RISING WHEN WE FALL: UNDERSTANDING RESILIENCE IN ORANGUTANS AND OTHER GREAT APES

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by

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Abstract

Great apes in rehabilitation centres and other captive environments must have the capacity to overcome adversity. Research in humans and other animals has shown that psychological resilience can help individuals ‘bounce back’ from stress. However, there is limited existing knowledge about how resilience might underpin the survival of great apes released back into the wild, or their wellbeing in long-term captivity. The first step towards understanding the importance of resilience in these contexts is identifying techniques to measure and increase resilience in great apes. This thesis lays the groundwork for a new field of research by evaluating appropriate and effective resilience interventions for captive great apes, exploring how species and individual differences may affect stress and resilience. This research involved conducting a scoping review of resilience interventions in humans and other animals, identifying several interventions with potential applicability to great apes (Chapter 2). Building on these results, a novel resilience intervention was trialled in captive orangutans and gorillas, showing promising results in terms of the potential of this intervention to increase persistence and skill in tool-using (Chapter 3). An investigation was also conducted into the effects of a potential major stressor, i.e. the effects of a period of zoo closures in England, due to the Covid-19 pandemic (2021), on orangutans and gorillas, identifying several species-specific effects and complex visitor effects (Chapter 4). Lastly, the implications of individual variation on welfare and resilience were explored in a case study of a neurologically and physically divergent orangutan, which highlighted several welfare implications as well as challenges in individually tailoring resilience interventions (Chapter 5). This thesis lays the foundation for future research into great ape resilience, contributing to wider efforts to return great apes to the wild and, where this is not possible, to maximise the wellbeing of great apes in long-term captivity.

For my mum, Rachel, who gave me an education.

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Declaration of author's contribution

Chapter 1: Entirely my own work.

Chapter 2: LBS conducted the literature review. JC and SKST assisted with discussion of the analysis and writing of the manuscript.

Chapter 3: LBS designed and conducted the experiment, collected and analysed the data, and wrote the manuscript, with input from JC and SKST.

Chapter 4: LBS and Charlotte King collected the data. LBS analysed the data and wrote the manuscript, with input from JC and SKST.

Chapter 5: LBS designed and conducted the case study, and wrote the manuscript, with input from JC and SKST.

Chapter 6: Entirely my own work.

Thesis contents

CHAPTER 1 – GENERAL INTRODUCTION 1
  1.1 Introduction 2
    1.1.1 IUCN conservation status of wild orangutans and gorillas 4
    1.1.2 Challenges in rehabilitation centres 5
    1.1.3 Challenges in captivity 11
  1.2 Resilience in humans 13
    1.2.1 Introducing resilience and protective factors 13
    1.2.2 Environmental factors 15
    1.2.3 Social factors 16
    1.2.4 Individual factors 16
  1.3 Resilience in non-human great apes 20
    1.3.1 Environmental factors 20
    1.3.2 Social factors 21
    1.3.3 Individual factors 22
    1.2.6 Necessity for further research 24
  1.4 Research aims 25
  1.5 Thesis outline 26
    1.5.1 Chapter Two 26
    1.5.2 Chapter Three 26
    1.5.3 Chapter Four 27
    1.5.4 Chapter Five 27
    1.5.5 Chapter Six 28
CHAPTER 2 – RESILIENCE INTERVENTIONS FOR ORANGUTANS(PONGO SPP.): A SCOPING REVIEW OF INTERVENTIONS IN HUMANS AND OTHER ANIMALS ... 29
  2.1 Introduction 31
  2.2 Methods 35
  2.3 Human interventions 36
    2.3.1 Resilience interventions 37
    2.3.2 Stress inoculation 39
  2.4 Animal interventions 41

2.4.1 Generic stressors/stress schedules 54
2.4.2 Separation 58
2.4.3 Environmental conditions 61
2.4.4 Social stress 66
2.4.5 Exercise 68
2.5 Discussion 69
2.5.1 Study limitations 70
2.5.2 Main findings 72
2.5.3 Animal welfare implications 74
2.6 Conclusion 76
2.7 Next steps 76

CHAPTER 3 – EFFECTS OF A PROGRESSIVELY CHALLENGING TOOL-BASED INTERVENTION ON BEHAVIOURAL RESILIENCE IN GREAT APES 78
3.1 Introduction 80
3.2 Methods 83
3.2.1 Location and subjects 83
3.2.2 Materials 84
3.2.3 Study design 88
3.2.4 Data collection 93
3.2.5 Analysis 97
3.5.6 Ethical considerations 99
3.3 Results 99
3.4 Discussion 105
3.5 Conclusion 110
3.5 Next steps 111

CHAPTER 4 – THE EFFECT OF LOCKDOWN RESTRICTIONS LIFTING ON CAPTIVE GREAT APE BEHAVIOUR AND POSTURE AS INDICATORS OF WELFARE 112
4.1 Introduction 114
4.1.1 Visitor absence during Covid-19 117
4.1.2 Measures of stress 120
4.1.3 Aims and objectives 122

4.2 Methods 122
4.2.1 Location and research subjects 122
4.2.2 Data collection 125
4.2.3 Statistical methods 131
4.3 Results 134
4.3.1 Effects of lockdown 138
4.3.2 Effects of total zoo visitors 141
4.3.3 Effects of visitor noise 146
4.3.4 Effects of visitor presence at enclosure 148
4.4 Discussion 150
4.4.1 Stress behaviours 151
4.4.2 Hunched and closed posture 153
4.4.3 Focus on humans 154
4.4.4 Object-holding and enrichment 155
4.4.5 Affiliative behaviours 156
4.4.6 Head covering (orangutans) 157
4.4.7 Spatial use (gorillas) 157
4.4.8 General study limitations 159
4.5 Conclusion 160
4.6 Next steps 160

CHAPTER 5 – UNDERSTANDING THE WELFARE REQUIREMENTS OF A NEUROLOGICALLY AND PHYSICALLY DIVERGENT CAPTIVE MALE SUMATRAN ORANGUTAN (PONGO ABELII) 162
Abstract 163
5.1 Introduction 164
5.1.1 Divergence and welfare 164
5.1.2 Existing knowledge of divergent primates 166
5.1.3 Benefits of research 168
5.2 Methods 170
5.2.1 Life history and development 170
5.2.2 Adaptation of cognitive enrichment 171
5.3 Results 174

5.3.1 Birth and physical development 174
5.3.2 Developmental milestones 179
5.3.3 Sexual development 181
5.3.4 Cognitive abilities 182
5.3.5 Cognitive enrichment 184
5.4 Discussion 185
5.4.1 Study limitations 185
5.4.2 Notable differences in development 186
5.4.3 Implications for wellbeing 188
5.4.4 Benefits of enrichment 190
5.4.5 Implications for animal management 190
5.5 Conclusion 191

CHAPTER 6 – GENERAL DISCUSSION 193
6.1 Summary of thesis aims and main findings 194
6.2 Implications for orangutans in rehabilitation 196
6.2.1 Further development of experimental intervention 196
6.2.2 Alternative forms of intervention 199
6.3 Visitor presence following lockdown 202
6.3.1 Stress behaviours 202
6.3.2 Visitor measures 204
6.3.3 Posture scales 204
6.4 Thesis limitations 205
6.4.1 Limitations related to Covid-19 205
6.4.2 General limitations 207
6.5 Contributions and recommendations for future research 208
6.6 Conclusion 210
References 214
Appendix A: Overview of common tools to measure resilience in humans 269
Appendix B: Overview of common types of nonhuman animal behavioural measurements relevant to resilience 273
Appendix C: Resilience experiment prior distributions 275
Appendix D: Resilience experiment MCMC diagnostics 276

Appendix E: Resilience experiment MCMC chain convergence 278
Appendix F: Resilience experiment WAIC scores 282
Appendix G: Lockdown study prior distributions 283
Appendix H: Lockdown study MCMC diagnostics 284
Appendix I: Lockdown study MCMC chain resolution 290
Appendix J: Lockdown study WAIC scores 304
Appendix K: Lockdown study posterior predictive check 306
Appendix L: Lockdown study effect sizes 326
Appendix M: Jiwa experimental procedures 332

List of figures

Figure 1.1 *Environmental, social, and protective factors contributing to resilience.* 14
Figure 3.1. *Orangutan apparatus.* 85
Figure 3.2 *Resilience treatment apparatuses* 86
Figure 3.3 *Gorilla apparatus* 88
Figure 3.4 *Timeline of apparatus positions given to control and intervention groups* 90
Figure 3.5 *Effects of resilience intervention on outcome variables* 100
Figure 3.6 *Effects of zoo on time spent attempting to use the apparatus* 102
Figure 3.7 *Mean attempt durations* 103
Figure 3.8 *Total number of dips* 104
Figure 3.9 *Mean number of stress behaviours* 105
Figure 4.1 *Timeline of lockdowns and data collection* 123
Figure 4.2 *Enclosure floorplans for orangutans (left) and gorillas (right)* 125
Figure 4.3 *Hunched and closed posture scales*). 130
Figure 4.4 *Activity budgets for each lockdown period* 136
Figure 4.5 *Indoor/outdoor observations* 137
Figure 4.6 *Effects of lockdown restrictions lifting on orangutans* 138
Figure 4.7 *Effects of lockdown restrictions lifting on gorillas* 140
Figure 4.8 *Effects of total visitor numbers on orangutans.* 142
Figure 4.9 *Effects of total visitor numbers on gorillas* 144
Figure 4.10 *Effect of total visitor numbers on height in enclosure (gorillas only)* 145
Figure 4.11 *Effects of visitor noise on orangutans* 146
Figure 4.12 *Effects of visitor noise on gorillas* 147
Figure 4.13 *Effects of visitor presence on orangutans* 149
Figure 4.14 *Effects of visitor presence on gorillas* 150
Figure 5.1 *Jiwa research apparatus.* 172
Figure 5.2 *Jiwa's growth in body weight compared to expected rates* 175
Figure 5.3 *Jiwa's deciduous dental emergence compared with expected rates* 176
Figure 5.4 *Jiwa at four years old* 178
Figure 5.5 *Jiwa's development of independence compared with expected rates* 180
Figure 5.6 *Cheek pad development* 182
Figure 5.7 *Number of stick removals per session.* 185

List of tables

Table 2.1 *Common themes in human resilience interventions* 37

Table 2.2 *Summary of resilience intervention effects* 43

Table 3.1 *Resilience study demographic information* 84

Table 3.2 *Conspecifics visible to focal individual* 91

Table 3.3 *Mean session duration in minutes (m) and seconds (s)* 94

Table 3.4 *Resilience intervention ethogram* 95

Table 4.1 *Demographic information of study participants* 124

Table 4.2 *Lockdown study ethogram* 127

Table 4.3 *Number of observations* 135

Table 5.1 *Jiwa experimental schedule* 173

Glossary of terms

Acute stress	Short-term stress, often relatively intense. In the context of this thesis, acute stress occurs within a single day, often combining multiple forms of stressor (see ‘Stress’).
Anxiety	Long-term tension in response to anticipated danger (American Psychological Association, 2023).
Agency	Proactive and flexible engagement with the environment beyond immediate needs to promote individual wellbeing (Špinka & Wemelsfelder, 2011).
Chronic stress	Stress that occurs over a period of time. In the context of this thesis, chronic stress is categorized as occurring over at least ten days (see ‘Stress’).
Cognitive skills	Skills in cognitive processes related to sensory input, e.g. memory, learning, and causal reasoning (Clark, 2011).
Depression	Chronic negative affective state (see ‘Positive/negative affect’) (American Psychological Association, 2023).
Elevated platform stress	A rodent stress protocol involving placing subjects on an elevated platform in a brightly-lit environment (e.g. Yang et al., 2003).
Emotional intelligence	The capacity to make intelligent use of emotional information (Armstrong, Galligan, & Critchley, 2011).
Fear	Intense emotion and physiological responses as a short-term alarm reaction to immediate threat (American Psychological Association, 2023).
Flexibility	The ability to adapt to different kinds of situations and challenges.
Hardiness	A combination of self-control, persistence, and self-motivation to overcome challenges (Maddi, 2006).
Learned helplessness	The inability to avoid stressor(s), having experienced inescapable stress (Overmier & Seligman, 1967).
Meditation	An umbrella term for various methods of regulating focus and emotions (Lutz, Slagter, Dunne, & Davidson, 2008).

Mindfulness	The practice of intentionally maintaining focus on the present moment in a non-judgmental way (Las Hayas et al., 2019).
Neural plasticity	Structural and functional changes in the nervous system in response to particular experiences, e.g. injury (von Bernhardi, Eugenín-von Bernhardi, & Eugenín, 2017).
Optimism/pessimism	The tendency to believe that future events will be favourable/unfavourable (Forgeard & Seligman, 2012).
Persistence	Maintaining a course of action despite the obstacles or effort involved (American Psychological Association, 2023).
Positive psychology	Psychological perspective which emphasises helping patients to flourish, rather than focusing only on pathology (Seligman & Csikszentmihalyi, 2000).
Positive/negative affect	Positive/negative emotional state.
Resilience	Successful adaptation to, or competence despite, stress or trauma (Masten, Best, & Garmezy, 1990, in Egeland, Carlson, & Sroufe, 1993; Garmezy, 1993)
Self-awareness, self-reflection	The capacity/activity of being aware of one's own thoughts, behaviour, emotions, and influences.
Self-confidence, self-esteem	Positive conceptualisation and feelings about oneself (Mandleco & Peery, 2000).
Self-control/ behavioural inhibition	The ability to self-regulate behaviour and control impulses, for example to delay gratification.
Social defeat	Subordination by a dominant, usually physically larger, intruder of the same species (Gardner et al., 2005).
Stress	Psychological and/or physical response to stressors (American Psychological Association, 2023).
Stress inoculation	Exposure to manageable stress leading to resistance against future stress (Meichenbaum & Cameron, 1983; Parker et al., 2004).
Trauma	Response to experiencing or witnessing events which threaten, or are perceived to threaten, the life or bodily integrity of oneself or others (American Psychiatric Association, 2013; NCTSN, 2023)

"Our greatest glory is not in never falling, but in rising every time we fall."

Oliver Goldsmith

CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

Across the globe, great ape populations are under increasing threat from anthropogenic pressures like habitat loss, hunting, and the illegal wildlife trade (Plumptre et al., 2016; Strindberg et al., 2018; Walsh et al., 2003; Wich et al., 2015, 2016). These combined pressures are making the situation for wild great apes increasingly fragile. All non-human great ape species are declining in numbers, but this thesis will largely focus on orangutans (*Pongo spp.*) and gorillas (*Gorilla spp.*), both of which are categorised by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species as critically endangered in the wild (Ancrenaz et al., 2018; Maisels, Bergl, & Williamson, 2018; Plumptre, Robbins, & Williamson, 2019; Singleton et al., 2018). Alongside in-situ conservation methods, like habitat protection, local education programmes, and law-enforcement (Ancrenaz et al., 2018; Farmer & Courage, 2008; Plumptre et al., 2016; Singleton et al., 2018), there are also ex-situ conservation measures in place. Orangutan rehabilitation centres routinely rescue infants who have been illegally kept as pets, or adult orangutans who stray onto human settlements, with the intention of rehabilitating them and releasing them back into the wild (Russon, 2008). It is the policy of the Indonesian government that ex-captive orangutans must be returned to the wild where possible (Sherman, Ancrenaz, & Meijaard, 2020). Rehabilitation centres are constrained by time, space, resources, and gaps in scientific knowledge about the effectiveness of different rehabilitation practises. However, there are potentially very severe consequences for orangutans if they are released without adequate practical and psychological preparation for life in the wild, with the ultimate risk being their premature death (Russon, 2009). Because of the heightened pressure on orangutan rehabilitation centres to adequately prepare and release orangutans, research into effective orangutan rehabilitation techniques is imperative. In contrast, there is not the same urgency or opportunity for release with African great apes (King, Chamberlain, & Courage, 2005). Although gorilla releases have also taken place, this is less common, and there are some high-profile examples which have been controversial (e.g. Chant, 2014). In addition, ex-situ conservation efforts are constrained by the diminishing areas of available habitat which can support self-sustaining populations of released great apes (Farmer & Courage, 2008; Russon, 2008). However, despite these challenges, rehabilitation and release programmes can tackle the immediate issue of addressing the welfare of displaced great apes, and successful releases can complement in-situ conservation methods.

For great apes to be successfully returned to the wild, it is essential that they can demonstrate the necessary skills and mental strength before release decisions can be made. However, preparing great apes for release is a complex issue, as individuals can struggle to cope with the stressors involved with life in the wild (Basalamah et al., 2018; Russon, 2008; Utami-Atmoko et al., 2017). In addition, because not all great apes can be released, it is important to consider the needs of great apes who spend their whole life in zoos and sanctuaries. Captivity is associated with a range of stressors (e.g. Choo, Todd and Li, 2011; Lewis et al., 2020; Wells, 2005), and having the capacity to manage and overcome these stressors is essential for maintaining wellbeing in the long term.

In recognising the scope for improvement in helping great apes prepare for unavoidable stress, this thesis seeks to identify practical interventions with the potential to improve the resilience of captive great apes. In doing so, a contribution is made to methodological advances in the rehabilitation of wild-born great apes who will be returned to the wild, as well as promoting the wellbeing of individuals staying in long-term captivity. The following sections provide an overview of some of the challenges facing great apes in rehabilitation centres and long-term captivity. After these challenges are described, the concept of psychological resilience is introduced, before this chapter concludes with the research objectives and an outline of the thesis structure.

1.1.1 IUCN conservation status of wild orangutans and gorillas

By 2025, it is estimated that the population of Bornean orangutans (*Pongo pygmaeus*) will have decreased by 82% since 1950 levels (Ancrenaz et al., 2018). A similar population decline is projected for Sumatran orangutans (*Pongo abelii*), who have lost 60% of their forest habitat between 1985 and 2007 (Wich et al., 2008, 2011), and are currently under threat from continuing land use changes and habitat conversion (Singleton et al., 2018). The world's most recently discovered great ape species, the Tapanuli orangutan (*Pongo tapenuliensis*), has the smallest population of all great apes, with less than 800 individuals estimated to remain in the wild (Wich et al., 2016). Due to habitat loss, and the resulting closer contact with human populations, orangutans displaced from their natural habitat can be killed or injured while trespassing or food-stealing, or killed for meat consumption (Davis et al., 2013). Often as a by-product of human conflicts with adult orangutans, it is common for infant orangutans to be taken from the wild to be sold as pets (Singleton et al., 2018).

Gorilla populations are similarly affected by many of the human activities which threaten orangutans. Alongside habitat loss and degradation, gorillas face particular threats from disease and illegal hunting for bushmeat consumption (Maisels et al., 2018). Although Western lowland gorillas (*Gorilla gorilla gorilla*) have a wide geographic range, the gorilla population of Gabon alone has more than halved between 1983 and 2000 (Walsh et al., 2003). There is an estimated annual population decline of 2.7% for Western lowland gorillas (Strindberg et al., 2018) and

5% for the world’s largest primate, Grauer’s gorillas (*Gorilla beringei graueri*) (Plumptre et al., 2016). Grauer’s gorillas are situated in a politically unstable region spanning the borders of three countries in central Africa (Plumptre et al., 2019). The related proliferation of firearms and commercial human activity in this region has facilitated illegal hunting, leading to a 77% population reduction of Grauer’s gorillas within a single generation (Plumptre et al., 2016).

It is clear from these statistics that the conservation status of orangutans and gorillas is alarming, and the situation is continuing to deteriorate due to continued habitat loss and direct conflict with humans. Although efforts to resolve the higher-level anthropogenic causes behind population decline are essential, the immediate issues experienced by individual great apes due to human-wildlife conflict must also be addressed. The next section introduces rehabilitation and release efforts and discusses some of the potential challenges in this area.

1.1.2 Challenges in rehabilitation centres

Since the 1960s, growing numbers of orangutan rehabilitation centres have been established across Borneo and Sumatra. The aim of these rehabilitation centres is to rescue and rehabilitate orangutans subjected to human-wildlife conflict, with the intention of preparing them to eventually be released back into the wild (Russon, 2008). In some cases, e.g. where there are no immediate health concerns, orangutans are directly translocated to a new habitat, bypassing the rehabilitation process altogether (e.g. Kaye, 2016; ProKal, 2017; in Sherman, Ancrenaz and Meijaard, 2020). The reintroduction process is more established for orangutans than for other great apes, partially because the Indonesian government mandates the release of all orangutans, where possible (Sherman et al., 2020). For example, although there are examples of gorillas being released back into the wild (e.g. Farmer and Courage, 2008), there is a lack of suitable habitat which does not overlap with the existing ranges of wild gorillas, and this is particularly problematic due to their complex social structure (King, Chamberlain, & Courage, 2005). Therefore, this section will primarily focus on orangutan rehabilitation and re-introduction processes.

1.1.2.1 Confiscation and immediate care

Under Indonesian law (No. 5/1990), the capture, trading, killing, or keeping of orangutans is prohibited. When these activities occur, rehabilitation centres work with Indonesian authorities to confiscate and rescue illegally held orangutans (SOCP, 2023a), although law enforcement is weak and resulting prosecutions are rare (Nijman, 2005). Some rehabilitation centres have several hundred orangutans in their care (e.g. Bornean Orangutan Survival Foundation sites at Nyaru Menteng and Samboja; BOSF, 2023), ranging in age from infants to fully grown adults (Russon, 2008). However, arrivals are predominantly infants under seven years old (Nijman, 2005; Russon, 2008). Following arrival at the rehabilitation centre, orangutans undergo health checks and a quarantine period (Beck et al., 2007; BOSF, 2023a; SOCP, 2023b). Extremely young infants will require a surrogate mother for at least the first 18 months of their life; this would ideally be an older orangutan, but is usually a human surrogate (Beck et al., 2007). Surrogacy is extremely important in providing infants with affection and psychological support, and contributing to their normal emotional, social, and behavioural development (Beck et al., 2007; Russon, 2008). However, for orangutans destined to be released back into the wild, reliance on human caretakers is not conducive to the development of independence; therefore, interactions with humans are gradually phased out during the first six years of life (Beck et al., 2007), as orangutans are socialised with peers of a similar age (SOCP, 2023b). Balancing caretaker input is one of the biggest challenges throughout the rehabilitation process, and an issue that is not easily solvable.

1.1.2.2 Forest school

The next stage of orangutan rehabilitation is usually referred to as ‘forest school’ and takes place in open forest within the centre’s grounds during the day, with orangutans returning to enclosures at night. Orangutans attend forest school until between five and nine years old (Nadine Sugianto, personal communication; Preuschoft et al., 2021; SOCP, 2023b), which gives them an opportunity to learn the necessary skills they need to survive in the wild (BOSF, 2023a; SOCP, 2023b). Orangutans are typically separated into different age groups, to help prevent stress and physical injury to their conspecifics (Russon, 2008). Where there is sufficient capacity to do so, each age group attends forest school on a daily basis (Nadine Sugianto, personal communication; SOCP, 2023b), and some centres allow sufficiently skilled orangutans to stay in the forest overnight (Russon, 2008). Providing orangutans with the opportunity to develop wild skills is essential if they are to be released successfully into the forest. Wild orangutans face a diverse range of physical, cognitive, and emotional challenges, some of which are outlined in section 1.1.2.3.

1.1.2.3 Skills required for successful release

As the world’s largest arboreal animal (Cant, 1992), travelling through the forest canopy is energetically demanding for orangutans, particularly as food sources such as leaves, buds, and fruit are often on the lightest and most flexible branches, requiring muscular stabilisation to counteract branch flexibility (Halsey et al., 2017). Wild orangutans, who demonstrate a greater variety of positional behaviours than any other primate, can use branch elasticity to their advantage in locomotion methods such as tree swaying and catapulting (Thorpe & Crompton, 2005; Thorpe, Crompton, & Alexander, 2007; Thorpe, Holder, & Crompton, 2009). However, captive environments do not necessarily provide the same opportunities for orangutans to learn about the mechanical properties of flexible and dynamic supports.

There are also cognitive aspects to route planning through the forest canopy, with the most efficient way involving low energy expenditure, risk avoidance, and using direct routes (Thorpe, Holder, & Crompton, 2009). Unlike monkeys, great apes often use the same crossing places when traversing gaps in the canopy. This may be because remembering set routes is less risky and less cognitively demanding for great apes than innovating individual routes each time (Halsey et al., 2017). However, it seems likely that captive orangutans have a limited amount of 'ranging' space, and therefore are constricted in practising route planning, and retaining information about routes.

Alongside individual practise, social learning is probably the 'default' method for orangutans to learn complex skills as it is more efficient and less risky than individual learning (Schuppli *et al.*, 2016; Whiten & Mesoudi, 2008). Wild orangutans primarily rely on their mothers for opportunities to learn skills like food processing and nest-building (Jaeggi et al., 2010). Orangutan nests are stronger and more complex than those of the African great apes (van Casteren et al., 2012). As a result, nest-building requires technical knowledge of the mechanical properties of different kinds of branches and tree types, as well as weaving techniques and the different ways branches can be bended, broken, or detached (van Casteren et al., 2012; Videan, 2006). However, because infant orangutans in rehabilitation are typically orphans, they will need to learn these skills by observing their peers, or human demonstrators, rather than their own mothers.

Some orangutan habitats can demonstrate a high temporal variation in fruit availability. For example, during ‘tree masting’ events, <88% trees fruit simultaneously (Knott, 1998). Wild orangutans have the capacity to increase their calorific intake during these periods, exploiting temporal high food abundance and insuring against periods of food scarcity (Knott, 1998). This is particularly important in Borneo, which has harsher ecological conditions than Sumatra (Delgado & Van Schaik, 2000; Wich et al., 2011). However, it is unclear how effectively released orangutans cope with temporal variation in food availability, as they are accustomed to a regular supply of food during rehabilitation (Schmidt, 2004). Reintroduced primates can experience a range of difficulties when adapting to foraging in the wild. For example, a study on golden lion tamarins (*Leontopithecus rosalia*) found that 20% of post-release mortality was caused by starvation, or by consuming toxic fruits (Beck et al., 1991). Another study, which monitored 10 orangutans post-release, found that nearly all of them returned to the release cages in search of food within 6-12 months following release (Basalamah et al., 2017). Reintroduced orangutans eat more fruit and less flowers and insects than their wild counterparts (Basalamah et al., 2018), and spend less time feeding in proportion to resting and travel time (Russon, 2008). A recent study indicates that wild orangutans may balance nutrients by actively selecting nonfruit foods (Digiorgio et al., 2023). Therefore, the heightened focus on fruit seen in rehabilitated orangutans could lead to a nutrient imbalance. The drastic change in food availability for released orangutans, compared to the regular, secure food supply provided by rehabilitation centres, is likely to be unexpected and stressful.

Orangutans must also avoid threats such as humans and snakes. Having been acclimatised to human presence, there is a risk that orangutans will approach human settlements following release (Russon, 2008). This could result in fatal conflict, or in orangutans being rescued for a second time. Orangutans must also learn to avoid other dangerous animals they might encounter in the forest (Damerius, 2017). For example, rubber snakes are sometimes used as a prop in forest school to prompt cautiousness in orangutans (Neme, 2010). The skills outlined above, which are required for orangutans to survive and thrive in the wild, present rehabilitation centres with a complex challenge. Orangutans must acquire these skills during their time in rehabilitation, whether during forest school, in enclosures, or on pre-release islands, before they are deemed to be suitable for release.

1.1.2.4 Release strategies and post-release challenges

Orangutans who have been approved for release may first be transferred to an enclosure and/or a semi-provisioned ‘pre-release island’, the latter helping them acclimatise to semi-independent living (Chappell & Thorpe, 2022). During this period, enclosure design and other management changes can help to promote wild-type behaviours, for example by providing flexible and dynamic support structures with interventions such as roof-feeding, to promote locomotion (see Thorpe et al., 2022). When release does take place, strategies can range from ‘soft’ to ‘hard’. Softer strategies involve helping orangutans adjust by holding them in enclosures close to the reintroduction site, as well as provisioning them with supplemental food following release (Beck et al., 2007). Hard releases involve releasing orangutans immediately, with no post-release support (Beck et al., 2007).

Assessing whether individuals are ready for release is a complex issue. Released orangutans often struggle to adapt to the wild (Basalamah et al., 2018; Russon, 2008; Utami-Atmoko et al., 2017), with one study reporting post-release survival rates of 20% to 80% and an estimated mean survival rate of 40% (Russon, 2008). This reflects the challenges involved with preparing orangutans to support themselves in the wild, outlined in the previous section (1.1.2.3). Although improvements can be made to the rehabilitation process, this will never substitute for the close and extended bond wild orangutan infants share with their mothers, and the associated learning opportunities and direct experience of the wild environment. Therefore, it is inevitable that orangutans undergoing rehabilitation will face stressful challenges once they are released back into the wild. Alongside all the necessary skills they learn through the rehabilitation process, orangutans must have the capacity to bounce back from these challenges and demonstrate perseverance in the face of adversity.

In addition, up to 45% of orangutans in rehabilitation centres will remain in a sanctuary environment for the rest of their life (BOSF, 2023b). This includes individuals rescued from captivity too late in life to acquire the necessary skills to support themselves in the wild, individuals with physical or cognitive disabilities, and individuals at risk of transmitting diseases like tuberculosis into wild populations (BOSF, 2023b; SOCP, 2023c). Some rehabilitation centres have the capacity to move orangutans with no physical impairments onto provisioned forested islands (BOSF, 2023b; SOCP, 2023c). However, where this is not possible, long-term sanctuary inhabitants will remain confined in an enclosure.

1.1.3 Challenges in captivity

The capacity to overcome stress is not only important for great apes and other nonhuman animals (hereafter ‘animals’) living in the wild, but it is also necessary for captive apes in sanctuaries and zoos. There is not a clear dividing line between zoos and sanctuaries in terms of their activities, but the primary purpose of modern zoos is displaying animals to the public to support research, ex situ conservation, and education goals, while sanctuaries' primary purposes are the rescue and subsequent lifelong care of trafficked animals. In zoos, sanctuaries, and rehabilitation centres, captive great apes face a combination of long-term pressures of a different nature to those experienced by their wild counterparts.

In all captive environments, there is a substantial limitation on ‘agency’, or control over one’s environment, as humans must make significant decisions on behalf of the great apes in their care. For example, decisions about which individuals to group together are made by humans. Therefore, captive great apes have limited (or no) agency to leave groupings or form new social connections. Although dietary decisions are made with each individual’s welfare in mind, and great apes have a regular supply of food in captivity (Schmidt, 2004), there are constraints over what and when they eat. In highly social species such as gorillas, the pressure around feeding time can cause tension and conflict (Jersey Zoo Senior Mammal Keeper, Mark Beresford, 2022 - personal communication). Animal caretakers also make decisions around reproduction, and it is normal practise for female great apes to be given contraceptive pills to manage their ability to conceive, e.g. if there are concerns about available space and resources (Asa, 1997). In addition, in zoo environments, there is a near-continuous visitor presence throughout the day, alongside associated human noises and smells. Although visitors can have positive, neutral, or negative effects (Sherwen & Hemsworth, 2019), visitor presence can be stressful for great apes (e.g. Wells, 2005; Choo, Todd and Li, 2011; Lewis et al., 2020). Lastly, due to the enclosed nature of captive environments, it is not possible for great apes to travel the long distances they are accustomed to travelling in the wild. For example, wild Sumatran orangutans travel over 850 metres daily, with an average monthly range size of 423±139 hectares for males and 131±46 hectares for females (Campbell-Smith et al., 2011). Similarly, a troop of wild Western lowland gorillas were found to travel an average of 1,527±575 metres a day, with a monthly range size of 3.0±0.74 square kilometres (Cipolletta, 2004). Even though the size of zoo enclosures can vary, depending on the context and available space, captive environments do not allow for this extent of natural ranging behaviour.

Many constraints on agency associated with captive environments are unavoidable for logistical reasons. However, it is important for great apes to be able to manage the short- and long-term stressors associated with life in captivity. Whether in rehabilitation centres, zoos, or in the wild, great apes must demonstrate ‘psychological resilience’, or the ability to ‘bounce back’ after stressful or difficult experiences (Fletcher & Sarkar, 2013). Having described some of the challenges facing great apes, section 1.2 explores the concept of psychological resilience in more depth and relates this to great apes in rehabilitation centres and other captive environments.

1.2 Resilience in humans

1.2.1 Introducing resilience and protective factors

The term ‘resilience’ is rooted in the Latin *resilire*, which means ‘to leap back’ (Fletcher and Sarkar, 2013: p4). As very little is currently known about psychological resilience (hereafter ‘resilience’) in great apes, current knowledge in this area is largely based on our understanding of human behaviour. Therefore, the following section is based on human research, and discusses the environmental, social, and individual factors which are thought to contribute to resilience.

Resilience can be interpreted in different ways, and has been defined as a trait, a process, or an outcome (Fletcher & Sarkar, 2013). Rather than being directly measured, resilience can be inferred by positive adaptation in response to adversity (Luthar & Zelazo, 2003). Within this thesis, resilience is understood to mean the successful adaptation to, or competence despite, stress or trauma (Masten, Best and Garmezy, 1990, in Egeland, Carlson and Sroufe, 1993; Garmezy, 1993). Some aspects of resilience can be altered through resilience interventions which are designed to have a beneficial effect. These are also sometimes referred to as resilience ‘treatments’ or ‘programmes’, particularly in the human literature. However, the term ‘intervention’ is more commonly used in the animal literature and will be used throughout this thesis.

In humans, there are thought to be three levels at which resilience can be influenced: environmental, social, and individual (Figure 1.1). The aspects of each of these areas are sometimes referred to as ‘protective factors’ (Greenberg, 2006), because their presence can protect against detrimental responses to adverse events. The remainder of this section will summarise what is known about protective factors in humans, and the extent to which these may be relevant for orangutans in rehabilitation centres and other captive great apes.

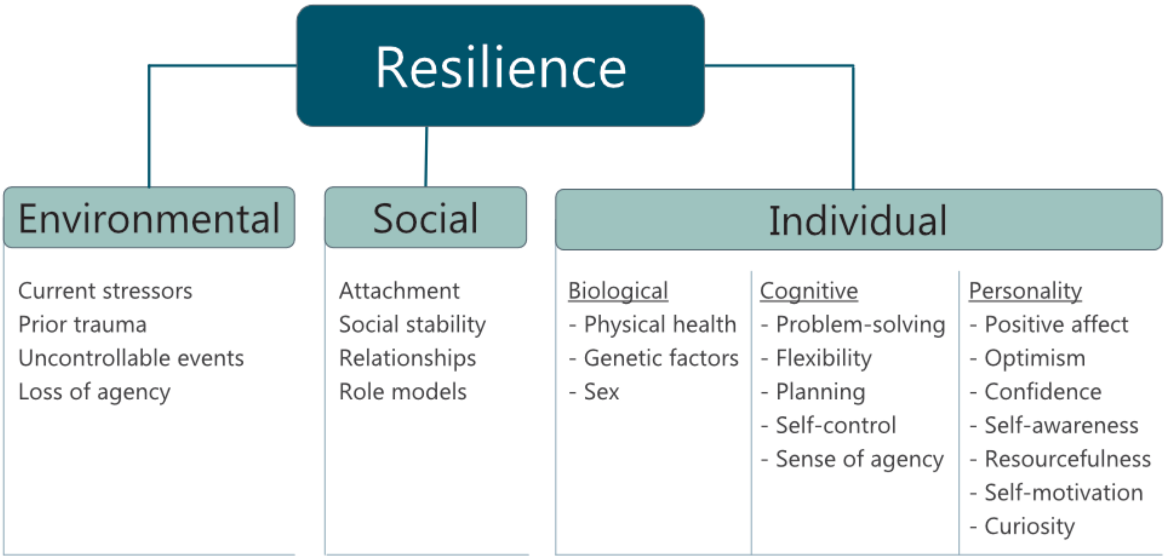


Figure 1.1 *Environmental, social, and protective factors contributing to resilience.* Based on Mandleco & Peery (2000).

1.2.2 Environmental factors

Resilience in humans can be affected by current life stressors and previous experiences of trauma (Bonanno et al., 2007; Kessler, 1997). The National Child Traumatic Stress Network (NCTSN) defines a potentially traumatic event as a "frightening, dangerous, or violent event that poses a threat to [one's] life or bodily integrity" (2023; brackets added); and traumatic events include witnessing a loved one's life or physical security being threatened (NCTSN, 2023). Traumatic events can include, but are not limited to, physical, sexual, and psychological abuse, serious accidents and illness, natural and man-made disasters, or the sudden or violent loss of a loved one (NCTSN, 2023). However, traumatic events do not necessarily result in traumatic stress, depending on prior experience of trauma and other protective factors (NCTSN, 2023). This definition of potentially traumatic events aligns with the 5th edition of the American Psychiatric Association's Diagnostic and Statistical Manual of Mental Disorders (DSM-V) definition of 'post-traumatic stress (disorder)' as occurring in response to experiencing or witnessing death, serious injury, or sexual violence, or the threat of any of these things (American Psychiatric Association, 2013). The term 'disorder' is bracketed here because there are some criticisms about the practise of categorising common responses to potentially traumatic events as being disordered. For example, in a survey of 359 women who had been raped, 79% were subsequently diagnosed with a mental disorder after seeking professional support for their trauma, indicating that their responses to this kind of traumatic event were not unusual, and should therefore not be thought of as disordered (Taylor, 2022). Throughout this thesis, the term 'disorder' will be avoided where possible, for example using 'anxiety' rather than 'anxiety disorder', unless referring to a specific instance of a diagnosis.

Resilience to stress has been found to decrease when additional life stressors are present, e.g. chronic disease or recent widowhood, as well as when individuals have experienced more than one potentially traumatic event (Bonanno et al., 2007). As stress increases, there is a correlated increase in negative affective states, as well as disturbance in behavioural repertoires and increased abnormal behaviours (Colditz & Hine, 2016). However, despite the clear potential for harm from exposure to severe stress, research indicates that some adversity can help individuals develop a sense of agency and prepare them for future stressors (see Fletcher and Sarkar, 2013).

1.2.3 Social factors

The quality of the bond between parent and infant can have an impact on resilience in humans. In a study of two-year-old human children, those rated as ‘securely attached’ to their parents at 12 months old later approached problems with enthusiasm and persistence, being more likely to seek help from adults than becoming upset or angry (Nolen-Hoekseme et al., 2014). In contrast, children rated ‘insecurely attached’, "easily became frustrated and angry, seldom asked for help, tended to ignore or reject directions from adults, and quickly gave up trying to solve the problems" (Nolen-Hoekseme et al., 2014; p91). Wider social factors can also influence resilience. Resilience can be promoted by supportive environments within and outside social groups, which demonstrate stability and cohesiveness, and involve good interpersonal relationships (Bonanno et al., 2007; Fletcher & Sarkar, 2013; Masten et al., 1990).

1.2.4 Individual factors

There are several protective factors relating to individual differences that influence resilience in humans. These are relevant at different stages of development, from infancy to adulthood, and include biological, cognitive, and personality factors.

1.2.4.1 Biological factors

Biological protective factors include general health and physical capability, strength, and endurance; genetic predisposition, including the absence of hereditary physical or psychological illnesses; temperament, which can help to mediate adaptation to stress and change; and sex, for example with male humans being more vulnerable to all risk factors apart from during adolescence, when females are more vulnerable (Mandleco & Peery, 2000). Although some biological factors are inflexible, there is at least some neural plasticity in resilience. Neural plasticity can be defined as the ability of the nervous system to change, structurally and functionally, after being exposed to injury, or other experiences (von Bernhardi et al., 2017). For example, epigenetic changes in the expression of some genes, e.g. those thought to convey risk or vulnerability, can be triggered by traumatic events, but can also be influenced by interventions (Hornor, 2017). One study of a family-based intervention program, for African-American families in rural areas of the United States, focused on young people genetically more likely to engage in high-risk behaviours such as alcohol and drug use and high-risk sexual activity (Brody et al., 2009). These individuals were identified by the presence of a polymorphism of the SCL6A4(5HTT) gene at 5-HTTLPR, which is connected to risky behaviours, negative affect, and attention levels. Following the intervention program, young people were half as likely to develop internalising (e.g. depression) and externalising (e.g. aggression) behaviours compared to the control group (Brody et al., 2009). Although this example of neural plasticity is human-specific, it shows that, at least in humans, there is the potential for resilience interventions to influence individuals at the level of gene expression.

1.2.4.2 Cognitive factors

The cognitive factors which affect resilience in humans include: problem solving ability, flexibility, self-control, and planning ability (Bridgeland, 1971; Hornor, 2017; Mandleco &

Peery, 2000; Rutter, 2012; Shure, Spivack, & Jaeger, 1971). Intelligence levels and 'cognitive style', i.e. the particular skills and methods used to problem-solve, can also influence resilience (Mandleco & Peery, 2000). Resilient individuals demonstrate confidence and self-motivation in meeting challenges, balanced with self-reflection and impulse control (Hornor, 2017; Rutter, 2012). To overcome challenges and problem-solve in a resilient way, the activity of planning is important: more so than possessing specific planning skills (Hornor, 2017; Rutter, 2012). Individual coping style (in response to adverse events) is also influential, with resilient coping styles consisting of independent and flexible behaviours, where frustrations are managed and coping is orientated around effective problem-solving (Mandleco & Peery, 2000).

Resilience can also be affected by the self-perception of one's own abilities, e.g. the perceived achievability of goals (Scheier and Carver, 2001; in Forgeard & Seligman, 2012), and the level of perceived control over events (Janoff-Bulman & Brickman, 1982; Langer, 1975; Seligman, 1975). An individual's belief that they can influence events through their own actions is sometimes described as self-efficacy, or agency (Rutter, 2012). One study on Australian business owner-managers following a hurricane found that managers with an internal locus of control (rather than feeling that external influences were controlling events) were less stressed and more likely to employ task-centred, rather than emotion-centred, coping behaviours (Anderson, 1977). The lack of agency, or the perception of an external locus of control, can result in the phenomenon of 'learned helplessness'. This term was first used to describe a situation where animals who have experienced inescapable electric shocks fail to avoid shocks in future, which were avoidable by performing a simple action (Overmier & Seligman, 1967). Later, learned helplessness was also identified in humans by Hiroto (1974). In this study, people who had learned that it was impossible to turn off an unpleasant noise by pressing a button were subsequently unable to turn off the same noise in situations where only a simple movement of the hand was required.

1.2.4.3 Personality factors in humans

For humans, there are certain elements of personality found to be particularly relevant to resilience. These include: 1) a tolerant temperament with positive affect (‘happy’ emotions), 2) high levels of optimism, 3) self-esteem, stemming from confidence and self-reliance; 4) self-awareness, i.e. awareness of one’s own strengths and weaknesses, while being autonomous and independent; 5) resourcefulness (which helps in adapting to constantly varying situations: Farkas and Orosz, 2015); 6) self-motivation; and 7) high levels of activity and curiosity (Block and Block, 1980; Mandleco and Peery, 2000; Fletcher and Sarkar, 2013). Positive affect is associated with more effective problem-solving and decision-making, resulting in more innovative and flexible cognitive processing (Isen, 2001). Interpersonal personality traits, for example sociability, can also affect resilience (Mandleco & Peery, 2000), for example by strengthening social support networks. However, Armstrong, Galligan and Critchley (2011) argue that interpersonal emotional intelligence (emotional awareness and management of others) is less important for resilience than intrapersonal emotional intelligence (emotional self-awareness, expression, self-control, and self-management). The second relevant element of personality, optimism, can be defined as a tendency towards believing that events in the future are likely to be favourable (Forgeard & Seligman, 2012). The presence of optimism in humans can be affected by environmental and indirect genetic influences, and the presence and input of socially influential figures like mothers (Seligman et al., 1984) and teachers (Heyman, Dweck & Cain, 2016).

1.3 Resilience in non-human great apes

1.3.1 Environmental factors

Prior experience of stress is very relevant to the resilience of orangutans in rehabilitation. As highlighted in section 1.1.2, every orangutan in rehabilitation will have experienced traumatic events, including being removed from their natural habitat and other forms of human-wildlife conflict. Nearly all infant orangutans in rehabilitation will have witnessed their mother being killed (Sherman et al., 2020), and many arrive with physical or psychological problems following neglect or abuse, as described by Russon (2008: p331), below:

> "Physical damage includes gunshot and machete wounds, amputated, maimed or broken limbs, deep neck or waist wounds and scars from chaining, paralysis, blindness, and internal damage... Behavioral and psychological damage include physical and sexual abuse, prolonged isolation as young infants, identification with humans, and abnormal experience that subverts learning forest competencies and fosters counterproductive learning."

Some of the issues described above can result in visible behavioural abnormalities, for example self-clinging, rocking back and forth repeatedly, and self-abuse (Russon, 2008). However, much of the trauma is likely to be internalised and therefore difficult to measure. Therefore, it is challenging to determine how prior trauma may affect the current behaviour of orangutans and their resilience to future stress.

Environmental factors like fluctuations in food availability are likely to affect the resilience of orangutans after being released into the wild (see section 1.1.2.3). It is essential that released orangutans have the resilience to overcome food-related stress while they are still adapting to their new environment, so that they can persist in trying to obtain different kinds of food and ultimately avoid starvation. They may also need to cope with environmental disasters like forest fires (e.g. NASA, 2003). However, environmental stressors can also affect great apes in captivity. Alongside relatively mild disruptions like moving enclosure or accepting a new group member, some stressors cannot be anticipated and mitigated by human caretakers. For example, during the Covid-19 pandemic, captive great apes had to overcome an unprecedented environmental stressor in the form of prolonged national zoo lockdowns. In normal conditions, visitor presence can have both beneficial and detrimental effects on the behaviour and psychological state of zoo-held animals (Sherwen & Hemsworth, 2019). However, having to repeatedly adapt to extended, fluctuating periods of absence and presence of zoo visitors is likely to have required great apes and other animals to demonstrate flexibility and resilience.

Fostering a sense of agency may be an important factor for orangutans in rehabilitation and great apes in captivity, who have very little control over their own lives while they are in captivity. The concept of learned helplessness may also be pertinent to orangutans in rehabilitation, many of whom will have experienced traumatic events during their lives over which they had no control. In addition, the necessary level of external control in rehabilitation centres and zoos over living space, food provision, and medical care may reinforce learned helplessness. Therefore, it is important to identify other ways in which agency and an internal locus of control can be fostered in a captive setting.

1.3.2 Social factors

The effect of disrupting the mother-infant bond (section 1.2.3) is extremely relevant to orangutans, who have an exceptionally long infant-mother bonding period in the wild, with almost constant bodily contact for the first few months, and staying with their mother until six to nine years old (van Adrichem et al., 2006; van Noordwijk et al., 2009). As most orangutans in rehabilitation have experienced significant disruption to this bonding period, this could influence the way problems are approached later in life. Alongside disrupted attachment, separating orangutan infants from their mothers also deprives them of the learning opportunities afforded by watching their mothers solve problems in the wild.

Wider social factors are also important for resilience in animals. An individual's position within the group social structure can affect the immune system and physiological responses, as well as influencing affective state (feeling positive or negative emotions) (Colditz & Hine, 2016). This may be particularly influential for great apes with close social structures, like gorillas. However, as orangutans have a relatively loose social structure, living in dispersed societies with temporary aggregations (Galdikas, 1985; Malone, Fuentes, & White, 2012; Roth et al., 2020), the extent to which wider social factors are likely to affect their resilience is unknown. Social factors may be more relevant in captive environments, where orangutans are often housed in groups (see section 1.1.3).

1.3.3 Individual factors

Personality factors have also been found to influence behaviours relevant to resilience in great apes. One study of orangutans, gorillas, chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*) identified a connection between personality traits and individual differences in behaviour during a range of scenarios, including situations designed to elicit frustration, responses to novelty, and reactions to sudden noises and distractions (Uher, Asendorpf, & Call, 2008). In humans, variation in subjective wellbeing, i.e. ‘happiness’, is thought to be around 50% heritable, with most subjective well-being accounted for by aspects of personality, particularly extraversion and neuroticism, rather than being strongly affected by external circumstances (Costa & McCrae, 1984; Costa & McCrae, 1980; Lykken & Tellegen, 1996). However, human personality traits relevant to happiness can vary in heritability, with neuroticism being significantly heritable, but not extraversion (Power & Pluess, 2015). A subjective wellbeing scale based on human studies was applied to chimpanzees by King and Landau (2003). They found that personality traits accounted for around 50% variance in wellbeing, with 'extraversion', 'agreeableness' and 'low neuroticism' in chimpanzees being related to subjective well-being. Although these results are interesting, and the idea that personality is related to wellbeing is well-documented in humans, it should be noted that both methods of data collection in this study involve subjective human assessments, and therefore may be affected by anthropomorphism, or preconceptions based on theories of wellbeing and personality in humans.

The connection between personality and wellbeing in great apes is also supported by a study of 283 wild-born and captive-born (both mother- and human- raised) western lowland gorillas across 43 institutions in North America (Weiss et al., 2013). This study compared gorilla mortality rates over an 18 year period with a human-rated personality assessment previously carried out by Gold and Maple (1994). The results found that extraversion was associated with longer lifespans, and that this was not confounded by age, sex, rearing background, or the number of transferrals between institutions (Weiss et al., 2013). Because of the dynamic between personality and resilience, there is likely to be individual variation in the response of great apes to different stressors, as well as in their receptiveness to resilience interventions.

If optimism in great apes is affected by socially influential figures, as it is with humans (section 1.2.4.3), this may be relevant to orangutans in rehabilitation, where human surrogates and caretakers partially substitute for a mother and/or teacher role model (see section 1.1.2.1). Therefore, their behaviour may influence orangutan optimism. Despite the benefits of optimism, temporary pessimism may be more appropriate and realistic in the face of danger, by preparing for worst-case scenarios, and lowering expectations of success to prevent disappointment (Forgeard & Seligman, 2012); therefore, both optimism and pessimism may be relevant in the context of orangutan reintroductions.

1.2.6 Necessity for further research

As established above, resilience is a fundamental factor in the ability of humans and other animals to overcome stress. It is evident that resilience is flexible and can be altered over time, through life experiences or specific interventions. Despite the considerable amount of research into human resilience interventions, animal resilience studies largely feature rodents as subjects (discussed in more depth in Chapter Two), and there is very little knowledge about the resilience of great apes. Resilience is important for all great apes in captivity, but it is also paramount for the capacity of wild animals to survive in challenging environments. Orangutans in rehabilitation are faced with the shock of leaving behind the security of captivity for the danger and adversity they will undoubtably encounter in the wild. In future, the reintroduction process for gorillas and other great apes may become more established, in which case resilience will have similar importance. The extent to which resilience underpins the survival rate of released great apes has not yet been explored. However, the first step towards understanding this dynamic is identifying techniques to measure and increase resilience in great apes. Once developed, these resilience interventions can be tested for their efficacy in various contexts, including helping orangutans and other great apes successfully adapt to the wild, and helping captive great apes bounce back from unexpected stressors to live a more fulfilling and confident life in captivity.

Having provided an overview of the context within which this research is situated, and highlighted areas which require further investigation, section 1.4 specifies the project aims and research questions, before this chapter concludes with a description of the thesis structure (section 1.5).

1.4 Research aims

This thesis explores the gap in existing knowledge about great ape resilience and species-appropriate resilience interventions. The overarching aims of this research are to identify potential resilience interventions for captive great apes, and to determine how stress and resilience may be influenced by individual and species differences. The following research questions seek to address these aims:

- RQ1: Which form(s) of resilience intervention could be used to promote aspects of resilience in orangutans in rehabilitation and other captive environments?
- RQ2: Can experimental interventions promote persistence, an aspect of resilience, in orangutans and gorillas?
- RQ3: How does human presence, following extended periods of absence due to the Covid-19 lockdowns in England, affect stress and other behaviour in captive orangutans and gorillas?

- RQ4: Do individual or species differences affect the wellbeing of orangutans and gorillas and their likelihood of resilience to stress?

1.5 Thesis outline

1.5.1 Chapter Two

Resilience interventions for orangutans in rehabilitation and other captive environments can only succeed if they are logistically possible and appropriate. Recognising the current gap in knowledge about great ape resilience, Chapter Two, 'Resilience interventions for orangutans (*Pongo spp.*): a scoping review of interventions in humans and other animals', answers RQ1 by establishing a comprehensive overview of resilience interventions found to be effective in human and non-human animals. This is achieved through a systematic literature review of resilience interventions, which spans the fields of human psychology and animal behaviour. This review evaluates interventions which are effective in promoting aspects of resilience, and critically analyses them in terms of their appropriateness for orangutans in rehabilitation. This provides an essential foundation for future research into great ape resilience, acting as a starting point for the development of effective resilience interventions.

1.5.2 Chapter Three

Before applying resilience interventions more widely, it is essential to test them first, to ensure that they are effective and beneficial, rather than harmful. Building on the findings of the systematic review, Chapter Three, 'Testing a tool-based resilience intervention for captive great apes', addresses RQ2 by testing the efficacy of a novel resilience intervention. The intervention introduced in this chapter was tailored to fit the tool-using abilities of orangutans and gorillas and was subsequently tested at two different zoos in the UK. The findings of Chapter Three will help to inform future efforts in designing resilience interventions for great apes.

1.5.3 Chapter Four

Chapter Four, ‘The effect of Covid-19 lockdown restrictions lifting on zoo-held great ape behaviour and posture as indicators of welfare’, addresses RQ3 and RQ4 with an observational study of orangutans and gorillas at a UK zoo during varying degrees of lockdown, as Covid-19 restrictions lifted and zoo visitors returned. This provides an insight into the impacts of a major, potentially stressful event, contributing to an understanding of how the return of visitors following extended zoo closures influenced welfare-related behaviours in orangutans and gorillas. This chapter demonstrates that the lifting of restrictions affected gorillas and orangutans in separate ways. Chapter Four contributes to the Covid-19 zoo lockdown literature in helping caretakers understand how the lockdowns, and the subsequent return of visitors, impacted zoo-held great apes.

1.5.4 Chapter Five

To develop a fuller understanding of how captive great ape welfare is influenced by stress and environmental factors, it is important to look beyond the species level to the individual level. Chapter Five, ‘Understanding the welfare requirements of a neurologically and physically divergent captive male Sumatran orangutan (*Pongo abelii*)’, addresses RQ4 with a case study of a captive orangutan who has an array of physical and cognitive impairments, to critically analyse how these individual differences are likely to affect his welfare. This case study involved comparing the development of the study subject with expected rates of development in orangutans. In parallel, a cognitive enrichment apparatus was tailored to a suitable level of challenge for this individual. Chapter Five establishes key areas where wellbeing may be impacted by individual differences, and discusses some of the benefits and challenges associated with tailoring resilience interventions to accommodate atypical individuals.

1.5.5 Chapter Six

Chapter Six, 'General discussion', draws the results of the previous chapters together in a general discussion. This chapter summarises the main findings in this thesis and discusses the resulting implications for great apes in rehabilitation and other captive environments. Based on the findings of Chapters Two and Three, suggestions are made about the further development of resilience interventions and enquiry into related fields of research. Consideration is given to the issue of accommodating individual differences in the application of resilience interventions, with reference to Chapter Five. In addition, the complex findings in Chapter Four are discussed within the context of the existing Covid-19 and visitor presence literature. Chapter Six concludes with an overview of the limitations of these studies, followed by recommendations for future research, and a discussion of the key theoretical and practical contributions of this thesis.

CHAPTER 2

RESILIENCE INTERVENTIONS FOR ORANGUTANS (*PONGO SPP*.): A SCOPING REVIEW OF INTERVENTIONS IN HUMANS AND OTHER ANIMALS

This chapter, largely in its current form, is under review as:

Bridgeland-Stephens, L., Thorpe, S. K. S., Chappell, J., Resilience treatments for orangutans (*Pongo spp*.): A scoping review of interventions in humans and other animals. *Animal Welfare*.

Abstract

Wild orangutans (*Pongo spp.*) rescued from human-wildlife conflict must be adequately rehabilitated before being returned to the wild. It is essential that released orangutans can cope with stressful challenges like food scarcity, navigating unfamiliar environments, and regaining independence from human support. Although practical skills are taught to orangutans in rehabilitation centres, post-release survival rates are low. Psychological resilience, or the ability to 'bounce back' from stress, may be a key missing piece of the puzzle. However, there is limited knowledge about species-appropriate interventions which could help captive orangutans increase resilience to stress. This scoping review summarises and critically analyses existing human and non-human animal resilience literature and provides suggestions for the development of interventions for orangutans in rehabilitation. Three scientific databases were searched in 2021 and 2023, resulting in 63 human studies and 266 non-human animal studies. The first section brings together human resilience interventions, identifying common themes and assessing the applicability of human interventions to orangutans in rehabilitation. The second section groups animal interventions into categories of direct stress, separation stress, environmental conditions, social stress, and exercise. In each category, interventions are critically analysed to evaluate their potential for rehabilitation centres. The results show that mild and manageable forms of intervention have the greatest potential benefit with the least amount of risk. Potential interventions include brief separations from conspecifics, exercise programmes, increasing environmental complexity, providing challenging cognitive enrichment, and indirect exposure to difficult, but manageable, social interactions. The study concludes by emphasising the need for further investigation and experimentation, to develop appropriate interventions and measure their effect on the post-release survival rate of orangutans.

2.1 Introduction

Orangutans (*Pongo spp.*) are critically endangered in the wild and face substantial population decline (Ancrenaz et al., 2018; Singleton et al., 2018). They are threatened by a combination of factors, including habitat loss, degradation, and fragmentation (Wich et al., 2016, 2015). Many are deliberately killed as a by-product of habitat conversion, or during human-wildlife conflict, which can lead to infants being captured and trafficked in the illegal wildlife trade (Ancrenaz et al., 2018; Singleton et al., 2018). Since pioneering efforts in the 1960s, orangutan rehabilitation centres have been established across Borneo and Sumatra, with the aim of rescuing injured and/or trafficked orangutans and providing them with long-term rehabilitation (Russon, 2008). These centres endeavour to prepare capable individuals for release back into the wild, and to provide life-long care for those unable to be released, e.g. individuals with a severe physical disability, or an inability to acquire the necessary skills for independent living. Infants orangutans rescued from the illegal wildlife trade (Russon, 2008) will spend a large proportion of their development in rehabilitation before they are old enough to be released back into the wild.

Wild orangutan infants stay with their mothers until between six and nine years old (van Adrichem et al., 2006; van Noordwijk & van Schaik, 2005), learning the essential skills required to survive as an adult. Life in the wild for the world's largest arboreal mammal (Cant, 1992) is extremely demanding. Released orangutans face challenges like the physical and cognitive requirements of travelling through the forest canopy and building appropriate nests (Halsey et al., 2017; Thorpe et al., 2007; van Casteren et al., 2012), coping with unpredictable food scarcity (Knott, 1998), encountering unfamiliar or difficult-to-process food (Jaeggi et al., 2010), interacting with other orangutans, and managing conflict with humans and other dangerous animals (Chappell & Thorpe, 2022; Meijaard et al., 2011). In addition, when female orangutans reproduce successfully after being released, they must face all these challenges while providing their infants with extensive care until weaning, without having had the opportunity to experience species-typical maternal care from their own mothers.

As many orangutans in rehabilitation are orphaned at a young age, they are completely dependent on the support and care of human caretakers, and being able to learn from their peers, to help them acquire these life skills and prepare for independent living in the forest. Despite the extensive current efforts of rehabilitation centres to help orangutans develop each of these skills, there are continuing issues with post-release survival (Basalamah et al., 2018; Russon, 2008; Utami-Atmoko et al., 2017). The survival rates of released orangutans are uncertain, with estimates ranging from 20% to 80% (Russon, 2008). Therefore, even if orangutans appear to exhibit individual life skills while in rehabilitation, this does not necessarily translate into the capacity for independent survival. This indicates that there is a missing piece of the puzzle, and suggests that there may be broader, less tangible, factors underpinning the successful adaption of orangutans to the wild.

In a survey of Orangutan Veterinary Advisory Group (OVAG) members (n = 43), 93% of respondents (40/43) agreed that an orangutan's 'drive to survive' was an important factor in deciding whether to release orangutans back into the wild (unpublished OVAG questionnaire; Bridgeland-Stephens, 2020). This idea of individual variation in the 'drive to survive' arguably overlaps with resilience, which can be defined as a successful adaptation or competence despite stress or trauma (Masten, Best and Garmezy, 1990, in Egeland, Carlson and Sroufe, 1993; Garmezy, 1993). Although stress is often thought of as 'bad', it should be noted that there are thought to be different types of stress, with distress generally having a negative effect on the individual, and eustress generally having a positive effect (Lu, Wei, & Li, 2021). This nuance is important in the context of resilience research, as some forms of stress may be more likely to promote or decrease resilience than other forms of stress.

There is limited knowledge about resilience in nonhuman great apes. However, it seems likely that resilience, and the ability to ‘bounce back’ from stress, would be important for orangutans in rehabilitation centres. Resilience may also underpin the ‘drive to survive’, highlighted by OVAG members as an important aspect of successful orangutan releases. All orangutans in rehabilitation will have experienced at least one major life stressor, in being captured and then travelling to the rehabilitation centre. Many will also have witnessed the death of their mother, experienced physical injuries from humans or other orangutans, poor living conditions in small cages, or emaciation from lack of food (Sherman et al., 2020). They will probably continue to experience stressors during rehabilitation, e.g. conflict with conspecifics, veterinary interventions like surgeries or routine health checks, spending long periods of time in enclosures, being near dominant males, and moving to unfamiliar environments (e.g. pre-release islands). As well as overcoming stressors during rehabilitation, resilience is likely to be particularly important when orangutans are released, so that they can adapt to unfamiliar challenges in the wild. Low levels of resilience could explain why some orangutans appear to simply ‘give up’, despite their skillset, because persistence is an important aspect of resilience (Brown, 2015; Grotberg, 1995). Therefore, resilience may be an important missing piece of the puzzle, potentially underpinning the chances of a successful release by providing orangutans with a more flexible and generalised ability to ‘bounce back’ from previously unencountered challenges, rather than having to rely on specialised, situation-specific skills.

In humans, resilience is considered to be a malleable, rather than fixed, characteristic (Fletcher & Sarkar, 2013). Similarly, although little is known about orangutan resilience, 70% of OVAG respondents (n = 30/43) felt that an orangutan's 'drive to survive' could be influenced through rehabilitation (unpublished OVAG questionnaire; Bridgeland-Stephens, 2020). Despite the potential importance of resilience in the rehabilitation and release process, this factor has not yet been addressed scientifically. In order to begin filling this gap in scientific knowledge, this review draws together human and animal research on resilience interventions, to establish an understanding of the foundations of resilience, and to identify possible resilience-promoting interventions for orangutans. 'Resilience interventions' are defined here as interventions designed to influence one or more attributes of resilience in an individual. In reviewing the existing literature, the word 'intervention' is taken to mean an experimental condition, including interventions expected to have a negative impact. It is important to understand the potential negative effects of specific interventions to avoid replicating them and thereby causing further harm. It should be noted that resilience is a latent variable and can only be measured or influenced indirectly. Therefore, interventions designed to promote resilience are likely to overlap and inter-relate with tools to measure resilience, as both are proxies of 'true' resilience.

This review aims to outline key recommendations for developing practical interventions that can be used to promote resilience in orangutans in rehabilitation centres and other captive contexts. Section 2.3 addresses human resilience interventions. Although most of these methods are not applicable to great apes, it is important to understand the essential elements of resilience and identify common themes that underpin successful interventions. Therefore, this section draws out key concepts with the potential to be translated into interventions for orangutans. Section 2.4 summarises the most common resilience interventions in studies of non-human animals. The animal resilience interventions described in section 2.4 all overlap with at least one human resilience theme described in section 2.3. Each intervention type is critically analysed to evaluate its relevance for orangutan rehabilitation centres, and practical suggestions are made for integrating similar techniques into appropriate interventions for orangutans.

2.2 Methods

An electronic search was conducted on 7th February 2021 using three search engines: ProQuest Biological Science Collection, Scopus, and Web of Knowledge. Boolean operators were used for the following search terms: “psychological resilience” OR “resilience interventions” OR “resilience program” OR “stress inoculation” OR “stress immunity” OR “foster resilience”; and “psychological resilience” AND “animal”. The language filter was set to English, and sources included books, conference papers and proceedings, dissertations & theses, government & official publications, reports, scholarly journals, and working papers. There was no exclusion based on publication date.

The initial search returned 1680 results, reduced to 1241 articles of potential relevance after removing duplicates. The reference lists of the animal articles were also searched for relevant articles, as a greater diversity of intervention type was identified in the animal literature compared to the human literature. Only resources which had institutional access were used, excluding 20 articles from the final list. Irrelevant articles, and those which related to a very specific aspect of resilience, for example in a particular activity or relating to a particular illness or pain threshold, were removed in favour of articles with more general relevance. Studies on prenatal stress, and studies proposing medicinal aids to resilience, were excluded. Finally, only interventions which were targeted at building individual resilience (rather than family resilience, or group resilience) were included, even if the resilience interventions were provided in a group setting.

The search and filtering process resulted in 63 human papers and 240 animal papers. An additional search of animal articles was carried out on 11th May 2023, using the same search terms and filtering criteria as before, to ensure that the literature was up to date. This returned 202 results, and, after removing duplicates (n = 1) and articles that did not meet the criteria (n = 175), resulted in a further 26 relevant animal studies, bringing the total number of animal studies to 266. Due to the breadth of fields drawn together in this review, lesser-known terms can be found in the glossary at the beginning of this thesis.

2.3 Human interventions

The human resilience studies encompassed a broad range of age groups and spanned five continents (Asia, Australia, Europe, and North and South America). An overwhelming majority of interventions used talking therapies, in a group or individual setting. The in-text descriptions of the content of each resilience programme were coded into different categories and collated into broader recurring themes, listed in Table 2.1. Many of these themes match those described by OVAG members as important factors in an orangutan's 'drive to survive', e.g. flexibility, hardiness, self-efficacy, independence, social skills and interest in conspecifics, physical activity, problem-solving, and the ability to overcome stress (unpublished OVAG questionnaire; Bridgeland-Stephens, 2020). Interventions included training in one or more of these themes, with a mean of 6.5 different themes per intervention and a range of 1-15. Studies can broadly be divided into those based on a type of cognitive behaviour therapy called Stress Inoculation Therapy (see Glossary) (Meichenbaum, 1985), further detailed in section 2.3.2.1, and those using alternative methods. Over 80 different types of questionnaire were used to measure aspects of resilience, shown in Appendix A. These were either carried out by an experimenter/professional or were self-administered.

Table 2.1 *Common themes in human resilience interventions.* 'Number of studies' includes all studies which mention each theme; some studies include multiple themes. Refer to Glossary for definitions of terms.

Type of intervention	**Number of studies**
Stress inoculation	31
Emotional intelligence	25
Social skills, peer support	23
Self-awareness, self-reflection	22
Optimism, positive affect, positive thinking	21
Cognitive skills	19
Self-confidence, self-esteem	19
Relaxation, meditation, mindfulness	18
Self-control, behavioural inhibition	17
Agency, self-efficacy, independence	15
Problem-solving	14
Planning	11
Exercise, physical activity, healthy lifestyle	9
Persistence, hardiness	9
Goal orientation	7
Flexibility	7
Other	5

2.3.1 Resilience interventions

Several interventions were found to significantly increase resilience (Agteren, Iasiello, & Lo, 2018; Henshall, Davey, & Jackson, 2020; Joyce et al., 2018; Peng et al., 2014; Pluess et al., 2017; Rogerson et al., 2016; Steinhardt & Doblier, 2010), particularly in individuals who initially had low levels of resilience (Agteren, Iasiello, & Lo, 2018; Peng et al., 2014). In applying a resilience training programme to female prisoners, which focused on mindfulness techniques, ‘positive psychology’ (see Glossary), and cognitive behavioural therapy, Lo et al. (2020) found that the programme was more beneficial for long-term prisoners. This is encouraging for orangutans unable to be released into the wild who need to cope with pressures connected with long-term life in captivity, for example relative limitations to space and environmental complexity. Despite the clear differences between human prisoners and animals in long-term captivity, particularly regarding the intentions and causes underlying each situation, there are arguably similarities in the physical limitations and psychological stress (Morgan & Tromborg, 2007) resulting from long-term life in captivity. In a resilience training programme with similar methods to Lo et al. (2020), Smith et al. (2018) found that the longer participants engaged with resilience training, the greater the benefit they experienced. This indicates that it is beneficial to integrate resilience-building interventions throughout the whole rehabilitation period, to maximise the potential benefits.

A range of studies that focussed on talking therapies found benefits in measures of specific aspects of resilience, including the ability to cope, proactivity, self-esteem, confidence, and lower levels of stress, depression, anxiety, inflexibility, and negative or suppressed emotions (Agteren et al., 2018; Akeman et al., 2020; Gallegos-guajardo et al., 2015; Henshall et al., 2020; Joyce et al., 2018; Kozina, 2020; Lo et al., 2020; Peng et al., 2014; Pluess et al., 2017; Foster et al., 2018; Steinhardt & Doblier, 2010). Pluess et al. (2017) identified long-lasting beneficial effects in school children who had participated in a resilience intervention programme, when tested six and twelve months after the intervention. Neither Chandler and Roberts (2015) nor

Delaney et al. (2020) found a statistically significant difference between resilience intervention and control groups, although both studies had a relatively low number of participants (n = 28 and 40 respectively) and benefits were self-reported by participants through written reflections or in-depth interviews. Reported benefits included building personal strengths, creating supportive connections with others (Chandler & Roberts, 2015), learning stress-relieving techniques, and sharing experiences of stress with others (Delaney et al., 2016)

These results suggest that humans can build skills and attributes that contribute to resilience and protect against stress. However, the interventions above are all talking therapies, and non-linguistic methods are required for orangutans. In addition, human resilience therapies may have an underlying benefit by providing a degree of social support, same-species contact, and the feeling of 'being understood', and these benefits may not translate in a straightforward way for orangutans. Therefore, the most common themes in human resilience interventions, shown in Table 2.1, offer a starting point from which to design interventions for orangutans.

2.3.2 Stress inoculation

2.3.2.1 Stress Inoculation Therapy

Stress Inoculation Therapy (SIT) (Meichenbaum, 1985) involves a form of cognitive behavioural therapy, and is based on the theory that behaviour and feelings are determined by individual perceptions, and can therefore be cognitively reframed. SIT is intended to break the 'stress cycle' of negative reactions and ineffective responses to stressful events by teaching a range of coping skills and behaviours. The three-stage process involves patients reconceptualising their responses to specific stressors, before learning coping skills and applying these to imaginary (role-played) and real-life stressors (Meichenbaum & Cameron, 1983). SIT was used as an intervention in 27 of the papers reviewed, and several randomised controlled trials identified beneficial effects (Hourani et al., 2016; Law, Logan, & Baron, 1994; Navaee & Kaykha, 2019; Szabo & Marian, 2012; Varker & Devilly, 2012), with some positive effects still present two years after the intervention (Hourani et al., 2016). However, in the context of orangutan rehabilitation, the cognitive reframing element of SIT would be extremely difficult to achieve in a non-linguistic form and may be counterproductive in blunting responses to stressors, e.g. by inhibiting appropriate reactions to stressful events during the 'skills acquisition' phase of the intervention (Meichenbaum & Cameron, 1983). It is important for caretakers to be able to identify stressors for orangutans by reading their behaviour, to avoid further harm. This is already a challenge, as nonhuman primates are adept at masking overt expressions of pain and illness (Pelsker & Mayer, 2008). SIT has also received criticism for moving the locus of control away from the patient towards the therapist, and for framing certain responses to stress as 'irrational' (Hurley, Barrett, & Reet, 2006). As will be discussed in section 2.4.1.1, a sense of agency and control over the environment is thought to be beneficial for a range of taxonomic groups. Although SIT is not appropriate here, certain coping skills involved in the intervention may be beneficial, e.g. problem-solving skills.

2.3.2.2 Major lifetime stressors

Alongside daily stressors related to life in captivity, all orangutans in rehabilitation will have experienced at least one major life stressor, i.e. capture and travelling to the rehabilitation centre. However, depending on the prior history of each orangutan, they are likely to have experienced additional major stressors leading up to their rescue, such as witnessing the death of their mother, as well as stressors during their time in rehabilitation, e.g. veterinary interventions. Although some studies identified a positive linear relationship between cumulative lifetime adversity and the odds of being diagnosed with a stress-related disorder

(Fernandez et al., 2020; Gerber et al., 2018), there is more robust evidence for a U-shaped relationship. In a large study involving a stratified random-digit-dial telephone survey with 2,398 members of the public, Seery et al. (2010) found that individuals with some experience of lifetime adversity had lower ratings for distress, functional impairment, and post-traumatic stress symptoms, higher ratings for life satisfaction, and were least affected by recent adversity than those with no experience of prior adversity, or those with high exposure to adversity (categorised as mean + 1 SD; ~87th percentile). These results are supported by Seery et al. (2013), who reported a similar U-shaped relationship between lifetime adversity and pain-induced catastrophising and negative affect, with moderate numbers of prior major life stressors (two to seven) associated with the highest resilience to stress. If a U-shaped relationship between life stressors and resilience exists for orangutans, it is very important that an 'upper limit' of life stressors is established, so it can be avoided. However, because orangutans' life histories prior to arrival at the rehabilitation centres are often unknown, this will be difficult to achieve.

2.4 Animal interventions

In this section, stress and resilience interventions for animals are broadly separated into five categories: direct stress procedures designed to elicit pain/fear/discomfort, separation from the group/mother, environmental deprivation/enrichment, social stress, including exposure to strangers or dominant individuals, and exercise regimes. These are different to the human resilience categories shown in Table 2.1 as the five categories described here relate to forms of intervention, rather than themes of resilience within different types of talking therapies. There were one to four interventions per study, with a mean of 1.36 interventions and the great majority of papers using a single experimental intervention, alongside a control group (where applicable) (201/266). Many studies, particularly those involving rodents, used well-established behavioural tests to measure aspects of resilience and stress indicators, summarised in Appendix B. A comprehensive overview of animal resilience interventions is shown in Table 2.2. Sections 2.4.1 to 2.4.5 will expand on the studies most pertinent to the context of orangutan rehabilitation.

Table 2.2 *Summary of resilience intervention effects.* (Grey-shaded cells highlight primate studies; S = sex (F = female, M = male, B = both/mixed, ? = not stated). Colour shading is specified in key below:

Strength of evidence (E) (The number and proportion of studies which support, i.e. provide evidence for, the effect on resilience category - see 'effect on resilience' key, below)				
Weak evidence	Limited evidence	Inconclusive	Some evidence	Strong evidence
Single study	*<5 studies*	*5+ studies,* *40-59% support effect*	*5+ studies,* *60-79% support effect*	*5+ studies,* *80-100% support effect*
🟦	🟪	🟥	🟧	🟨
Effect on resilience (R)				
Negative	Neutral-Negative	Neutral/unclear	Neutral-positive	Positive
>70% studies have negative effect	*>70% studies have negative and/or no effect*	*Either no studies with a clear positive/negative effect, or equal numbers of studies with conflicting effects*	*>70% studies have positive and/or no effect*	*>70% studies have positive effect*
🟦	🟪	🟥	🟧	🟨

Type	**Intervention**	**Taxonomic group**	**S**	**E**	**R**	**Notes on intervention**	**Most relevant studies**
Generic stressors/ stress schedules	Acute stress (see Glossary)	Rodents	B	🟨	🟦	Strong evidence that 'single prolonged stress' and other acute stressors can cause a range of negative effects, including heightened fear expression during re-exposure to stressors, increased anxiety	(Adamec & Shallow, 1993; Bazak et al., 2009; Chen et al., 2018; Denny et al., 2021; Eagle, Fitzpatrick, & Perrine, 2013; Gonzalez et al., 2021; Le Dorze &

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
(99/266 papers reviewed)	*(single acute stress session)*			🟧	🟦	and depression, and reduced behavioural flexibility.	Gisquet-Verrier, 2016; Liu, Atrooz, Salvi, & Salim, 2017; Nahvi et al., 2023; Perrine et al., 2016; Tsoory, Cohen, & Richter-Levin, 2007)
			F	🟪	🟥	Conflicting studies, unclear effect on female rodents.	
		Dogs	?	🟪	🟦	Two studies intentionally induced learned helplessness (see Glossary) in dogs (*Canis familiaris*) in an electric shock session.	(Overmier & Seligman, 1967; Seligman, Maier, & Geer, 1968)
	Short periods of stress (e.g. electric shock, predator odour, forced swim, or elevated platform stress) (see Glossary) *(3-7 days)*	Rodents	M	🟥	🟪	Contradictory evidence of effects, mostly negative, and possibly age-dependent.	(Avital et al., 2006; Baugher & Sachs, 2022; Peleg-Raibstein & Feldon, 2011; Toledo-Rodriguez & Sandi, 2007; Tsoory & Richter-Levin, 2006; Wilkin et al., 2012)
			F	🟦	🟥	Contradictory evidence of positive and negative effects, possibly age-dependent. One study found reduced freezing in response to a fear cue in adolescent females, but not males.	
		Birds	F	🟦	🟧	One study of Japanese quail (*Coturnix japonica*) found that one week of unpredictable stress improved spatial learning and behavioural flexibility.	(Calandreau et al., 2011)

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
	Chronic stress (see Glossary) *(10-48 days)*	Rodents	B	🟧	🟪	Strong evidence of chronic stress causing a range of negative effects. Contradictory evidence regarding importance of age and sex. Mixed evidence of the effect of mild/predictable chronic stress, with some studies showing benefits and others showing increased anxiety and depression	(Bondi et al., 2008; Bourke & Neigh, 2011; Burgdorf, Kroes, & Moskal, 2017; Castro et al., 2012; Chaby et al., 2015a; Chaby et al., 2013; Chaby et al., 2015b; Cotella et al., 2019; Ducottet & Belzung, 2004; Garcia-Marquez & Armario, 1987; Katz, Roth, & Carroll, 1981; Li et al., 2022; Lyte et al., 2022; Mineur, Belzung, & Crusio, 2007; Muhammad & Kolb, 2011; Pohl et al., 2007; Remus, Jamison, & Johnson, 2013; Strekalova et al., 2022; Swiergiel, Zhou, & Dunn, 2007; Toth et al., 2008; Walker et al., 2022; Yohn & Blendy, 2017)
	Restraint stress *(usually 6 hours daily from 10 days to 4 weeks)*	Rodents	M	🟥	🟥	Contradictory results, with some studies showing negative effects. However, some forms of restraint stress, particularly shorter periods of restraint (i.e. 5 minutes to 1 hour), supporting positive effects of restraint stress; e.g. reduced anxiety and depression, and increased exploration, spatial memory, and novel object recognition.	(Beck & Luine, 2002; Bowman, Zrull, & Luine, 2001a; Campos-Cardoso et al., 2023; Chiba et al., 2012; Doremus-Fitzwater, Varlinskaya, & Spear, 2009; Eiland & McEwen, 2012; Hoffman et al., 2011; Luine, 2002; Luine et al., 1996; Luine et al., 1994; Lyte et al.,

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
			F	🟪	🟪	Most studies had negative effects, but one study found a positive effect of restraint stress on spatial memory in females only, particularly those in proestrus, compared to controls.	2022; Parihar et al., 2011; Shi et al., 2021; Torrisi et al., 2021; Wood et al., 2008; Yan et al., 2023)
		Agricultural	F	🟦	🟨	One sheep (*Ovis aries*) study showed that three days of 6h restraint sessions led to a more optimistic judgement in a positive/negative bias test than unrestrained controls.	(Doyle et al., 2010)
	Controllable/ predictable stress	Rodents	M	🟧	🟨	Most studies showed positive effects of being able to control stress, in protecting against stress and depression when exposed to later stressors, as well as enhancing social learning and the ability to discriminate between positively and negatively reinforced odours. Some of these benefits emerged over time.	(Amat et al., 2010; Baratta et al., 2018; Brown et al., 2001; Christianson et al., 2008; Kubala et al., 2012; Lucas et al., 2014; Prince & Anisman, 1984; Suo et al., 2013)
			F	🟦	🟥	Only one study, which did not show an effect of being able to control stress.	
		Agricultural	F	🟦	🟥	One study found a positive effect of being able to control stress in sheep (*Ovis aries*), another study found no effect of stress predictability.	(Greiveldinger, Veissier, & Boissy, 2009; Greiveldinger, Veissier, & Boissy, 2007)

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
		Dogs	?	🟪	🟧	Two dog (*Canis familiaris*) studies induced learned helplessness through loss of controllability. In one study, this was later reversed by physically forcing the dogs to escape the stressor.	(Overmier & Seligman, 1967; Seligman et al., 1968)
		Birds	F	🟦	🟧	One chicken (*Gallus domesticus*) study found that loss of both controllability and predictability increased frustration.	(Zimmerman & Koene, 1998)
Maternal/ group separation *(96/266 papers reviewed)*	Brief separations *(15 minutes to 1 hour)*	**Primates**	B	🟧	🟧	Moving squirrel monkeys (*Samiri sciureus*) next to an unfamiliar group for one hour weekly for ten weeks during adolescence led to reduced anxiety, increased exploration and interaction with novel objects, and enhanced inhibitory control.	(Lyons & Parker, 2007; Parker et al., 2004, 2005, 2012, 2019)
		Rodents	B	🟧	🟥	In some studies, 15 minute daily maternal separation and handling had no effect compared to controls. Where an effect was seen, brief separations tended to protect against stress, reduce emotionality, anxiety, depression, and fear, and increase playfulness, exploration, and vigilance.	(Caldji et al., 2000; McIntosh, Anisman, & Merali, 1999; Mrdalj et al., 2016; Núñez et al., 1995, 1996; Siviy & Harrison, 2008; Stamatakis et al., 2008)
	Longer separations	**Primates**	B	🟦	🟦	Marmosets (*Callithrix jacchus*) experienced a range of negative effects after 26 days of 30-120	(Pryce et al., 2004)

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
	(2-4.5 hours daily for 1-3 weeks)			🟦	🟦	minute daily separations, e.g. reduced levels of activity, play, social contact, motivation, and increased impulsivity.	
		Rodents	M	🟧	🟦	Longer separations generally led to a range of negative effects, including increased anxiety, fear, emotional reactivity, and depression, cognitive impairments, and reduced exploration. However, one study showed that predictable maternal separations can reduce anxiety resulting from stress (Shi et al., 2021).	(Aisa et al., 2007, 2008; Baudin et al., 2012; Baugher & Sachs, 2022; Bian et al., 2015; Bowman, Zrull, & Luine, 2001b; Caldji et al., 2000; Colorado et al., 2006; Daniels et al., 2004; Eiland & McEwen, 2012; Farrell et al., 2016; Gardner et al., 2005; Grassi-Oliveira et al., 2016; Hulshof et al., 2011; Kalinichev et al., 2002; Lee et al., 2007; Leussis et al., 2012; Marais et al., 2008; Marco et al., 2013; Mourlon et al., 2010; Ogawa et al., 1994; Penke et al., 2001; Romeo et al., 2003; Shi et al., 2021; Shu et al., 2015; Sun et al., 2014; Uysal et al., 2005; Wei et al., 2018; Zalosnik et al., 2014)
			F	🟧	🟪	Most studies show a negative effect, or no effect, but a small number of mixed-sex studies show a sex-specific positive effect in females, in the form of decreased fearfulness and/or anxiety. One study identified these benefits in females in diestrus only (Romeo et al., 2003).	
	Prolonged isolation	**Primates**	B	🟨	🟦	Infant macaque species (*Macaca mulatta/fascicularis*) in laboratory environments	(Corcoran et al., 2012; Feng et al., 2011; Novak & Harlow, 1975; Röder,

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
	(>24 hours) or surrogacy			🟨	🟦	were negatively affected by prolonged separation or surrogacy (either peer, or inanimate wire/cloth 'surrogate'). Negative effects included increased stereotypies, reduced activity and exploration, and abnormal social interactions.	Timmermans, & Vossen, 1989; Sackett, 1972; Suomi & Harlow, 1972; Suomi, Harlow, & Domek, 1970)
		Rodents	M	🟪	🟪	Mixed results, with most studies showing no effect or a negative effect, and a small number of studies showing a positive effect.	(Abraham & Gruss, 2010; Grippo et al., 2007; Grippo et al., 2008; Han et al., 2011; Hong et al., 2012; Weintraub, Singaravelu, & Bhatnagar, 2010)
			F	🟪	🟥	Mixed results, with most studies showing no effect, and equal numbers of studies showing positive and negative effects.	
Env. conditions *(41/266 papers reviewed)*	Env. stress/ deprivation *(for rodent studies, 'early life stress' consists of 1 week of wire floors and*	**Primates**	B	🟦	🟦	One bonnet macaque (*Macaca radiata*) study found that variable foraging demand (i.e. periodically having to search for food under woodchip) had a negative effect on infant exploration, as infants were less likely to break contact with their mother to explore a novel environment.	(Andrews & Rosenblum, 1993)
		Rodents	M	🟧	🟦	Most studies show a negative effect of early life stress, e.g. increased anxiety, impaired spatial memory and novel object recognition, and reduced	(Bath et al., 2017; Brunson et al., 2005; Dalle Molle et al., 2012; Goodwill et al., 2019; Machado et al., 2013)

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
	restricted bedding)			🟧	🟦	exploration. Some (limited) evidence to suggest that negative effects are more prolonged in males than females.	
			F	🟨	🟦	Most studies show a negative effect of early life stress, e.g. increased anxiety in an open space. Some evidence of a sex-specific depressive effect of early life stress on females. Possible improved recovery from early life stress in females compared to males.	
		Birds	B	🟪	🟥	Two zebra finch (*Taeniopygia guttata*) studies support some benefits of low food conditions, including faster spatial learning and exploration. A small study (6 individuals) of starlings (*Sturnus vulgaris*) found a detrimental effect of environmental enrichment followed by deprivation.	(Bateson & Matheson, 2007; Krause et al., 2009; Kriengwatana et al., 2015)
		Fish	B	🟦	🟧	One Panamanian bishop (*Brachyrhaphis episcopi*) study found that high-risk environments were associated with increased activity and exploration, both of which are indicators of resilience..	(Archard & Braithwaite, 2011)

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
	Env. enrichment	Rodents	B	🟧	🟧	There is a strong body of evidence that environmental enrichment can protect against stress, anxiety, depression, fear, and emotional reactivity, as well as increasing activity levels, learning ability, and spatial memory. Some of these effects may be dependent on age, severity of stress, and type of enrichment. However, these benefits may be lost when enriched conditions are reverted back to baseline conditions.	(Benaroya-Milshtein et al., 2004; Crawford et al., 2020; Cui et al., 2006; Francis et al., 2002; Harati et al., 2013; Hattori et al., 2007; Ilin & Richter-Levin, 2009; Kent et al., 2022; Lambert et al., 2016; Leggio et al., 2005; Luo et al., 2022; Sampedro-Piquero et al., 2016; Schrijver, et al., 2002; Strzelewicz et al., 2019; Zambrana et al., 2007)
		Agricultural	B	🟧	🟧	Strong evidence for a positive effect of environmental enrichment on pigs (*Sus domesticus*), including greater mobility, diversity of behaviours, and reduced emotionality. However, enrichment followed by deprivation had a negative effect, e.g. increasing pessimism in a cognitive bias test.	(Bolhuis et al., 2006; De Jong et al., 2000; Douglas et al., 2012; Puppe et al., 2007; Wemelsfelder et al., 2000)
Social stress *(26/266 papers reviewed)*	Social defeat stress (see Glossary)	Rodents	M	🟧	🟦	Strong evidence to support a negative effect of social defeat stress, even if the subject is only witnessing a conspecific experiencing social defeat, and the defeat is not experienced directly. These negative effects include increased anxiety,	(Bravo-Tobar et al., 2021; Calpe-López et al., 2022; Jacobson-Pick et al., 2011; Jing et al., 2021; Lee et al., 2021; Li et al., 2021; Lu et al., 2021; Patki, Solanki, & Salim, 2014; Santarelli et al., 2017;

Type	Intervention	Taxonomic group	S	E	R	Notes on intervention	Most relevant studies
				🟧	🟦	impulsivity, and depression, impaired social interactions, and memory deficits.	Shi et al., 2023; Wang et al., 2022; Willmore et al., 2022; Wommack et al., 2004)
			F	🟦	🟦	One study showing increased anxiety in an open field test, particularly in the metoestrus and dioestrus phase, but no effects in other behavioural tests of anxiety and depression.	(van Doeselaar et al., 2021)
	Indirect (no physical contact) exposure to dominant individual	Rodents	M	🟪	🟧	Evidence to support a protective effect of exposure to a dominant individual against depression and anxiety, and a positive effect on exploration and social interaction.	(Ayash et al., 2020; Brockhurst et al., 2015)
			F	🟦	🟧	One study found evidence for a more active coping strategy when exposed to a dominant individual. This was characterised by increased exploration, reduced fearfulness, and reduced immobility in a tail-suspension test.	(Lyons, Buckmaster, & Schatzberg, 2018)
	Chronic social stress/social instability stress	Rodents	M	🟪	🟦	Some evidence to support negative effects of social instability stress, although these are not necessarily permanent.	(dos Santos Guilherme et al., 2022; Green, Barnes, & McCormick, 2013; McCormick, Smith, & Mathews, 2008; Sterlemann et al., 2008)
			F	🟦	🟥	Two studies showed negative effects of social instability stress, including increased depression,	

Type	**Intervention**	**Taxonomic group**	**S**	**E**	**R**	**Notes on intervention**	**Most relevant studies**
	(repeated exposure to strangers)			🟦	🟥	anxiety, and impaired social interactions. However, one study found reduced anxiety in females in oestrus.	
Exercise *(21/266 papers reviewed)*	Voluntary exercise *(wheel running)*	Rodents	M	🟧	🟧	Evidence to support beneficial effect of voluntary wheel running in protecting against stress when exposed to later stressors, particularly in individuals with high baseline levels of physical activity. However, two studies report negative effects on anxiety in male rats. One study found improved fear extinction and reduced fear renewal in males, but not females.	(Bouchet et al., 2017; Calpe-López et al., 2022; Dishman et al., 1997; Fuss et al., 2010; García-Capdevila et al., 2009; Greenwood, et al., 2003, 2005, 2007, 2012; Leasure & Jones, 2008; Mul et al., 2018; Robinson et al., 2019; Tanner et al., 2019; Zhang et al., 2021)
			F	🟪	🟧	Low number of studies, but evidence to support beneficial effect of voluntary wheel running in protecting against future stress. One study found improved active coping strategies in females, but not males.	
	Forced exercise *(treadmill/ wheel running)*	Rodents	M	🟧	🟧	Evidence to support a protective effect of forced exercise against anxiety, depression, and spatial memory.	(Fulk et al., 2004; Greenwood et al., 2013; Kochi et al., 2017; Lalanza et al., 2015; Leasure & Jones, 2008; Pietrelli et al., 2018; Yan et al., 2023)
			F	🟪	🟥	Conflicting evidence, effect on resilience is unclear.	

2.4.1 Generic stressors/stress schedules

It is important to understand the effects of direct stress procedures designed to elicit pain, fear, or discomfort, not only to investigate how prior stress influences resilience, but also whether milder forms of stress can have an inoculating effect. There is strong evidence that acute (single stress session) and chronic (over a period of at least 10 days) stressors (see Glossary) cause a range of long-lasting negative effects in rodents, including increased anxiety and depression, heightened fear expression during stress re-exposure, and reduced cognitive and behavioural flexibility (see Table 2.2). However, the evidence for the effects of restraint stress, or short periods (three to seven days) of various stressor, such as electric shock, predator odour, forced swim, and/or elevated platform stress (see Glossary), on rodents is less clear-cut. There is contradictory evidence, with some studies showing positive outcomes, and others showing negative outcomes. Companionship with a conspecific may protect against the negative effects of direct stress. For example, one study of the effect of chronic unpredictable stress on male mice found that 30 minute periods spent with a female mouse in between stressors ameliorated some depressive effects (Li et al., 2022). Another study found that human stimulation of rats, i.e. stroking them at a rate of 5 cm/second for ten minutes prior to chronic unpredictable mild stress, helped to protect against increased anxiety and depression in subsequent behavioural tests (Walker et al., 2022).

However, some taxonomic groups may experience benefits from stress interventions. For example, one week of unpredictable stress in Japanese quail (*Coturnix japonica*) led to increased spatial learning and behavioural flexibility when tested the next day (Calandreau et al., 2011). One sheep (*Ovis aries*) study found that three days of six-hour restraint sessions led to more optimistic judgements than unrestrained controls in a positive/negative bias test (Doyle et al., 2010). However, as the subjects were not later retested, the duration of these benefits is unclear.

Some rodent studies indicate that certain characteristics are conducive to resilience against stress, e.g. low anxiety and exploration, low emotionality, and positive affect (see Glossary) (Castro et al., 2012; Ducottet & Belzung, 2004; Mällo et al., 2009). It is interesting that Castro et al. (2012) found that a combination of low anxiety and low exploration led to resilience against stress in rats, as this contradicts the fact that curiosity, physical activity, and self-motivation are all thought to contribute to resilience. In addition, once released into the wild, orangutans will need exhibit enough targeted exploratory behaviours appropriate to specific situations to be able to locate food and establish a home range without taking unnecessary risks. It is possible that the importance of low anxiety and exploration is specific to resilience in rats, or the laboratory environment. Therefore, further research needs to be done to understand the relationship between individual characteristics and levels of resilience. Liu et al. (2017) identified a resilient group of subjects who showed earlier signs of anxiety and depression following acute stress, but had no behavioural deficits later in life. In another rat study, rough-and-tumble play during chronic unpredictable stress protected against any negative effects (Burgdorf et al., 2017). These protective characteristics should be further explored, to see whether they are relevant in other contexts.

2.4.1.1 Stress controllability/predictability

Uncontrollable stress can lead to 'learned helplessness' (see Glossary), which describes the failure to respond to avoidable shocks due to prior experience of inescapable traumatic shock (Overmier & Seligman, 1967). This should be taken seriously in the context of orangutan rehabilitation, where space is limited and orangutans have very little control or ability to change their situation. For example, they are restricted in what and when they eat, who they have social contact with, and where they can go while in the rehabilitation centre. Maier (2001) found that inescapable stress followed by repeated exposure to the specific context in which stress took place prolonged depression and learned helplessness in rats indefinitely. Sanctuary housed orangutans may be repeatedly exposed to stressful contexts, e.g. relatively small enclosures or veterinary interventions. Repeatedly 'refreshing' the stress associated with captivity and small environments may have long-lasting detrimental effects. It would be beneficial to identify coping strategies currently used by orangutans in rehabilitation to manage long-term stressors.

There is strong evidence that the ability of male rodents to control electric shock stress helps to protect against stress and depression when exposed to future stressors, as well as enhancing social exploration and the ability to discriminate between positively and negatively reinforced odours (see Table 2.2). Similar benefits are seen in sheep. Greiveldinger et al. (2009) found that teaching lambs to control an airblast to the muzzle during feeding led to lower emotionality and vigilance compared with subjects who did not have the opportunity to control the stressor. Predictability can also reduce the impact of stress. Lambs that experienced a predictable sudden event – either due to regularity of appearance, or because it was associated with a cue – had a reduced startle response and less disruption to feeding than those that experienced an unpredictable event (Greiveldinger et al., 2007). Although neither predictability or controllability of the stressor had a noticeable effect on chicken (*Gallus domesticus*) behaviour, loss of both had the effect of increasing their frustration, measured by higher levels of vocalisations (Zimmerman & Koene, 1998). When learned helplessness has occurred, two studies on dogs and rats respectively found that it can be reversed by force, i.e. a human physically dragging the animal away from the source of an electric shock (Seligman et al., 1968; Seligman, Rosellini, & Kozak, 1975). Although the ethical problems with these methods are substantial, it does indicate that recovery from learned helplessness is possible.

2.4.1.2 Summary

This section clearly demonstrates the potential harms from both acute and chronic stressors. However, some forms of milder, less extended, and more controllable forms of stress may have potential benefits. It is natural for orangutans to experience stressful situations in the wild, and it is therefore important for rehabilitant orangutans to be given the opportunity to develop resilience by successfully overcoming a range of different challenges prior to release. These challenges can be presented to animals in a controlled way by developing interventions which provide a mildly frustrating – but ultimately rewarding – challenge that can be resolved through persistence and problem-solving. The importance of effort-based reward is something that has been addressed in human studies. For example, Dweck (1975) found a way to 'treat' learned helplessness in human children, by teaching them to take responsibility by attributing failures to a lack of effort, rather than ability. Appropriate difficulty levels of cognitive enrichment will be discussed further in section 2.4.3. There may also be specific personality traits that help to protect against stress, such as low anxiety, low emotionality, and positive affect, which may help orangutans adapt to the wild. However, although generally low levels of anxiety may be beneficial, it is important that orangutans are still responsive to genuine threats, so that these can be avoided. Therefore, interventions that induce an anxious response to specific threats, e.g. snakes and humans, can still be utilised, even if overall low anxiety levels are desirable for resilience in orangutans.

2.4.2 Separation

This section is particularly relevant for three reasons. The first is that nearly all orangutans in rehabilitation have been separated from their mothers at a young age, which is likely to cause considerable distress and persisting trauma considering the long-lasting mother/infant bond in orangutans (van Noordwijk & van Schaik, 2005). The second reason is that human caretakers will not have the same intensity and duration of contact that the orangutans would normally have with their mother. On the other hand, too much contact with humans may increase dependence on human care (unpublished OVAG questionnaire; Bridgeland-Stephens, 2020) and lead to orangutans seeking out humans after they have been released into the wild, which could pose a considerable risk to the orangutans. Therefore, it is important to understand the effects of the presence and/or absence of a caretaker, so that an optimal amount and appropriate form of contact between humans and orangutans in a rehabilitation setting can be determined. Lastly, understanding the effects of separation has implications when considering the logistics of housing orangutans in groups, and the potential effects of isolation if this is not possible.

2.4.2.1 Brief separations

Brief daily separation interventions (15-60 minutes) can have a range of beneficial effects, and this is supported by a strong body of evidence. Over the past two decades, a series of stress inoculation studies were carried out on squirrel monkeys (*Samiri sciureus*) raised in a normal, species-typical way in a laboratory environment. These involved moving subjects from their natal group to an enclosure adjacent to an unfamiliar group for one hour weekly, for 10 weeks during adolescence, with the purpose of inoculating the monkeys against future stress. This intervention resulted in benefits such as reduced anxiety, increased time spent exploring and interacting with novel objects, and enhanced inhibitory control (Parker et al., 2019, 2005, 2012, 2004, 2007). However, it should be noted that these studies were all carried out by the same research team, and some research subjects were used for multiple studies, so caution should be taken in generalising the results to other populations. Many rodent studies found positive effects in adulthood of 15 minutes of daily keeper handling (involving separation from the litter) during infancy or adolescence, including protection against stress, a reduction in anxiety, depression, and fear, and increased playfulness and exploration (see Table 2.2). These brief separation interventions may be transferable to the context of orangutan rehabilitation. Exposing young infant orangutans to mild separation stress by removing them from their social group and placing them next to unfamiliar orangutans may have stress-inoculating benefits. However, careful management decisions would need to be made on an individual basis about the appropriateness of this method. In rehabilitation centres, detailed knowledge of prior traumatic events experienced by individual orangutans is usually not available. As the studies detailed above are carried out on normally-reared laboratory animals with known histories, there is less risk of unexpected trauma surfacing during the separations. This potential interaction between prior stress and the effect of separation is related more generally to the nature of the relationship between life stressors and resilience, discussed in section 2.3.2.2.

2.4.2.2 Longer separations

There is fairly consistent evidence that longer periods of separation (2-4 hours daily) can have a range of negative effects in rodents (see Table 2.2), and this is also supported by a primate study (Pryce et al., 2004). Wild orangutan infants are in near-continuous bodily contact with their mother for the first two years of life, only gaining full locomotory independence at five to six years, and sharing her nest until weaning at six to eight years old (van Adrichem et al., 2006; van Noordwijk & van Schaik, 2005). Even years after gaining independence, orangutans have been observed to occasionally ‘visit’ their mother at 11 years old (Noordwijk et al., 2009).

However, early maternal separation is inevitable for nearly all orangutans rescued from the illegal wildlife trade, as the process of capture usually requires the death of the infants' mother (Nijman, 2005). Therefore, infant orangutans rely mostly on a combination of human caretakers and peer-rearing. A study of laboratory chimpanzees (*Pan troglodytes*) found that individuals separated from their mothers earlier, and isolated for longer, were less social, less dominant, and more affected by stressful experiences (Reimers, Schwarzenberger, & Preuschoft, 2007). Compared with maternally-raised individuals, same-species surrogacy has been found to reduce locomotion and time spent exploring in a number of other studies (Corcoran et al., 2012; Röder et al., 1989; Sackett, 1972). In the context of orangutan rehabilitation, early maternal separation will unavoidably have a detrimental impact. However, social support may help to ameliorate stress. In one marmoset study (*Callithrix kuhli*), anxiety upon moving to a new enclosure was reduced by the presence of their breeding partner during the transition (Smith, McGreer-Whitworth, & French, 1998).

2.4.2.3 Prolonged isolation

Orangutans in the illegal wildlife trade may spend years with no conspecific contact. However, it may be possible to reverse some behavioural effects of isolation. Some 1970s primate studies measured the consequences of extreme forms of separation in rhesus macaques. Although disturbing in their methods, two studies demonstrated successful reversals of the traumatic effects of prolonged isolation. Suomi and Harlow (1972) managed to reverse the effects of six months of isolation in four male rhesus monkeys, by socially exposing them to younger, normally reared female monkeys. After six months of 'social rehabilitation', isolated monkeys demonstrated similar social behaviour to controls and an absence of stereotypies. Similar results were achieved in another study of the same species after an entire year of total isolation (Novak

& Harlow, 1975). Particularly traumatised orangutans may therefore benefit from peer support in carefully arranged group housing, so that individuals who are coping more effectively can experience a positive effect by association (see section 2.4.4 for potential risks).

2.4.2.4 Summary

There are many potential harms from extended periods of maternal/group separation. However, brief separations could be used as a mechanism to create a positive, stress-inoculating effect, as seen in the squirrel monkey studies by Parker and colleagues. Maintaining contact with a conspecific during separations may help to reduce associated stress. These kinds of 'gentle', sporadic separations should be explored as a potentially appropriate intervention for orangutans in rehabilitation, applying a principle of caution and initially trialling with very short periods of time.

2.4.3 Environmental conditions

Despite best efforts, captive environments can never equal the spatial and temporal complexity of life in the forest, and the level of enrichment provided by wild environments. Long-term captivity has been associated with increased anxiety and compulsivity in other great apes, e.g. chimpanzees (Ferdowsian et al., 2012). However, there is great potential here, as environmental conditions can be relatively easily controlled in a rehabilitation setting. The interventions in this section either involve environmental enrichment or environmental stress/deprivation. Understanding the negative effects of environmental deprivation is important for orangutan rehabilitation, as most individuals will experience poor conditions before arriving at the centre. Even during rehabilitation, captive environments are relatively deprived of enrichment compared to the complex and dynamic forest environment, so it is important that opportunities for enrichment are maximised within these constraints.

2.4.3.1 Environmental enrichment

Environmental enrichment can have a variety of benefits in rodents, including protecting against the negative effects of future stress on anxiety, depression, fear, and emotional reactivity, as well as increasing activity levels, learning ability, and spatial memory (see Table 2.2). Cognitive challenges can also have beneficial effects, with effort-based reward training in rats leading to improved persistence and problem-solving (Bardi et al., 2012; Lambert et al., 2014). This makes sense in terms of having the opportunity to exercise agency (see Glossary), and overcoming a certain degree of challenge having the effect of eliciting a positive emotional state (Clark, 2011; Meehan & Mench, 2007). There is also strong evidence that environmental enrichment improves the wellbeing of pigs (*Sus domesticus*), including promoting long-term memory, mobility, diversity of behaviour, and reducing emotionality (De Jong et al., 2000; Puppe et al., 2007; Wemelsfelder et al., 2000). However, the form of enrichment may be important. In a study comparing the effects of natural and artificial (e.g. plastic/manufactured) novel object enrichment on rats, Lambert et al. (2016) observed that rats interacted nearly three times more with natural enrichment items than artificial items matched according to their functionality and purpose (i.e. climbing, shelter, or manipulation), as well as having a greater reduction in anxiety-like behaviours. Although natural enrichment may be preferable, the practicalities of this with larger animals can be complicated, as enrichment and enclosure features must also be durable and not easily destroyed. Chappell and Thorpe (2022) argue that non-natural enclosure modifications can simulate the mechanics of a natural environment and provide similar physical and cognitive challenges to those found in wild environments.

However, moving from an enriched to a barren environment can be more harmful than only experiencing barren environments (Bolhuis et al., 2006). In studies of pigs, moving from an enriched to a barren environment has been found to reduce activity levels (Bolhuis et al., 2006), and increase pessimism in a cognitive bias test used to measure attitudes towards an ambiguous cue (Douglas et al., 2012). Similarly, starlings (*Sturnus vulgaris*) who had moved from enriched to barren environments had increased pessimism in a cognitive bias test (Bateson & Matheson, 2007). This has implications for rehabilitation centres, as orangutans are likely to experience a fluctuation of environmental conditions, from wild environments to extremely poor captive conditions (for illegally traded individuals), to improved conditions at the rehabilitation centre with varying levels of enrichment, depending on the stage of rehabilitation. It is not clear from the literature how a series of multiple changes in condition would affect individuals, and this makes it difficult to predict how changing environmental conditions might impact orangutans in rehabilitation. However, it seems likely that an increasing trajectory of environmental complexity would be beneficial, with orangutans in rehabilitation experiencing gradual increases in enrichment and autonomy and, as far as possible, avoiding a reversal in conditions.

2.4.3.2 Environmental stress/deprivation

Most evidence suggests that environmental deprivation, i.e. wire floors and restricted bedding during infancy, has a range of negative effects in rodents, for example increased anxiety, impaired spatial memory and novel object recognition, and reduced exploration (see Table 2.2). However, the studies on environmental stress in birds and fish have less straightforward results. In zebra finches (*Taeniopygia guttata*), a low quality diet led to faster spatial learning and exploration than individuals on a high quality diet (Krause et al., 2009; Kriengwatana et al., 2015), although spatial memory was impaired (Kriengwatana et al., 2015). In the Panamanian bishop fish (*Brachyrhaphis episcopi*), high-predation environments were associated with increased activity and exploration (Archard & Braithwaite, 2011). Exposure to environmental stressors such as food availability, or risk of predation, may therefore have some benefits in fish and birds, e.g. increased motivation and exploration. However, a study of foraging demand on bonnet macaques (*Macaca radiata*) found - perhaps surprisingly - that infants whose mothers had to periodically forage in woodchip were less likely to explore a novel environment than those for whom food was easily available (Andrews & Rosenblum, 1993). This indicates that there may be taxonomic and context-specific differences in how various types of environmental stress is experienced, and that human-controlled environmental deprivation may have different effects to more naturally arising situations such as competition for food.

2.4.3.3 Summary

The damaging effects of early life stress are extremely relevant to the context of orangutan rehabilitation, as many infant orangutans rescued from the illegal wildlife trade are found in deprived conditions. When an orangutan is rescued from a human environment, it is reasonable to assume that some detrimental effects of early life stress, e.g. increased anxiety and reduced exploration, may carry through into adulthood, emerging over time. Environmental enrichment can protect against stress, reduce anxiety, depression, and fear, and promote physical activity and spatial memory. However, moving animals from enriched to unenriched environments may have unintended negative effects. This shift in environmental conditions could occur in several circumstances. For example, orangutans who have been living in the wild before arriving at a rehabilitation centre will experience a large shift in conditions, from a complex forest environment to the relative deprivation of captivity. However, even within rehabilitation centres there is limited space, and orangutans may need to be temporarily moved to smaller enclosures. For example, infant orangutans too old for forest school may need to be housed for some years in an enclosure before they are old enough to be released into the wild (Ricko Jaya, personal communication). Similarly, orangutans experiencing semi-independent living on a ‘pre-release island' may temporarily be returned to an enclosure before being released into the wild. In these situations, regressing back to an enclosed environment may have negative effects, including increasing pessimism, which is discussed below. This could be heightened if enclosed environments have negative associations, e.g. for orangutans who have experienced life in the illegal wildlife trade. Regression to a smaller environment is also likely to reduce levels of physical activity, which in turn could negatively impact resilience.

In humans, optimism and pessimism are considered to influence resilience, e.g. by affecting self-perception, environmental perception, and how information is processed and actioned (Forgeard & Seligman, 2012). Hobfoll (2002) argues that optimism, self-esteem, and a sense of agency, overlap and tend to be correlated. Optimists can actively approach challenges in a constructive way, perceiving the possibility to act in order to alter outcomes (Forgeard & Seligman, 2012). Therefore, an optimistic outlook may help orangutans maintain a sense of control over their surroundings. However, it could also be argued that temporary realistic pessimism may be more appropriate in the face of danger, to prepare for worst-case scenarios and lower expectations of success to prevent disappointment (Forgeard & Seligman, 2012). Therefore, a careful balance should be maintained. For example, enrichment could be used in tangent with environmental challenges that encourage persistence and problem-solving. This requires an understanding of appropriate difficulty levels, so that challenges elicit some frustration, but ultimately lead to a positive emotional state, rather than apathy, boredom, or a negative emotional state (Clark, 2011; Meehan & Mench, 2007). In addition, long-term planning is important to ensure that positive effects are long-lasting and maintained up until the point orangutans are released. It would also be helpful to establish an understanding of current enrichment practises in rehabilitation centres, to measure the effectiveness of different methods and explore the relationship between environmental enrichment and optimism/pessimism in orangutans.

2.4.4 Social stress

As orangutans are semi-solitary primates who live in dispersed societies, only forming temporary aggregations (Galdikas, 1985; Malone et al., 2012; Roth et al., 2020), proximity with large numbers of other orangutans may cause stress during rehabilitation, particularly where direct conflict between conspecifics occurs. However, orangutan sociability may partially depend on resource availability. For example, Schuppli et al. (2017) found that Sumatran orangutans (*Pongo abelii*) in an area with higher food availability were more sociable, and, in turn, more exploratory, than Bornean orangutans (*Pongo pygmaeus warmbii*) in an area with lower food availability. This indicates some degree of behavioural flexibility, and/or species differences, in orangutan sociability. Therefore, appropriate levels of sociability in rehabilitation centres may vary depending on a number of factors, including localised differences and individual tendencies.

While in captivity, and after release, it is important that orangutans can communicate appropriately and navigate social situations in an effective way. Among interventions reviewed, the most common type of social stress included brief (often 15 minutes) exposure to a larger, more dominant, strain of rat, with the interaction ending in 'social defeat' (see Glossary), i.e. forced subordination for the focal animal. Another intervention, called 'chronic social stress' or 'social instability stress', involved rotating individuals around unfamiliar conspecifics over consecutive days. Both forms of stress were found to negatively impact rodents (see Table 2.2). As with other forms of stress (see section 2.4.1), the negative effects of social defeat stress in male rodents can be ameliorated with regular female companionship throughout the period of stress (Shi et al., 2023). There is also evidence for social stress being contagious, and observing a conspecific experiencing social defeat can lead to depressive and anxious behaviours and memory deficits in rats (Patki et al., 2014). The close social structure in rats may heighten the impact of this intervention. However, if applicable to orangutans, this aspect of social stress would be particularly relevant in rehabilitation centres, where individuals will be exposed to other stressed individuals, potentially exacerbating their own stress, leading to copying stress-related behaviours such as stereotypies, and/or complicating or prolonging the rehabilitation process. Conversely, indirect exposure to a dominant individual can have a stress-inoculating effect in rodents. This intervention does not involve social defeat, but rather confinement to a small part of an enclosure which houses a dominant individual. This can lead to a range of positive effects, including a more active coping strategy, increased exploration and social interaction, and reduced anxiety (Ayash et al., 2020; Brockhurst et al., 2015; Lyons et al., 2018).

In summary, social stress can cause a range of negative effects and can also be contagious, as exposure to stressed rats can cause similar effects to direct stress. However, milder and less direct forms of social stress may have an inoculating effect, promoting a more active coping strategy, reducing depression and anxiety, and increasing exploration and social interaction. Therefore, exposing individuals to mildly challenging social situations may be beneficial, if less dominant individuals are not subjected to prolonged or repeated aggression from more dominant conspecifics. The potential dynamics of stress contagion, balanced with the therapeutic effects of conspecifics (see section 2.4.2.3), should be explored further, to identify potential benefits while minimising further harm.

2.4.5 Exercise

Building locomotion skills is an important aspect of orangutan rehabilitation, as orangutans must be cognitively and physically capable of traversing the forest canopy (Halsey et al., 2017; Tecwyn, 2013; Thorpe et al., 2007). However, locomotion can also have beneficial psychological side-effects as a form of exercise. There is strong evidence that voluntary wheel running in rodents can protect against stress, and additional evidence that forced exercise can be beneficial in some situations (see Table 2.2). Zhang et al. (2021) found that mice that subjected to social defeat stress who had a high baseline levels of physical activity, measured by voluntary wheel running, were more sociable in a social interaction test than subjects with low levels of activity. Voluntary exercise is preferable for several reasons, including ethical considerations, and Leasure and Jones (2008) found that forced exercise increased anxiety. This suggests that a lack of agency constrains the potential benefits of exercise in this context. However, these results contrast with Greenwood et al. (2003), who found that both forced and voluntary exercise in rats improved response to fear conditioning and escape in a shuttle-box test. The authors explain this as being due to the experimental apparatus: instead of a treadmill, a wheel was designed to simulate a natural stop-start running pattern and distance that closely resembled voluntary wheel running. As well as replicating a more natural style of movement for rats, this apparatus also replicates the ‘stop/start’ structure of high-intensity interval training in humans. Interval training, where exercise involves short bursts of intense activity alternated with periods of recovery, is thought to help generate fitness and improve cardiac health in humans more quickly than prolonged ‘endurance’ periods of moderate exercise (Gillen & Gibala, 2014; Wisløff, Ellingsen, & Kemi, 2009), as well as having benefits for psychological wellbeing (Martland et al., 2022). For orangutans, species-appropriate exercise may involve guided exercise which simulates natural physical activities such as travelling through the canopy, gap-crossing, or bending and breaking branches for nest building. However, providing them with any opportunity or reason to move will encourage physical activity.

Species-specific, voluntary exercise can have numerous benefits, particularly in protecting against the effects of future stress and recovering from past stress. ‘Forest school’, where infant orangutans are taken into the forest by human caretakers to learn a variety of skills, already involves a certain degree of physical activity (Preuschoft et al., 2021). This is arguably the best exercise opportunity prior to pre-release islands or living in the wild, followed by large, complex enclosures that provide plenty of locomotion opportunities. Although many orangutans will learn by trial and error, less active individuals may require more encouragement to engage in physical activity. Social learning could be utilised here, as well as solutions like using ropes to pull food higher into the canopy to encourage climbing. In some circumstances, human caretakers have learned tree-climbing skills to encourage orangutans to climb to higher levels in the canopy (Epstein & Reed, 2019). However, there is a wide variety of forest school capacity among different rehabilitation centres, and not all centres have access to pre-release islands. Therefore, careful consideration should be given to possible in-cage physical enrichment and roof feeding (Chappell & Thorpe, 2022), and, in the longer-term, building larger enclosures.

2.5 Discussion

In order to effectively integrate resilience interventions into orangutan rehabilitation programmes, it is essential to strike the right balance, by exposing orangutans to opportunities where they can build resilience and prepare for challenges in the wild, while protecting them against further harm. In this review, resilience themes have been drawn from human and animal interventions, and interventions have been assessed in terms of their potential to be adapted for rehabilitation centres.

2.5.1 Study limitations

Although this scoping review has spanned multiple disciplines, from animal biology to human psychology, the results were limited by the search terms. As these terms centred around ‘resilience’ and ‘stress’, the search may have missed related topics which do not use either of these terms, for example ‘coping’ and ‘eustress’. In addition, as the results show such a diversity of different aspects and expressions of resilience, each of the themes described above could have their own scoping review.

Due to the diversity of species included in this review, from mice to humans, caution must be applied in extrapolating these findings to orangutans. Although rodents are not closely related to great apes, rodent studies have long been used as a starting point for pre-clinical medical research due to similarities in anatomy, physiology, and genetics (Bryda, 2013) (though for limitations of animal studies in human psychology, see Shapiro, 1998). However, interventions such as social stress may be expressed differently in close-knit, hierarchical taxonomic groups such as mice and rats compared with orangutans, who live in dispersed societies (Galdikas, 1985; Malone et al., 2012; Roth et al., 2020). In addition, most of the animal research presented here was carried out in a laboratory environment, with human-manipulated genetics, where life histories of the research subjects are already known. These conditions contrast with those in rehabilitation centres, where life histories are rarely known, and orangutans are likely to have had complex life experiences which intrinsically affect resilience.

In terms of the findings on human resilience interventions, some themes may be easier to translate to orangutan rehabilitation centres than others. Interventions such as problem-solving, social interactions, and physical activity are relatively straightforward to use as a measure of resilience and/or apply as an intervention in orangutans. In addition, the animal resilience literature indicates that these aspects can be influenced through practical interventions. However, other attributes relevant to human resilience, such as emotional intelligence, self-awareness, and a sense of agency, are more difficult to identify and measure, let alone 'teach', through non-linguistic means. Despite the lack of examples of non-linguistic resilience-building techniques in humans, it is still possible to draw meaningful insights from section 2.3. It is not unlikely that many of the main factors underpinning resilience in humans are shared by other great apes, because of the close phylogenetic relationship and cognitive overlap among great ape species, and the resulting 'psycho-socio-biological continuity'(Brüne et al., 2006). There is a longstanding tradition of comparative research on aspects of psychology, for example theory of mind (Premack & Woodruff, 1978), attachment theory (Harlow, 1958), learned helplessness (Overmier & Seligman, 1967), and psychopathology (Fabrega, 2002). Although the 'talking therapy' methods described in section 2.3 cannot be directly translated to orangutans, there is still value in developing an understanding of the underlying mechanisms of action and themes of these treatments. In other words, by understanding how talking therapies work, it is possible to work out how to translate these core components to non-talking therapies. There is an opportunity for future comparative research here, in applying resilience techniques devised for animals to human participants.

2.5.2 Main findings

The recurring theme in this review is that mild and manageable interventions are the safest form of resilience intervention. Benefits were found from interventions that involved short-term and/or manageable forms of stress, including brief separations, exercise regimes, mildly frustrating cognitive enrichment, and opportunities to indirectly navigate difficult social interactions. Many of these can be integrated into existing management schedules as part of enrichment provision at rehabilitation centres.

However, there are potential conflicts between different types of stress-related interventions. For example, although mild stress inoculation appears to be beneficial, the possible U-shaped relationship between lifetime stressors and resilience should be considered. There may be a stress ‘threshold’ for orangutans that would be nearly impossible to identify, considering the frequently unknown life histories of orangutans in rehabilitation. Research into this topic might be easier to conduct in a zoo environment, where there are records of entire life histories and major stressors, e.g. moving to a new zoo. Orangutans in rehabilitation must be shielded as much as possible from severely stressful experiences. Unavoidable known stressors, e.g. moving enclosure or veterinary interventions, should be spaced out as much as possible to allow sufficient recovery time. Peer support may also help orangutans to support one another during stressful experiences. However, more research needs to be carried out on stress contagion and the potential positive and negative effects of housing more stressed individuals with less stressed individuals. This type of arrangement may be beneficial for the more stressed individual, but could lead to the negative effects of stress contagion for their conspecifics.

Bearing in mind the risks of introducing stressful experiences, any investigation of these kinds of interventions should begin with the mildest form, building from this only if found to be appropriate and effective. Cognitively demanding challenges through enrichment may be an appropriate way of providing opportunities to overcome controllable frustration and foster independence without causing harm. There are many different forms of enrichment that can be provided to primates, including food-based, occupational (including cognitive), structural, sensory, and social (Bloomsmith, Brent, & Schapiro, 1991), and each of these categories has the potential to address a number of different factors contributing to resilience. Clark (2011) highlights the importance of maintaining interest and long-term engagement in enrichment, ensuring that the level of complexity is appropriate for the individual, and rotating or modifying enrichment at regular intervals. Physical enrichment is also important, as voluntary exercise can have numerous benefits and protective effects against future stress. Regarding opportunities for exercise, further research is needed into the extent to which orangutans of different age groups have access to forest school, and the frequency/duration of forest school sessions.

In addition to adding enrichment to an enclosure, the design of the enclosure itself is something that can be enriched and modified to encourage cognitive and physical activity, e.g. by using the Enclosure Design Tool to promote wild-type behaviours (Thorpe et al., 2022). Enrichment provision spans a large proportion of the human resilience themes identified in this review, including optimism/positive affect, exercise/physical activity, cognitive skills, agency/independence, problem-solving, planning, persistence, hardiness, goal orientation, and flexibility. However, the findings of this review indicate that long-term planning is essential to ensure that later exposure to less enriched conditions does not reverse the benefits. A negative change in environmental conditions could be severely detrimental to resilience: for example, during the change from forest school to enclosed environments, or moving an orangutan back into an enclosure from a pre-release island. It would be useful to monitor the effectiveness of existing enrichment methods and explore the relationship between enrichment and optimism/pessimism in orangutans.

Some studies identified a role of resilient personality traits, e.g. low anxiety, low emotionality, and positive affect. This makes sense in terms of the wider literature on animal personality, where research indicates that personality traits can influence cognitive styles (the way information is acquired and processed), strategies for balancing risk and reward, and wellbeing (Capitanio, 2011; Cole & Quinn, 2014; Sih & Del Giudice, 2012; Zandberg et al., 2017). Personality traits like extraversion, agreeableness, and low neuroticism have been found to contribute to wellbeing in chimpanzees, and extraversion has been associated with longer lifespans in gorillas (Weiss et al., 2013). Therefore, it is likely that individual orangutans will have different resilience 'baselines', with their response to resilience interventions depending to some extent on personality traits. Further research is needed into expected resilience levels in orangutans, and individual variation in coping styles, to be able to measure the effectiveness of interventions.

2.5.3 Animal welfare implications

Because so little is known about great ape resilience, it is difficult to know where to start with more 'risky' interventions like stress inoculation, which have the potential to cause further harm. It could be argued that the risks outweigh any potential benefits to orangutans. In zoo environments, for example, where the main consideration for caretakers is the wellbeing of the animal, deliberately causing stress or frustration might be seen as unacceptable. However, there is a strong justification for investigating these types of resilience interventions, as long as a principle of caution is applied throughout the process. For orangutans who are likely to be returned to the wild, the justification is clear: these individuals will face unavoidable stress and new challenges, probably daily, and preparing them for this reality is essential for their ability not only to cope, but to thrive in their new environment. Although rehabilitation centres strive to teach essential life skills to the orangutans in their care, some challenges will be experienced for the first time after orangutans are released into the wild. For example, orangutans in rehabilitation receive a balanced, regular diet to maximise their wellbeing in captivity (Schmidt, 2004). However, due to the temporal availability of food in the wild due to tree masting (mass fruiting) events, wild orangutans experience a dramatic fluctuation of weight loss and gain (Knott, 1998). Having prior experience of manageable stress and frustration will help orangutans develop the persistence and hardiness to endure this kind of difficult experience, and the flexibility and problem-solving skills to overcome them. However, orangutans and other great apes in lifelong captivity, in environments like zoos, can also benefit from the experience of overcoming challenging situations. As well as general stressors associated with zoos (Birke, 2002; Hosey, 2000; Skynner, Amory, & Hosey, 2004), great apes are also likely to experience major challenges throughout their life, including moving to a new zoo, welcoming a new group member into their enclosure, construction/maintenance work, and medical treatment. Therefore, resilience is important for captive great apes to be able to bounce back from these stressors and maximise their wellbeing.

These findings indicate substantial scope for further research into great ape resilience and the potential benefits of resilience interventions. More work must be done to develop and test individual interventions in each of the areas mentioned above, tailoring each intervention to maximise their effectiveness in captive environments, and trialling different combinations of interventions. Ultimately, the purpose of these investigations would be to prepare for the implementation of a long-term study, to trial and measure the effect of a resilience intervention programme on the survival rate of orangutans released back into the forest. This could act as an essential resource for rehabilitation centres in helping to prepare orangutans as much as possible during their time in rehabilitation, and inform decisions on when each individual is ready to face independent life in the wild.

2.6 Conclusion

This review has identified key overarching themes within the human and animal resilience literature, and has critically analysed the applicability of different interventions within the context of orangutan rehabilitation. Several starting points have been suggested, with the caveat that further research is necessary into each potential intervention and that a principle of caution should be applied. In general, interventions which offer a mild, but manageable, challenge appear to be the most effective and appropriate in the context of orangutan rehabilitation. Due to the lack of existing knowledge about non-human great ape resilience, it is essential that there is a foundation from which effective interventions can be developed. Therefore, this review aims to be a starting point for future research into this essential field, with implications not only for the survival of orangutans released into the wild, but also for the wellbeing of great apes in all captive environments.

2.7 Next steps

By evaluating the effects of different types and intensities of intervention, Chapter 2 has established that mild and manageable forms of stress are likely to comprise the most appropriate and effective resilience interventions for orangutans in rehabilitation. One way of applying mild stress without risking further harm is by providing orangutans with difficult and engaging cognitive enrichment, which can be frustrating for the individuals, but is ultimately rewarding. Chapter 3 introduces a novel apparatus which is intended to elicit frustration but provides an appropriate level of challenge and motivation for increasing persistence, an aspect of resilience. This resilience intervention was tested in a controlled experiment with orangutans and gorillas in two UK zoos. The efficacy of this intervention can help to inform the future development of great ape resilience interventions.

CHAPTER 3

EFFECTS OF A PROGRESSIVELY CHALLENGING TOOL-BASED INTERVENTION ON BEHAVIOURAL RESILIENCE IN GREAT APES

This chapter, largely in its current form, will be submitted for publication.

Abstract

Great apes in the wild and in captivity must have the resilience to be able to bounce back from stressful and challenging experiences. This is particularly pressing for orangutans in rehabilitation centres, who must develop resilience during their time in captivity to have a greater chance of adapting and thriving after being released back into the wild. The aim of this study was to test a new, tool-based resilience intervention for captive great apes. In two UK zoos, species-appropriate apparatuses were designed for orangutans and gorillas, which necessitated attributes of resilience such as problem-solving, frustration, agency, and persistence. The subjects were divided into an intervention and a control group, with the intervention group receiving an incrementally more challenging apparatus each week for four weeks, and the control group receiving an unchanging difficulty level of the apparatus across the same period. The prediction was that the intervention group would be more persistent in a final, more challenging version of the apparatus than the control group. There was no meaningful effect of the resilience intervention on any of the outcome variables, for either species. However, the intervention group demonstrated trends towards increased numbers of successful interactions with the apparatus, and decreased mean attempt time, in both species. There was also a trend towards the intervention gorillas being more engaged in the apparatus than the control group, whereas intervention orangutans were less engaged than the control group. Suggestions are made for improving the intervention for orangutans, and for exploring future avenues of research.

3.1 Introduction

As described in Chapter One, released great apes must adapt to a variety of challenges in the wild, including moving through dynamic forest environments (Halsey et al., 2017; Thorpe et al., 2007), fluctuating food availability (Knott, 1998), and responding appropriately to dangerous and stressful situations (Damerius, 2017). Because of these difficulties, released great apes can struggle with adapting to the wild (Basalamah et al., 2017). Orangutan rehabilitation centres have reported that the 'drive to survive in the wild' is an important factor in successful releases (unpublished Orangutan Veterinary Advisory Group questionnaire; Bridgeland-Stephens, 2020), indicating that some individuals are more resilient than others. As argued in Chapters One and Two, it is essential that orangutans released back into the wild are resilient to new challenges and have the capacity to cope with stressful situations.

However, psychological resilience is not only important for orangutans in rehabilitation centres, but for all great apes in captivity. There are unavoidable stressors associated with long-term life in captivity, e.g. relative lack of space, moving to new enclosures, veterinary interventions, and changing social dynamics when individuals leave or arrive within a group. With a tighter social structure than orangutans, Western lowland gorillas (*Gorilla gorilla gorilla*) face particular challenges in captivity. Gorillas in zoos can be sensitive to environmental noise (Clark et al., 2012), and high visitor density can cause increased aggression and stereotypies (Wells, 2005). Visitor presence can also result in reduced feeding in gorillas (Clark et al., 2012; Hashmi & Sullivan, 2020). The hierarchical nature of gorilla groups can restrict the access of lower-ranking individuals to enrichment (Lonsdorf et al., 2009; Ryan, Proudfoot, & Fraser, 2012). In addition, gorillas in zoos are known to exhibit particularly high levels of regurgitation and reingestion ('R/R'), which may be related to stress or boredom (Lukas, 1999). Resilience is important for gorillas and other captive apes to be able to bounce back from these stressors without experiencing lasting harm.

Chapter Two identified key elements of psychological resilience and resilience interventions potentially applicable to orangutans in rehabilitation. Among other types of intervention, mild and manageable stress was found to have potential resilience-building benefits. One way of achieving this is by providing mildly frustrating cognitive enrichment motivated by a food reward, which, when successfully used, may help to increase agency by fostering a sense of control over the environment (Chapter Two). This is related to the concept of ‘appropriate challenge’, highlighted by Meehan and Mench (2007), where enrichment for captive animals provides problems which may be frustrating, but are ultimately resolvable by applying cognitive and other skills. As established in Chapter Two, withstanding stressful situations can have an ‘inoculating’ effect, by presenting the opportunity to practice dealing with stress effectively, as well as being connected with elements of resilience seen in humans, e.g. cognitive skills, self-control, problem-solving, persistence, and goal orientation. However, chronic unmanageable stress can cause long-lasting problems and have a detrimental effect on resilience to future stress (see Chapter Two).

Bloomsmith, Brent and Schapiro (1991) describe five main categories of enrichment for captive animals: social, occupational, structural, sensory, and nutritional. ‘Occupational’ enrichment includes psychological tasks and puzzles, which may require hand-eye coordination and control over the environment (Bloomsmith, Brent and Schapiro, 1991). In current implementations of great ape enrichment, Clark (2011) highlights the common lack of long-term engagement due to a mismatch between skill and level of challenge, leading to apathy, boredom, or anxiety

(Meehan & Mench, 2007). In designing appropriate and effective resilience interventions, it is important to incorporate species-specific knowledge of cognitive abilities, skill level, and individual variation (Clark, 2022). For example, unlike orangutans, gorillas are not usually tool users in the wild (van Schaik, Deaner, & Merrill, 1999), although there are some isolated examples of tool use in wild gorillas (Breuer et al., 2005; Kinani & Zimmerman, 2015). However, both species have been known to use tools in captivity (van Schaik et al., 1999), and the use of probing tools to access a food reward is a commonly used form of enrichment for great apes (Clark, 2011).

Extractive tool use is a cognitively demanding activity (van Schaik et al., 1999) that can heighten motivation through positive reinforcement when obtaining a food reward. This form of enrichment seems highly appropriate for adapting as part of a resilience intervention, as it has the potential to fulfill several requirements. When initially faced with the apparatus, problem-solving skills are required to understand how to obtain the food reward. In using the apparatus, the hand-eye coordination and dexterous manipulation (van Schaik et al., 1999) required for tool use necessitate persistence and patience. The apparatus can be made challenging enough to elicit frustration, leading to manageable stress which could have an inoculating effect against future adversities (Fletcher & Sarkar, 2013). Lastly, successfully obtaining the food reward may lead to a sense of agency and control over the environment, as well as positive affect (Berridge & Robinson, 2003; Greiveldinger et al., 2009). All of the above are important aspects of resilience (see Chapter Two).

While tool use in general is an appropriate form of enrichment for great apes, and relates to many different aspects of resilience, it is important to maintain engagement and provide a continuing challenge to avoid boredom and habituation (Meehan & Mench, 2007). This can be achieved by periodically increasing the difficulty level, or changing the form, of enrichment apparatuses (Clark, 2011). Gradual increases in the difficulty of enrichment are also appropriate for resilience interventions, as they are likely to contribute to an increase in confidence and agency, while continuing to provide an engaging challenge. Bearing this in mind, the aim of this study was to pilot an intervention designed to foster resilience in captive orangutans and gorillas, by presenting the intervention group with an increasingly difficult cognitive enrichment apparatus, to develop persistence, self-control, and problem-solving skills. The expectation was that the intervention group would experience a positive effect on their persistence in using the apparatus compared with a control group, particularly in the number of successful dips and the time spent engaging with, and attempting to use, the apparatus.

3.2 Methods

3.2.1 Location and subjects

The resilience study research took place between 10th May 2021 and 24th February 2022 at Twycross Zoo (United Kingdom) and Jersey Zoo (British Channel Islands). The resilience study at Twycross Zoo took place between 17th May and 19th July 2021. There was a two-week break between study weeks two and three (31st May to 13th June 2021), to allow for school holidays, as this was a particularly busy time for the zoo staff. The resilience study at Jersey Zoo took place between 17th January and 24th February 2022. The study subjects included 21 great apes, comprised of five Bornean orangutans (*Pongo pygmaeus*), five Sumatran orangutans (*Pongo abelii*), and 11 Western lowland gorillas (*Gorilla gorilla gorilla*). The demographic information for the study animals is shown in Table 3.1.

Table 3.1 *Resilience study demographic information*. Individuals later removed from the study are shown in italics. HR = individual was hand reared; D = dominant male/female.

Group	Name	Sex	Age	Born	Location	Species
Intervention	Kibriah (HR)	F	Adult	1977	Twycross	*Pongo pygmaeus*
	Kayan	F	Infant	2017		
	Batu (D)	*M*	*Adult*	*1989*	*Twycross*	
	Dana	F	Adult	1988	Jersey	*Pongo abelii*
	Kea	F	Adolescent	2013		
	Dagu (D)	*M*	*Adult*	*1985*	*Jersey*	
	Asante (HR)	F	Adult	1985	Twycross	*Gorilla gorilla gorilla*
	Lope	M	Adolescent	2013	Twycross	
	Biddy	*F*	*Adult*	*1973*	*Twycross*	
	Kahili	F	Adult	1988	Jersey	
	Kishka	*F*	*Adult*	*1978*	*Jersey*	
Control	Maliku	F	Adult	1994	Twycross	*Pongo pygmaeus*
	Basuki	M	Infant	2017		
	Annette	F	Adult	1983	Jersey	*Pongo abelii*
	Jantho	M	Adolescent	2017		
	Oumbi (D)	M	Adult	1992	Twycross	*Gorilla gorilla gorilla*
	Ozala (D)	F	Adult	1994	Twycross	
	Shufai	M	Infant	2016		
	Badongo (D)	M	Adult	1999	Jersey	
	Bahasha (D)	*F*	*Adult*	*1994*	*Jersey*	
	Amari	*F*	*Infant*	*2019*		

3.2.2 Materials

Because of the difference in tool-using ability between orangutans and gorillas, two different apparatuses were designed. The orangutan apparatus required more dexterity and was positioned outside the enclosure. This apparatus was constructed from a 50 cm length of 5 cm diameter hollow plastic pipe. This was suspended 25 cm away from the wire mesh, so that it could only be reached using a stick (see Figure 3.1).

Figure 3.1. *Orangutan apparatus*. Showing apparatus suspended from the ceiling outside Dagu's bed den (lower left wire mesh) in Position 1.

The tube was suspended from the ceiling using 15 cm lengths of 4 mm nylon cord. This was attached at the tube end using M8 eye bolts that were screwed into pipe clips clamped around the pipe. At the ceiling end, the cord was tied to carabiners, which hung from eye hooks at 5 cm intervals along 60 cm wooden batons that were fixed to the ceiling outside the enclosure. 5 cm intervals were marked along the tube to indicate the five positions of the cord. These positions are shown in Figure 3.2a.

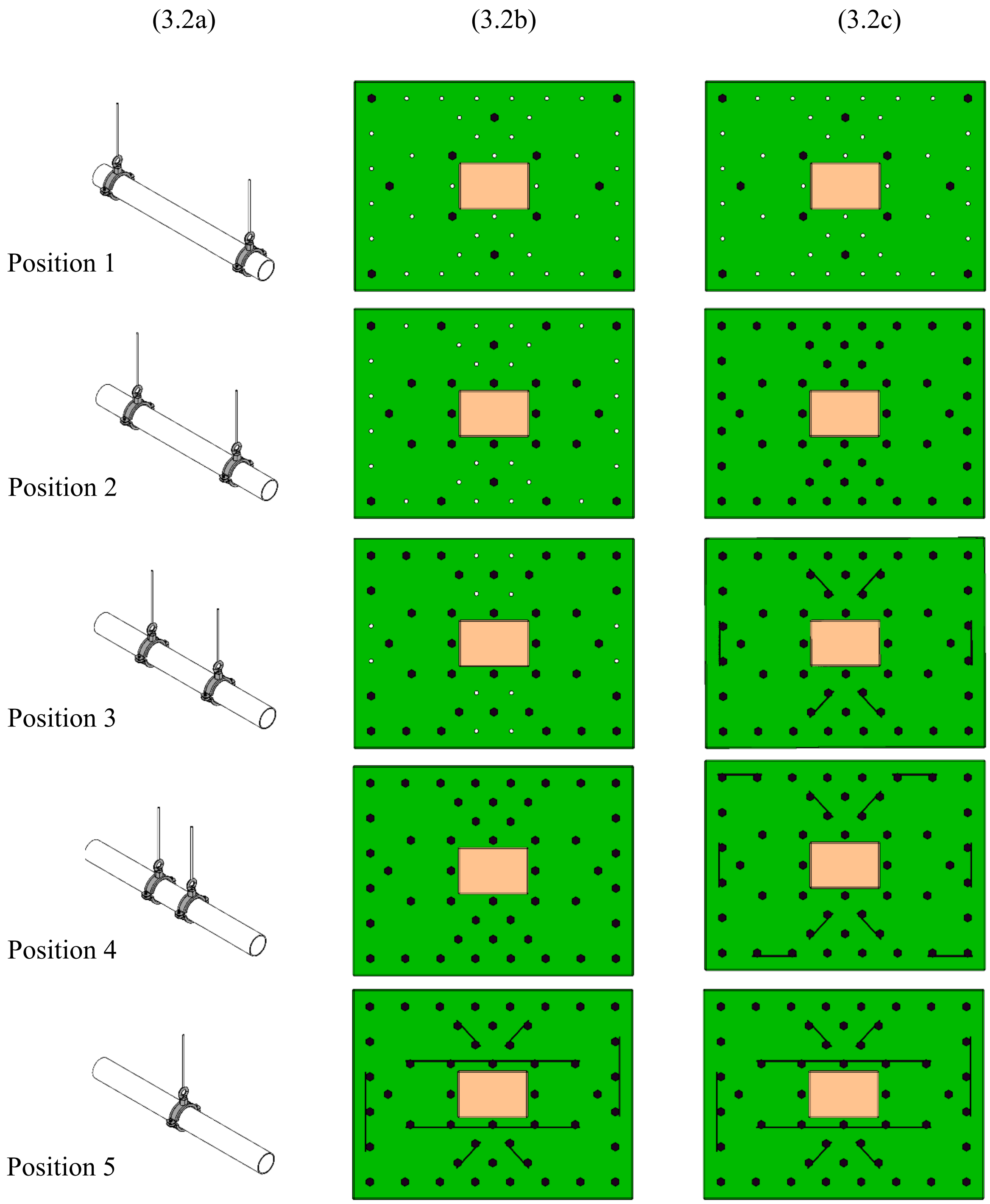


Figure 3.2 *Resilience treatment apparatuses*. Positions 1-5 of (3.1a) orangutan apparatus, showing location(s) of tube suspension from ceiling; (3.1b) Twycross gorilla apparatus and (3.1c) Jersey gorilla apparatus. For (3.1b) and (3.1c), the brown rectangles indicate the area of peanut butter; the white dots indicate the position of empty bolt holes in the apparatus; the black dots indicate the position of the bolts; and the black lines indicate the positions of the internal barriers.

Position 1 was 5 cm in from each of the ends of the tube (at the 5 cm and 45 cm markers, 40 cm apart). For each subsequent position, the cords moved towards the centre of the tube by 5 cm, until Position 4 (20 cm and 30 cm markers, 10 cm apart). This increased the difficulty level, by making the tube less stable and more likely to swing from side to side when touched. For Position 5, the tubes were suspended by a single cord, at the midpoint (25 cm) of the tube. The apparatus was filled with four teaspoons (approximately 60 ml) of a food reward. This consisted of honey at Twycross Zoo and peanut butter at Jersey Zoo. At both zoos, the chosen food reward was part of the orangutans' normal diet.

The gorilla apparatus was easier to use than the orangutan apparatus as it was inside the enclosure, so the gorillas could hold it with one hand and use a tool to access the food reward with the other hand. One of the main considerations in designing the gorilla apparatus was that it could withstand the strength of the largest gorilla, bearing in mind that even built-in artificial termite mounds made of concrete are known to have been destroyed by silverback (dominant male) gorillas (Jersey Zoo Senior Mammal Keeper, Mark Beresford; personal communication). The gorilla apparatus in this study (Figures 3.2b and 3.2c) was constructed from two parallel sheets of high-density polyethylene board (width: 1.2 cm x length 60 cm x height 45 cm), joined together with M10 hex bolts and nylon threaded nuts. The sheets were kept 35 mm apart by sheathing 12 of the bolts with lengths of copper pipe (15 mm diameter). A 10 x 15cm rectangle in the centre of the boards designated an area that was spread with two tablespoons (approximately 35 ml) of peanut butter. Position 1 consisted of 12 bolts. For subsequent positions, bolts or internal barriers were added to increase the difficulty of the apparatus.

Starting with 12 bolts in Position 1, each subsequent position at Twycross Zoo involved adding an additional 12 bolts, until Position 4 (n = 48 bolts) (Figure 3.2b). For Position 5, internal barriers were added by stretching a heavy cotton cloth tape ('gaffer tape') between pairs of bolts. This design was modified for Jersey Zoo, as the original Positions 1-4 were completed fairly easily by the gorillas at Twycross Zoo. Therefore, for Jersey Zoo, Position 1 remained the same; Position 2 increased to 48 bolts (i.e. the Twycross Position 4); Positions 3 and 4 introduced internal 3 mm x 35 mm aluminium strips, and Position 5 was the same pattern as at Twycross Zoo, using metal strips instead of tape (Figure 3.2c). Figure 3.3 shows the apparatus being used by Kahili (Jersey Zoo).

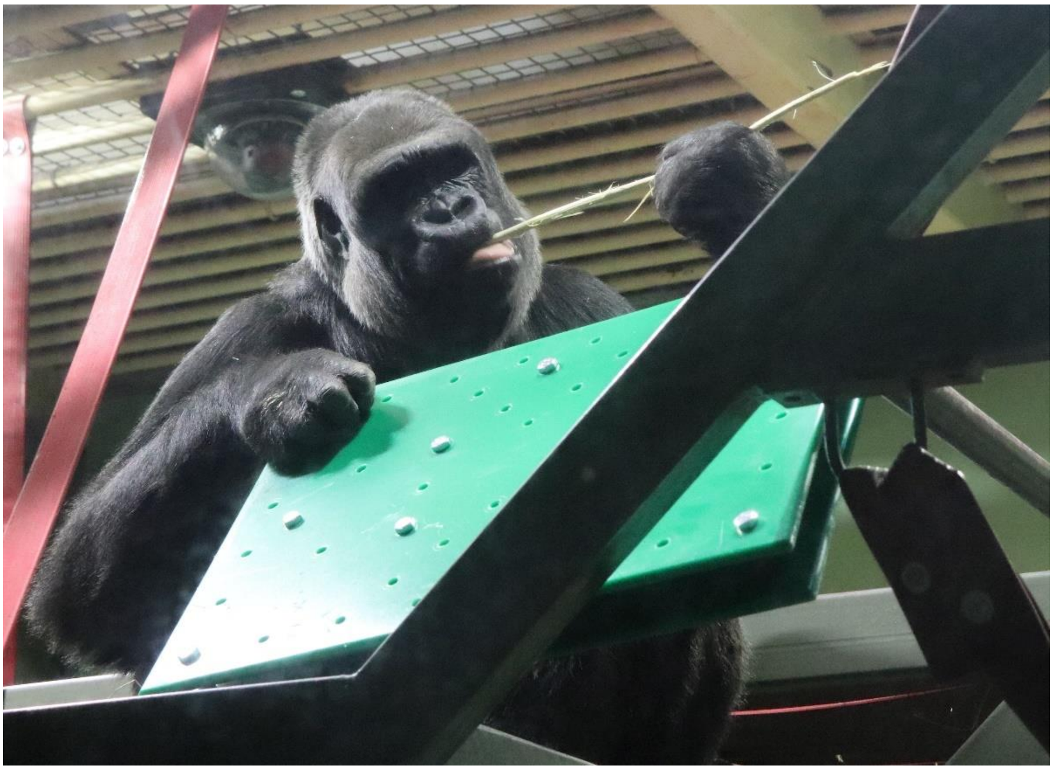


Figure 3.3 *Gorilla apparatus*. Showing Kahili holding the gorilla apparatus and licking a stick after successfully obtaining the food reward.

3.2.3 Study design

There was a familiarisation day for the orangutans on 10th May 2021 at Twycross Zoo and 13th January at Jersey Zoo. This involved placing identical versions of the study tubes inside the main enclosure for one day, with no food reward inside. There was a familiarisation period for the gorillas between 10th and 14th May 2021 at Twycross Zoo and between 11th and 14th January 2022 at Jersey Zoo. This involved installing the apparatus in the main enclosure, in Position 4, with no food reward inside. This allowed the study subjects to become familiar with the apparatus and approach it in their own time.

Following familiarisation, there were five weeks of the resilience intervention. Orangutans were randomly allocated to a control or intervention group. At Twycross Zoo, gorillas were assigned to each group in a structured way, matching for age and sex as far as possible. However, this inadvertently resulted in the most dominant gorillas being in the control group, and the least dominant individuals being in the intervention group. Therefore, at Jersey Zoo, gorillas were matched as much as possible for dominance, to balance any related effects. All individuals were given an apparatus once a week in individual areas or as mother/infant dyads (orangutans: Kibriah/Kayan, Maliku/Basuki, Dana/Kea, and Annette/Jantho; gorillas: Bahasha/Amari and Ozala/Shufai). The control group received Position 4 of the apparatus for four weeks, while the intervention group initially received Position 1, which incrementally increased in difficulty over the same period until the fourth week (Position 4). The control group was presented with Position 4 as a representation of the ‘whole’ challenge, whereas this challenge was broken down into more manageable steps for the intervention group. The intervention was therefore designed to promote persistence by gradually building confidence and skills over time in a manageable way. For the fifth week, a more challenging version of the apparatus (Position 5) was presented to both control and intervention groups, to assess their persistence and ability in accessing the food reward (Figure 3.4).

Intervention	Position 1	Position 2	Position 3	Position 4	Position 5
	Week 1	→			**Week 5**
Control	Position 4	Position 4	Position 4	Position 4	Position 5

Figure 3.4 *Timeline of apparatus positions given to control and intervention groups.*

Study animals could temporarily access the research apparatus as part of the normal daily schedule, along with browse which could be adapted for tool use by stripping away the leaves and side-branches. All other aspects of the normal husbandry routine remained the same. All interactions with the apparatuses were voluntary, and there was access to other food as part of the normal daily routine. Eight orangutans and seven gorillas successfully completed the task. Two orangutans and four gorillas were unsuccessful in obtaining the food reward and were subsequently removed from the study. The unsuccessful individuals are shown in italics in Table 3.1. Some subjects could see one or more of their conspecifics, and so there was the potential for social learning to take place. Table 3.2 shows which conspecifics were visible to the focal individual(s) during their study session. All subjects apart from Dagu had the opportunity to learn from conspecifics. However, Dagu was housed opposite a male orangutan (Jiwa) who was part of a separate study involving the researcher carrying out a social learning demonstration of the food reward being obtained from inside the tube using a stick (see Chapter 5). Therefore, Dagu did have some opportunity for social learning, even if this differed from the other subjects in this study.

Table 3.2 *Conspecifics visible to focal individual*. Showing the conspecifics who were visible to the focal individuals during the study period, and frequency of visibility. Individuals later removed from the study are shown in italics.

Group	Focal individual	Conspecifics visible	Frequency
Intervention	Kibriah & Kayan	Maliku & Basuki	Often
	Batu	*Maliku & Basuki*	*Often*
	Dana & Kea	Annette & Jantho	Always
	Dagu	*N/A*	*N/A*
	Asante	Ozala & Shufai	Always
	Lope	Oumbi	Always
	Biddy	*Ozala & Shufai*	*Always*
	Kahili	Kishka	Always
	Kishka	*Kahili*	*Always*
Control	Maliku & Basuki	Batu, Kayan & Kibriah	Often
	Annette & Jantho	Dana & Kea	Always
	Oumbi	Lope	Always
	Ozala & Shufai	Biddy & Asante	Always
	Badongo	Bahasha & Amari	Always
	Bahasha & Amari	*Badongo*	*Always*

3.2.3.1 Orangutan schedule

The orangutan research sessions took place during the morning or afternoon feed at Twycross Zoo, and the afternoon feed at Jersey Zoo, when the animals were separated into individual or mother-infant dyad sections of the enclosure. At Twycross Zoo, the apparatus was either installed prior to the orangutans entering the bed dens or following their arrival. The arrangement varied depending on daily keeper management decisions and was possible because the tubes could be safely hung outside the enclosure while the animals were inside (out of reach). The apparatus design for orangutans was modified after the first session, because Kibriah pulled down one of the ceiling batons. Galvanised metal banding was subsequently used to strengthen the fixings. In addition, a fine (2.5 cm) wire mesh panel was fixed to the outside of the bed dens with wire zip-ties to ensure that the infant orangutans could not reach through with their hands or arms. However, this was damaged and made ineffective by Kibriah in the first session onwards, meaning that Kayan was able to reach her hand through the wire mesh towards the tube, giving her a slight advantage over the other orangutans at Twycross Zoo. At Jersey Zoo, the tube for Dagu (dominant male) was hung from the ceiling outside his enclosure. Due to the building design, the mother-infant dyads had access to a raised hatch in the upper part of the building, which gave them access to the outside as well as an interlinking corridor between the two main enclosures. When open, this corridor enabled the keepers to move the orangutans to different parts of the building. However, the corridor was closed for the duration of the study sessions, and the tubes were hung from within either end of this corridor, depending on the location of the study subjects. This meant that the Jersey orangutans were able to sit on a ledge while using the tubes, rather than supporting their body weight by hanging from the wire mesh. For all orangutans at Jersey Zoo, the tubes were hung outside the enclosures while the orangutans were inside the enclosures.

3.2.3.2 Gorilla schedule

The gorilla research sessions took place during the morning feed at Twycross Zoo and the afternoon feed at Jersey Zoo, when subjects were separated into individual or mother-infant dyad bed dens. Browse was provided at all sessions. At Twycross, the apparatus was chained to wire mesh on the inside of the bed den prior to the gorillas entering the area. Due to the enclosure design at Jersey Zoo, three gorillas (Badongo and Bahasha/Amari) were in bed dens and two gorillas (Kahili and Kishka) were separated into individual sections of the main enclosure. The apparatus was initially lowered through skylights using a metal chain. However, the first session caused unforeseen distress to Bahasha and Amari due to the noise of the chain. Their session was terminated immediately, and the decision was made to introduce the apparatus to the silverback, Badongo, the following day to provide reassurance to Bahasha and Amari, as they had visibility of Badongo from their bed den. However, Bahasha and Amari were reluctant to even enter their bed den, so a decision was made to change the chain to firehose for all future sessions to minimise noise, and the apparatus was installed prior to these subjects entering the bed dens. Due to the building design, it was necessary to continue lowering the apparatus through skylights for both Kahili and Kishka. However, neither gorilla seemed distressed by this, and occasionally approached as the apparatus was lowered, although Kahili sometimes covered her ears with her hands (a common behaviour for Kahili during any unexpected noise; Mark Beresford, personal communication).

3.2.4 Data collection

The research sessions took place while keepers were cleaning the main enclosures, and therefore varied in length. Table 3.3 shows the session times for each zoo, species, and week. Sessions were defined by either the time the individual entered/exited the enclosure, or (orangutans only) the time the tubes were hung up or removed. This was either done by the keeper, or by the researcher under supervision of a keeper. Each session was recorded on an ‘APEMAN’ A77 video camera. For the orangutans and two gorillas (Kahili and Kishka), the camera was mounted on a tripod outside the enclosure. However, there were keeper concerns about the presence of tripods causing distress to the other gorillas at both zoos, so for these individuals the camera was unobtrusively mounted on a wall adjacent to the enclosure. The videos were subsequently coded as continuous behavioural observations. Videos were viewed in real time and were paused and rewound as necessary.

Table 3.3 *Mean session duration in minutes (m) and seconds (s), by zoo, week, and species.* Standard deviation shown in brackets.

	Week 4		**Week 5**	
	Orangutans	Gorillas	Orangutans	Gorillas
Twycross	23m 35s (± 8m 10s)	48m 9s (± 13m 59s)	30m 9s (± 16m 28s)	33m 52s (± 10m 10s)
Jersey	23m 2s (± 3m 25s)	38m 22s (± 5m 59s)	22m 33s (± 8m 4s)	32m 27s (± 2m 0s)

The ethogram used to code the continuous observations is shown in Table 3.4. All apparatus-directed behaviours were tailored to this study. ‘Dipping’ was defined by the stick entering the apparatus, i.e. some part of the stick being inside the mouth of the tube of the orangutan apparatus, or between the two boards of the gorilla apparatus. ‘Attempt at dipping’ was defined by the focal individual directing the stick towards the apparatus, but without the stick entering any part of the apparatus. Whereas gorillas were only seen to hold the stick with their hands when using the apparatus, orangutans tended to alternate between using their hands and mouth to hold the stick while using the apparatus. Therefore, each second of video footage for orangutan attemping/dipping was categorised as either predominantly using their hand, or predominantly using their mouth. Indicators of stress, frustration, and negative affect included agonistic behaviours (Chamove, Hosey, & Schaetzel, 1988), displays, as an indicator of aggression in gorillas (Kuhar, 2008), and stereotypies (Kuhar, 2008). Yawning and scratching were included as they correlate with anxiety and are thought to indicate stress in primates (Maestripieri, Schino, Aureli, & Troisi, 1992). Other gorilla-specific behaviours which may indicate frustration were included retrospectively, including slamming the apparatus into the wire mesh, and rapidly waving the stick back and forth inside the apparatus in a frustrated manner.

Table 3.4 *Resilience intervention ethogram.* Based on (Chamove, Hosey, & Schaetzel, 1988; Kuhar, 2008; Maestripieri et al., 1992)

Type	**Behaviour**	**Description**
Apparatus	Looking at apparatus	Gaze is orientated towards apparatus.
	Touching apparatus	Touching apparatus using any body part.
	Attempt at dipping	Using stick to try and reach food reward. Stick is outside tube/apparatus. (Orangutans divided into predominantly using hand or predominantly using mouth).
	Dipping	Successful dip. Stick is inside tube/apparatus. (Orangutans divided into predominantly using hand or predominantly using mouth).
	Licking food reward	Licking food reward off stick.
Indicators of stress, frustration, or negative affect	Agonistic	Hitting, biting, threats, submission, or avoidance.
	Display	Chestbeat/charging (gorillas only)
	Stereotypies	Repeated, unchanging behaviour, including pacing, rocking, hair plucking, and regurgitation and reingestion ('R&R')
	Scratching	Scratching self
	Yawning	Yawning
	Other	E.g. slamming apparatus into wire mesh; or rapidly waving stick back and forth inside apparatus in a frustrated manner
Browse	Holding browse	Individual is holding browse with hand, mouth, or foot.
Other	Other	Other behaviour.
	Out of sight	Out of range of the camera.

Each side of the gorilla apparatus was photographed before and after each session, to measure the difference in area of peanut butter. The photos at Twycross Zoo were taken in JPEG (.jpg) format using a Samsung J10 Android phone. However, there were some issues with image quality, glare, and consistency of the height of the camera in the earlier weeks of the study (prior to weeks 4 and 5). To resolve these issues, the photos at Jersey Zoo were taken in RAW (.CR3) format using a Canon EOS 250D DSLR camera, with a tripod to ensure a consistent distance between the camera and apparatus, and a light diffuser sheet to remove glare. For week five at Twycross, there was one occasion when additional areas of peanut butter were added after the bolts had been added to the apparatus. To resolve this, a second pre-session photograph was taken with the bolts in place, and the additional areas of peanut butter were manually identified using the steps in section 3.2.5.1 and added to the final pre-session area of peanut butter.

The following dependent variables were used as measures of success in interacting with the apparatus: 1) rate of dips per minute of session time, defined by the stick successfully entering the mouth of the orangutan tube/in between the sides of the gorilla apparatus; 2) rate of attempts per minute of session time, defined by the stick being directed towards the apparatus without actually entering it; 3) percent of session spent dipping; 4) percent of session spent attempting to use apparatus; 5) mean duration of dips; 6) mean duration of attempts; 7) percent of session spent interacting with apparatus (looking at, touching, and/or using the apparatus); 8) percent of session spent looking at apparatus; 9) percent of session spent touching apparatus; 10) percent of session spent holding a stick; and 11) area of peanut butter removed from the apparatus. Both rates and percentages of dips and attempts were included as measures, because two individuals might spend a relatively small percentage of the session duration dipping, but one might have a much higher rate of dips than the other (i.e. greater success). For orangutans, all outcome variables except 9 and 11 were measured, as the orangutans could not touch the apparatus and it was not possible to measure the amount of the food reward removed. The primary predictor variable was intervention/control group, and ancillary variables included individual ID, zoo, and week of study. Only the results for weeks 4 and 5 were included in the analysis, as this provided a direct comparison of persistence between the intervention and control groups.

3.2.5 Analysis

3.2.5.1 Image analysis

Image processing was conducted using the image processing package Fiji 2.1.0 (Schindelin et al., 2012). Images were analysed to calculate the difference in area of peanut butter between photographs taken before and after each research session, with the following steps. First, for the Jersey photos, the RAW (.CR3) image files were converted to TIFF files using Digital Photo Professional, version 4.12.0.4 (Canon, 2020). Then a reference image was created manually in the exact dimensions of the apparatus (45 cm x 60 cm). This ensured consistent sizing/dimensions for the rest of the images. The images were batch processed to split channels and isolate the red channel, which highlighted the peanut butter effectively as the apparatus boards were green. The 'Point Roi' tool was used to manually identify the corners of the apparatus in each image. The 'Landmark Correspondences' tool was then used to manipulate each image to fit the reference image, to ensure that the photographic images of the apparatus were all exactly the same size. The threshold level for distinguishing between the peanut butter and the apparatus was set automatically using Otsu's method (Otsu, 1979) and the 'Analyse Particles' tool was used to identify the area of each 'region of interest' (area of peanut butter). The results from the post-session images were subtracted from the pre-session images to obtain the area of peanut butter removed from each side of the apparatus. Finally, the mean area of peanut butter for each internal surface of the two parallel polyethylene boards (see section 3.2.2) was calculated.

3.2.5.2 Statistical analysis

Bayesian, rather than frequentist, analysis was used because of its flexibility in fitting models that are appropriate to the data, as well as being able to generate robust credible intervals which do not rely on specific statistical tests or large amounts of data (Kruschke, 2021; McElreath, 2020). The analysis was conducted in R version 4.2.0 (22/04/2022) (R Core Team, 2022) using 'ulam()', a Markov chain Monte Carlo function from the 'rethinking' package 2.21 (McElreath, 2021). Additional packages included: 'tidyverse' version 1.3.1 (Wickham et al., 2019), 'ggplot2' 3.4.0 (Wickham, 2016), and 'readxl' 1.4.0 (Wickham & Bryan, 2022). The formal model specification is shown below. A total of 500 warmup and 2,000 actual iterations of each chain was used for each model:

```
model <- ulam(alist(
outcome_variable ~ dnorm(mu, sigma),
mu <- a[control_intervention] + b[ID] + c[week] + d[zoo],
a[control_intervention] ~ dnorm(a_bar, sigma_a),
b[ID] ~ dnorm(0,sigma_b),
c[week] ~ dnorm(0, 1.5),
d[zoo] ~ dnorm(0,sigma_d),
a_bar ~ dnorm(0,1.5),
sigma ~ dexp(1),
sigma_b ~ dexp(1),
sigma_a ~ dexp(1),
sigma_d ~ dexp(1)
), data = data, chains = 4, cores = 4, warmup = 500, iter = 2000,
control = list(adapt_delta = 0.99), log_lik = TRUE)
```

Each model was multilevel, by clustering the control/intervention group, ID, and zoo variables. All outcome variables were normalised. Weakly informative priors were chosen, which were appropriate for the possible range of data (Wesner & Pomeranz, 2021). The prior distribution of the clustered variables was chosen to have a mean of zero and an exponential distribution of sigma with a rate of 1. The mean parameter for the normally distributed control/intervention group prior, 'a_bar', had a normal distribution with a mean of zero and a standard deviation of 1.5. This was the same as the prior distribution for the unclustered variable 'week'. The prior distributions for week and a_bar were adapted for some models, when the diagnostics were poor and/or the models were not converging correctly. The full list of priors can be found in Appendix C, alongside a visualisation of each of these priors. The means, standard deviations, 89% credible intervals (CIs), number of effective samples, and the Gelman-Rubin convergence diagnostic Rhat (Gelman & Rubin, 1992) for the control/intervention group predictor variables are shown in Appendix D. Trankplots showing the exploration of the posterior distribution for each chain are shown in Appendix E. The chains for all models reported here explored the posterior distribution effectively and were centred around the mean. Appendix F contains the Widely Applicable Information Criterion (Watanabe, 2010) scores for all models.

3.5.6 Ethical considerations

Ethical approval was obtained for this study from the University of Birmingham Animal Welfare and Ethical Review Body (ERN_19-1935), the Twycross Zoo Research Committee (TZR-2021-014), and the Durrell Wildlife Conservation Trust Ethics Committee (ETH21/2019). The Association for the Study of Animal Behaviour (ASAB) ethical guidelines were adhered to throughout the experiment (ASAB Ethical Committee, 2023). The subjects were provided with food as part of their normal daily schedule throughout the experiment, and participation was entirely voluntary (ASAB Ethical Committee, 2023). Although some frustration during more difficult versions of the apparatus was expected due to the nature of the research, the sessions would have been terminated by the keepers at the first sign of more severe stress or anxiety.

3.3 Results

Only 15 subjects successfully used the apparatus. Both dominant male orangutans (Batu and Dagu) made brief initial attempts to use the apparatus in the first session, but ceased to use the apparatus very soon afterwards. Two gorillas (Biddy and Amari) made no attempt to use the apparatus, and the remaining unsuccessful gorillas (Bahasha and Kishka) made very brief attempts in a later session, but soon gave up. Figure 3.5 shows the mean difference, for orangutans (Figure 3.5a) and gorillas (Figure 3.5b), between control and intervention groups for all outcome variables, as well as 89% credible intervals, representing 5.5% to 94.5% of the probability distribution (McElreath, 2020).

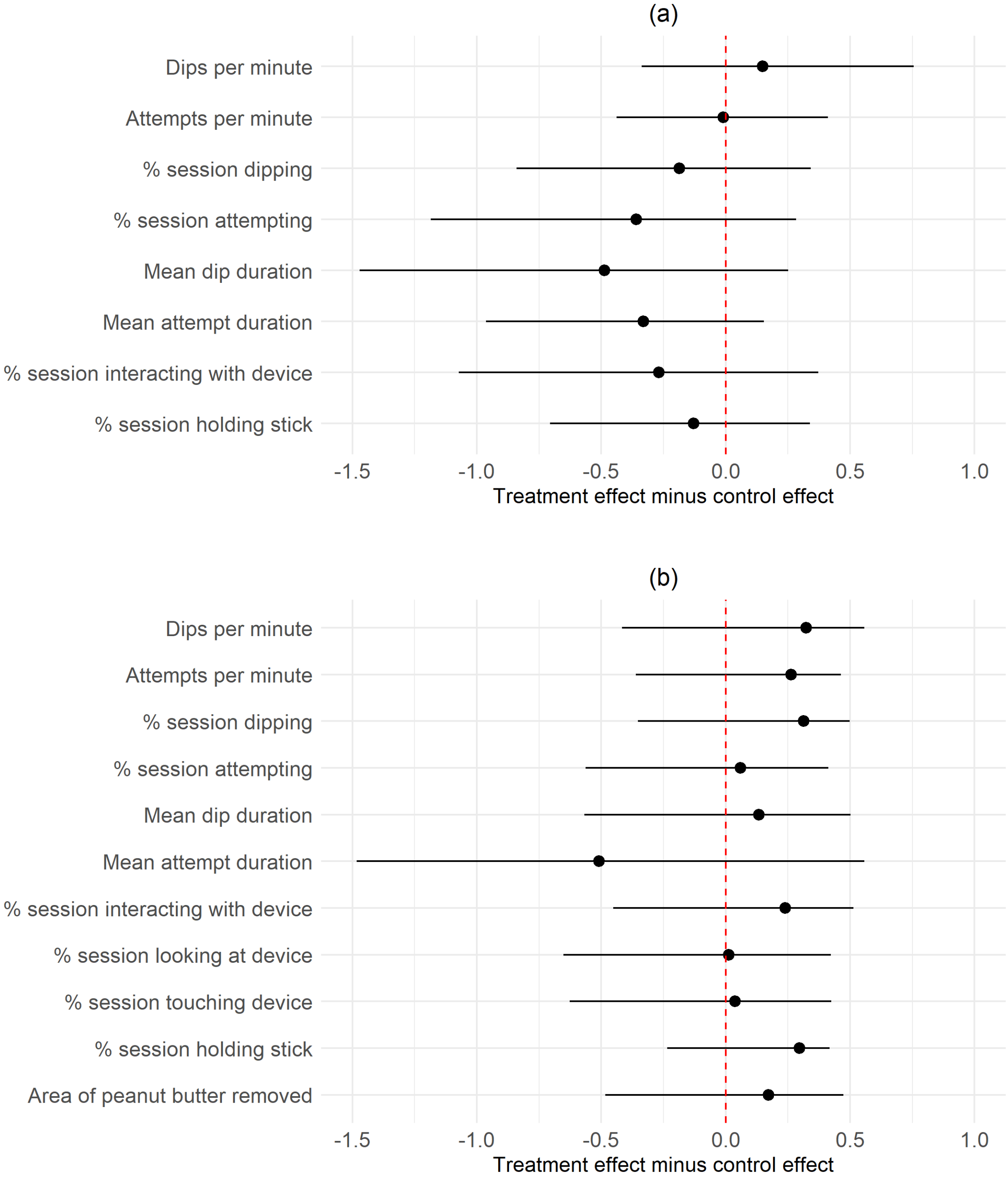


Figure 3.5 *Effects of resilience intervention on outcome variables.* Showing means (points) and 89% credible intervals (bars) for the differences between the effect of intervention and control groups on

each outcome variable for (a) orangutans and (b) gorillas. The left side of the dotted red line indicates a decrease in the outcome variable as a result of the intervention, the right side indicates an increase in the outcome variable.

There was no meaningful effect of the resilience intervention on any of the outcome variables, for either species. However, despite the large amount of uncertainty, there appears to be some species-specific trends. For gorillas, there was a general tendency towards a positive effect of resilience intervention on most outcome variables, whereas for orangutans, there was a general tendency towards a negative effect. There are two exceptions to these general species-specific tendencies: there was a trend towards the resilience intervention increasing the rate of dips per minute for both species; and a trend towards the intervention reducing the mean duration of each attempt to dip for both species.

Gorillas in the intervention group had a very small trend towards an increased mean dip duration, whereas orangutans in the intervention group had a more substantial trend towards a reduced mean dip duration. There was a trend towards gorillas in the intervention group spending more of their time dipping, holding a stick, and interacting with the apparatus. Conversely, there was a trend towards the intervention orangutans spending less time holding a stick and interacting with the apparatus.

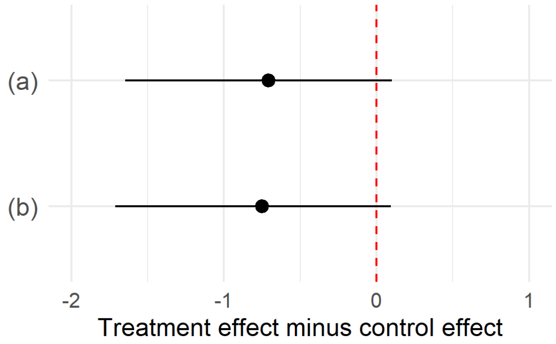


Figure 3.6 *Effects of zoo on time spent attempting to use the apparatus.* Showing means (points) and 89% credible intervals (bars) for the difference between zoos (the effect for Twycross Zoo subtracted from the effect for Jersey Zoo) on the percentage of the session spent attempting to use the apparatus for (a) orangutans and (b) gorillas. The left side of the dotted red line indicates a decrease in time spent attempting to use the apparatus in Twycross compared with Jersey, the right side indicates an increase in attempting time in Twycross compared with Jersey.

There was considerable individual variation for both species, as well as trends towards zoo-specific effects. Figure 3.6 shows that individuals of both species at Jersey Zoo spent more time attempting to use the apparatus than those at Twycross Zoo. For most measures, there was a trend towards the Jersey orangutans performing better than the Twycross orangutans. The trends towards zoo-specific effects were less clear-cut for gorillas, with a trend towards Jersey gorillas having a greater rate of dips per minute, percent of session spent dipping, mean attempt duration, and percent of session spent holding a stick, but lower proportion of session spent touching apparatus, and area of peanut butter removed from the apparatus than Twycross gorillas. Figure 3.7 shows the mean duration of attempts for each individual, week, and species. Orangutans (Figures 3.7a and 3.7b) generally had longer mean attempt durations than gorillas (Figures 3.7c and 3.7d). In addition, there was a clear increase in attempt duration for orangutans between week four (Figure 3.7a) and week five (Figure 3.7b).

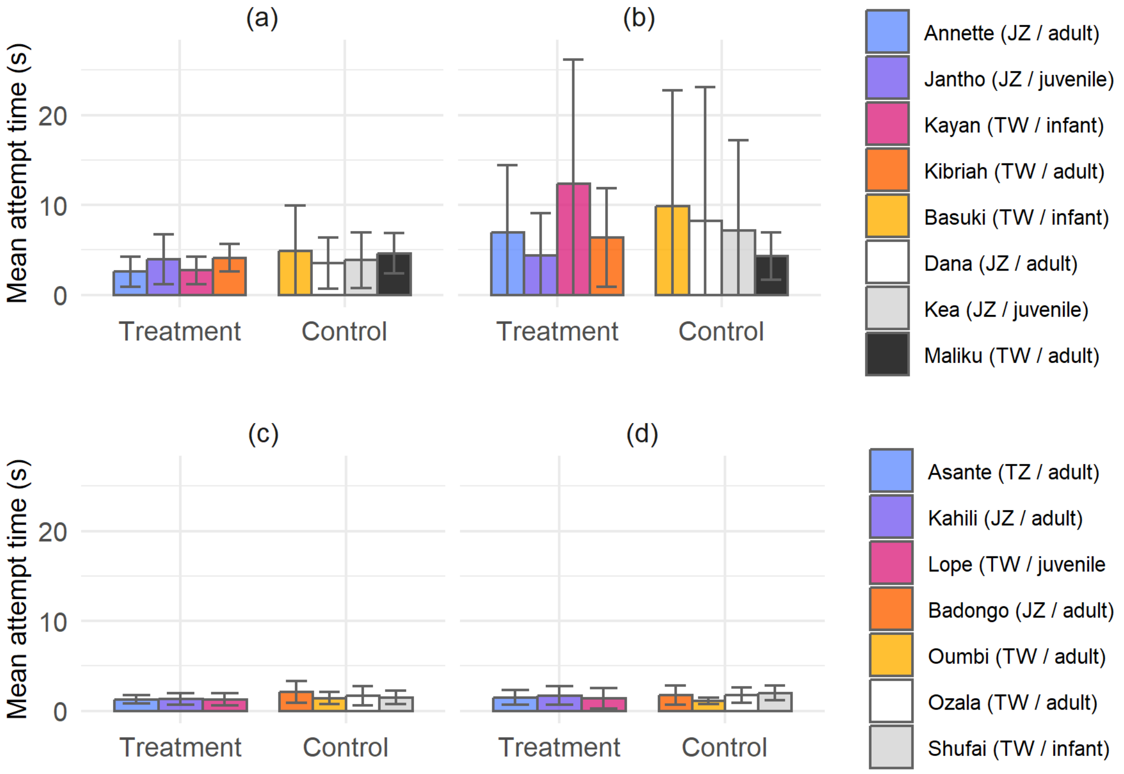


Figure 3.7 *Mean attempt durations.* Showing mean attempt durations for (a) orangutans in week 4, (b) orangutans in week 5, (c) gorillas in week 4, and (d) gorillas in week five. Error bars indicate standard deviation. The lower limits of the error bars were set to zero.

Figure 3.8 shows the total number of dips for each individual, week, and species. Orangutans (Figures 3.8a and 3.8b) generally had a lower number of dips than gorillas (Figures 3.8c and 3.8d), which reflects the longer attempt time for orangutans (Figure 3.7b and 3.7b). For both species there were lower numbers of total dips in week five (Figures 3.8b and 3.8d) than week four (Figures 3.8a and 3.8c). There were clear individual differences, with Lope (male juvenile gorilla at Twycross Zoo) having higher numbers of dips in both weeks than any other subject (Figures 3.8c and 3.8d).

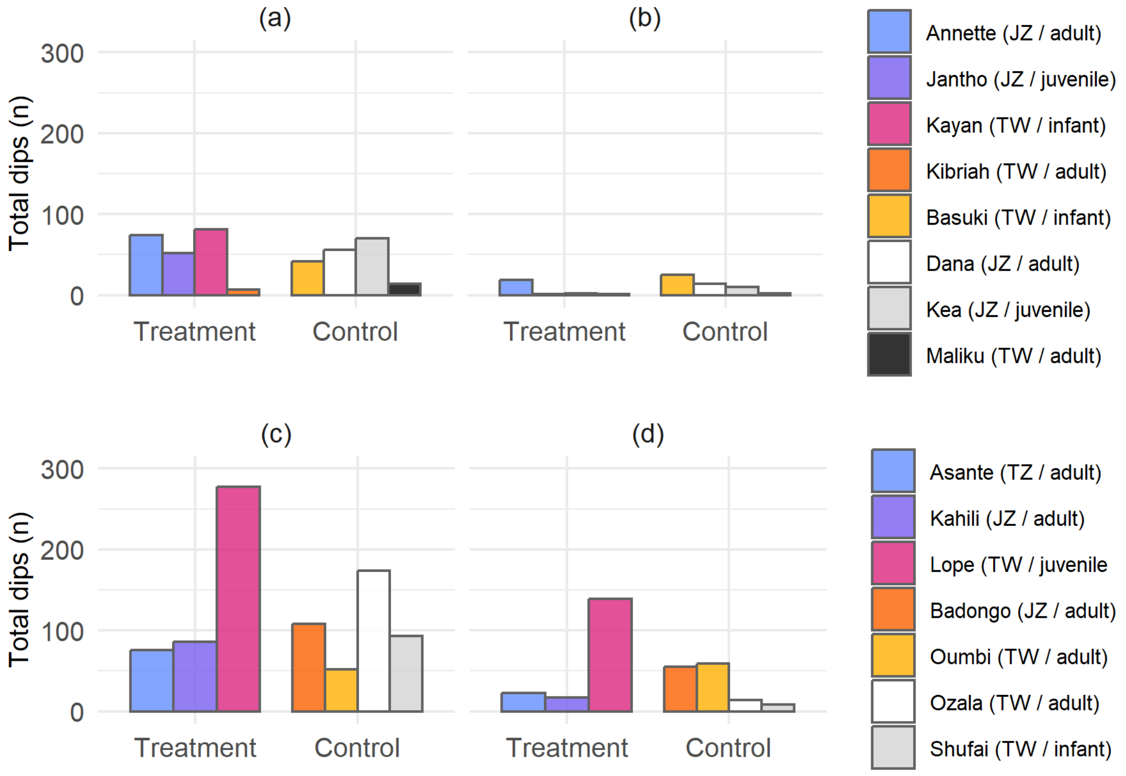


Figure 3.8 *Total number of dips.* Showing total number of dips for (a) orangutans in week 4, (b) orangutans in week 5, (c) gorillas in week 4, and (d) gorillas in week five.

Figure 3.9 compares the overall number of behaviours indicating stress, frustration, or negative affect in the intervention and control groups between weeks four (Figure 3.9a) and five (Figure 3.9b). The control group generally had higher numbers of these behaviours than the intervention group in both weeks. However, there was considerable individual variation in the number of behaviours indicating stress, frustration, or negative affect, with no stress-related behaviours exhibited by three gorillas (Asante, Kahili, and Badongo) and two orangutans (Basuki and Jantho) in week four; and by two gorillas (Kahili and Badongo) and one orangutan (Kayan) in week five.

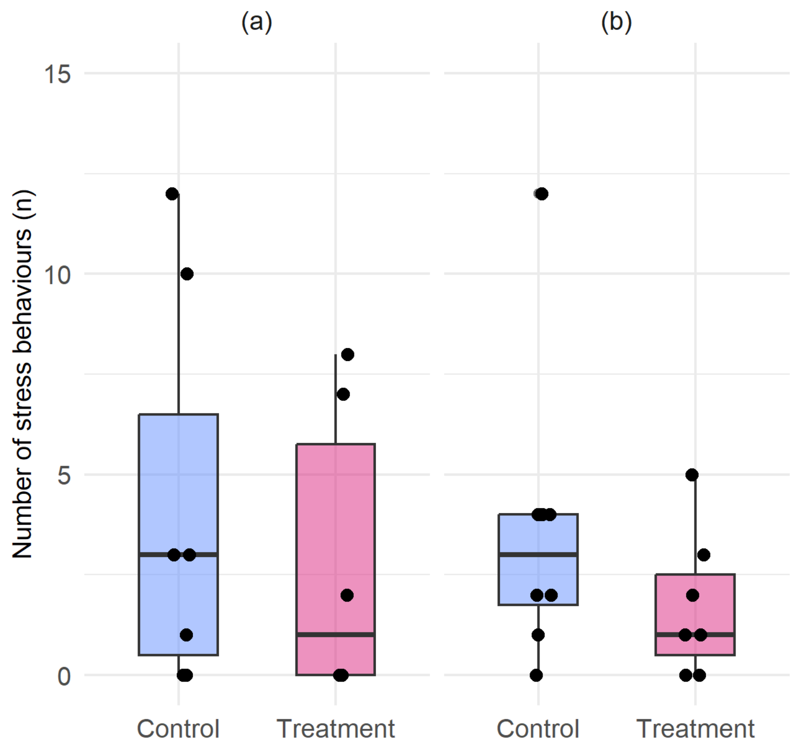


Figure 3.9 *Mean number of stress behaviours.* Mean number of stress behaviours in the control and intervention groups in (a) week four and (b) week five, with both species combined. Black dots indicate the total number of stress behaviours for each individual within each week.

3.4 Discussion

The aim of this study was to pilot a progressively challenging tool-based intervention designed to increase resilience in captive orangutans and gorillas. There was considerable statistical uncertainty presented in the posterior distributions of each model. The initial study design was for 10 orangutans and 11 gorillas to participate in the study, with approximately equal numbers of each species at each zoo. However, due to two orangutans and four gorillas failing to successfully use the apparatus, only eight orangutans and seven gorillas participated. The small number of subjects and individual variation is likely to have contributed to the statistical uncertainty. There were some location-specific effects, and the subjects at Jersey Zoo generally performed better than those at Twycross Zoo.

There were some differences in the presentation of the resilience intervention between zoos and species. To accommodate for gorillas having less skill and experience in tool-use, the gorilla apparatus was designed to be easier to use than the orangutan apparatus. This was reflected in the longer mean attempt times and shorter number of dips seen in orangutans compared to gorillas. There were also some unavoidable variations in each iteration of the apparatus between the two zoos. For orangutans, the food reward was changed from honey (Twycross Zoo) to peanut butter (Jersey Zoo), complementing the zoo dietary plans. However, there were more substantial changes in the gorilla apparatus configuration. Due to concerns about the difficulty level of the Twycross gorilla apparatus not being sufficiently challenging, additional internal barriers were added for Positions 2-4 at Jersey Zoo. Although the configuration of the internal barriers in Position 5 was the same in both zoos, the gaffer tape at Twycross Zoo was replaced with aluminium strips at Jersey Zoo, due to concerns about gorillas being able to force sticks between the apparatus and the edge of the gaffer tape.

Despite the lack of clear intervention effects for all outcome variables, there were some species-specific trends. There was a trend towards the apparatus being more enriching for gorillas than orangutans, with a trend towards increased interaction with the apparatus and time spent holding a stick compared with the control group. In contrast, intervention orangutans spent a lower proportion of the session dipping, attempting to dip, interacting with the apparatus, and holding a stick. These opposing trends may partly be due to differences between the apparatuses, as gorillas could physically touch and manipulate the apparatus, and this tactile feedback may have been engaging for them. In contrast, orangutans could not touch the apparatus, and configuration changes were minimal as the apparatus could only be made more challenging by moving the suspending cords closer together. For gorillas, the internal configuration of the apparatus changed weekly for the intervention group, which may have led to them deploying longer dips to ‘feel it out’, as they could not see clearly inside the apparatus. Conversely, there was no hidden internal configuration for the orangutan tubes, and there was clear visibility of the food reward when the tube was in its resting position. Therefore, the trend towards intervention orangutans having shorter dip lengths may indicate greater efficiency, particularly combined with the trend in the intervention group for shorter attempt durations.

In general, orangutans had longer attempt times, and shorter numbers of dips than gorillas. Although this suggests the orangutan apparatus was more difficult than the gorilla apparatus, as intended, there could still be a mismatch between the motor skill level of orangutans and the difficulty of the apparatus. Orangutans at both zoos were routinely given tool-based enrichment more frequently than gorillas, who were only given tool-based enrichment occasionally (Mark Beresford, personal communication; Research and Conservation Coordinator at Twycross Zoo, Dalma Zsalako, personal communication). Meehan and Mench (2007) highlight the importance of balancing cognitive challenge and ability in enrichment, to avoid apathy (low skill/low challenge), anxiety (low skill/high challenge), or boredom (high skill/low challenge) (Meyers & Diener, 1995). The ideal combination is high skill and high challenge, which can elicit the psychological state of ‘Flow’ in humans, a combination of satisfaction and pleasure (Csikszentmihalyi, 1988). Although the apparatuses described in this study do not qualify for eliciting Flow, as they involve extrinsic motivation in the form of a food reward (Clark, 2023), it remains important to avoid eliciting excess anxiety, apathy, or boredom through resilience interventions. As the control orangutans initially had a more difficult version of the apparatus, it is possible that they stayed more engaged with participating in the activity than the intervention animals, who were initially given a much easier version of the apparatus. However, although there were trends towards control orangutans being more engaged than intervention subjects, both apparatuses appear to have been popular with all orangutan and gorilla study participants who were successful at obtaining the food reward, and have subsequently been assimilated into the enrichment programs at both zoos.

There are some observations to make about the individuals who were unsuccessful in using the apparatus. Neither male orangutan at either zoo (Batu/Dagu) obtained the food reward, although both did make a brief attempt in the first session. This may partly be due to their larger hands making it more difficult to apply fine motor skills to successfully use the apparatus (Deputy Head of Mammals at Jersey Zoo, Gordon Hunt, personal communication). Neither of the older gorillas at each zoo, Biddy (48 years old) and Kishka (43 years old), were successful in using the apparatus. Although Biddy is thought to have some arthritis (Dalma Zsalako, personal communication), which could affect her motivation and ability to use the apparatus, a radiograph taken of Kishka in 2023 indicates that she is unaffected by arthritis (Mark Beresford, personal communication). Another possible explanation could be the combination of a lack of individual motivation combined with the cognitive effort and fine motor skills required to use the apparatus. However, such contributing factors are not possible to ascertain from this study.

Similarly to the results in this study, Lonsdorf et al., (2009) reported high individual variation in the ability of gorillas to attempt and succeed in using an artificial termite mound. Some gorillas did not attempt to use the apparatus, even after 60 baited trials. In addition, Lonsdorf et al., (2009) noted that the highest-ranking female gorillas in two different groups were the first individuals to successfully use the mound. Although both silverback gorillas and one dominant female (Ozala) showed a similar aptitude to tool-use in this study, the dominant female at Jersey

Zoo, Bahasha, did not succeed in this task. Bahasha was a first-time mother and newly dominant female and has been described by the keepers as having a nervous disposition (Mark Beresford, personal communication). She was the first gorilla at Jersey Zoo to use the apparatus, and during the first session there was some difficulty in lowering the apparatus into the enclosure (see section 3.2.3.2), which caused Bahasha some distress. This initial experience means that the apparatus was probably associated with a stressful experience. Although Bahasha did approach the apparatus in later sessions, and appeared to become more comfortable around it, she was not successful in using the apparatus. In addition, Amari has not been observed to use tools and, at the time the experiment took place, was probably too young to be able to use the apparatus (two years old). However, the *previous* dominant female at Jersey Zoo, Kahili, was the only other gorilla in this group, apart from the silverback, to succeed in using the apparatus. The gorillas at Jersey Zoo only receive tool-based enrichment occasionally (Mark Beresford, personal communication), and it is possible that lower-ranking gorillas have had less opportunity to practice using cognitive enrichment in the past, as higher-ranking gorillas may control access to these resources, either actively (i.e. territorial behaviours) or simply with their presence (Lonsdorf et al., 2009). The monopolising behaviour of dominant individuals over enrichment has also been observed in other great ape studies (e.g. Celli et al., 2003; Ryan, Proudfoot and Fraser, 2012). Therefore, even though in this study individuals were separated from the group while using the apparatus, position in the group hierarchy may affect individual confidence levels and prior experience of problem-solving and tool-use in similar tasks. Unfortunately, as the Twycross gorillas were matched for age and sex, this inadvertently led to the most dominant gorillas being in the control group, which may have influenced the outcome of the study.

Despite the species and individual differences noted above, the results of this study are somewhat encouraging for the potential of this method of resilience intervention. For both species, there was a trend towards a higher number of dips per minute in the intervention group. Combined with a trend towards reduced attempt times in the intervention group for each species, this indicates that intervention individuals may have become more skilled and faster at using the apparatus than the control group. In addition, there was a trend towards the intervention gorillas removing a greater area of peanut butter than the control group, which is arguably a more objective measure of success than number of dips per minute. However, this variable was not possible to measure for orangutans due to the apparatus design. It would be interesting to explore this form of resilience intervention further, with a greater number of subjects, to reduce statistical uncertainty. It would also be interesting to run a longer-term study, so that the longevity of any beneficial effects is determined. One of the limitations of this study is that the subjects were tested immediately after the last session, and no follow-up tests were conducted. In addition, it seems that the orangutan intervention was not as engaging as the gorilla intervention. Therefore, further research needs to understand whether this was due to the non-tactile nature of the apparatus, or because the difficulty level was set inappropriately low for the tool-using ability of orangutans.

3.5 Conclusion

The aim of this study was to test a new resilience intervention in orangutans and gorillas, to see whether persistence could be increased in the intervention group. Although no clear effects were identified, there were trends in both species towards increased numbers of dips. In addition, there was a trend towards shorter mean duration of attempts in both species, which indicates an improvement in ability in the intervention group. However, there were individual, location-based, and species-specific differences, with intervention gorillas generally engaging more with the apparatus than controls, and intervention orangutans generally engaging less with the apparatus than controls. This may indicate an inappropriate skill level for the orangutan apparatus and requires further research. Overall, this method appears to have potential for increasing persistence and skill in tool-using, and it is recommended that this resilience intervention is explored further in a larger study over a longer period of time.

3.5 Next steps

Although the results presented in Chapter 3 are inconclusive, there are trends towards the intervention group becoming more skilled and persistent in using the apparatus compared with the control group. Therefore, further research into this intervention is desirable, to determine its potential as a resilience intervention for orangutans in rehabilitation and other captive great apes. As well as measuring the effects of resilience interventions, it is also important to understand the effects of major unexpected events on captive great ape behaviour. In captivity, great apes have limited agency, and uncontrollable events have the potential to be very stressful, potentially impacting resilience. Chapter Four investigates the effects of the Covid-19 national lockdown restrictions lifting on orangutan and gorilla stress and other behaviours at a UK zoo.

CHAPTER 4

THE EFFECT OF LOCKDOWN RESTRICTIONS LIFTING ON CAPTIVE GREAT APE BEHAVIOUR AND POSTURE AS INDICATORS OF WELFARE

This chapter, largely in its current form, will be submitted for publication.

Abstract

Due to the Covid-19 pandemic, lockdowns in England between March 2020 and May 2021 led to zoo-held animals experiencing extended periods of time without visitors. There is a large body of literature addressing the effects of zoo visitors on animal wellbeing and behaviour, but limited understanding of the effect of extended, repeated periods of visitor presence and absence. The aim of this study was to understand the effect of lockdown restrictions lifting, and the subsequent return of visitors, on Bornean orangutan (*Pongo pygmaeus*) and Western lowland gorilla (*Gorilla gorilla gorilla*) behaviour and posture. Behavioural observations were collected at Twycross Zoo, UK, from 17th November 2020 to 28th July 2021, during three time periods that represented various stages of lockdown lifting. Instantaneous sampling was used, involving 30 minutes of 30 second observations per focal period. Once the zoo was reopened to visitors, visitor numbers and noise levels were also recorded. The results showed that the lifting of lockdown restrictions led to key changes in behaviour and posture. For orangutans, this included increased behavioural indicators of stress, object-holding, affiliative behaviours, and head covering, and reduced closed and hunched postures. For gorillas, lockdown restrictions lifting led to increased interaction with enrichment and reduced hunched posture and time spent at the top of the enclosure. However, the partial reopening of the zoo, i.e. the outdoor areas opening but the indoor areas remaining closed, had separate effects on gorilla behaviour. Wide ranging and sometimes contradictory results were also seen in the effects of three measures of visitor presence, once the zoo had reopened: total daily zoo visitors, visitor noise, and visitor presence at the enclosure. The results are discussed within the context of the wider literature, and suggestions for future research are made.

4.1 Introduction

During the Covid-19 pandemic, captive animals in zoos across the globe were presented with an absence of visitors for several months at a time, due to national lockdowns and resulting zoo closures. The closure of zoos due to disease is not unprecedented in the UK, as the foot-and-mouth disease outbreak in 2001 resulted in zoo closures for a period of six weeks (Davis, Schaffner, & Smith, 2005). However, the Covid-19 closures were arguably more substantial, due to their repeated and prolonged nature. In England, zoo-held animals had to adapt to sudden and prolonged periods of absence and the subsequent return of visitors during the three separate periods of national lockdown: from March to June 2020, September to December 2020, and January to April 2021.

Although the effects of the Covid-19 pandemic on zoo-held animals have not yet been fully established, there is a large body of existing literature on visitor effects in 'normal', pre-pandemic conditions. Zoo visitors can have both beneficial and detrimental effects on the behaviour and psychological state of captive great apes**.** One study of six zoo-housed gorillas found that significantly more aggressive behaviours, autogrooming, and abnormal behaviours were observed during periods of high visitor density than low visitor density (Wells, 2005). Abnormal behaviours included repetitive teeth clenching, body rocking, and spinning. In addition, significantly more resting time was observed during periods of low visitor density than high density (Wells, 2005), although more resting time does not necessarily indicate a negative impact on welfare (Sherwen & Hemsworth, 2019). Choo et al. (2011) found that close visitor proximity (within 10 metres) on a free ranging 'treetop' exhibit, with a visitor boardwalk up to 3 metres away, reduced play behaviour, and increased the probability that orangutans would be looking at visitors. In a more traditional exhibit with indoor and outdoor viewing areas, Lewis et al. (2020) found that large crowds of visitors were associated with increased visitor-directed vigilance and self-scratching in gorillas, which could indicate anxiety, as well as decreased use of the enclosure. Although visitors could approach more closely in this exhibit, within 1 metre of the window in the indoor area, there was more space for the gorillas to move away from the window, and the glass is likely to have shielded them from some of the visitor noise indoors compared with the treetop exhibit (Choo et al., 2011). However, in a long term study, which involved group scans alongside individual focal observations over 12 months, Bonnie et al. (2016) found no effect of visitor presence on gorilla and chimpanzee proximity to the indoor viewing area. This is despite the size of the indoor and outdoor enclosures in this zoo being smaller than the studies mentioned above. The gorilla enclosure comprised of 92 m^2 indoors and 485 m^2 outdoors, in comparison to 120 m^2 and 1600 m^2 in the gorilla enclosure described by Lewis et al. (2020). Therefore, the effects could be explained by the gorillas being more acclimatised to close proximity with visitors, or simply individual differences in personality.

Visitor noise and numbers may have separate effects on great ape behaviour. For example, Hashmi and Sullivan (2020) found a positive correlation between visitor noise and vigilance in orangutans, but no significant relationship between visitor numbers and vigilance. It should be noted that there was no freely available off-show access for the orangutans in this study (Hashmi & Sullivan, 2020), so the individuals did not have an option to move out of sight or hearing range of visitors. In contrast, Choo et al. (2011) used the same category for ‘high’ visitor presence as Hashmi and Sullivan (2020), i.e. more than 40 visitors, and found that high visitor levels increased focus on humans and food-begging behaviour in orangutans. Conversely, although Bonnie et al. (2016) found an effect of visitor presence on self-directed behaviours in gorillas and chimpanzees, there did not seem to be a positive correlation between large groups (>30) of visitors and increased prevalence of self-directed behaviours. This may be due to the fact that the categorisation of 'large' groups in this study had a lower threshold to those in Hashmi and Sullivan (2020) and Choo et al. (2011). However, there are contradictions here in whether large groups have a negative effect on orangutans. Similar variations in the effect of visitor noise and numbers are seen in gorillas. For example, in one gorilla study, activity was found to decrease with increasing visitor numbers, but there was no significant relationship between noise and activity levels (Hashmi & Sullivan, 2020). Clark et al. (2012) found that western lowland gorillas demonstrated more visitor-directed vigilance, i.e. staring, posturing, and charging at visitors, as noise levels increased. However, it is possible that the gorillas' behaviour resulted in increased noise levels, rather than the other way round (Clark et al., 2012). As well as the subtleties in the effect of visitor presence on great ape behaviour, depending on which measure of visitor presence is used, it is also important to note that group dynamics, sex, and individual differences can influence the way great apes respond to visitor presence (Stoinski et al., 2012), as well as habitat size, height, and complexity (see Thorpe et al. 2022).

Negative impacts of visitor presence in zoos have also been observed with other primates. In a zoo study of 15 different primate species, visitor presence (at least six visitors) was associated with more aggression towards conspecifics, and less grooming, inactivity, and affiliative behaviour, compared with periods when no visitors were present (Chamove et al., 1988). In a study of white-handed gibbons, visitor noise level and group size was associated with increased focus on humans, self-directed scratching, and open-mouthed displays, which in combination might indicate increased territoriality and anxiety (Cooke & Schillaci, 2007).

4.1.1 Visitor absence during Covid-19

It is clear that human visitors can have a range of effects on zoo-held animals. However, in normal conditions, animals living in zoos experience some degree of consistency. Visitor presence is regular, with visitors being present in the daytime but not (usually) at night. However, after periods of national lockdown, the return of visitors was likely to have a different effect on captive animals than during normal periods of time. This is not only because of the general disruption in routine, but also because it is likely that the animals became somewhat accustomed to relatively little visitor presence.

Evidence suggests that the effects of the Covid-19 lockdowns on captive animals varied considerably depending on the species. One cross-species primate study compared the effects of visitor presence, compared with absence during lockdown, on the same group of gorillas (*Gorilla gorilla gorilla*) observed in this study, as well as bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and olive baboons (*Papio anubis*) (Williams et al., 2022). There were different effects of visitor presence on each species, including reduced solitary time for gorillas and bonobos, more engagement with enrichment for chimpanzees, and reduced dominant and sexual behaviour for olive baboons. Williams et al. (2022) found that gorillas at Twycross Zoo spent less time alone and more time resting during lockdown than when the zoo was open. They also spent less time close to the visitor window. However, the period of research in this study was relatively short, with only nine days of six-hour observations: three during lockdown and six after lockdown. Also, the indoor areas had not yet been fully opened to the public, so the gorillas had a less direct experience of visitors during the post-lockdown phase, both in terms of noise and visibility. In another gorilla study, which compared long-term behavioural data of six gorillas to their behaviour during lockdown, there were no significant effects of visitor presence (Masman et al., 2022). However, there were trends towards increased regurgitation and reingestion (‘R&R’), which may be a sign of stress in gorillas (Lukas, 1999). Although great apes might be expected to interact more with objects and enrichment during zoo closures, due to less external stimulation from visitors, (Masman et al., 2022) found that gorillas manipulated objects more while the zoo was open, particularly younger individuals. This was interpreted as younger gorillas actively engaging more with visitors in order to prompt a response, e.g. clapping or filming (Masman et al., 2022). If great apes engaged less with objects and enrichment during lockdown, this could have led to understimulation and boredom, which sit under the ‘behavioural interactions’ domain in the Five Domains Model of animal welfare (Mellor et al., 2020).

In addition to behavioural measures, physiological effects of stress have also been identified in primates due to visitor presence. For example, a study of spider monkeys (*Ateles geoffroyii rufiventris*) during and after the 2001 foot and mouth outbreak found that numbers of zoo visitors were positively correlated with urinary cortisol levels (Davis et al., 2005). Varying effects of the Covid-19 lockdowns have also been seen in other taxonomic groups. For example, in a study of red kangaroos (*Macropus rufus*) in a walk-through exhibition, visitor presence following lockdown resulted in greater social proximity and more restricted spatial use (Jones, Gartland, & Fuller, 2021). Williams et al. (2021b) reported an increase in positive social interactions in meerkats (*Suricata suricatta*), alongside seemingly negative impacts like increased alert behaviour, reduced environmental interaction, and longer periods of time in areas of the enclosure furthest from viewing areas. However, in the same study, no effects of lockdown were seen in African penguins (*Spheniscus demersus*) (Williams et al., 2021b). Another mixed-species study of eight different species across a number of taxonomic groups found that most species did not experience behavioural changes during lockdown (Williams et al., 2021a). However, effects were seen in some species, with Grevy’s zebra (*Equus grevyi*) spending more time close to the visitor viewing area and exhibiting more ‘comfort behaviour’ (self-maintenance/grooming) during lockdown, while Chinese goral (*Naemorhedus griseus*) had more interactions with the environment during lockdown compared to when the zoo was open to the public. However, there were very small subject numbers of each species in this study, with two Grevy’s zebra and a single Chinese goral.

Behavioural changes during lockdown have also been reported by zookeepers. In a survey of 40 zoo and aquarium keepers of a wide range of taxa, mostly UK-based (n = 25), nearly half of the keepers surveyed (n = 19) reported behavioural changes in zoo animals during lockdown (Hunton, Rendle, & Carter, 2022). Although some reported impacts of lockdown seemed to indicate positive welfare, e.g. more relaxed behaviour, social play, and enclosure use, the keepers reported more negative than positive impacts. The most common negative impacts reported were increased interest in keepers, increased people-seeking, less activity and more ‘withdrawn’ behaviour, and increased aggression and stereotypies. However, this study took place over a year after the first lockdowns took place, from May to August 2021. Even though participants did recall differences between short- and long-term effects, their memories of events may have been unreliable (Hunton, Rendle, & Carter, 2022).

The inconsistent results reported above indicate that lockdowns, and the subsequent return of visitors, affected wellbeing in unpredictable ways, which could be positive, negative, or completely absent, depending on the species. In addition, because most lockdown studies collected data during lockdown and compared this to data collected either before or after lockdown took place, there is limited knowledge about the effects of partial lockdown restrictions. For example, before lockdown restrictions in England were fully lifted for the last time in May 2021, visitors were permitted to enter the outside, but not inside, areas of zoos. These periods of partial visitor presence, as well as the transitions between levels of restrictions, may have had a different effect on behaviour than when the zoos had fully reopened.

4.1.2 Measures of stress

The Five Domains Model of animal welfare (Mellor et al., 2020) describes several areas in which animal wellbeing can be affected. The four physical/functional domains are nutrition, environment, health, and behaviour; the fifth domain is psychological, comprising mental wellbeing, and is affected by the four physical domains. Mental wellbeing and affective state can be situation-related, reflecting an animal's perception of external circumstances (Mellor et al., 2020). This type of negative affect can include frustration, loneliness, boredom, depression, anxiety, fear, and hypervigilance. The extended periods of visitor absence and sudden return experienced by zoo animals during the Covid-19 pandemic may have affected zoo animals in several different ways. For example, on one hand, the lack of visitor presence during lockdown may have resulted in a less varied and interesting environment for zoo animals, leading to boredom, depression, and withdrawal (Mellor et al., 2020). On the other hand, the sudden and unpredictable return of visitors may have been stressful, leading to anxiety, fear, and hypervigilance (Mellor et al., 2020). Although some mild stress and environmental challenge can be beneficial (see Chapter Two), the fact that zoo animals experienced such prolonged and unprecedented disruption to their environment may have caused considerable stress.

There are several ways of measuring stress in captive animals. Physiological measures are sometimes used, e.g. urinary cortisol or faecal glucocorticoid metabolite concentrations (e.g. Davis et al. 2005, Sherwen et al. 2015). In addition, there are specific behaviours thought to indicate stress, which can include agonistic behaviour towards conspecifics and self-directed behaviour, e.g. self-grooming, hair-plucking, and rocking (e.g. Chamove et al. 1988, Blaney & Wells 2004, Wells 2005). Some of these stress behaviours have been correlated with physiological measures (e.g. Brand et al. 2016). However, not all stress is expressed in terms of specific behaviours or stereotypies. Alongside these more overt behavioural indicators of stress, physical posture may provide an alternative insight into an individual's psychological state. For example, the degree to which the torso is in a closed posture has been correlated with stress in humans (Mirigall et al 2020). Similarly, in orangutans, a 'body hug', where the forelimbs are flexed around the front of the torso, and the hands are wrapped around the back, has been documented as a stress indicator (Commitante, 2005). Furthermore, 'body lock' is another stress indicative posture for orangutans, where all limbs are flexed in a foetal position (Commitante, 2005). As well as reflecting an internal psychological state, posture can also influence self-perceptions of stress in humans. For example, Riskind & Gotay (1982) found that human subjects temporarily placed in a 'slumped, depressed' posture were less persistent than people placed in an 'expansive, upright' position, and that those placed in a 'hunched, threatened' posture had higher self-perceived stress levels than those placed in a relaxed posture. This is supported by a more recent randomised study, which found that participants strapped into an upright sitting posture (using physiotherapy tape) had increased self-reported measures of self-esteem, greater positive affect, and less fear than participants strapped into slumped postures (Nair et al., 2015). Therefore, whether psychological state influences posture, and/or posture influences psychological state, hunched and closed postures may be related to a negative internal state. Although Commitante (2005) has already identified defined the stress postures ‘body hug’ and ‘body lock’, these categories do not distinguish between different aspects of the posture, i.e. the degree to which shoulders are hunched, or the torso is closed and arms are wrapped around the body. If simple, isolated scales of hunched and closed postures are found to coincide with stress behaviours in great apes, this could be used as a quick and easy method to indicate degrees of stress alongside other behavioural measures.

4.1.3 Aims and objectives

The aim of this study was to understand the effect of lockdown restrictions lifting on the behaviour and posture of orangutans and gorillas at Twycross Zoo. There were two objectives: the first was to determine whether lockdown restrictions lifting affected behaviours linked to welfare, including stress behaviours, focus on humans, object-holding, interaction with enrichment, and affiliative behaviours; the second was to test a new methodology for categorising posture, to see whether hunched and closed postures followed a similar pattern to stress behaviours in response to visitors returning to the zoo.

4.2 Methods

4.2.1 Location and research subjects

Behavioural data was collected at Twycross Zoo from 17th November 2020 to 28th July 2021, spanning three distinct time periods (see Figure 4.1). The first period of data was collected between 17th November 2020 and 16th December 2020. The first half of this period overlapped with the second lockdown in England, which took place from 5th November to 2nd December. Although this lockdown ended on 2nd December, the gorilla house remained inaccessible to the public due to ongoing restrictions, and the gorillas were only observable by the public from the outside area. Therefore, the second period of data was categorised as 'semi-lockdown' for the gorillas, but 'post-lockdown' for the orangutans, whose enclosure did not have an indoor viewing area. The third national lockdown took place from 6th January to 11th April 2021, and no data was collected during this period. Once the zoo was reopened, semi-lockdown data collection continued until the final period of post-lockdown, when data was collected between 17th May and 28th July 2022. During this period, all areas of the zoo, including indoor areas, were reopened to the public.

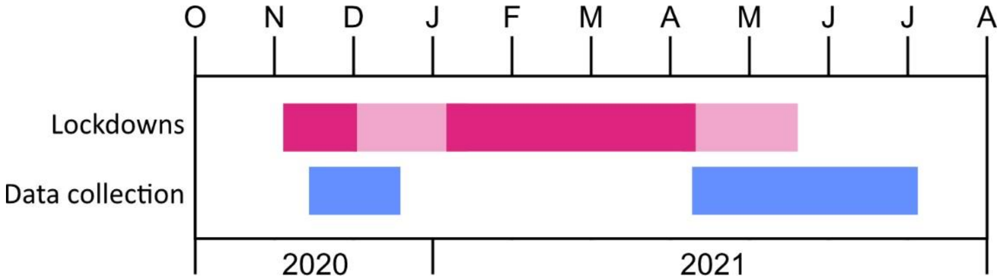


Figure 4.1 *Timeline of lockdowns and data collection.* Showing overlap between data collection period and lockdown (dark pink) / semi-lockdown (faded pink).

There were eleven research subjects, with six Western lowland gorillas (*Gorilla gorilla gorilla*), consisting of one silverback (Oumbi), three adult females (Biddy, Asante, Ozala), one adolescent (Lope), and an infant (Shufai) (see Table 4.1). In addition, there were five Bornean orangutans (*Pongo pygmaeus*): one adult male (Batu), two adult females (Kibriah and Maliku), and two infants (Kayan and Basuki). The gorilla enclosure measured 102 m², and the outdoor enclosure was 400 m² (see Figure 4.2). Two floor-to-ceiling visitor windows spanned the width of the enclosure and nearly the whole length of the indoor visitor area. There was a near-continuously available off-show section running down the length of the enclosure, measuring approximately 29 m². On the opposite side, and at the rear of the enclosure, there were windows and two slides giving gorillas visibility of, and access to, the outside area. The gorilla enclosure was situated at the far end of the zoo, adjacent to a café and the chimpanzee enclosure.

Table 4.1 *Demographic information of study participants.* Mother-infant dyads are shown within the same fields.

Name	**Sex**	**Age**	**Born**	**Species**
Maliku	F	Adult	1994	*Pongo pygmaeus*
Basuki	M	Infant	2017	
Kibriah	F	Adult	1977	
Kayan	F	Infant	2017	
Batu	M	Adult	1989	
Oumbi	M	Adult	1992	*Gorilla gorilla gorilla*
Ozala	F	Adult	1994	
Shufai	M	Infant	2016	
Asante	F	Adult	1985	
Lope	M	Adolescent	2013	
Biddy	F	Adult	1975	

Due to conflict between Batu and Kibriah, the orangutans were divided into two groups, which were changed by the keepers every few days in response to daily group dynamics. The group composition alternated between Batu alone and females and infants together, to Kibriah and Kayan alone and Batu with Maliku and Basuki. Although physically separated by a mesh barrier, the on-show group was able to see the off-show group in the indoor enclosure (see Figure 4.2). Access to the outdoor enclosure alternated between the groups. The indoor part of the orangutan enclosure that contained the focal individuals measured approximately 160 m^2, and the outdoor area measured approximately 370 m^2. Visitor windows ran along the whole length of the indoor area, and there was nowhere for the focal orangutans to move out of sight of the visitors, due to the rotations described above. The slide to the outside part of the enclosure was situated at the rear of the enclosure. The outdoor area overlooked the main zoo entrance, although the orangutan enclosure was not always obviously accessible from the central path in the zoo (depending on whether a large gate on this path was open or closed).

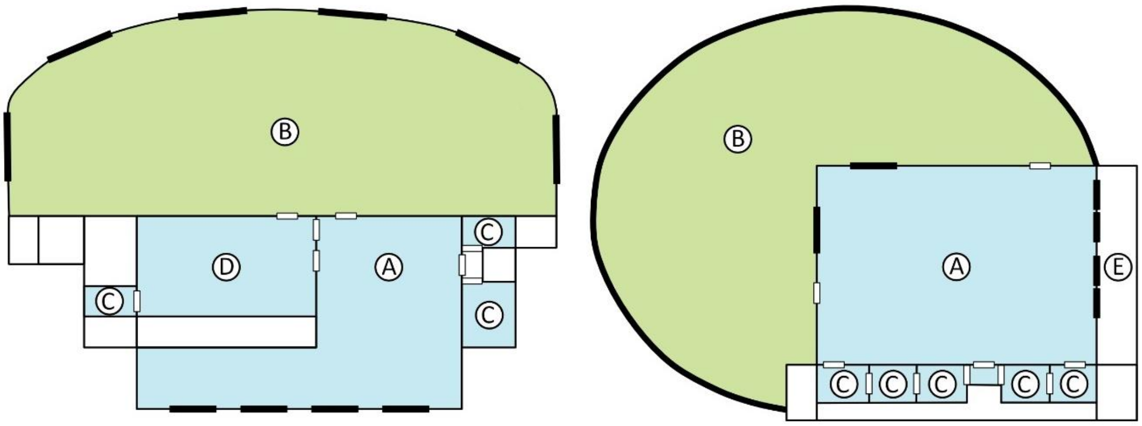


Figure 4.2 *Enclosure floorplans for orangutans (left) and gorillas (right)*. Birds eye view showing indoor viewing area (A), outdoor viewing area (B), off-show bed dens (C), off-show orangutan area (D), and indoor gorilla house viewing area (E). White rectangles indicate slides between different parts of the enclosure, thick black lines indicate the position of windows. Based on floorplans provided by Twycross Zoo.

This study complied with the ethical guidelines of Twycross Zoo and the ASAB ethical committee (2023), and ethical approval was obtained from the Twycross Zoo Research Committee (TZR-2021-014) and the University of Birmingham Animal Welfare and Ethical Review Body (ERN_19-1935). As a purely observational study, there was no interaction with any of the study subjects. Normal animal management conditions were maintained throughout the duration of the study. However, due to staff shortages, there was a reduced enrichment provision for both species during the periods of lockdown (Twycross Zoo Research and Conservation Coordinator Dalma Zsalako, personal communication).

4.2.2 Data collection

Data collection consisted of 30 minutes of 30 second instantaneous sampling for each focal individual and was collected by a single observer (LBS). Observations took place between

08:30 and 17:30 and the focal individual was selected on a rotational basis, ensuring sampling of multiple individuals across each day. Because individual orangutans were rotated on- and off-show for periods of several days, the alternation between species was flexible to accommodate for availability. Focal individuals were followed in indoor and outdoor parts of the enclosures. Whenever an individual was out of sight for over five minutes, the session was terminated. For gorilla posture and inside spatial use, data from a second observer (Charlotte King) was combined with the existing dataset. As this data involved 60 minutes of 1-minute instantaneous sampling, only every second observation for gorilla posture recorded by the first observer (LBS) was used in this analysis, so that the two datasets could be combined. As gorilla spatial use was not recorded by the first observer (LBS), only data collected by the second observer (Charlotte King) was used for this variable.

The ethogram in Table 4.2 shows the full list of behaviours recorded in this study. For orangutans, the stress indicators in Commitante (2005) was used (see Table 3 for detail of stress behaviours). Hair plucking was added to this list, as this is a well-known sign of anxiety and stress in great apes (Brand et al., 2016; Kutsukake, 2003). The list of stress indicators was expanded to include repetitive teeth clenching, body rocking, spinning, self-scratching, and ear covering using hands, all of which have previously been observed as signs of stress in gorillas (Blaney & Wells, 2004). During data collection, additional behaviours that may have been a sign of stress were observed and subsequently added. These were: finger tapping (repeatedly tapping fingers on self or object), thumb sucking, head banging (repeatedly banging head on arms or floor), banging glass, and urinating during conflict.

Table 4.2 *Lockdown study ethogram.* Based on Blaney & Wells (2004) and Commitante (2005).

Category	**Name**	**Description**
Location	Inside/outside	Whether the focal individual was in the inside or outside part of the enclosure.
Stress behaviours	Bang glass	Banging the glass using hands or another body part (gorillas only).
	Blank stare	Eyes are dull and lifeless with no particular focus.
	Body hug	Body hug, subject has arms tightly wrapped around its own body.
	Body lock	Entire body is locked in foetal position.
	Body melt	Subject is completely unresponsive; limbs are lifeless as if there were no bones or muscles.
	Charge	Charging display towards conspecifics or visitors (gorillas only).
	Chest beat	Beating chest with hands (gorillas only).
	Ear covering	Using hands to cover ears.
	Head bang	Hitting head repeatedly on crossed arms, the floor, or another environmental feature.
	Pacing	Walking in a repetitive, unchanging pattern.
	Rocking	Rocking body back and forth in a repetitive manner from a seating or standing position.
	Scratching	Scratching self
	Tapping	Repeatedly tapping an environmental feature or own body part using the fingers or hand.
	Teeth clenching	Clenching jaw in a repetitive way (gorillas only).
	Thumb sucking	Thumb held inside mouth.
	Urinate in conflict	Urinate in conflict
Posture	Hunched	Degree to which the shoulders are relaxed or hunched (with 1 being completely relaxed, and 5 being completely hunched).
	Closed	Degree to which a body position is open or closed (with 1 being very open and 5 being arms wrapped tightly around the torso).
Focus	Focus of subject	Orientation of subject's gaze, including: food, environmental features, keeper, researcher, self (e.g. resting or grooming self), and zoo visitor.
Object	Object of exploration	Object with which the subject is interacting (if any), including: attached enrichment (e.g. ball on rope), browse, food, enclosure furniture (permanent installed structures), unattached enrichment (e.g. cardboard box), wood wool, and other (grass, stones, etc.).

Mode of exploration	Touch	Touch object using hand, mouth, or other body part.
	Touch with tool	Touch object with another object (e.g. browse).
	Hold	Hold object using hand, mouth, or other body part.
	Manipulate	Manipulate (i.e. temporarily or permanently altering the form of the object) using hand, mouth, or other body part.
	Manipulate with tool	Manipulate (i.e. temporarily or permanently altering the form of the object) using another object, e.g. browse.
Contextual behaviour	Affiliative	Affiliative behaviours towards conspecifics, including grooming others, playing with others, 'kiss' (using mouth to touch another individual's mouth), and 'embrace' (wrapping arms around another individual).
	Agonistic	Agonistic behaviours towards conspecifics, including threatening, physically attacking, or chasing a conspecific (excluding play chasing).
	Cover head	Covering head using wood wool, cardboard, or another object (orangutans only).
	Feeding	Foraging and consuming food.
	Resting	Sleeping or resting; not engaged in any other observable behaviour.
	Travelling	Locomoting.
	Other	Other behaviours outside the categories reported above.
	Out of sight	Not visible to observer.

As unvarying, repetitive behaviours with no obvious purpose, finger tapping and head banging meet the requirements of stereotypies (Mason, 1991). Thumb sucking was observed to occur during periods of general tension in gorillas, e.g. prior to feeding, when keepers were in the off-show area. Banging glass is thought to be a form of visitor-directed vigilance or aggression (Clark et al., 2012; Lewis et al., 2020) and has been associated with high levels of visitors (Wells, 2005). Lastly, urinating during conflict has been observed as a stress response in orangutans (e.g. Lameira & Call 2018). The attentional focus of the individual was recorded, based on categories used by Commitante (2005): focussing on the self, the environment, food, others, or humans. Focus on humans was sub-divided into focus on visitors, keepers, and researchers. Affiliative behaviours included grooming others, playing with others, ‘kiss’ (using mouth to touch another individual’s mouth), and ‘embrace’ (wrapping arms around another individual).

In order to record posture, two five-point Likert scales were created (Figure 4.3). The first indicated the extent to which the shoulders were relaxed or hunched (1 = completely relaxed, 5 = completely hunched), and the second indicated the extent to which the body position was open or closed (1 = very open, 5 = arms wrapped tightly around the torso). Interaction with enrichment and other objects was recorded, specifying the type of object being manipulated (e.g. food, browse, wood wool, enclosure furniture, and enrichment items) and the type of manipulation observed (e.g. touching with hand/mouth, touching with tool, holding object, manipulating with hand/mouth, and manipulating with tool). For gorilla spatial data, the enclosure was divided in two dimensions, to record proximity to the visitor window (front third of the enclosure) and high positions (1 meter from the highest point of the enclosure).

While the zoo was open, visitor presence was measured by total daily visitors, visitor noise at the enclosure, and visitor presence at the enclosure. Total daily visitor numbers, as measured at the zoo gate for each day data, were collected and grouped into quartiles. These were then grouped into ‘low’, ‘medium’ and ‘high’ visitor levels. The ‘medium’ category included all figures within the interquartile range, the ‘low’ category included all visitor numbers in the first quartile, and the ‘high’ category included all numbers in the fourth quartile. Visitor presence at the enclosure was recorded in categories of ‘no visitors’, ‘less than 20 visitors’, and ’20 or more visitors’. The categorisation of high visitor presence in previous studies ranged from 8-40 (Birke, 2002; Bonnie et al., 2016; Choo et al., 2011; Hashmi & Sullivan, 2020).

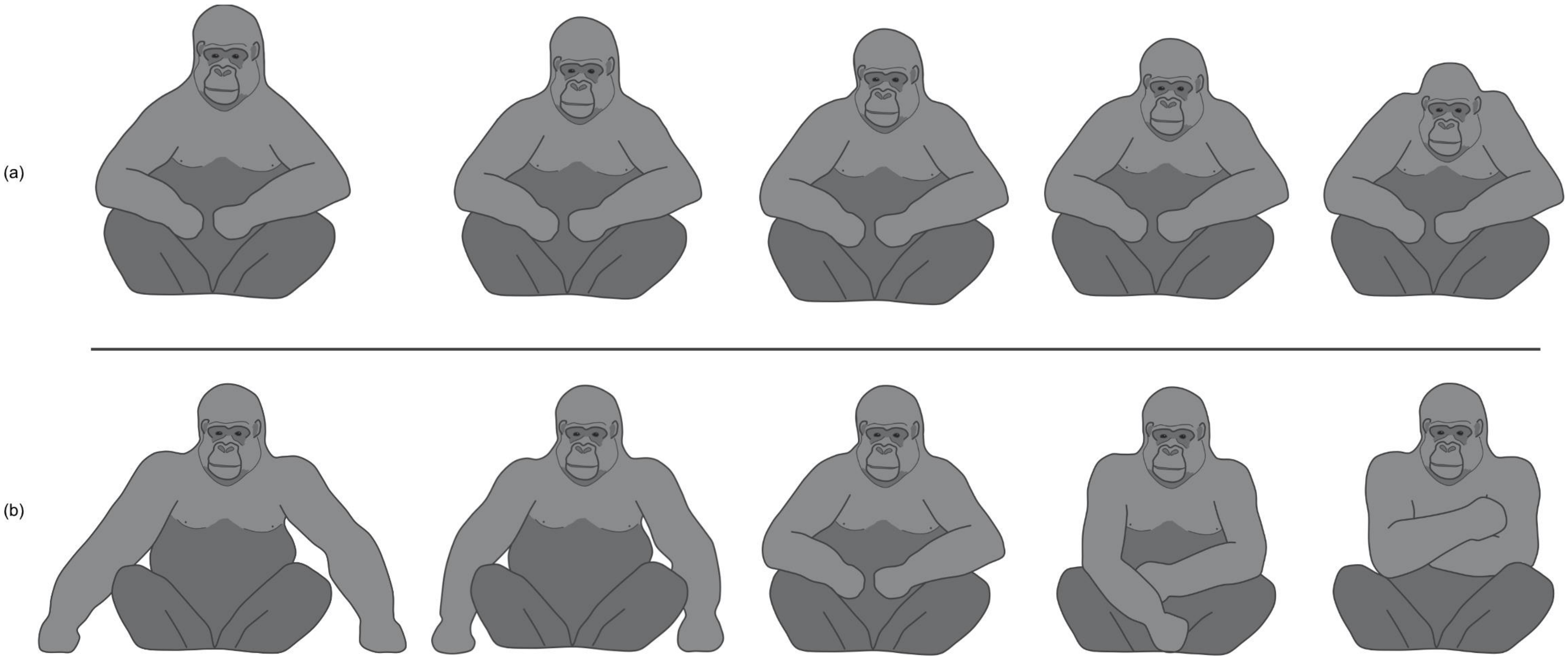


Figure 4.3 *Hunched and closed posture scales.* Showing Likert scales of hunched (a) and closed (b) posture, from least hunched/closed (left) to most hunched/closed (right). Figure hand drawn using Affinity Designer version 1.10.1.1142 (Serif, 2023).

As visitor density depends somewhat on the size of an indoor visitor area, 20 was chosen as the threshold for ‘high’ visitor presence, because this was roughly the size of a crowd that spanned the whole visitor window at the gorilla and orangutan enclosures (looking into the indoor enclosure). Visitor noise was measured subjectively by the observer(s) as ‘no noise’ (quiet), ‘some noise’ (conversational level noise), and ‘loud noise’ (shouting, screaming, or talking at a volume above a conversational level).

4.2.3 Statistical methods

4.2.3.1 Primary analysis

Bayesian, rather than frequentist, analysis was used for its flexibility in fitting models that are appropriate to the data, and the ability to generate robust credible intervals that do not rely on specific tests or large sample numbers (Kruschke, 2021; McElreath, 2020). The analysis was conducted in R version 4.2.0 (22/04/2022) (R Core Team, 2022) using the Markov Chain Monte Carlo (MCMC) function ‘ulam()’ from within the rethinking package version 2.21 (McElreath, 2021). Other packages used include: ‘tidyverse’ version 1.3.1 (Wickham et al., 2019), ‘ggplot2’ version 3.4.0 (Wickham, 2016), ‘readxl’ version 1.4.0 (Wickham & Bryan, 2022), and ‘ProbBayes’ version 1.1 (Albert, 2020b).

Separate models with the following outcome variables were used for each species: 1) stress behaviours, 2) hunched posture, 3) closed posture, 4) focus on humans, 5) object-holding, 6) interaction with enrichment, 7) tool-use, and 8) affiliative behaviours. Both species had additional, species-specific outcome variables. For orangutans, this was 9) covering their head with wood wool or cardboard; and for gorillas, this was 10) proximity to visitor window, and 11) height in enclosure. For all models, the primary predictor variable was the categorical variable of ‘lockdown status’. For gorillas, this corresponded to three stages: ‘lockdown’ (when the zoo is closed), ‘semi-lockdown’ (when visitors are allowed outside only), and ‘post-lockdown' (when visitors can enter the gorilla house). For orangutans, who do not have an inside visitor area, semi-lockdown was not included. Ancillary variables include individual ID, grouping (orangutans only), and number of researchers (gorillas only). For orangutans, 'grouping' refers to the grouping of the orangutans, as this was regularly rotated. For gorillas, 'number of researchers' refers to the number of researchers in the indoor area, as there were concurrent observational studies taking place on some days. Observations when the subject was out of sight were not included.

Both models relating to posture (2 and 3) used an ordinal outcome variable, as the data collected was in a Likert scale format. All other models used a binomial outcome variable with a logit link function, to constrain the model between zero and one. Normal distributions were used for the individual ID, lockdown status, and grouping priors. The priors for the stress behaviour models were informative, as stress behaviours were expected to be relatively uncommon (see Wesner & Pomeranz 2021 for justification of using informed priors). Other studies on gorillas and orangutans have reported stress-related behaviours like stereotypies to comprise under 15% of the activity budget (Clark et al., 2012; Hashmi & Sullivan, 2020; Masman et al., 2022). A generous allowance was used for the prior, with the prior median being 10% of total behaviour counts, and the 90th percentile being 25%. The beta.select() function in the ProbBayes package (Albert, 2020b), was used to find the correct shape parameters of the beta curve prior, based on the quantiles described above. These were converted to the logit parameter, using the method described by Albert (2020b), resulting in normally distributed priors with a mean of -2.31 and an exponential prior for sigma with a rate of 1. These priors were also used for affiliative behaviours, which were similarly expected to comprise a small proportion of the activity budget, based on previous research (Morales Picard et al., 2020; Sussman, Garber, & Cheverud, 2005).

The remaining models used normally distributed flat priors with a mean of zero and a standard deviation of 1.5 for individual ID, grouping, and lockdown status. Exponential priors for sigma with a rate of 1 were used for all clustered variables in multilevel models to indicate average, rather than maximum, deviation (McElreath 2020, p119).

A total of 1,000 warmup and 2,500 actual iterations of each chain was used for each model. The formal model specification for the ordinal posture models is shown below:

```
ordinal_model <- ulam(alist(
outcome_variable ~ dordlogit(phi, cutpoints),
phi <- a[ID] + b[lockdown_status] + c[group],
a[ID] ~ dnorm(a_bar, sigma_a),
a_bar ~ dnorm(0,1.5),
b[lockdown_status] ~ dnorm(0,sigma_b),
c[group] ~ dnorm(0, sigma_c),
sigma_a ~ dexp(1),
sigma_b ~ dexp(1),
sigma_c ~ dexp(1),
cutpoints ~ dnorm(0,1.5)
), data = data, warmup = 1000, iter = 2500, chains = 4, cores =
4, control = list(adapt_delta = 0.99))
```

The model specification for the remaining binomial models is shown below:

```
Binomial_model <- ulam(alist(
outcome_variable ~ dbinom(1, p),
logit(p) <- a[ID] + b[lockdown_status] + c[group],
a[ID] ~ dnorm(a_bar, sigma_a),
b[lockdown_status] ~ dnorm(0,sigma_b),
c[group] ~ dnorm(0,1.5),
a_bar ~ dnorm(0,1.5),
sigma_a ~ dexp(1),
sigma_b ~ dexp(1)),
data = data, warmup = 1000, iter = 2500, chains = 4, cores = 4,
log_lik = TRUE)
```

Visualisations of the prior distributions on the outcome scale are shown in Appendix G. The means, standard deviations, 89% credible intervals (CIs), number of effective samples, and the Gelman-Rubin convergence diagnostic Rhat (Gelman & Rubin, 1992) for all model structures are shown in Appendix H. Trankplot results showing how the posterior distribution is explored by each chain are shown in Appendix I, Widely Applicable Information Criterion (WAIC) (Watanabe, 2010) scores are shown in Appendix J, and posterior predictive checks for all models are found in Appendix K.

4.2.3.2 Secondary analysis

After using lockdown status as the main predictor variable, a secondary analysis was carried out on the effects of visitor presence, while the zoo was open, on all outcome variables that indicated an effect of lockdown status. Categorical predictor variables included total daily zoo visitors, visitor presence at the enclosure, and visitor noise levels at the enclosure. All three visitor predictor variables had three levels (low, medium, and high). For gorillas, lockdown status for semi- and post-lockdown were added into these models as an unclustered variable. In addition, a secondary analysis of the effect of lockdown on the focus variable was also conducted. Two separate binomial models were run, with lockdown status as the primary predictor variable. The outcome variables used were 12) focus on keeper, and 13) focus on researcher. As with stress and affiliative outcome variables, these two models used informed priors, as they were expected to comprise a relatively small proportion of the activity budget (Commitante, 2005).

4.3 Results

A total of 148 hours of data was collected, amounting to 17,746 observations. For each orangutan, there was an average of 4.8 (±0.73) hours of data collected during lockdown and 6.19 (± 4.27) hours during post-lockdown. For each gorilla, there was an average of 4.18 (±0.74) hours of data collected during lockdown, 5.45 (±1.11) hours during semi-lockdown, and 3.79 (±0.49) hours during post-lockdown. Added to this was 160 hours of observations for gorilla spatial use and posture from the second observer, amounting to 9,624 observations. This additional dataset amounted to an average of 9.18 (±0.31) hours during lockdown, 8.69 (±1.44) hours during semi-lockdown, and 8.86 (±0.58) hours during post-lockdown. The total number of observations for each outcome variable, after discarding every second observation for the posture models, are shown in Table 4.3.

Table 4.3 *Number of observations.* Showing number of observations for each outcome variable, species, and lockdown period. 'N/A' indicates that there are no observations classified as 'semi-lockdown' for orangutans.

Outcome Variable	**Species**	**Lockdown**	**Semi-lockdown**	**Post-lockdown**
1) Stress	Orangutan	2766	N/A	5078
	Gorilla	2593	2572	3519
2) Hunched	Orangutan	1601	N/A	2762
	Gorilla	2884	3119	3289
3) Closed	Orangutan	1601	N/A	2762
	Gorilla	2884	3119	3289
4) Focus on humans	Orangutan	2759	N/A	5053
	Gorilla	2578	3513	2550
5) Object-holding	Orangutan	2767	N/A	2278
	Gorilla	2589	1985	646
6) Interaction with enrichment	Orangutan	2767	N/A	2279
	Gorilla	2589	1985	652
7) Tool-use	Orangutan	682	N/A	1418
	Gorilla	988	1216	646
8) Affiliative	Orangutan	2887	N/A	5200
	Gorilla	2954	3897	2729
9) Covered head	Orangutan	2887	N/A	1563
10) Proximity to visitor window	Gorilla	2643	2649	2635
11) Height in enclosure	Gorilla	2643	2649	2635
12) Focus on keeper	Orangutan	2759	N/A	5053
	Gorilla	2578	3513	2550
13) Focus on researcher	Orangutan	2759	N/A	5053
	Gorilla	2578	3513	2550

Although most categories had at least 2,000 observations, there is some variation among lockdown periods and outcome variables. For example, there are fewer post-lockdown observations for object-holding, interaction with enrichment, and tool-use in gorillas compared with most other variables. There are also relatively low numbers of lockdown observations for tool use in both species. Activity budgets for each species across each lockdown phase are shown in Figure 4.4.

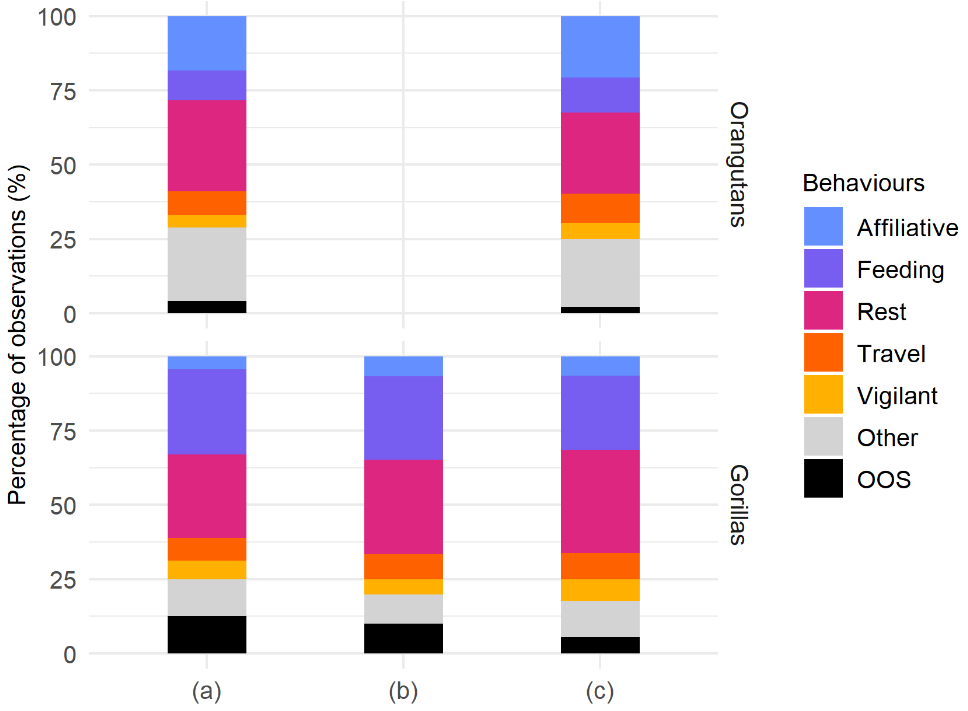


Figure 4.4 *Activity budgets for each lockdown period.* Showing activity budgets for (a) lockdown, (b) semi-lockdown, and (c) post-lockdown, for each species. OOS = out of sight.

In general, orangutans spent a greater percentage of their activity budget in affiliative behaviours (20%) than gorillas (6%), whereas gorillas spent a greater percentage of their activity budget feeding (27%) than orangutans (11%). Gorillas were also out of sight for a greater percentage of time (10%) than orangutans (3%). After lockdown restrictions lifted, orangutans spent a lower percentage of their activity budget resting (27%) compared to lockdown (31%), whereas gorillas spent a higher percentage of their budget resting (35%) compared to during lockdown (28%). However, these differences are relatively small. Lastly, gorillas were out of sight for a lower percentage of time during semi-lockdown (10%) and post-lockdown (6%), compared to when the zoo was closed (13%). The proportion of time focal individuals spent indoors and outdoors for each lockdown phase is shown in Figure 4.5. Orangutans generally spent a higher proportion of time outside than gorillas. However, both species were inside for more than 80% of the time. There was a very slight decrease in the time gorillas spent outside during semi-lockdown. However, there does not appear to have been a seasonal difference in time spent outside from lockdown (December) to semi- and post-lockdown (May to July).

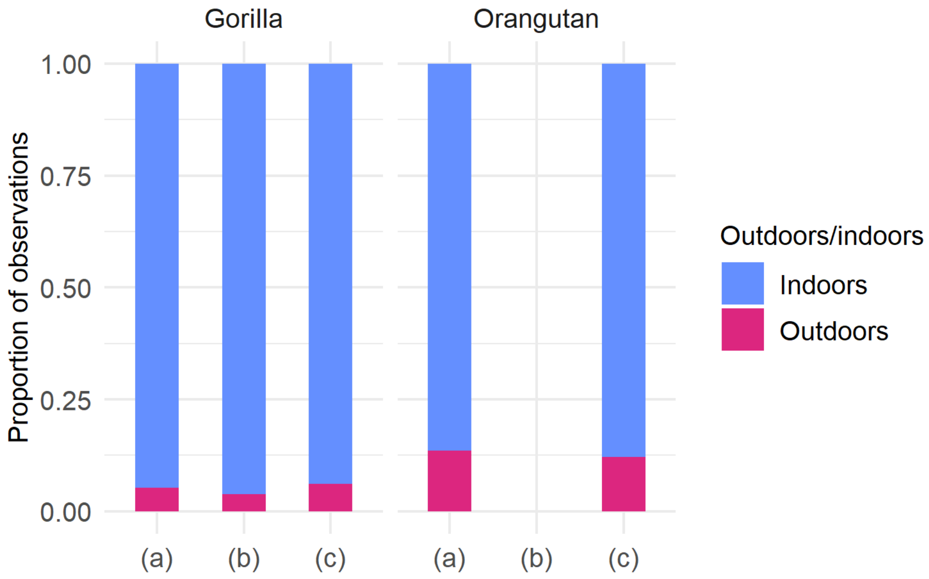


Figure 4.5 *Indoor/outdoor observations.* Showing proportion of observations when focal animal is indoors/outdoors in (a) lockdown, (b) semi-lockdown (gorillas only), and (c) post-lockdown.

Tables of the effect sizes for all outcome variables can be found in Appendix K. The remainder of this section will present the notable effects on outcome variables, categorised and ordered by predictor variable (lockdown, total visitors, visitor noise, and visitor presence), species, and outcome variable.

4.3.1 Effects of lockdown

4.3.1.1 Orangutans

The mean effects of lockdown status on each outcome variable are shown in Figure 4.6, along with 89% credible intervals (CIs) indicating 5.5% to 94.5% of the probability distribution (McElreath, 2020). There were no effects of lockdown restrictions lifting on focus on humans, interaction with enrichment or tool-use in orangutans. However, lockdown restrictions lifting increased the probability of stress behaviours (mean = 0.05, 5.5% = 0.01, 94.5% = 0.11), and also increased the probability of less hunched (mean = -0.09, 5.5% = -0.12, 94.5% = -0.07) and closed (mean = -0.09, 5.5% = -0.12, 94.5% = -0.07) posture ratings in orangutans.

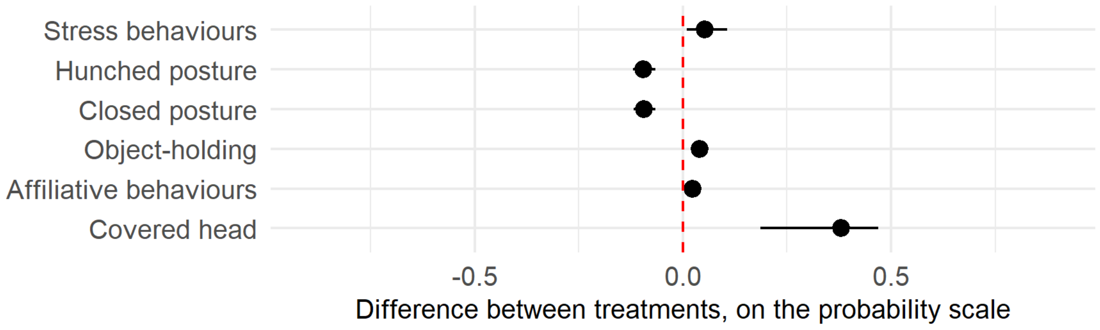


Figure 4.6 *Effects of lockdown restrictions lifting on orangutans.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability.

Lockdown restrictions lifting increased the probability that orangutans would be holding an object (mean = 0.04, 5.5% = 0.02, 94.5% = 0.06) and displaying affiliative behaviour (mean = 0.02, 5.5% = 0.01, 94.5% = 0.04). The zoo reopening also had the effect of increasing the probability of orangutans having their head covered (mean = 0.38, 5.5% = 0.19, 94.5% = 0.47), indicating that orangutans were around seven times more likely to have their head covered once lockdown restrictions had been lifted (proportional odds: 6.96).

4.3.1.2 Gorillas

Figure 4.7 shows the effects of lockdown restrictions lifting on gorilla behaviour. There were no effects of lockdown restrictions lifting on stress behaviours, tool use, or affiliative behaviours in gorillas. Overall, lockdown restrictions lifting increased the probability of less hunched posture ratings in gorillas (mean = -0.06, 5.5% = -0.08, 94.5% = -0.04, Figure 4.7a). However, there was initial increase in probability of more hunched posture ratings when the zoo reopened (mean = 0.07, 5.5% = 0.05, 94.5% = 0.09, Figure 4.7b), which then decreased once the gorilla house had been reopened to the public (mean = -0.13, 5.5% = -0.15, 94.5% = -0.10, Figure 4.7c).

For closed posture, there was no overall effect of lockdown restrictions lifting. However, the initial re-opening of the zoo increased the probability of less closed posture ratings in gorillas (mean = -0.08, 5.5% = -0.10, 94.5% = -0.06, Figure 4.7b), whereas the internal visitor area reopening increased the probability of more closed posture ratings (mean = 0.07, 5.5% = 0.05, 94.5% = 0.09, Figure 4.7c). There was no effect of lockdown status on focus on humans for gorillas. However, when human categories were narrowed down into researchers and keepers respectively, there were some effects of lockdown restrictions lifting on focus on keepers, but not focus on researchers. For example, lockdown restrictions lifting decreased the probability of gorillas focusing on keepers (lockdown to post-lockdown: mean = -0.09, 5.5% = -0.16, 94.5% = -0.03, Figure 4.7a, lockdown to semi-lockdown: mean = -0.06, 5.5% = -0.12, 94.5% = -0.02, Figure 4.7b).

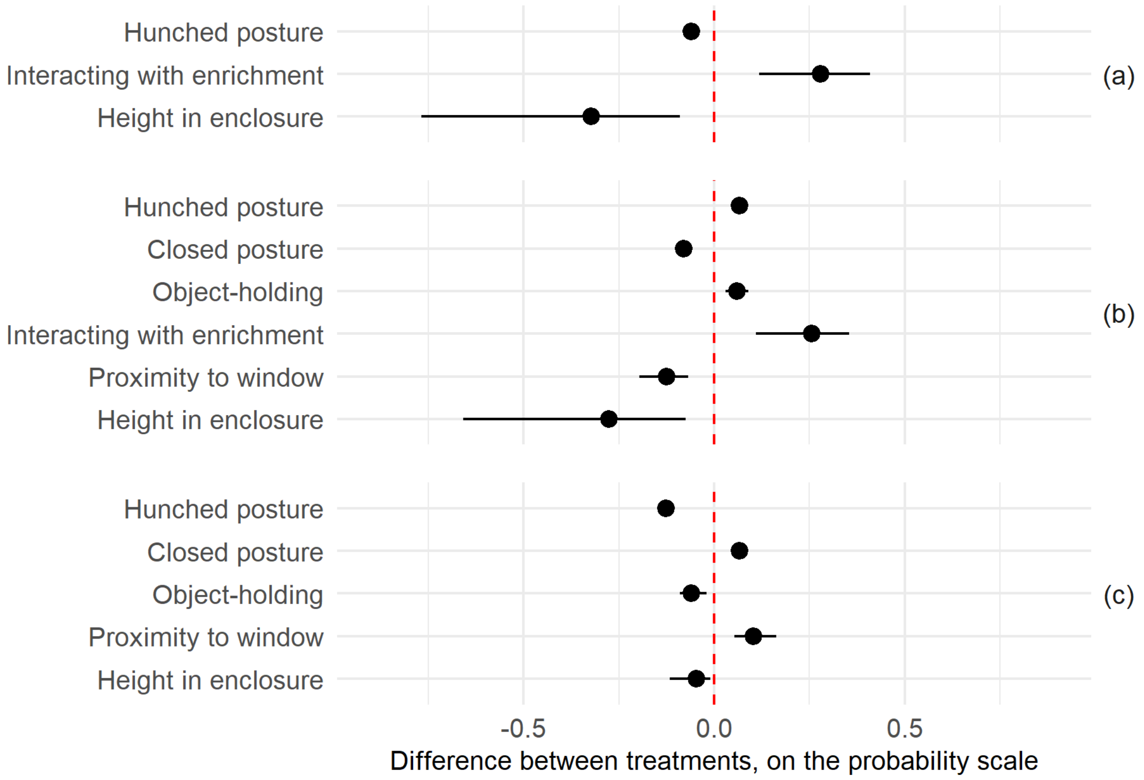


Figure 4.7 *Effects of lockdown restrictions lifting on gorillas.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (a) Lockdown to post-lockdown, (b) lockdown to semi-lockdown, (c) semi-lockdown to post lockdown.

The initial re-opening of the zoo increased the probability of gorillas holding objects (mean = 0.06, 5.5% = 0.03, 94.5% = 0.09, Figure 4.7b). However, when the zoo was fully reopened, this had the effect of reducing the probability of gorillas holding objects (mean = -0.06, 5.5% = -0.09, 94.5% = -0.02, Figure 4.7c). Lockdown restrictions lifting increased the likelihood of gorillas interacting with enrichment in semi-lockdown (mean = 0.28, 5.5% = 0.12, 94.5% = 0.41, Figure 4.7b) and post-lockdown (mean = 0.26, 5.5% = 0.11, 94.5% = 0.35, Figure 4.7a). There was a no effect of lockdown status on tool-use for gorillas. Gorillas demonstrated far fewer tool using behaviours than orangutans, with only seven observations of tool-using behaviours observed overall for gorillas, compared to 65 for orangutans. The initial re-opening of the zoo reduced the probability of gorillas being in the third of the enclosure closest to the visitor window (mean = -0.12, 5.5% = -0.20, 94.5% = -0.07, Figure 4.7b). However, this trend was reversed once the zoo fully reopened, and the opening of the visitor house increased the probability that gorillas would be close to the window (mean = 0.10, 5.5% = 0.05, 94.5% = 0.16, Figure 4.7c). The gorillas were 6% less likely to be close to the visitor window when the zoo was initially reopened (proportional odds 0.94), but 31% more likely to be close to the visitor window after the indoor visitor area was opened to the public (proportional odds 1.31). Lockdown restrictions lifting decreased the probability that gorillas would be situated at the top of the enclosure, with a stronger effect when the zoo initially reopened than when the visitor area was reopened to the public (lockdown to post-lockdown: mean = -0.32, 5.5% = -0.77, 4.5% = -0.09, Figure 4.7a, lockdown to semi-lockdown: mean = -0.28, 5.5% = -0.66, 4.5% = -0.07, Figure 4.7b, semi-lockdown to post-lockdown: mean = -0.05, 5.5% = -0.12, 94.5% = -0.01, Figure 4.7c).

4.3.2 Effects of total zoo visitors

4.3.2.1 Orangutans

Figure 4.8 shows the effects of total zoo visitor numbers on orangutan behaviour. There were no effects of total visitor numbers on closed posture in orangutans. Medium visitor levels increased the probability of stress behaviours compared with low visitor levels (mean = -0.08, 5.5% = -0.17, 94.5% = -0.02, Figure 4.8b). In addition, medium visitor levels increased the probability of less hunched posture ratings in orangutans (mean = -0.18, 5.5% = -0.22, 94.5% = -0.33, Figure 4.8b). However, this effect was reversed as visitor levels increased, with high visitor levels increasing the probability of more hunched posture ratings (mean = 0.16, 5.5% = 0.09, 94.5% = 0.23, Figure 4.8c). This means that orangutans were less hunched with medium visitor numbers compared with low or high visitor numbers. Increasing visitor levels decreased the probability of orangutans holding objects (low to high: mean = -0.05, 5.5% = -0.09, 94.5% = -0.02, Figure 4.8a, low to medium: mean = -0.13, 5.5% = -0.20, 94.5% = -0.06, Figure 4.8b, medium to high: mean = -0.18, 5.5% = -0.24, 94.5% = -0.12, Figure 4.8c) and interacting with enrichment (low to high: mean = -0.33, 5.5% = -0.52, 94.5% = -0.15, Figure 4.8a, low to medium: mean = -0.09, 5.5% = -0.17, 94.5% = -0.02, Figure 4.8b, medium to high: mean = -0.24, 5.5% = -0.44, 94.5% = -0.06, Figure 4.8c).

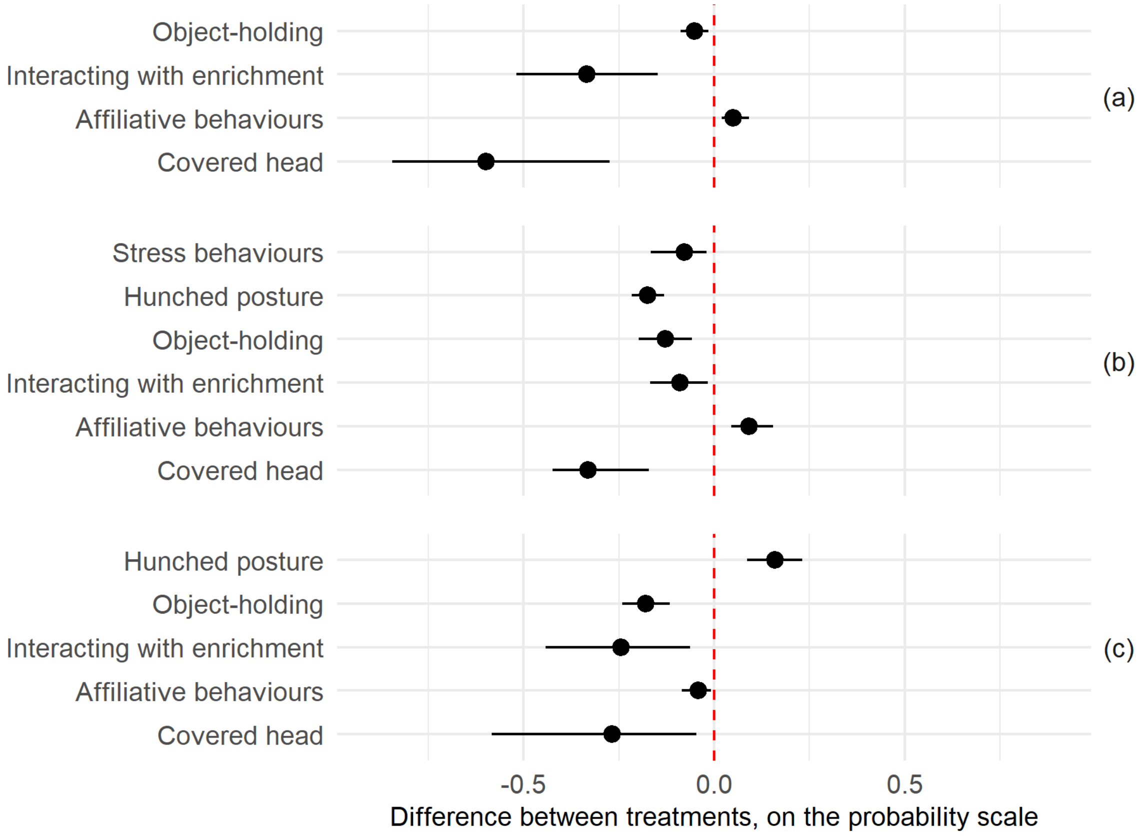


Figure 4.8 *Effects of total visitor numbers on orangutans.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (a) Low to high visitor levels, (b) low to medium visitor levels, (c) medium to high visitor levels.

Orangutans were 77% less likely to be interacting with enrichment when zoo visitors were high compared with when they were low (proportional odds: 0.23). However, medium and high visitor levels increased the probability of affiliative behaviour in orangutans (low to high: mean = 0.05, 5.5% = 0.02, 94.5% = 0.09, Figure 4.8a, low to medium: mean = 0.09, 5.5% = 0.04, 94.5% = 0.15, Figure 4.8b), although there was a lower probability of affiliative behaviours in high visitor levels compared with medium levels (mean = -0.04, 5.5% = -0.08, 94.5% = -0.01, Figure 4.8c). Increasing visitor levels also decreased the probability of orangutans having their head covered (low to high: mean = -0.60, 5.5% = -0.85, 94.5% = -0.27, Figure 4.8a, low to medium: mean = -0.33, 5.5% = -0.42, 94.5% = -0.17, Figure 4.8b, medium to high: mean =-0.27, 5.5% = -0.58, 94.5% = -0.05, Figure 4.8c).

4.3.2.2 Gorillas

Figure 4.9 shows the effects of total zoo visitor numbers on all variables except height in enclosure. Medium visitor levels reduced the probability of stress behaviours in gorillas compared to low visitor levels (mean = -0.07, 5.5% = -0.16, 94.5% = -0.02, Figure 4.9b), but no other effects were seen on stress. High visitor levels increased the probability of less hunched posture ratings compared with low (mean = -0.09, 5.5% = -0.12, 94.5% = -0.05, Figure 4.9a) or medium visitor levels (mean = -0.08, 5.5% = -0.11, 94.5% = -0.04, Figure 4.9c). Conversely, high visitor levels increased the probability of more closed posture ratings compared with low (mean = 0.09, 5.5% = 0.06, 94.5% = 0.12, Figure 4.9a) or medium visitor levels (mean = 0.19, 5.5% = 0.15, 94.5% = 0.22, Figure 4.9c). However, medium visitor levels increased the probability of less closed posture ratings compared with low visitor levels (mean = -0.10, 5.5% = -0.12, 94.5% = -0.07, Figure 4.9b). This means that gorillas were most likely to have less hunched, but more closed posture during high visitor levels. The probability of gorillas holding an object was greater with medium visitor levels than low (mean = 0.13, 5.5% = 0.04, 94.5% = 0.22, Figure 4.9b) or high (mean = -0.10, 5.5% = -0.20, 94.5% = -0.01, Figure

4.9c) visitor levels, with gorillas being less likely to hold an object in high visitor levels than low visitor levels (0.23, 5.5% = -0.27, 94.5% = -0.19, Figure 4.9a).

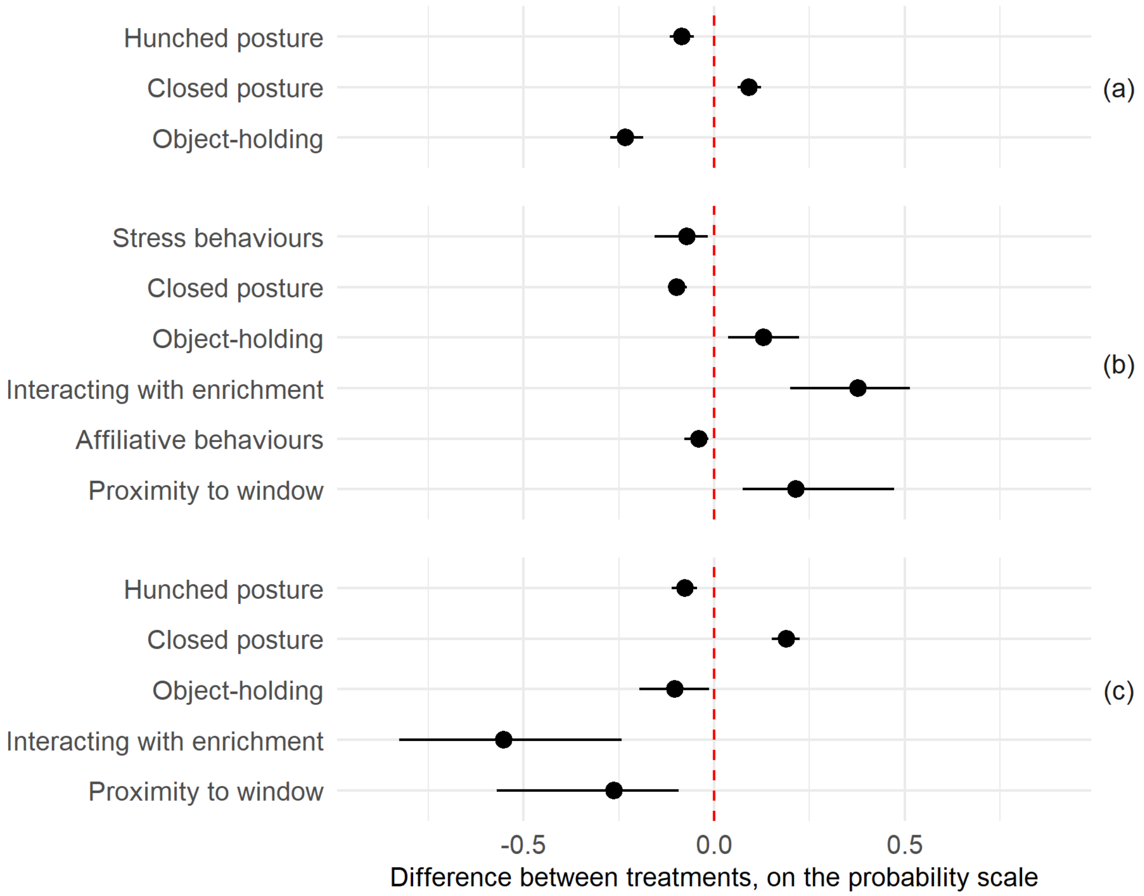


Figure 4.9 *Effects of total visitor numbers on gorillas.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (a) Low to high visitor levels, (b) low to medium visitor levels, (c) medium to high visitor levels.

Visitor numbers increasing from low to medium levels increased the probability of gorillas interacting with enrichment (mean = 0.38, 5.5% = 0.20, 94.5% = 0.51, Figure 4.9b). This was reversed when visitors increased from medium to high levels, decreasing the likelihood of interaction with enrichment (mean = -0.55, 5.5% = -0.83, 94.5% = -0.24, Figure 4.9c). This means that gorillas were seven times more likely to interact with enrichment during medium visitor levels (proportional odds: 7.22), but 93% less likely to do so when visitor levels were high (proportional odds: 0.07).

Medium visitor conditions decreased the probability of affiliative behaviour in gorillas compared with low visitor levels (mean = -0.04, 5.5% = -0.08, 94.5% = -0.01, Figure 4.9b). In addition, medium visitor levels increased the probability of gorillas being in the third of the enclosure closest to the visitor window (mean = 0.21, 5.5% = 0.07, 94.5% = 0.47, Figure 4.9b), although this was reversed with high visitor levels, where gorillas became less likely to be close to the visitor window (mean = -0.26, 5.5% = -0.57, 94.5% = -0.09, Figure 4.9c). As shown in Figure 4.8, gorillas were more likely to be high in the enclosure as visitor numbers increased to medium levels (mean = 3.13, 5.5% = 0.01, 94.5% = 7.85, Figure 4.10b) but were less likely to be high up with high visitor levels (-3.05, 5.5% = -7.32, 94.5% = -0.01, Figure 4.10c).

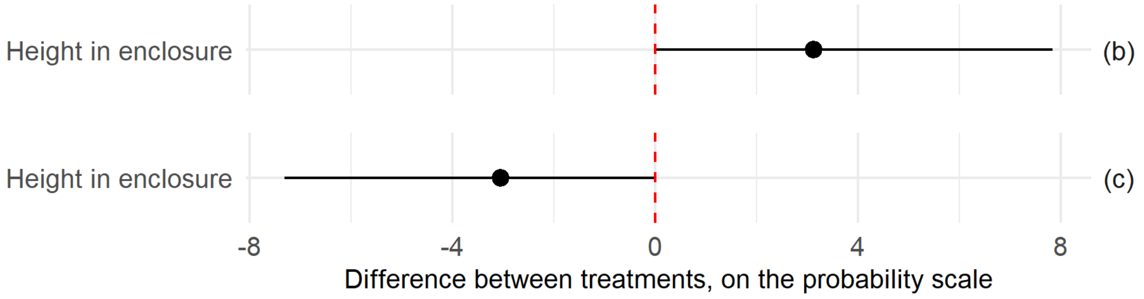


Figure 4.10 *Effect of total visitor numbers on height in enclosure (gorillas only).* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (b) low to medium visitor levels, (c) medium to high visitor levels. Note: A different scale is used for the x axis in this figure compared to the other figures, due to the larger effect sizes and wider credible intervals for this outcome variable.

4.3.3 Effects of visitor noise

4.3.3.1 Orangutans

Figure 4.11 shows the effects of visitor noise on orangutan behaviour. There were no effects of visitor noise on orangutan stress behaviours, closed posture, object-holding, or affiliative behaviour. Loud noise levels increased the probability of lower hunched posture ratings compared with some noise (mean =-0.13 , 5.5% = -0.23, 94.5% = -0.02, Figure 4.11c). Visitor noise at any level above quiet decreased the probability of orangutans interacting with enrichment (quiet to loud: mean = -0.48, 5.5% = -0.70, 94.5% = -0.24, Figure 4.11a, quiet to some noise: mean = -0.31, 5.5% = -0.40, 94.5% = -0.18, Figure 4.11b), although there was no difference between some noise and loud conditions.

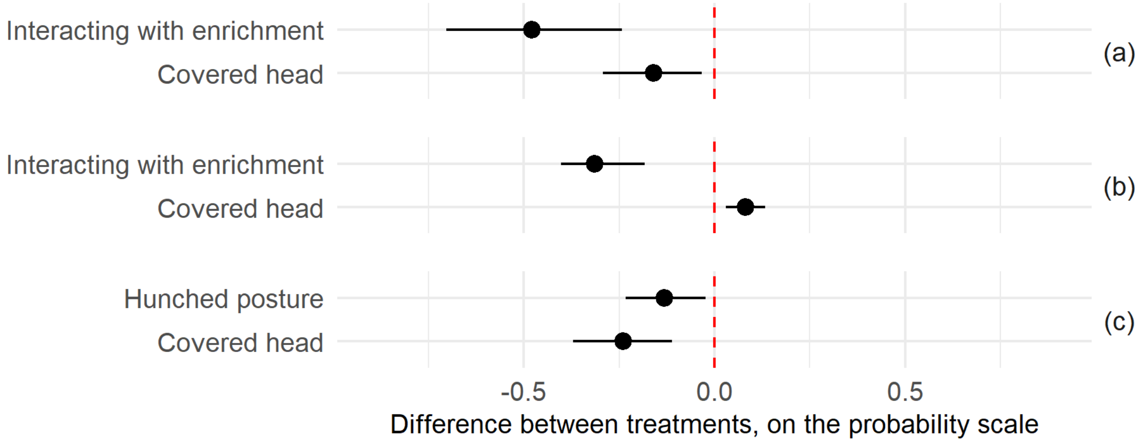


Figure 4.11 *Effects of visitor noise on orangutans.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (a) Quiet to loud noise, (b) quiet to some noise, (c) some noise to loud noise.

Loud visitor noise decreased the probability of head covering in orangutans compared to some or no noise (quiet to loud: mean = -0.16, 5.5% = -0.29, 94.5% = -0.03, Figure 4.11a, some noise to loud: mean = -0.24, 5.5% = -0.37, 94.5% = -0.11, Figure 4.11c), whereas some visitor noise increased the probability of head covering in orangutans compared with quiet conditions (mean = 0.08, 5.5% = 0.03, 94.5% = 0.13, Figure 4.11b).

4.3.3.2 Gorillas

Figure 4.12 shows the effects of visitor noise on gorilla behaviour. There were no effects of visitor noise on gorilla object-holding, interaction with enrichment, proximity to the visitor window, or height in the enclosure. Loud noise levels increased the probability of stress behaviours compared with some noise (mean = 0.02, 5.5% = 0.02, 94.5% = 0.08, Figure 4.12c).

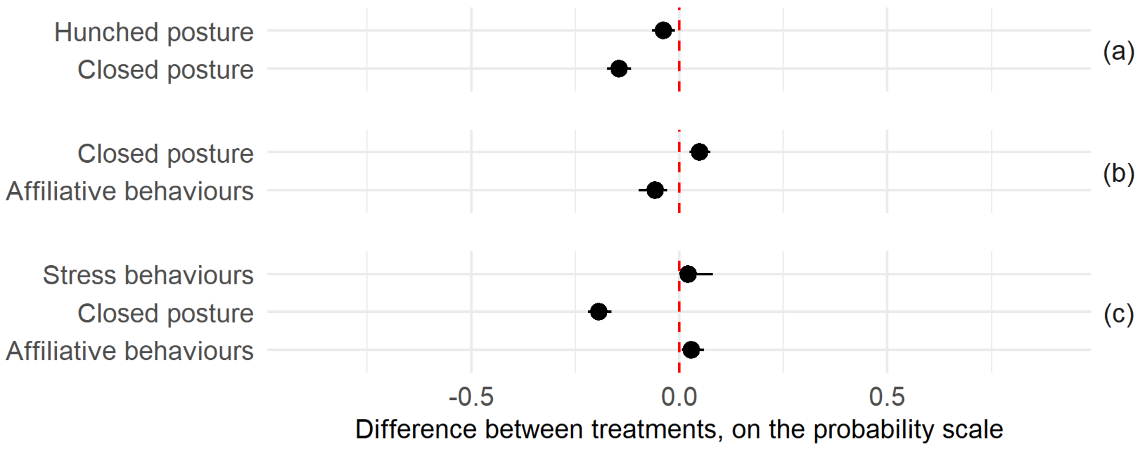


Figure 4.12 *Effects of visitor noise on gorillas.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (a) Quiet to loud noise, (b) quiet to some noise, (c) some noise to loud noise.

Loud noise also increased the probability of less hunched posture ratings in gorillas compared with quiet conditions (mean = -0.04, 5.5% = -0.07, 94.5% = -0.01, Figure 4.12a). Similarly, loud noise increased the probability of less closed posture ratings compared with quiet (mean = -0.15, 5.5% = -0.17, 94.5% = -0.12, Figure 4.12a) or some noise (mean = -0.19, 5.5% = -0.22, 94.5% = -0.16, Figure 4.12c) conditions. However, some noise increased the probability of more closed posture ratings compared with quiet conditions (mean = 0.05, 5.5% = 0.02, 94.5% = 0.07, Figure 4.12b). This indicates that gorillas were likely to have a more closed posture when noise levels were neither quiet nor loud. Some visitor noise reduced the probability of affiliative behaviours compared with quiet conditions (mean = -0.06, 5.5% = -0.10, 94.5% = -0.03, Figure 4.12b); however, when noise levels from some noise to loud noise, the probability of affiliative behaviours was increased (mean = -0.06, 5.5% = -0.10, 94.5% = -0.03, Figure 4.12c).

4.3.4 Effects of visitor presence at enclosure

4.3.4.1 Orangutans

Figure 4.13 shows the effects of visitor presence at the enclosure on orangutan behaviour. There were no effects of visitor presence on orangutan hunched posture, closed posture, or affiliative behaviour. There was a small effect of <20 visitors, which decreased the probability of orangutan stress behaviours compared with no visitor presence (mean = -0.04, 5.5% = -0.09, 94.5% = -0.01, Figure 4.13b). Some visitor presence increased the probability of object-holding in orangutans compared with no visitor presence (none to <20: mean = 0.12, 5.5% = 0.08, 94.5% = 0.15, Figure 4.13b). Conversely, there was a strong effect of visitor presence on interaction with enrichment, with orangutans being less than half as likely to be interacting with enrichment when some visitors were present compared with no visitor presence (proportional odds: 0.45) (none to 20+: mean = -0.38, 5.5% = -0.68, 94.5% = -0.11, Figure 4.13a, none to <20: mean = -0.18, 5.5% = -0.25, 94.5% = -0.09, Figure 4.13b). However, there was no difference between the presence of <20 and 20+ visitors. Visitor presence had a strong effect on orangutan head covering, with higher visitor presence decreasing the probability of head covering (none to 20+: mean = -0.40, 5.5% = -0.69, 94.5% = -0.11, Figure 4.13a, none to <20: mean = -0.07, 5.5% = -0.12, 94.5% = -0.02, Figure 4.13b, <20 to 20+: mean = -0.33, 5.5% = -0.63, 94.5% = -0.06, Figure 4.13c).

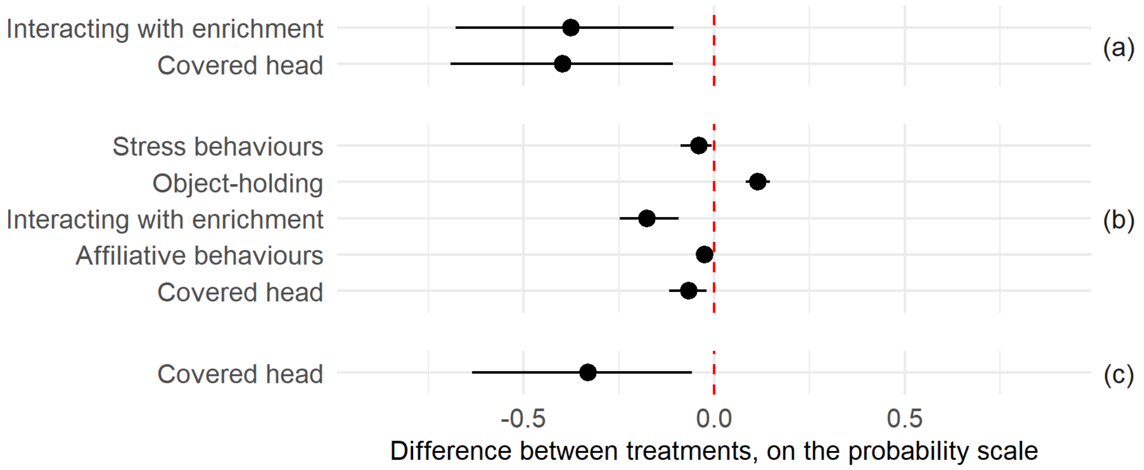


Figure 4.13 *Effects of visitor presence on orangutans.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (a) No visitors to 20+ visitors, (b) No visitors to <20 visitors, (c) <20 visitors to 20+ visitors.

4.3.4.2 Gorillas

Figure 4.14 shows the effects of visitor presence at the enclosure on gorilla behaviour. There were no effects of visitor presence on gorilla stress behaviour, hunched posture, affiliative behaviour, proximity to the visitor window, or height in the enclosure. The presence of 20+ visitors increased the probability of gorillas having less closed posture ratings compared with no visitors (mean = -0.09, 5.5% = -0.12, 94.5% = -0.06, Figure 4.14a) or <20 visitors (mean = -0.09, 5.5% = -0.12, 94.5% = -0.05, Figure 4.14c). The presence of <20 visitors at the gorilla enclosure decreased the probability of object holding (mean = -0.07, 5.5% = -0.11, 94.5% = -0.02, Figure 4.14b) and interaction with enrichment (mean = -0.22, 5.5% = -0.36, 94.5% = -0.08, Figure 4.14b) compared to when there were no visitors. However, larger crowds of 20+ visitors reversed this effect and increased the probability of interaction with enrichment compared with <20 visitors (mean = 0.27, 5.5% = 0.10, 94.5% = 0.44, Figure 4.14c). This means that gorillas were 62% less likely to interact with enrichment when some visitors were present (proportional odds 0.38), but nearly one and a half times more likely when 20+ visitors were present compared with <20 visitors (proportional odds 1.43).

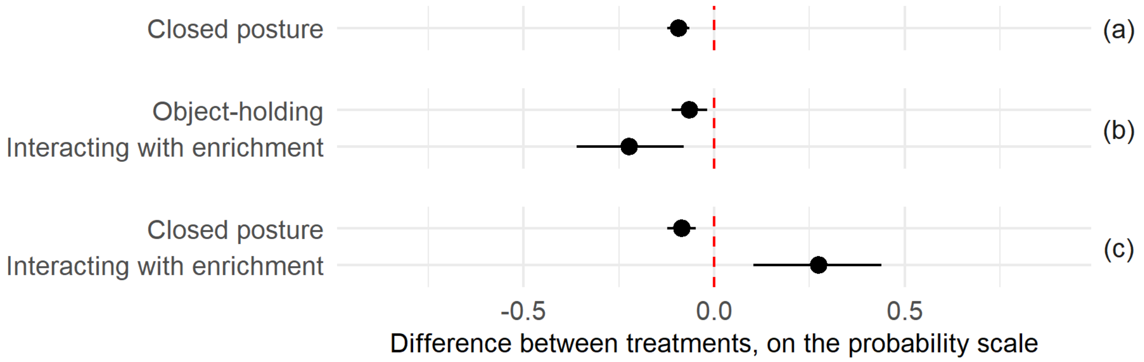


Figure 4.14 *Effects of visitor presence on gorillas.* Showing mean effects (points) and 89% credible intervals (bars). The left side of the dotted red line indicates decreased probability, the right side indicates increased probability. (a) No visitors to 20+ visitors, (b) No visitors to <20 visitors, (c) <20 visitors to 20+ visitors.

4.4 Discussion

This study aimed to establish the effects of lockdown restrictions lifting on behaviours linked to welfare in orangutans and gorillas. In addition, a new method for categorising posture was trialled to determine whether changes in hunched and closed postures were affected by the zoo reopening in a similar way to stress behaviours. The results show that there are clear species differences between gorillas and orangutans. For example, the lifting of lockdown restrictions only caused increased stress behaviours in orangutans, whereas gorillas were unaffected. For gorillas, the initial reopening of the zoo had effects on some variables which reversed once the indoor visitor area had been opened to the public, for example proximity to the visitor window, which initially decreased before increasing again. The effects of lockdown restrictions lifting on the posture measures were unclear and at times contradictory; it appears that hunched and closed postures were affected differently by the zoo reopening, and that this varied between species. The secondary analysis of three measures of visitor presence revealed some surprising effects, some of which contradicted the effects of the zoo reopening. To untangle this complicated picture, the effects of lockdown restrictions lifting, total zoo visitors, visitor noise, and visitor presence at the enclosure are discussed for each outcome variable below.

4.4.1 Stress behaviours

After the zoo reopened, orangutans exhibited more stress behaviours than during lockdown. As orangutans are semi-solitary animals who live in dispersed societies in the wild, only forming temporary aggregations (Galdikas, 1985; Malone et al., 2012; Roth et al., 2020), they may cope better without visitors than gorillas, who are highly social animals. However research on wild orangutans have shown that sociability in orangutans is higher in areas with more food resources (Schuppli et al., 2017). Therefore, this explanation may not make sense in this situation, where there is no scarcity in food resources. Another explanation may be the differences in visibility between the two enclosures. The gorillas had access to an off-show area nearly all the time, except during cleaning, whereas, because of the temporary housing arrangements in the orangutan enclosure, only one group at a time had access to an off-show area.

However, it is interesting that, once visitors had returned to the zoo, visitor presence was generally associated with less stress in orangutans and more stress in gorillas. Stress was decreased in both orangutans and gorillas during medium levels of visitors. However, whereas loud visitor noise increased stress in gorillas, no effect of noise was seen in orangutans. These results align with Clark et al. (2012), who found that increasing noise levels were correlated with visitor-directed vigilance in gorillas. Although orangutans were unaffected by noise levels, some visitor presence at the enclosure led to reduced stress in orangutans compared to no visitors, despite the fact there was no off-show area. This contrasts with Hashmi and Sullivan (2020), who found that vigilance in orangutans was positively correlated to noise, but not visitor numbers. It is possible that the presence of visitors at the enclosure was enriching for the orangutans. For example, Bloomfield et al. (2015) found that orangutans preferred to spend time near an uncovered part of the visitor window compared to a covered part. However, the conditions in Bloomfield et al. (2015) were very different to this study, with the visitor viewing area facing a platform within an outdoor enclosure, giving the orangutans an opportunity to voluntarily move away.

These findings are unexpected, because it seems logical that the species most negatively affected by lockdown restrictions lifting, i.e. orangutans, would also be negatively affected by visitor presence in general. The results presented here indicate that daily changes in visitor numbers, noise, and presence have a different effect on stress than visitor presence/absence as a categorical predictor. However, it should be noted that the effect sizes were small in all stress models and demonstrated considerable uncertainty, with the 89% credible intervals (indicating 5.5% to 94.5% of the probability distribution; McElreath 2020) approaching zero in both species.

When visitor presence does seem to result in stress for primates, there are ways to reduce or avoid this effect through enclosure modification. For example, Carder and Semple (2008) found a positive relationship between visitor numbers and duration of self-scratching behaviour in gorillas, but no significant relationship after feeding enrichment was provided. Another helpful intervention can be reducing the visibility of visitors. For example, Blaney & Wells (2004) found that gorillas who had a camouflage net barrier installed into the public viewing area demonstrated less aggressive and stereotypic behaviours than without the presence of the barrier. Similarly, Clark et al. (2012) found that negative visitor-directed behaviours decreased in gorillas when semi-opaque ‘privacy screens’ were used. The benefits of obscuring visibility of visitors in zoos have been seen in other primates, with one-way glass helping to reduce the negative impacts of visitor presence in black-capped capuchins (*Cebus apella*) (Sherwen et al., 2015). This suggests that enclosure modification can reduce anxiety levels related to visitor presence (Carder and Semple, 2008).

4.4.2 Hunched and closed posture

There results do not indicate a clear link between posture and stress behaviours because, after the zoo reopened, orangutans were more stressed, but less hunched and closed. For gorillas, there was an opposing pattern of hunched and closed posture during semi-lockdown, with more hunched, but less closed, postures. In addition, once the zoo had re-opened, visitor presence affected hunched and closed posture in different ways. Orangutans were less hunched during medium visitor levels, but more hunched during high visitor levels and in ‘some noise’ conditions. In contrast, gorillas were less hunched and more closed with high visitor numbers and some noise, but less closed with medium visitor numbers. A large visitor presence of >20 people also reduced closed posture in gorillas. Therefore, for total visitor numbers, there are u-shaped relationships for closed posture in gorillas and hunched posture in orangutans.

These results are difficult to interpret but indicate clear species differences in how posture is exhibited and influenced by lockdown restrictions lifting and visitor presence. This is not surprising, considering the behavioural and anatomical differences between gorillas and orangutans. There are some potential issues with drawing conclusions from simple Likert scales of posture in non-humans. Both body lock (extreme contraction of limbs) and body melt (extreme relaxation of muscles) are indicators of stress in orangutans (Commitante, 2005), which is a contradiction of the posture scales described here, where body melt could be categorised as open and unhunched posture. One issue here is that the stress categories described by Commitant (2005) are defined behaviours, whereas the posture scales introduced in this study measure two separate variables on a scale. Therefore, it is difficult to draw a comparison between the two studies. Due to the uncertainty presented by the results above, it would be useful to explore whether the two posture variables described can be related to other behaviours or internal psychological states. It is also possible that hunched or closed postures could be affected by other factors, for example ambient temperatures, particularly when the great apes are outside.

4.4.3 Focus on humans

There was no effect of lockdown restrictions lifting on focus on humans in general. However, when the zoo reopened, gorillas were less likely to focus on keepers. This aligns with the keeper-reported increase in zoo animal orientation towards keepers during lockdown (Hunton et al., 2022). In this study, the regular presence of observers during the lockdown data collection period may have ameliorated the effects of visitors returning after the zoo had reopened. One study of the effects of visitor presence on giant otters (*Pteronura brasiliensis*) found that the otters' behaviour was impacted to a greater extent by observers than zoo visitors (Brereton et al., 2023). More specifically, both observers and visitors were associated with increased standing alert behaviour, but only observer presence was associated with increased grooming and decreased resting behaviour. In addition, observers had a greater effect than visitors on spatial use, with inside areas being used more and pools being used less frequently when observers were present (Brereton et al., 2023). Although there was no notable change in focus on researchers in either species, it may have been better from a methodological perspective to have installed cameras in the enclosure to monitor behaviour remotely. However, this was prevented by limitations in keeper time due to the skeleton staff during lockdown.

4.4.4 Object-holding and enrichment

Lockdown restrictions lifting increased object-holding in orangutans but had no effect on interaction with enrichment. A more complicated picture was seen in gorillas, with increased object-holding and enrichment use when the zoo initially reopened, but a subsequent decrease in object-holding when all restrictions were lifted. Once the zoo reopened, orangutans were less likely to hold objects or interact with enrichment as total visitor numbers and noise levels increased. However, gorillas were more likely to hold objects and interact with enrichment during medium visitor levels, rather than low or high visitor levels. There was a contrasting effect of some visitor presence (<20), with orangutans being more likely to hold objects, but less likely to engage with enrichment, during some visitor presence. Interestingly, although gorillas were less likely to hold objects and interact with enrichment during some visitor presence, they were more likely to engage with enrichment during high visitor presence (20+), indicating another u-shaped function. The increase in object-holding and/or interaction with enrichment shown in each species when the zoo reopened aligns with the trend towards increased object manipulation prior to zoo closures reported by Masman et al. (2022). This might partially be explained by the fact that the keepers were on a skeleton staff during lockdown, and enrichment provision was lower than normal due to limited resources (Dalma Zsalako, personal communication).

However, the fact that gorillas were less likely to hold objects when the zoo fully reopened, while also being negatively affected by high total visitors, may indicate a threshold of visitor presence in gorillas, where some visitor presence is helpful but too much can have a negative effect. The picture is complicated by the fact that visitor presence at the enclosure had a different effect on object-holding and enrichment, with gorillas being more likely to interact with enrichment during high visitor presence (20+). This contradicts a study on chimpanzees by Wood (1998), who found that larger crowds of visitors were associated with reduced object-using, foraging, grooming, and play.

4.4.5 Affiliative behaviours

Affiliative behaviours in orangutans increased as lockdown lifted and during medium visitor levels. This is interesting, as orangutans also had a higher probability of stress behaviours when the zoo reopened. This might indicate that affiliative behaviours were a form of peer support and comfort during this period of increased stress. However, there was a lower probability of affiliative behaviours in high levels of total zoo visitors, as well as high visitor presence (20+) at the enclosure. Therefore, there might be a threshold where particularly large visitor presence is associated with reduced affiliation in orangutans. This does not necessarily contradict the idea that affiliative behaviours are related to social support, as high visitor presence may draw focus away from other orangutans and towards members of the public. Alternatively, high visitor presence might cause a kind of shutdown in normal social functioning. In gorillas, affiliative behaviours increased when the zoo initially reopened, but decreased again when the zoo fully reopened. Similarly, affiliative behaviours in gorillas reduced as visitor numbers increased from low to medium levels, indicating that affiliation in gorillas generally decreased as the zoo returned to normal. This aligns with a study of 15 different primate species, which found that the presence of at least six visitors was associated with a reduction in affiliative behaviour, compared to when there was no visitor presence (Chamove et al., 1988). Interestingly, although the presence of noise reduced affiliation in gorillas, loud noise increased affiliation. This supports the idea of affiliation providing a form of peer support.

4.4.6 Head covering (orangutans)

When the zoo reopened, orangutans were around seven times more likely to have their head covered than during lockdown. However, confusingly, nearly all measures of visitor presence were associated with a reduction in head covering, with the exception being ‘some noise’, where head covering was more likely than no noise conditions. These results contrast with Birke (2002), who found that adult orangutans covered their heads with paper sacks more when there were more than eight visitors in a group. However, the results align with (Hashmi & Sullivan, 2020), who found that covering behaviour reduced as visitor presence and noise increased. Hashmi and Sullivan (2020) also found that orangutans were more vigilant as noise levels increased, suggesting that a reduction in covering behaviour is due to increased vigilance. However, the pattern shown in this study is slightly less straightforward, as orangutans displayed greater head covering after lockdown, but also higher levels of stress. As visitor presence increased, this pattern reversed, with lower head covering and generally lower levels of stress. Although stress behaviours and vigilance are not synonymous, it is difficult to understand what is underlying the differences in probability of head covering in this study, but it seems that it is not necessarily visitor presence itself that is causing an increase in head covering when the zoo is open. There may be other important factors associated with zoos being open or closed that are unrelated to visitors. It would be interesting to conduct further research into head covering in orangutans, to see whether different measures of visitor presence affect other orangutan groups in a similar way.

4.4.7 Spatial use (gorillas)

Although gorillas were less likely to be close to the visitor window when the zoo initially reopened, they were more likely to be close to the window when the indoor visitor area was reopened to the public. These results contradict the findings by Williams et al. (2022), who found that the Twycross Zoo gorillas were less likely to spend time in the fifth of the enclosure nearest the visitors when the zoo was reopened to the public. However, it should be noted that the six observation days reported by Williams et al. (2022) that represented ‘post-lockdown’ took place in December 2020 and January 2021. While the zoo was briefly open during these two months, 79% of the time (11/14 days) the total zoo visitor numbers would be categorized as ‘low’ visitor levels (below the interquartile range), as defined in this study. The results of this study found that gorillas were more likely to be close to the visitor window during medium visitor levels than low visitor levels, a trend that reversed during high visitor levels. Therefore, it seems likely that this study actually shows similar results to those reported by Williams et al. (2022), as both studies show a negative effect of low visitor presence on gorilla proximity to the window. This indicates that medium visitor presence was enriching for the gorillas, rather than being stressful. However, the time spent in the back den areas out of view of visitors was not recorded. This might have given a greater insight into the effect of visitor presence on the areas of the enclosure used by gorillas.

Gorillas were also less likely to be in the highest part of the enclosure once the zoo had reopened. It is possible that, during semi-lockdown, there was greater visibility of visitors from the slides and windows at the back of the enclosure, which faced onto the outside part of the enclosure and the café, which had a considerable amount of visitor traffic. There was a high window near the enclosure ceiling overlooking access to the keeper area (personal observation), which may have encouraged gorillas to climb higher in the enclosure when there was less human presence at the zoo, particularly considering the increased focus on keepers during lockdown. However, in contrast to the results for proximity to visitor window, gorillas were more likely to be high in the enclosure with medium visitor levels, but less likely once total visitors had increased to high levels. Again, this may be related to the vantage point afforded by a high position in the enclosure. Neither proximity to the window or height in the enclosure were affected by visitor noise, which is consistent with a gorilla study by Hashmi & Sullivan (2020), who found that activity was influenced by visitor numbers but not noise.

4.4.8 General study limitations

There are several key limitations to this study. The first is the stage of lockdown during which the data was collected. It would have been optimal to have collected data prior to the first lockdown. As this study commenced during the second UK lockdown, the great apes had already experienced one lockdown and subsequent return of visitors. Therefore, it was not an entirely new situation for them, and the effects of lockdown may not have been as strong the second time round. In addition, the third lockdown occurred in the middle of the semi-lockdown period. This means that the research subjects did not experience a clear progression from lockdown to semi-lockdown to post-lockdown, but rather a fluctuation of conditions during the study period. The second study limitation is that there was only one group of each species participating, so an inter-group comparison was not possible. It is important to note that group dynamics, sex, and individual differences can influence the way great apes respond to visitor presence (Stoinski et al., 2012). As group composition may influence the way visitor presence affects great apes (e.g. Kuhar 2008), these subtleties would have been ignored in this study. For the hunched and closed posture variables, data was collected by two different observers. However, no formal inter-observer reliability testing was performed to take this into account, which is a limitation of this study. Lastly, because the secondary analysis looked at each measure of visitor presence separately, some of the relationships between these variables may have been obscured.

4.5 Conclusion

This study set out to investigate the effects of Twycross Zoo reopening after the Covid-19 lockdowns on the behaviour and posture of orangutans and gorillas. In addition, a new method for measuring closed and hunched posture was introduced, to see whether posture was affected by visitor presence. There were species-specific effects of lockdown restrictions lifting on orangutans and gorillas. Orangutans showed more stress behaviours, object-holding, affiliative behaviours, and head covering when the zoo was open, and less closed and hunched postures. Overall, gorillas demonstrated more interaction with enrichment, and less hunched posture and time spent at height when the zoo was fully open. However semi-lockdown had effects on several variables in gorillas, including closed posture, object-holding, and proximity to the visitor window, which reversed when the visitor house was reopened to the public. The results are further complicated by the wide-ranging effects of total zoo visitors, visitor noise, and visitor presence. These findings represent the complex picture seen in the wider literature regarding the effect of lockdowns, and the subsequent reopening of zoos, on captive great ape behaviour. It is also evident that conclusions about the effect of lockdown restrictions lifting on great ape behaviour cannot simply be attributed to visitor presence. It is hoped that the findings of this study will help zoos plan and prepare for future lockdown-related disruptions by providing the necessary support to meet the species-specific needs of great apes in their care.

4.6 Next steps

Chapter 4 found that the return of zoo visitors following lockdown had a number of different effects on gorillas and orangutans. One key finding is that orangutans were more stressed following lockdown, whereas there were no changes in stress behaviours in gorillas. In addition, the presence of zoo visitors had different effects on each species, depending on whether visitors were measured by total daily zoo visitors, visitor noise at the enclosure, or visitor presence at the enclosure. However, to understand stress and resilience in great apes, it is important to not only look at species differences, but also individual differences. Although there is variation in all animals, some individuals are different to the extent that they have unique welfare needs. Chapter 5 addresses this by presenting an in-depth case study of a male Sumatran orangutan with atypical physical and cognitive development, to identify how these differences may affect his wellbeing in captivity.

CHAPTER 5

UNDERSTANDING THE WELFARE REQUIREMENTS OF A NEUROLOGICALLY AND PHYSICALLY DIVERGENT CAPTIVE MALE SUMATRAN ORANGUTAN (*PONGO ABELII*)

This chapter, largely in its current form, has been submitted for publication as:

Bridgeland-Stephens, L., Thorpe, S. K. S., Price, E., Hunt, G., Chappell, J., Understanding the welfare requirements of a neurologically and physically divergent captive male Sumatran orangutan (*Pongo abelii*). *F1000Research*.

Abstract

Understanding the needs of animals with physical and cognitive impairments is essential for zoos, rehabilitation centres, and other captive contexts. This case study describes the atypical physical and cognitive development of Jiwa, an adult male Sumatran orangutan (*Pongo abelii*), to evaluate how these differences may impact Jiwa and to explore how cognitive enrichment can be tailored to his skill level. Keeper records from Jiwa's birth (1999) to February 2022 were scrutinised to identify key developmental milestones, changes in body weight, and deciduous dental emergence. These were compared with expected milestones for wild and captive orangutans. In addition, a probe feeder enrichment apparatus was gradually tailored to an appropriate skill level between January and March 2022. Many of Jiwa's developmental milestones were consistent with expected orangutan development, although there were noticeable differences in body weight, dental emergence, locomotion, and cognition. The welfare domains most likely to be negatively impacted by these differences were physical health, expression of agency, and mental wellbeing. After the enrichment apparatus was tailored to an appropriate level of challenge, Jiwa showed marked improvement in engagement and ability to use the apparatus. This study helps to inform future case studies of atypical great apes by detailing the physical and cognitive development of an individual orangutan. Although Jiwa's differences may impact his own wellbeing in some areas, he has largely been able to overcome them. However, this case study highlights the challenges involved in tailoring enrichment apparatuses and resilience interventions for atypical individuals.

5.1 Introduction

5.1.1 Divergence and welfare

Humans responsible for the care of non-human animals (hereafter animals) have a responsibility to ensure that positive welfare is promoted in those individuals, and that they are free from harm. Over the past few decades, there has been a concerted effort to develop a system to measure wellbeing in captive animals. In the 1990s, the UK Farm Animal Welfare Council's original 'five freedoms' of welfare (FAWC, 1992) were adapted by Mellor and Reid (1994) into a grading system known as the Five Domains Model. These overlapping domains are: 1) thirst, hunger, and malnutrition; 2) environmental challenge; 3) disease, injury, and functional impairment; 4) behavioural restriction; and 5) anxiety, fear, pain, and distress. Rather than measuring the presence or absence of each 'freedom', this system takes a more nuanced approach, acknowledging the degrees of compromise made in each of these areas of welfare, or 'wellbeing' (Mellor & Reid, 1994). The fifth domain, which relates to mental wellbeing, is a cumulative measure of the four physical domains, and therefore determines the overall score. The five domains were extended in 2015, with changes that included broadening the negative affective states with those related to an individual's cognitive assessment of external circumstances, e.g. anxiety, fear, frustration, anger, helplessness, loneliness, and boredom (Mellor & Beausoleil, 2015). In addition, positive welfare states were taken into consideration. In the mental wellbeing domain, this includes states such as security, confidence, calmness, control, affectionate sociability, playfulness, and sexual gratification (Mellor & Beausoleil, 2015). These are related to behaviours encompassing agency, exercised through activities like environmental challenges, making choices, exploration, bonding with others, playing, and being able to retreat or defend oneself from attack. The latest iteration of the Five Domains Model incorporates both positive and negative human-animal interactions (Mellor et al., 2020).

Identifying the welfare needs of animals in captivity who diverge neurologically and/or physically from the species-typical ‘norm’ is a complicated issue, partly due to the individual nature of such conditions. Although there is variation within all species, some individuals are divergent to the extent that they experience life differently to others. This means that socio-environmental conditions which are deemed to meet welfare needs in most members of a species may not be able to meet the needs of all individuals. In humans, the 1975 declaration of the Union of the Physically Impaired Against Segregation marked a shift towards emphasising the constraints of external, socio-structural barriers preventing humans from fully participating in society, rather than disability being defined by individual, internal limitations (Edwards & Imrie, 2008). This is relevant for non-human animals in captivity, as there is potential for management changes and enclosure modifications to enable atypical individuals to lead a fulfilling life. However, the first step is to begin to understand the diversity of neurologically and physically atypical characteristics, and the extent to which captive environments can be adapted without compromising the welfare of other individuals.

Understanding of the needs of divergent animals is important in all captive contexts. However, for wild-born animals rescued from human-wildlife conflict and undergoing rehabilitation, there is an additional motivation. For example, orangutan (*Pongo spp.*) rehabilitation centres, which care for orangutans rescued from the illegal wildlife trade and other harmful situations, must make decisions on whether injured and otherwise atypical individuals can and should be released back into the wild or moved to semi-wild environments (Russon, 2008). If great apes are released into more natural environments, where individuals must be self-supporting, physical and cognitive impairments may result in difficulties such as obtaining food (Domain 1), building nests for resting safely (Domain 2), maintaining physical fitness and being able to reach and navigate the forest canopy (Domain 3), and defending against threats (Domain 4). All of these are likely to have a negative impact on mental wellbeing (Domain 5), leading to hunger, anxiety, fear, pain, and distress (Mellor et al., 2020). In some rehabilitation centres, great apes with physical or psychological disabilities remain in enclosures rather than being released into partially free-range forested islands (Litchholt, 2021). These careful management decisions made by rehabilitation centres will depend on the specific nature of an individual's differences, whether physical or cognitive, and the extent to which they are likely to affect an individual's ability to support themselves with a reasonable degree of wellbeing. There are complex ethical issues surrounding these decisions (see Palmer, 2018), particularly as it is difficult to predict the outcome of any release effort, and these risks must be balanced against potentially sub-optimal welfare in captivity. There may be differing perspectives on the extent to which great apes might be debilitated in the wild due to cognitive or physical impairments. However, arguably at the very least, released orangutans should have the capacity to search for and consume food, and to move away from danger.

5.1.2 Existing knowledge of divergent primates

There is poor knowledge of divergent individuals in animal research. There are some examples of studies with primates with physical impairments (Antilla et al., 2013; Cole, 1989, in Taylor, 2020; Hobaiter & Byrne, 2010; Hopper, Shender, & Ross, 2016; Matsumoto et al., 2016; Nakamichi et al., 1983; Turner et al., 2014), but few long-term studies (e.g. Sakuraba, Tomonaga and Hayashi, 2016), and limited research on the life history and development of atypical individuals, although there are some isolated examples (e.g. Savage and Snowdon, 1982; Hirata et al., 2017). Although life in the wild is challenging for any individual, particularly those released from captivity, the challenge may be exacerbated for individuals with physical and/or cognitive differences. For example, severe physical injury can lower the dominance rank for chimpanzees and baboons (*Papio cynocephalus*) (e.g. Reynolds and Reyonlds 1965, Drews 1996), indicating a reduction in competitive ability (Beamish & O'Riain, 2014).

However, there are examples of divergent primates coping well in the wild. For example, a male free-ranging Japanese macaque (*Macaca fuscata*) called Tanago, who had missing hands and 'distorted' feet, was assessed during his first year of life and found to have impaired locomotion and social interactions (Nakamichi et al., 1983). Although Tanago's physical impairments meant he struggled to keep up with other infants, leading to lower levels of play behaviours, Tanago was also less likely to receive aggression than other infants, and more likely to be groomed by other juveniles, usually females (Nakamichi et al., 1983). Tanago had a closer relationship with adults and female juveniles than other infant macaques, despite the rigid hierarchy in Japanese macaques which would normally have prevented him interacting with older troop members (Nakamichi et al., 1983). Therefore, Tanago generally adapted well to his physical impairments.

As well as altering social interactions, physical impairments can also influence the length of time atypical individuals spent in different activities. For example, activities like locomotion may be more tiring with a physical impairment. In a long-term study of free-ranging Japanese macaques, disabled females spend more time resting and less time socialising than nondisabled females (Turner et al., 2014). However, as with Tanago, this was not due to social alienation, as disabled females received less aggression, and their groom solicitations were as successful as nondisabled females (Turner et al., 2014). Another study showed similar increased resting time for disabled baboons, but no changes in grooming or social vigilance behaviours (Beamish & O'Riain, 2014). Physical divergence does not necessarily prevent wild animals from living a long and fulfilling life. A wild female Japanese macaque called Mozu, whose hands and feet had an abnormal morphology (possibly from pesticide pollution), became a prominent troop member, living for 28 years and rearing five offspring (Cole 1989, in Taylor 2020).

5.1.3 Benefits of research

In captive contexts where long-term care is being provided, there are several key motivations for understanding divergent individuals. The first is that understanding the needs of these individuals is fundamental to promoting their welfare. As there is currently limited research in this area, sharing knowledge about specific cases can help caretakers know what to expect, particularly during an individual's development. By understanding of how the needs of atypical individuals can be fulfilled in relation to the Five Domains Model, a knowledge base can be established which caretakers can use to guide individual care and husbandry to optimise the quality of life for atypical individuals. Not only does this have clear benefits for animal welfare, but there are also financial implications for zoos. Atypical individuals whose needs are not being met may exhibit behaviours related to negative affect, e.g. anger and frustration. As well as having the potential to negatively affect visitor perceptions, such behaviours could be destructive and costly and could even put the wellbeing of other individuals in the group at risk. Additional keeper time may be required to manage and care for some individuals with cognitive impairments, e.g. where there are difficulties training an animal to move to a specific area of the enclosure to enable cleaning. An inability to socially coexist with other conspecifics could mean complicated housing arrangements, and additional space requirements to avoid conflict.

Therefore, when the needs of atypical individuals are understood and being met, there is likely to be less pressure on the workload of caretakers and less financial pressure on the zoo.

Research involving atypical animals can also contribute to improved wellbeing for the individuals themselves, as taking part in research can be enriching. There can be both cognitive and physical benefits from taking part in research. For example, cognitive enrichment was used for rehabilitating movement in an adult male chimpanzee (*Pan troglodytes*) called Reo, who experienced acute transverse myelitis at the age of 24 which resulted in impaired walking ability (Sakuraba, Tomonaga and Hayashi, 2016). Reo was provided with a puzzle task linked to a feeder two meters away, designed to encourage him to walk between the puzzle and the feeder. This led to an increased total travel distance from 136.7 meters to 506.3 meters within a period of 10 days, and an increase in percentage of walking during the study sessions from 1.2% to 27.2%. Research can also help to identify the skill levels of an individual, which can lead to the development of targeted interventions (e.g. Ernst et al., 2005) with ongoing benefits beyond the scope of the study. However, determining an appropriate level of challenge depends on the individual abilities of each animal (Meehan & Mench, 2007), which may be particularly difficult to determine for divergent individuals. Therefore, case studies which involve appropriately tailored enrichment apparatuses could be used as an important point of reference.

In order to address the gap in research on individuals with unique welfare needs, a case study was carried out on an adult male Sumatran orangutan (*Pongo abelii*), Jiwa, who is cognitively and physically divergent from other orangutans. The aim of this study was to evaluate areas of the Five Domains Model where Jiwa's differences may be associated with an impact on wellbeing; and to determine an appropriate difficult level of cognitive enrichment for Jiwa, to aid in tailoring future enrichment to his individual needs.

5.2 Methods

5.2.1 Life history and development

There were two main sources of information on Jiwa's development. The first was his full daily keeper records from 17/10/1999 (his birth) to 07/02/2022, obtained through his specimen report on the Zoological Information Management System ('ZIMS'). The second was an unpublished internal report that summarised Jiwa's development during his first year of life. This was written by a keeper, Rupert Beck, on 22/10/2000. These documents were scrutinised for indications of Jiwa's developmental milestones, which were then compared with expected milestones for wild (van Noordwijk et al., 2009; van Noordwijk & van Schaik, 2005) and/or captive (Lethmate, 1977b, 1977a; Miller and Nadler, 1981; Beck, 2000; Nakamichi, 2004) orangutans. These milestones were: first break in continuous body contact with his mother, first time being carried by an individual other than his mother (captivity only), first time supporting his body weight on the barwork of the enclosure (captivity only), first independent locomotion from his mother, first attempt at nest-building, first locomotion more than 10 metres away from his mother, first attempt at using tools, first attempt at making tools, and being fully weaned.

Although wild Sumatran orangutans as young as three may be able to build arboreal nests adequate for a brief rest (van Noordwijk et al., 2009), fully functional nest-building is rarely possible in the zoo environment due to a lack of appropriate base structures and limited nesting materials (Chappell & Thorpe, 2022). Therefore, only the first attempt at 'practising' nest building (van Noordwijk et al., 2009), i.e. arranging nesting materials without building an adequate nest for sleeping, is included as a milestone. The milestone for the first attempt at using tools encompasses tools discarded by mother or peers (van Noordwijk & van Schaik, 2005). Milestones which are not normally possible within the zoo context were excluded, e.g. travelling more than 50 meters away from the mother. Milestones based on activity budgets were also excluded, due to lack of comparative data in the keeper reports.

In addition to developmental milestones, physical measurements of Jiwa's growth were compared with expected rates for a male Sumatran orangutan. These included body weight in kilograms and age of deciduous ('baby teeth') dental emergence (Beck, 2000; Fooden & Izor, 1983). Male orangutans are known to demonstrate distinctive bimaturism, with secondary sexual characteristics developing at very different ages and, in some individuals, taking as long as 30 years to develop (Utami et al., 2002). However, there is very little data available for the weight of unflanged male orangutans, since in captivity males nearly always develop flanges (Pradhan, van Noordwijk, & van Schaik, 2012). Therefore, as Bornean and Sumatran orangutans are considered to be approximately the same size (Smith & Jungers, 1997), the comparative data includes a range of different sources, including captive (Fooden & Izor, 1983) and wild-born (Markham & Groves, 1990; Smith & Jungers, 1997) Sumatran orangutans, wild-born Bornean orangutans living in rehabilitation centres with no flanges or developing flanges (Prasetyo, 2019), and unflanged orangutan skeletal data (species unknown) (Kralick et al., 2023).

5.2.2 Adaptation of cognitive enrichment

The second part of the study took place from 17th January to 5th March 2022 and involved tailoring a cognitive enrichment apparatus to a suitable level for Jiwa. This involved a probe feeder apparatus which had been previously presented to Jiwa's peers (in Chapter Three). This was constructed from a 50 cm length of 5 cm diameter hollow plastic pipe with a food reward inside (Figure 5.1). The food reward was initially peanut butter, but this was changed to porridge from session 3 onwards, as Jiwa's preferred food type and therefore a greater incentive. A full description of the probe feeder is provided in Chapter Three, section 3.2.2.

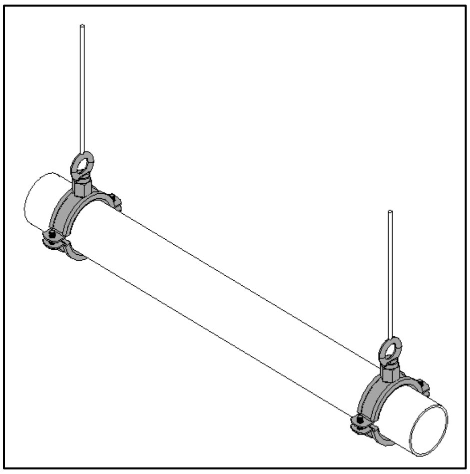


Figure 5.1 *Jiwa research apparatus.* Research apparatus used in Week 1, which was suspended from the ceiling from the two cords and orientated with the end of the tube facing Jiwa. A food reward was inside the tube which could only be reached using a stick.

The study methods were adapted on a weekly basis according to Jiwa's success at reaching the food reward, and the contents of each session are shown in Table 5.1. Each session lasted 30 minutes and was filmed using two 'APEMAN' A77 video cameras, one on a tripod and the other clipped to the front of the researcher. Initially, the same version of the apparatus was given to Jiwa as had been presented to his peers (see Chapter Three), to see whether he could successfully obtain the food reward. The intention was that, if Jiwa was successful, the apparatus would be gradually increased in difficulty by moving the cords closer together until Jiwa was no longer to access the food reward, which would provide an indication of Jiwa's skill level. However, as Jiwa did not use a tool to access the food reward when the probe feeder was hung outside the enclosure, out of reach of his hands (session one), the difficulty of the enrichment was lowered to a very basic level.

Table 5.1 *Jiwa experimental schedule*

Date	**Intervention**
17th January	Probe feeder hung from ceiling in keeper corridor 25cm away from the wire mesh, only reachable by using a stick.
24th January	Loose probe feeder given to Jiwa inside his bed den, with peanut butter at either end in reach of his fingers.
31st January	Loose probe feeder given to Jiwa inside his bed den, with peanut butter in the middle out of reach of his fingers (20cm from each end).
7th February	Loose probe feeder given to Jiwa inside his bed den, with researcher conducting social learning demonstration outside the bed den (see Appendix M).
14th February	Researcher held probe feeder outside bed den with stick already inside tube. It was possible to remove the stick from the tube, but not hold the tube.
21st February	Researcher held probe feeder outside bed den with stick already inside tube. It was possible to remove the stick from the tube, but not hold the tube.
25th February	Researcher held probe feeder outside bed den with stick already inside tube. It was possible to remove the stick from the tube, but not hold the tube.
28th February	Researcher held probe feeder outside bed den with stick already inside tube. It was possible to remove the stick from the tube, but not hold the tube.
5th March	Researcher held probe feeder outside bed den but provided Jiwa with sticks separately to see if he would insert the stick into the tube himself.

When given a loose tube inside his enclosure, Jiwa obtained the food reward when within reach of his fingers (session two), but not when the peanut butter was out of reach (20 cm from either end of the tube), even while the researcher was conducting a social learning demonstration using a second tube outside the enclosure and vocalising to draw Jiwa's attention (sessions three and four). The subsequent four sessions (sessions five to eight) were bi-weekly and required

Jiwa to remove the stick (already touching the food reward) while the probe feeder was being held outside the enclosure by the researcher. As Jiwa did participate in this form of enrichment, the difficulty level was increased in the final session (session nine) by providing Jiwa a stick, to see whether he would insert this into the probe feeder himself to obtain the food reward.

The full details of the social learning and stick withdrawal procedures can be found in Appendix M. The first five sessions took place weekly (17th January until 14th February 2022), and the last four sessions took place biweekly (21st February to 5th March 2022). Ethical approval for this research was obtained from the University of Birmingham Animal Welfare and Ethical Review Body (ERN_19-1935) and the Durrell Wildlife Conservation Trust Ethics Committee (ETH21/2019).

5.3 Results

5.3.1 Birth and physical development

Jiwa was born in 1999 at Jersey Zoo (UK) and was 23 years old at the time of the study. Although the cause of Jiwa's atypical development is unknown, Beck (2000) considered the possibility that excessive lip and face sucking behaviour from his mother resulted in a lack of sufficient nutrition and oxygen. However, it is also possible that Jiwa was deprived of oxygen prior to birth, e.g. due to complications with the umbilical cord or function of the placenta, and that his mother's behaviour was in reaction to Jiwa's lack of response. Although this behaviour was stopped through keeper intervention with negative reinforcement (water jets), for the following five months "Jiwa appeared to be in a semi vegetative state… giving the impression that he was temporarily brain damaged" (Beck, 2000).

Figure 5.2 shows Jiwa's growth rate compared with the expected growth rate of male orangutans with flanges, males developing flanges, and unflanged males (Fooden & Izor, 1983; Kralick et al., 2023; Prasetyo, 2019). On average, captive orangutans are 80% heavier than their wild counterparts (Fooden & Izor, 1983). Jiwa's weight, last measured in 2001 as 36.8 kg, sits just below the expected range for unflanged males, although it should be noted that both his mother and grandmother were smaller than average in size (Beck, 2000; Fooden & Izor, 1983), weighing 42kg and 40kg in adulthood respectively (Deputy Head of Mammals at Jersey Zoo, Gordon Hunt, personal communication).

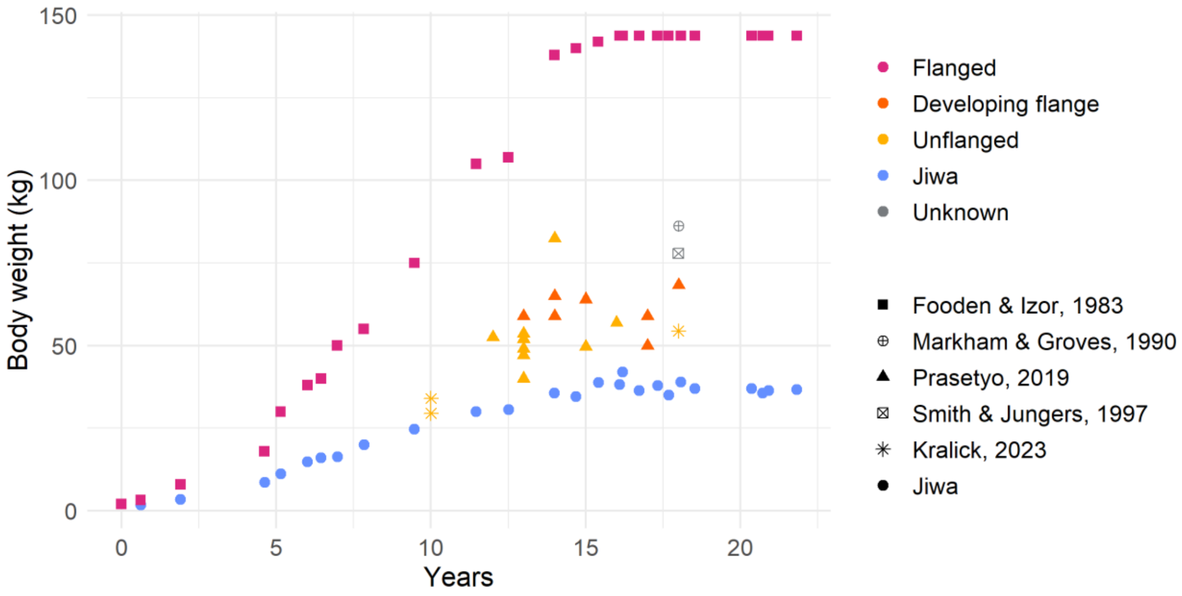


Figure 5.2 *Jiwa's growth in body weight compared to expected rates.* Comparative data includes expected growth in flanged males where species is unknown (Fooden & Izor, 1983), wild-born Bornean (*Pongo pygmaeus*) males in rehabilitation centres with developing flanges or no flanges (Prasetyo, 2019), wild Sumatran (*Pongo abelii*) males with unknown flange status (Markham & Groves, 1990; Smith & Jungers, 1997), and data based on unflanged male orangutan skeletons where species and exact age is not specified (Kralick et al., 2023). For the skeletal data, exact age was not specified, and so subjects characterised as 'young adult' and 'adult' by Kralick et al. (2023) were recorded here as 10 years and 18 years, respectively.

Expected dental emergence rates for orangutans in captivity can be seen in Figure 5.3, showing that the eruption of Jiwa's deciduous teeth generally appears to have taken place later than, or at the late end of, expected ranges of dental emergence reported by Beck (2000) and Fooden and Izor (1983). The exception to this is with his upper lateral incisors, which erupted well within the expected age range of 6.5-13 months for male Sumatran orangutans (Fooden & Izor, 1983). It appears that Jiwa's teeth emerged within a three-month period, contradicting the expected staggered dental emergence (Figure 5.3). There was no available data for the eruption of Jiwa's canines or secondary premolars. There was also insufficient data to compare the eruption of Jiwa's permanent (adult) teeth with expected emergence rates, although he was observed to have a possible full set of permanent mandible teeth by eight and a half years old (recorded on 07/06/2008 in the keepers' contemporaneous notes).

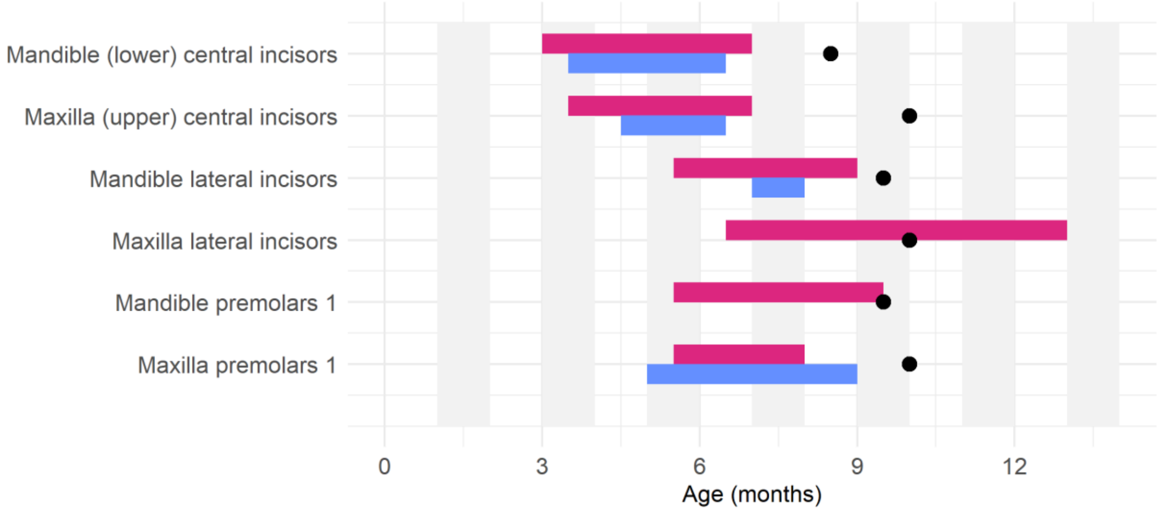


Figure 5.3 *Jiwa's deciduous dental emergence compared with expected rates*. Black dots indicate time Jiwa's dental eruptions are first observed by keepers, either in the keeper records or as reported by Beck (2000). Expected milestone ranges (rounded to the nearest half-month) reported by Fooden and Izor (1983) are indicated by the upper pink bars; the lower blue bars indicate ranges reported by Beck (2000). The dental emergence of Jiwa's peers at Jersey Zoo is mixed-sex and based on four individuals for lower incisor emergence, and two individuals for all other dental eruptions (Beck, 2000).

In addition to Jiwa's small size, his physical abilities were also impaired at some points in his development. Jiwa was described as being noticeably weak from 11 weeks old, with an insufficient grip that necessitated bodily support from his mother; when this did not take place, Jiwa fell on a number of occasions (Beck, 2000). However, at seven months old, a physical examination found that Jiwa "appeared perfectly healthy with normal audio and visual responses, normal heartbeat, good grip/overall strength, and normal blood count and chemistry" (Beck, 2000).

Orangutan infants would normally be expected to explore away from their mothers, but in very close proximity to them, from around six months old (Gordon Hunt, personal communication). However, Jiwa's first observed independent locomotion occurred at one year old (milestone four). This involved climbing one foot up the barwork, during which the keeper noted that Jiwa was "still quite slow and shaky" (30/10/2000). A few months later, at 15 months, Jiwa was still unable to walk quadrupedally (26/02/2001), although he started crawling across the floor at 21 months "with his hands holding each other, and pushing himself with his back legs" (13/07/2001). Elsewhere, he was described as crawling as if he was "climbing on a flat surface" (05/09/2001). Despite his difficulty with moving across the floor, as well as finding "smooth right-angle ledges" particularly challenging (08/11/2001), Jiwa's climbing skills improved considerably during this period (14/08/2001; 22/12/2001). At just over two years old, Jiwa was observed standing bipedally for the first time, using a rope to steady himself (17/11/2001). At around two and a half years old, keepers noted a concern with Jiwa not clinging properly ventro-ventrally and was either having to be supported by his mother's arm, or carried ventro-dorsally, on his mother's shoulders (18/04/2002). Approaching three years of age, Jiwa was described as being "confident and competent" walking quadrupedally outside, relatively competent walking quadrupedally inside, with his mobility and arm/leg strength having noticeably improved over the preceding few months (04/09/2002). Although Jiwa was at this point capable of walking "more normally" quadrupedally on the indoor floor, he was still often seen "moving along the floor as though he is swimming" (11/04/2003). This was partially attributed to the 'slippery' floor surface (i.e. smooth and flat) and was seen to improve when Jiwa was moving through deep litter, giving him more grip and therefore the opportunity to build strength in his legs (15/01/2004). A photo of Jiwa at around this age is shown in Figure 5.4.

Figure 5.4 *Jiwa at four years old.* Jiwa (right) with mother Mawar (left). Photo credit: Gregory Guida, 2004.

By five years old, Jiwa's quadrupedal walking and bipedal standing had noticeably improved, and "his overall movement continues to improve gradually" (16/10/2004). However, even today, Jiwa's style of locomotion is visibly distinctive compared to his peers (personal observation). For example, when walking quadrupedally, Jiwa's right shoulder is often hunched; he lands heavily on his limbs and walks with his arms out to the side (rather than in front) of his body, possibly for greater stability. In addition, Jiwa generally moves more slowly than his peers.

In summary, Jiwa is a particularly small orangutan, even for an unflanged male. His deciduous dental emergence generally took place later than expected, with some exceptions, and occurred within a three-month period, rather than the expected staggered dental emergence rates. Early in life, Jiwa was physically weak, with some difficulty locomoting, and his first independent locomotion took place six months later than expected, at one years old. Jiwa experienced considerably difficulty with quadrupedal walking in his early years, and, even now, continues to have a distinctive and slow locomotion style.

5.3.2 Developmental milestones

The expected developmental milestones for wild and captive orangutans (where available) are shown in Figure 5.5. Although Jiwa's first break in body contact with his mother was observed around the expected time of one to three months (milestone one), he reached the next two milestones somewhat later. Jiwa was not observed being carried by an individual other than his mother (milestone two) until seven months old (31/05/2000), four months later than other infants born at Jersey zoo (Beck, 2000). However, this would not have been possible for the first five months, as Jiwa and his mother were restricted to a separate part of the enclosure for observational purposes, away from the main group (Beck, 2000). As the initial instance of Jiwa breaking body contact was of Jiwa transitioning from his mother to his grandmother, it is not clear whether Jiwa was taken against his mother's will. However, Beck (2000) indicates that it would not have been surprising for Jiwa to have been given up voluntarily to his grandmother, due to the close familial relationship. Although Jiwa moved from his mother to the barwork in a stationary position (milestone three) at a later point than the expected range of two to four months, at 11 months old (25/09/2000), Jiwa was observed moving independently soon afterwards (30/10/2000), at an early point within the expected range of one to two years. However, Jiwa's first attempt at nestbuilding (milestone five) was considerably delayed beyond the expected one to two years.

Figure 5.5 *Jiwa's development of independence compared with expected rates.* Black dots indicate time Jiwa's milestones are first observed by keepers. Expected milestones (rounded to the nearest half-month) for wild orangutans are indicated by the upper pink bars and are based on van Noordwijk & van Schaik (2005) and van Noordwijk et al.(2009). Expected milestones for captive orangutans are indicated by the lower blue bares, and are based on Lethmate (1977a, 1977b), Miller & Nadler (1981), Miles (1990), Beck (2000), and Nakamachi (2004). Jiwa's data for the weaning milestone indicates the earliest possible data Jiwa could have been weaned (23/07/2004).

The first observed instance of Jiwa being more than 10 metres distance from his mother (milestone six) occurred when a conspecific stole Jiwa and carried him inside while his mother remained outside, presumed to be unaware of the incident (26/03/2002). Jiwa’s first intentional distancing from his mother may take place much later but is not detailed in the keeper records. The exact time of weaning (milestone seven) is unclear; it is likely to have taken place at some point between four years and nine months (when the keepers become doubtful of Jiwa’s mother’s milk production) (23/07/2004) and the point at which Jiwa’s younger brother was born, at five years seven months (24/05/2005). Not long after this, Jiwa initiated spending the night apart from his mother and seven-week-old brother (milestone eight), by refusing to enter the back den with them (11/07/2005). Approximately one year after Jiwa started sleeping alone, he was observed sleeping at the far end of the outside island, which is as far away as possible in the orangutan enclosure at Jersey Zoo (11/08/2006).

5.3.3 Sexual development

Jiwa’s first recorded mating attempt occurred at just over five and a half years old and was with his mother (21/05/2005). Some secondary sexual characteristics started to emerge at just over eight years old, with a small ‘beard’ (03/12/2007). Soon afterwards, keepers started to encourage him to regularly sleep alone as “he is now maturing” (17/03/2008). The next notable change occurred at just over fourteen years old, after a nine-year-old male conspecific, Jaya (born 13/05/04), left the zoo (14/11/2013). Six weeks later, the keepers observed that “Jiwa’s locomotion and co-ordination seem to have improved markedly; he has shown increased facial development: widening of his face, with cheek pads emerging, and his libido (has) rapidly developed” (25/12/2013). Soon after this, Jiwa’s frequent - and sometimes physically rough - sexual attention towards conspecifics became problematic, and he was put on a one-off, six-week course of cyproterone acetate to reduce testosterone levels and manage his libido (04/02/2014). Five months later, Jiwa was castrated (24/07/2014).

It is not until over four years later, at the age of eighteen, that Jiwa's repertoire of vocalisations changed to emulate typical mating calls, with one display-like instance of "a deep guttural vocalisation building up higher in short bursts", and a few months later "almost producing a long call" (17/05/2018; 01/10/2018). Jiwa's long call seemed to mature over the next year and was "almost a proper call" by 20 years old (18/11/2019). However, despite some development of secondary sexual characteristics, Jiwa was physically very different from his flanged father, Dagu, and had not yet developed full cheek pads or a throat sac (Figure 5.6).

Figure 5.6 *Cheek pad development.* Jiwa aged 21 (left) and his dominant male father Dagu (right). Photo credit: Jersey Zoo.

5.3.4 Cognitive abilities

Jiwa's cognitive differences were apparent from a young age. At nine months old, keepers noted that Jiwa "shows little or no obvious behavioural development. Appears to only react to objects that are within 6 inches of his face, though he appears fine in every other respect" (08/07/2000). 52 days later, Jiwa began interacting with the keeper (29/08/2000) and with other objects, such as a sunflower leaf and stem (11/09/2000), and a piece of bamboo (15/09/2000). However, at one year old, Jiwa was described as being "to all intents and purposes a 3-4 month old infant" (Beck, 2000). When introduced to glass at nearly two and a half years old, Jiwa "(looks) a little confused when touching the glass, trying to work out why he could not touch (the) keeper behind it" (10/02/2002). However, the keeper noted here that Jiwa responded well to his own name at this stage, as well as visual cues. Around this time, Jiwa was observed to be "increasingly playful and confident, especially when not mixed with other orangs" (03/04/2002). Approaching three years old, Jiwa was recognising familiar people, and showing interest and curiosity toward unfamiliar people, demonstrating that he could tell them apart (10/07/2002). After Jiwa's younger brother was born, the keepers noted difficulty with Jiwa understanding routines without the direction of his mother: "Jiwa does not appreciate the necessity to move to different parts of the enclosure during routines" (25/05/2005). However, Jiwa appeared to settle into a routine fairly easily after this (18/06/2005).

Jiwa displayed some possible nest-building behaviour (milestone five) with wood wool and a paper bag in the nest basket at nearly three and a half years old (17/11/2002), well beyond the expected one to two years (Figure 5.5). The next mention of nesting behaviour was five years later, at nearly eight and a half years old although, from the casual tone of the keeper's note ("Jiwa…made his nest in there"), this does not appear to be the first time Jiwa was seen nest-building (21/02/2008). By five years old, tool use is not uncommon in orangutans, and is seen at a younger age in both captivity and in the wild (Galdikas, 1982; Miles, 1990; Nakamichi, 2004). Although Jiwa has been seen by keepers to pick up extractive tools dropped by others, he has never been observed to use a tool to dip for food rewards (Gordon Hunt, personal communication). However, there were some instances where Jiwa used simple tools, i.e. knocking down a thermometer using a piece of bamboo at 20 years old (07/04/2020). Later in the same year, it was noted that "Jiwa (was) very alert and interactive with (the) Keeper this morning, more so than Keeper… has ever seen before, his movements were quick, he made eye contact several times" (11/10/2020).

5.3.5 Cognitive enrichment

During the nine experimental sessions, Jiwa did not use a tool to access the food reward, whether the apparatus was hanging outside the enclosure, being held by the researcher outside the enclosure, or loose inside the enclosure. However, Jiwa did access the food reward by withdrawing sticks that were placed inside the tube by the researcher. In addition, over the four sessions which involved this activity, Jiwa was consistently successful and showed a marked improvement over time in the number of sticks he withdrew per session (Figure 5.7). This is despite several occasions when Jiwa because frustrated, evidenced by repeated 'distress' vocalisations (Gordon Hunt, personal communication).

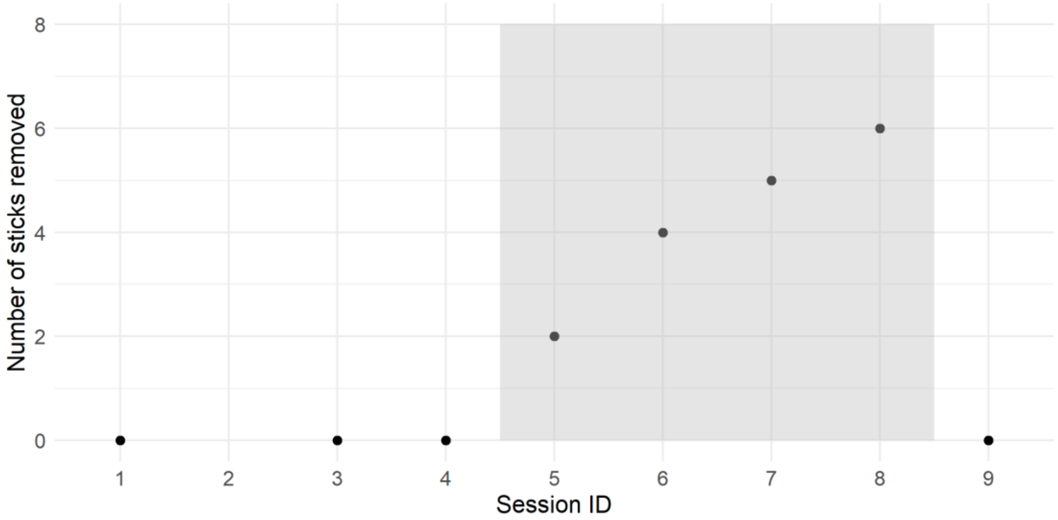


Figure 5.7 *Number of stick removals per session.* Highlighted area indicates sessions 5-8, during which Jiwa was required to withdraw a stick already placed inside the probe feeder. Note: Session 2 did not involve sticks.

5.4 Discussion

5.4.1 Study limitations

There are several limitations with the fact that nearly all information regarding Jiwa was obtained from keeper records and a single report made when Jiwa was one years old. The first limitation is that the keeper records compile observations from several different keepers, who may have interpreted Jiwa's behaviour in different ways over the two-decade time period. The second limitation is that keepers are not able to continually observe the animals in their care, so first observations of a particular behaviour may not reflect the first occurrence of that behaviour. Lastly, as the study was carried out in hindsight, not all developmental milestones have been recorded for Jiwa. For example, although Jiwa's initial nest-building behaviour was recorded, there is no further mention of his full nest-building behaviour until years later. Despite these limitations, valuable insights can be drawn about Jiwa's development and ability.

5.4.2 Notable differences in development

Jiwa reached many developmental milestones at an expected rate: the first break in body contact with his mother, first independent locomotion, first instance of being more than 10 metres away from his mother, and the first night spent apart from his mother. Although some of these milestones were not initiated by Jiwa himself, e.g. being taken by a conspecific and moved 10 metres away from his mother, others were. For example, Jiwa himself initiated spending the night apart from his mother for the first time when his younger brother was seven weeks old. There are other instances where Jiwa exercised agency and independence, for example spending the night at the far end of the outside enclosure when he was approaching seven years old.

However, there were also several key differences between Jiwa and other orangutans, particularly in his cognitive development, which appears to have been noticeably slow. Jiwa's first observed attempt at nest building does not take place until nearly three and a half years old, considerably longer than the expected age of one to two years for both wild and captive Sumatran orangutans (Lethmate, 1977a; van Noordwijk et al., 2009). It was not possible to determine Jiwa's nest-building ability from the keeper records. Nest building in the wild is more cognitively demanding than in captivity (van Casteren et al., 2012), but even in captive environments great apes can employ varying levels of complexity (Videan, 2006). However, it is likely that Jiwa and his peers would not have had the opportunity to learn more complex nest-building techniques, such as bending and weaving (Videan, 2006), as the main nesting material provided to the orangutans was wood wool. As well as the delay in nest-building behaviours, Jiwa had not yet learned how to use extractive tools, unlike his peers. However, he was observed using a simple form of tool, i.e. knocking down a thermometer using a bamboo stick, at around 20 years old.

Jiwa is physically atypical, with an unusually low weight, generally late deciduous dental eruptions, some difficulty with locomotion, and only ‘half-developed’ secondary sexual characteristics. Thompson et al. (2012) found that male orangutans (*Pongo spp.*) with noticeable changes in their secondary sexual characteristics before 14 years old had higher levels of testosterone as adults than those who completed their development from 14 onwards. Although Jiwa's testosterone levels are not specified in the keeper records, Jiwa comfortably fits into the latter category, as his facial structure widened and cheek pads started to emerge a couple of months after his 14th birthday. In addition, within the following year, Jiwa received a six-week course of a testosterone-lowering medication and was subsequently castrated. This is likely to be a contributing factor to Jiwa having not yet developed full flanges at 24 years old, in addition to the presence of his flanged father in the adjacent enclosure. However, although secondary sexual characteristics are also thought to be delayed by the presence of a dominant male (Maggioncalda, 1995), most males in captivity usually do develop these characteristics, even in the presence of another flanged male (Pradhan et al., 2012). Therefore, it seems more likely in this case that the medical interventions had a greater restrictive effect on the development of Jiwa’s secondary sexual characteristics than the presence of his father.

The physical and cognitive differences seen in Jiwa are reminiscent of a 1982 case study of two Bornean orangutan twins, with the second born infant suspected to have perinatal hypoxia (oxygen deficiency during birth) (Savage & Snowdon, 1982). Both orangutans were tested at around six years of age, with the second born orangutan exhibiting physical and cognitive differences to her brother. Physical differences included less frequent brachiation and more clumsy and uncoordinated locomotion, with an inability to perform fine motor movements (Savage & Snowdon, 1982). Cognitive differences included deficiencies in learning and short-term memory, and an inability to use tools (Savage & Snowdon, 1982). Although Jiwa was not assessed using the same battery of tests as in this study, it is possible that he was similarly deprived of oxygen, either during birth, or due to his mother's unusual face- and lip-sucking behaviour immediately afterwards.

5.4.3 Implications for wellbeing

Regarding the Five Domains Model, it seems likely that Jiwa's nutritional and environmental needs are largely unaffected by his condition. The keeper records do not mention difficulties with Jiwa's food or water intake. The only environmental constraint which may have affected Jiwa and his mother was during his first five months of life, when the mother-infant dyad was kept in the back dens for close observation. Although this may not have been ideal, it was a justifiable - and arguably necessary - intervention due to the concerns regarding Jiwa's survival and wellbeing at the start of his life. As an adult, Jiwa's wellbeing is affected in the 'health' domain, with a particularly low body weight, low levels of strength, and functional impairments in locomotion. Although Jiwa is able to access the same areas in the enclosure as the other orangutans, it would not be surprising if locomotion in general was more physically demanding for him than for his peers. There may also be more complex locomotion behaviours that Jiwa has not been able to acquire. It would be interesting to conduct a study on activity budgets of Jiwa and his peers, to see whether Jiwa spends more time resting than the other orangutans (e.g. Beamish and O'Riain, 2014; Turner et al., 2014) to compensate for his physical impairments.

It is somewhat difficult to determine how Jiwa's differences may affect his wellbeing in the fourth domain, which relates to the exercise of agency. Although Jiwa has access to the same enrichment programme as the other orangutans at Jersey Zoo, his impaired cognitive ability means that is not able to use some forms of enrichment which are accessible to his peers, e.g. extractive foraging. This may be detrimental to his ability to express agency and exercise control over the environment. Regarding social interactions, Jiwa generally appears to have a positive relationship with his peers (Gordon Hunt, personal communication). Although Jiwa has had the opportunity to engage in sexual activity, which is a form of agency, his attention towards his peers was so frequent - and sometimes rough - that it was deemed problematic. To resolve this situation, Jiwa was given a libedo-reducing medication. Although Jiwa's sexual agency was curbed by this medication, there was a trade-off involved, as this intervention arguably improved the wellbeing of Jiwa's peers, who were sometimes distressed by his mating attempts.

It is not possible to know the extent to which Jiwa's mental state was affected by the limitations in the physical/functional domains of welfare described above. However, there are several areas which have the potential to result in a negative affective state. For example, it is possible that Jiwa's physical difficulties lead at times to pain, weakness, or physical exhaustion. Regarding limitations to his agency, Jiwa may experience frustration or helplessness, e.g. when faced with cognitive enrichment he is unable to use. It is possible that he has also experienced sexual frustration, although this is likely to have been tempered by his medication. However, in general, Jiwa does not appear to be a particularly anxious individual, and seems relatively secure, with positive social relationships and the opportunity to play with younger conspecifics (Gordon Hunt, personal communication). Therefore, despite the potential impairments to Jiwa's wellbeing, it seems that he is still able to live a fulfilling and well-rounded life.

5.4.4 Benefits of enrichment

Although Jiwa did not use tools to obtain the food reward within the assessment period, he did show a marked improvement in the number of sticks he withdrew from the probe feeder over the four sessions that involved this activity. This improvement occurred despite the frustration Jiwa appeared to exhibit on several occasions. The increased frequency in stick withdrawal not only indicates continuing engagement in the activity, but also suggests that Jiwa learned how to use this version of the enrichment, evidenced by his increase success at the task over time. These results suggest that the activity was successfully tailored to Jiwa's abilities, which is an important requirement when providing captive animals with cognitive enrichment (Clark, 2011; Meehan & Mench, 2007). Jiwa's participation in this activity is connected with a number of areas of wellbeing, but the most relevant is the opportunity to express agency. By exercising control over his environment, despite the challenge and initial stress involved, Jiwa managed to obtain a food reward. Reward is linked to a number of benefits, including enhanced learning, positive affect, and motivation (Berridge & Robinson, 2003). In turn, agency, effective problem-solving, self-motivation, and positive affect are all aspects of psychological resilience, or the ability to 'bounce back' from stress (Hornor, 2017; Isen, 2001; Mandleco & Peery, 2000; Rutter, 2012). Therefore, ongoing participation in cognitive enrichment of this kind may have some very real, long-term benefits for Jiwa's welfare. In future, this apparatus could be adapted by building a permanent tube into the side of Jiwa's enclosure, where keepers can place food rewards and sticks in advance, so that Jiwa can use the enrichment by himself without being supervised or encouraged.

5.4.5 Implications for animal management

Jiwa's differences raise a number of considerations for animal management. At the beginning of Jiwa's life, his behavioural differences and concerns about his mother's maternal behaviour raised challenges for the zoo. These included additional keeper time, general psychological stress that may have been experienced by the keepers due to anxiety about Jiwa's welfare (e.g. Jensvold, 2022; Marino, 2023), and the financial impact of additional medical requirements relating to Jiwa's care, i.e. the course of medication to limit his libido. Even now, there are some challenges posed by Jiwa's needs, for example the fact that he is unable to participate in extractive foraging enrichment, which is regularly provided to the orangutans at Jersey Zoo (Gordon Hunt, personal communication). Although this study shows how cognitive enrichment can be tailored to meet Jiwa's needs, it should be noted that this process took two and a half hours over a period of five weeks; as keeper time is limited, this may not always be logistically possible to achieve. However, despite these challenges, Jiwa's conditions have been successfully managed by the zoo, to the extent that Jiwa has managed to develop independence, functional social relationships, and is strong and skilled enough to freely move around the enclosure. As well as benefiting Jiwa's wellbeing, this is logistically beneficial for the zoo, as it reduces the level of resources required to care for Jiwa.

5.5 Conclusion

Jiwa is an important reminder of the individuality present in all animals, and the importance of considering diversity in life experience, development, cognitive and physical abilities, and personality. Understanding how to meet the welfare requirements of individuals like Jiwa is a fundamental need for zoos and other caretakers of animals in captivity. Not only can this directly impact the quality of life of atypical individuals, but it can also help to avoid or reduce the potential financial, logistical, and time pressures associated with their care. In addition, understanding the requirements of divergent individuals is essential for contexts where animals may be returned to the wild. For example, orangutan rehabilitation centres must be able to assess whether an individual’s welfare needs will be met through independent life in the wild, or if they are likely to have a better quality of life remaining in captivity. It was surprising to learn that Jiwa’s life history had not been academically reviewed until this point, considering his unusual development and behaviour. It is hoped that this case study will not only help other animal caretakers know what to expect during the development of a divergent orangutan, but that it also provides an insight into the potential areas of wellbeing which might be constrained by these differences, requiring additional care and resources. This is exemplified by the fact that it took several hours, over a five-week period, to identify an appropriate difficulty level for Jiwa’s cognitive enrichment apparatus. However, the increase in engagement and ability demonstrated by Jiwa indicates that tailoring enrichment can contribute towards meeting welfare needs within the ‘expression of agency’ domain. Although animal caretakers may not have the capacity to fine-tune enrichment in this way, developing cognitive enrichment with adaptable difficulty levels could be a useful future avenue for research. It would be beneficial to carry out a follow-up study, to see whether Jiwa can still use this form of enrichment.

Jiwa’s unique array of physical and cognitive differences distinguish his life experiences from those of his peers. Although some of these differences may negatively impact his wellbeing, the vast majority of Jiwa’s welfare needs are met despite these barriers. In addition, the extra time and resources required to take care of Jiwa have gradually decreased as Jiwa has grown older and developed independence. Although every case is likely to be unique, it is hoped that Jiwa can be the start of a database on physically and neurologically diverse individuals. Such a database could be expanded by future researchers, to enhance knowledge in this area and help caretakers know what to expect, so that individuals like Jiwa can live a rewarding and fulfilling life.

CHAPTER 6

GENERAL DISCUSSION

6.1 Summary of thesis aims and main findings

As established in Chapter One, the aims of this thesis were to identify potential resilience interventions for captive great apes, and to determine how stress and resilience may be influenced by individual and species differences. These aims were initially addressed by comprehensively reviewing the human and non-human literature to identify appropriate forms of resilience interventions (Chapter Two). Based on these findings, a species-appropriate experimental intervention was developed and trialled with captive orangutans and gorillas at two UK zoos (Chapter Three). In addition, investigations were carried out into the effects of individual and species differences on wellbeing and exposure to stress in great apes. These studies explored the effect of human presence following extended periods of absence (Chapter Four) and the extent to which individual variation may influence wellbeing in captivity and inform the development of tailored enrichment apparatuses (Chapter Five).

The literature review on resilience interventions (Chapter Two) established that mild and manageable interventions are the methods least likely to be detrimental to resilience, and most likely to promote resilience in the context of orangutan rehabilitation centres and other captive environments. Potential interventions include interventions such as brief separations from conspecifics, exercise programmes, increasing environmental complexity, providing challenging cognitive enrichment at an appropriate skill level, and indirect exposure to difficult, but manageable, social interactions. Based on these findings, a novel experimental resilience intervention, which involved challenging cognitive enrichment designed to promote persistence, was trialled in orangutans and gorillas at two UK zoos (Chapter Three). Although no clear intervention effects were identified, the results showed a trend in both species towards the intervention group having greater numbers of successful interactions with the research apparatus compared with the control group, as well as a decreased mean attempt time. There was also a trend towards the intervention gorillas having greater engagement in the apparatus than the control group. However, a trend towards the reverse was seen in orangutans.

The study on Covid-19 lockdown restrictions lifting (Chapter Four) found that the zoo reopening increased the probability of stress behaviours in orangutans, alongside increased object-holding, affiliative behaviours, and head covering. Orangutans also displayed less hunched and closed postures after lockdown restrictions had lifted. In contrast, stress behaviours were unaffected by the zoo reopening in gorillas, who demonstrated more interaction with enrichment, and less hunched posture and time spent at the top of the enclosure. The initial reopening of the zoo, when the indoor gorilla viewing area was still closed to the public, had separate effects on several variables, including reduced closed posture and proximity to the visitor window, and increased object-holding, which reversed once all lockdown restrictions had been lifted. In addition, once the zoo had reopened, there were complex and sometimes contradictory effects of visitors, as measured by total zoo visitors, visitor noise, and visitor presence at the enclosure.

Lastly, the case study of Jiwa, an atypical Sumatran orangutan (Chapter Five) identified key areas where individual physical and cognitive differences could impact wellbeing, particularly regarding Jiwa’s physical health and his ability to express agency. In addition, after an enrichment apparatus was tailored to an appropriate skill level for Jiwa, he demonstrated a marked improvement in successfully interacting with the apparatus over a four-week period.

This chapter will discuss the implications of these findings in the context of orangutan rehabilitation centres and other captive environments. Firstly, suggestions will be given about how to develop and improve the experimental resilience intervention introduced in Chapter Three. After this, the application of alternative forms of intervention will be discussed, including suggestions for additional research areas which may have relevance. In addition, methods of accommodating individual variation in resilience interventions will be considered. In section 6.3, the implications of the lockdown study (Chapter Four) will be discussed, including an evaluation of the novel method of categorising posture in great apes. The remainder of the chapter will outline some of the general thesis limitations, provide suggestions for future research, and will summarise the key contributions of this research.

6.2 Implications for orangutans in rehabilitation

This thesis has addressed RQ1 by identifying several starting points which can be used to develop resilience interventions for captive great apes. Precaution is recommended in the development of interventions, starting with the mildest and most manageable forms of stress. Potential forms of research interventions include: separation stress, social stress, exercise regimes, environmental complexity, and challenging forms of cognitive enrichment.

6.2.1 Further development of experimental intervention

The novel resilience intervention introduced in Chapter Three was designed to promote resilience by providing great apes with cognitive enrichment which gradually increased in difficulty. The purpose of this was to address RQ2 in determining whether experimental interventions can alter an aspect of resilience (i.e. persistence) in captive great apes. Although there was no clear effect of the intervention, the trends towards increased success and skill at obtaining the food reward in the intervention group indicate some potential for this technique to be developed further and trialled with a greater number of study subjects. It should be noted that zoo-held great apes and orangutans in rehabilitation may differ in their response to resilience interventions. For example, wild-born great apes in rehabilitation centre enclosures may be relatively under-stimulated compared with captive-born great apes in zoos. Therefore, they may demonstrate greater enthusiasm in interacting with enrichment and problem-solving. However, conversely, great apes in rehabilitation centres are likely to have experienced prior trauma, and therefore may be more sensitive to stress-based resilience interventions. This is unchartered territory, as nearly all of the resilience interventions described in Chapter Two involved humans, rodents, or primates in laboratory settings (e.g. Parker et al., 2004; Feng et al., 2011). Because the subjects in the experimental resilience intervention (Chapter Three) were zoo-held great apes, it is not certain how generalisable these results are to orangutans in rehabilitation centres.

There was a trend towards the orangutan intervention group engaging less with the apparatus than the control group. This may indicate that the easier configurations of the apparatus, in the early weeks of the experiment, were not challenging enough keep the orangutans engaged. The orangutan apparatus should be adapted to resolve this issue before replicating the study or applying the resilience intervention elsewhere. One difference between the orangutan and gorilla apparatuses is that the orangutans could directly see the food reward inside the apparatus, and the cords from which it was suspended, whereas the gorillas had limited visibility of the food and barriers inside the apparatus. Therefore, it was possible that seeing the mechanism of the apparatus made the task too easy for the orangutans and induced boredom. However, this would contradict the findings of another study on captive great apes, which found that tasks with visual feedback (i.e. the mechanism of the puzzle could be solved) reduced latency to solving easier tasks, and increased success rate in solving more difficult tasks, compared with puzzles that had visually obstructed mechanisms (Völter & Call, 2012).

If visibility of the apparatus mechanism is not the issue, it is possible that the actions required to operate the orangutan apparatus were less engaging or challenging than those required for the gorilla apparatus. Whereas the orangutans were required to make the same basic action throughout the study period, i.e. insert a stick through the wire mesh and into the tube, the gorillas had to physically manipulate the apparatus to find the most efficient point of entry from which to access the food reward. One way of varying the actions required to solve the orangutan apparatus would be by incorporating additional actions each week, requiring planning to obtain the food reward. Orangutans and bonobos have been observed to demonstrate sequential, step-by-step planning, for example in a study which involved a paddle-box apparatus that necessitated an appropriate sequence of actions to obtain a reward (Tecwyn, Thorpe, & Chappell, 2013). As well as maintaining engagement and being able to alter difficulty levels, incorporating sequences of actions would have an additional benefit as a resilience intervention, since planning skills are another aspect of resilience (Hornor, 2017; Rutter, 2012).

The orangutan resilience intervention could be improved further by changing the way success is measured. For example, the quantity of food removed from the apparatus would arguably be a better measure of success than the rate of successful ‘dips’; as, even when the stick was inside the apparatus, there was no guarantee that the food reward had been extracted. However, it was not possible to measure this for the orangutans at Twycross Zoo, as honey was used as a food reward and dripped from the end of the tube throughout the session. In future iterations of the orangutan intervention, a more solid form of food (e.g. peanut butter) could be weighed before and after the session to measure success.

Despite these limitations, most subjects of both species were very engaged with the enrichment, and the apparatuses were subsequently incorporated by both zoos into the enrichment programme. Although both apparatuses were easy to install, the gorilla apparatus is time-consuming to reconfigure, as the bolts must first be removed. While suitable in its current form as cognitive enrichment, this apparatus would need to be redesigned with a simpler mechanism for regular use as a resilience intervention, due to time constraints at zoos and rehabilitation centres.

6.2.2 Alternative forms of intervention

Alongside developing the resilience intervention introduced in Chapter Three, it would also be beneficial to explore the other forms of intervention outlined in Chapter Two. It is important to establish the opportunities for exercise currently available to orangutans in rehabilitation. For example, which age groups have access to forest school? Do all forest school outings involve physical exercise? What is the frequency and duration of exercise opportunities? It is important here to consider how changes in environmental conditions can affect resilience. For example, orangutans who are too old for forest school, but who have not yet been transferred to a pre-release island, may not have sufficient opportunities for exercise. The literature indicates that a negative reversal in environmental conditions can be detrimental to resilience in some species (Bateson & Matheson, 2007; Bolhuis et al., 2006; Douglas et al., 2012). Therefore, it would be beneficial to determine whether orangutans are similarly affected by changes in environmental conditions. The first step is to establish how common it is for orangutans to move from more to less enriched conditions, and to measure the duration of time spent in each condition. A subsequent study could compare the resilience (and post-release success rate) of orangutans who only experience a positive, more enriched, change in environmental conditions to orangutans whose conditions fluctuate prior to release. One area of research which has not been addressed by this thesis is the opportunity to incorporate computer technology into resilience interventions. Although this would not be suitable for great apes which may be released to the wild, due to the risk of humanisation, computerised tasks may be an effective and fast way to provide an appropriate level of challenge by tailoring interventions to individual skill levels (Calapai, Cabrera-Moreno, Moser, & Jeschke, 2022; Fagot & Paleressompoulle, 2009).

Because the systematic review in Chapter Two was limited by its search terms, there is scope for investigating areas of study where the term ‘resilience’ might not be used. For example, there is a large body of existing literature on play behaviour in humans and other great apes, which is relevant to several aspects of resilience, including physical exercise, problem-solving, inhibitory control, positive affect, and social bonds (see Pellegrini and Smith, 2005). Another area of potential interest is the well-established field of sports science. For example, in a recent study of 86 sport performers, Mcloughlin and colleagues identified a U-shaped relationship between exposure to lifetime stressors and cardiovascular adaption to social stress (Mcloughlin et al., 2022), which aligns with the findings on cumulative lifetime adversity reported in Chapter Two (Seery et al., 2013; Seery et al., 2010). It is extremely important to determine whether a similar U-shaped relationship between prior stress and current resilience exists in orangutans, as all orangutans in rehabilitation will have experienced prior trauma. Therefore, it could be risky to subsequently apply stress-based resilience interventions. However, as orangutans are almost certain to encounter stressors in the wild, it is perhaps better to expose them to mild stressors in a controlled environment, where the effects can be monitored and intervened with if necessary. Establishing a relationship between major stressors and resilience in great apes may be easier to carry out in a zoo context, where life histories are usually known. Examples of stressful events in the zoo environment could include individual stress, like moving to a new zoo or a mother losing her infant; or group stress, for example fluctuating lockdown restrictions during Covid-19 (See Chapter Four) or surviving an enclosure fire (e.g. Chester Zoo, 2018).

6.2.3 Individual variation

It is clear from the findings presented in Chapters Two to Five that individual factors like age, personality, and dominance should be considered when developing resilience interventions. Some individuals are physically or neurologically divergent to the extent that their needs may be difficult to meet in captivity, and these individuals may not have the capacity to be released into the wild. Physical disabilities, e.g. blindness resulting from being shot in the eyes, are relatively common in rehabilitation centres and one reason for individuals needing lifelong care (e.g. Neme, 2016; Gunawan, 2019). The case study of Jiwa in Chapter Five demonstrated that, although most of Jiwa's needs were being met under the Five Domains Model of animal welfare (Mellor et al., 2020), his wellbeing may be impacted in the areas of physical health and mental wellbeing. These findings address RQ4 in indicating that individual differences can affect the wellbeing of great apes and their exposure to stressors. In addition, Jiwa was unable to participate in the resilience intervention (Chapter Three) alongside his peers, because he had not been seen to use extractive tools.

Taking individuals like Jiwa into consideration, it is difficult to design appropriate resilience interventions that can be adapted to accommodate such a range of individual variation in skills and capabilities. Chapter Five described how the enrichment apparatus was gradually adapted until Jiwa was successful at obtaining the food reward. However, it is not immediately apparent how this form of enrichment (i.e. withdrawing sticks from tubes) could be adapted into an effective resilience intervention aspect (i.e. gradual increase in difficulty, or manageable frustration). In addition, it was time consuming to develop an appropriate difficulty level for Jiwa, which may not be logistically possible in a rehabilitation setting. Therefore, where there are cognitive impairments of this kind, other forms of resilience intervention might be more appropriate and easier to facilitate. Alternative methods might include exercise regimes, environmental enrichment, or, where there is a prohibitive physical condition, separation stress or social stress. These forms of intervention may also be useful for individuals who choose not to participate in cognitive enrichment (despite having the capacity to do so), which was the case for two orangutans and three gorillas in the resilience intervention study in Chapter Three.

6.3 Visitor presence following lockdown

The observational study in Chapter Four addresses RQ3 and RQ4 in demonstrating several key species differences in the effects of lockdown restrictions lifting on orangutan and gorilla behaviour. These differences align with the species-specific effects reported in many other lockdown studies (Masman et al., 2022; Williams et al., 2021a, 2021b, 2022). Sections 6.3.1 to 6.3.3 will discuss the key findings of Chapter Four within the context of this thesis and the wider literature.

6.3.1 Stress behaviours

Although orangutans had a higher probability of stress behaviours after lockdown, this experience did not necessarily have a long-term detrimental impact. As the ‘post-lockdown’ data was collected within seven months of lockdown ending, and no long-term follow-up study has been conducted, it is not clear how long the effects persisted. This is also a limitation of the resilience intervention experiment (Chapter Three) and the Jiwa case study (Chapter Five), as it was not established whether any benefits were retained over time. It is possible that the repeated lockdowns, though disruptive, had an inoculating effect and will help to protect against future stress. However, as some form of Covid-19 lockdown was probably experienced by all captive great apes around the world, there is no control group available for comparison. As more lockdown studies are published, it may be possible in future to conduct a meta-analysis on the effects of lockdown in countries with different degrees of lockdown restrictions, to see whether the length or severity of restrictions affected great ape stress and future levels of resilience. It would also have been interesting to measure stress behaviours over time, to see whether there was any variation within the post-lockdown time period, for example a decrease in stress over time as orangutans gradually adapted to lockdown restrictions lifting. However, this would have been difficult to interpret in this study due to the interim lockdown (January to April 2021), which took place within the post-lockdown data collection period.

The fact that only orangutans exhibited increased stress after lockdown raises an important point about species differences in stress responses. Just as the concept of resilience may be understood differently in different human cultures (Fletcher & Sarkar, 2013), the way resilience is exhibited is likely to vary between different species. Although different species may vary in their baseline levels of resilience in response to the same stressor, an alternative explanation is that there were species-specific differences in external signs of stress, even if both species were internally affected in the same way. This is an important distinction, but would be difficult to determine outside a controlled experimental setting. One option would be to use physiological parameters to measure responses to stressful situations, an approach frequently used in sports science research. For example, in a study of footballers, Brimmel et al. (2019) found that cardiovascular response to pressure can predict performance, with higher cardiac outputs and lower peripheral resistance reactivity associated with improved performance. Physiological measures of stress could be used, in parallel with behavioural observations, in a multi-species study of stress in great apes, to determine the degree to which different species are likely to externalise signs of stress.

6.3.2 Visitor measures

Another key finding reported in Chapter Four was that there was not a clear link between the effects of lockdown restrictions lifting and the effects of other measures of visitor presence. For example, orangutan stress behaviours were higher after lockdown, but lower when visitors were present. In contrast, although gorilla stress behaviours were unaffected by the zoo reopening, their stress behaviours increased with loud visitor noise. Similarly, orangutans were seven times more likely to have their head covered when the zoo reopened, but nearly all subsequent measure of visitor presence reduced the probability of head-covering. Differences in the effect of visitors, depending on how visitor presence is measured, have also been observed in other zoo studies (Choo et al., 2011; Hashmi & Sullivan, 2020). Due to the complexity of the results of this study, it is important not to assume that the effects of the zoo reopening are solely due to visitor presence; it is likely that there are other factors at play.

6.3.3 Posture scales

The lockdown study in Chapter Four introduced a new method to categorise ‘hunched’ and ‘closed’ posture, based on a simple Likert scale. Although body posture has previously been associated with stress behaviours in humans (e.g. Riskind and Gotay, 1982; Nair et al., 2015) and great apes (e.g. Commitante, 2005), neither hunched nor closed posture was associated with changes in stress resulting from lockdown restrictions lifting. In addition, the two variables were not affected in the same way by lockdown stages. For example, during the 'semi-lockdown' period, gorillas displayed more hunched, but less closed, postures; a pattern which reverted once the zoo had fully reopened. Although hunched and closed postures were affected by lockdown restrictions lifting, and some forms of visitor presence, it is very unclear whether the postures are associated with any other behaviours. Therefore, it would be interesting to investigate these measures of posture further, perhaps seeing whether certain contextual behaviours are associated with specific postures.

6.4 Thesis limitations

6.4.1 Limitations related to Covid-19

There are number of limitations to the research presented in this thesis. The clearest limitation is the constraints of the geographic location of this research, which was heavily influenced by Covid-19 restrictions. It would have been more informative to carry out this research on orangutans in rehabilitation centres. As most zoo-housed great apes were born in captivity, and are likely to spend their whole life in zoos, their previous experiences of stress - and potential for future encounters with stress - are very different to those of wild-born orangutans in rehabilitation. Therefore, there are some limitations with generalising the results of this research. However, this thesis has established a foundational understanding of resilience and resilience interventions, which can later be expanded upon and applied in the context of rehabilitation centres. In addition, as the research was carried out with zoo-held great apes, sometimes spanning more than one zoo, some of the results presented here are generalisable within a zoo context.

The second limitation relating to the zoo-based nature of this research was the number of subjects available. Due to the delays and uncertainty caused by Covid-19, there was only enough time to conduct research at two different UK zoos. While there are several hundred orangutans at some rehabilitation centres, zoos in the UK have relatively small numbers of great apes. Because the resilience intervention in Chapter Three divided subjects into control and intervention groups, study numbers were relatively small and difficult to interpret statistically. However, the initial results of the intervention are encouraging, and indicate that a longer-term study with a greater number of subjects, particularly within a rehabilitation context, may yield firmer results.

The final limitation from Covid-19 relates to the observational study on the effect of lockdown restrictions lifting (Chapter Four). Ideally, an observational period prior to the first lockdown would have been incorporated into the study design, so that a representation of the initial effects of lockdown on stress (and other) behaviours could be established. However, the first lockdown took place approximately six months into the project, when the aims and objectives of the thesis were still being conceptualised. Even if this had not been the case, it would have been nearly impossible to anticipate the lockdowns with enough notice to obtain the necessary permissions and approval for the research to take place. In addition, the uncertainty and difficulties faced by zoos, particularly at the beginning of the pandemic, meant that research was put on hold in many cases, partly due to concerns about staff availability. However, despite these limitations, the research period of the lockdown study did span three key conditions which represented the varying stages of lockdown restrictions lifting. Therefore, meaningful conclusions can still be drawn about the effect of these periods on captive great ape behaviour.

6.4.2 General limitations

The systematic literature review (Chapter Two) was limited by the range of taxonomic groups commonly involved in resilience research, with rodents being the most common subjects. However, there are issues with generalising the potential effects of interventions on rats and mice to great apes. For example, interventions involving social stress are likely to affect animals with a tight, hierarchical social structure differently to orangutans, who live in dispersed societies in the wild and only aggregate temporarily (Galdikas, 1985; Malone et al., 2012; Roth et al., 2020). In addition, as the human resilience interventions usually involved 'talking therapies', these methods could not be directly translated for use in non-human captive great apes. The search terms used in the systematic literature review may also have excluded relevant aspects of resilience, or synonyms for stress and resilience. Because the research reviewed was so broad, an in-depth discussion of each specific aspect of resilience was not possible within the scope of this study. However, this review achieved its aim in establishing a foundation and essential starting point from which further research can be carried out.

Lastly, the case study of Jiwa (Chapter Five) is limited by the fact only one individual was addressed by this research. Considering the extremely individual nature of Jiwa's conditions, it would have been more informative to conduct case studies on several atypical individuals, so that more generalisable conclusions could have been drawn. However, due to the small numbers of these individuals, this would have been logistically difficult to achieve. Another limitation of this study is that it was primarily based on subjective keeper records and so there may be some issues with consistency between keepers and thoroughness of the keeper records, which limit the conclusions that can be drawn from this research. However, without establishing a long-term study at the start of Jiwa's life, the limitations of retrospectively relying on keeper records are inevitable. Such a long-term study is well beyond the time constraints of a single thesis; and, regardless, may not always be possible as cognitive or physical differences may not be observable from birth.

6.5 Contributions and recommendations for future research

This thesis makes several key contributions, not only to our knowledge of fundamental concepts in great ape resilience interventions but also to orangutan rehabilitation centres, zoos, and the wellbeing of great apes in captivity. Firstly, the systematic review in Chapter Two addresses a large gap in academic knowledge about how resilience can be improved in ways that could be applied to non-human great apes. Because this area has been relatively unexplored to date, the findings of this thesis can act as a foundation for researchers to investigate resilience interventions further, and to develop a better understanding of the mechanisms underlying changes in resilience levels over time. In terms of practical benefits, the most significant potential benefit of this research is to orangutan rehabilitation centres, who must make decisions on when and whether to released captured orangutans back into the wild. These decisions carry a great burden, as survival rates of released orangutans are currently low, and having guidance in techniques to psychologically prepare orangutans for stress and adversity in the wild provides an essential resource. Although this thesis only represents the first step towards such research, it fulfils a necessary role in establishing a starting point from which this field can be expanded. In addition, this research has also contributed to raising awareness in the general public about some of the difficulties facing orangutans in rehabilitation centres, and the potential importance of psychological resilience in the success of orangutan releases. This was achieved through a contribution to the orangutan chapter of ‘An Atlas of Endangered Species’, a popular science book by Megan McCubbin which was published in 2023 (McCubbin, 2023).

This thesis lays the foundation from which a focused, in-depth, and long-term study can be carried out in orangutan rehabilitation centres in Borneo and Sumatra. Such a study may build from the theory behind the novel intervention introduced in Chapter Three, or may alternatively focus on another form of resilience intervention introduced in Chapter Two. Ideally, several different methods would be carried out on separate groups of orangutans, to compare the efficacy of each resilience intervention. This would help to inform rehabilitation centres about which method is most appropriate and effective, and whether some interventions could be combined for an even greater benefit. A range of different age groups should be included in future research, to see whether some interventions are suited to specific stages in an orangutan's development. In addition, different durations of resilience intervention should be compared and follow-up studies implemented, to determine the optimal length of intervention and measure how long beneficial effects can last. Even if increases in resilience are relatively short-lived, for example lasting only six months post-release, this may be sufficient to help orangutans overcome the initial shock of returning to the wild. Maximising resilience during this early period, when orangutans are particularly vulnerable, may have direct implications for survival rates. However, it is hoped that interventions can be developed which can permanently increase resilience in orangutans. Not only will this help individuals face challenges more effectively throughout their lifetime, but at a group level it may increase the resilience of populations of orangutans released back into the wild. As well as helping these groups establish themselves and become more self-supporting, this might assist orangutans in raising the next generation of individuals, thereby helping to expand self-supporting reintroduced orangutan populations and contributing towards the larger picture of orangutan conservation.

As well as developing resilience interventions in rehabilitation centres, it is also important that future research builds on the findings presented here to help captive great apes who are unable to be released back into the wild. There is arguably less urgency in these contexts, as the survival of captive great apes depends more on human care than individual resilience. However, resilience can contribute to the wellbeing of captive animals by increasing their sense of agency and protecting them against unpredictable and unavoidable stressful events: from minor disturbances like unexpected construction noise near an enclosure, to substantial changes like national lockdowns during a pandemic. Therefore, it would be beneficial for future research to expand on the enrichment-based resilience intervention presented in Chapter Three, with a greater number of subjects across several different zoos, in order to see whether a notable long-term benefit can be identified from this intervention. In addition, it is important to take atypical individuals like Jiwa into account when evaluating the wellbeing of great apes in captivity. It is hoped that the case study presented in Chapter Six will be replicated in other zoos with atypical individuals. With a large enough number of examples, a database could be compiled, drawing a picture of the extent of the individual physical and cognitive variation of great apes in captivity, and this could be used as an invaluable resource for caretakers and researchers.

6.6 Conclusion

The aim of this thesis was to identify interventions which had the potential to promote resilience in captive great apes, and to establish how variations between individuals and species may influence stress and resilience. This research brings together the human and animal resilience literature, critically evaluates potential interventions, and introduces a novel experimental resilience intervention which has been trialled on two species of captive great apes. In doing so, the foundations have been laid for a new and important field of research, with the potential for numerous practical applications to benefit captive great apes. In addition, the findings presented here emphasise the importance of considering individual variation in understanding the relationship between stress, resilience, and wellbeing in non-human great apes.

Several forms of resilience intervention have been identified for further investigation and adaptation for great apes, including cognitive challenges, physical exercise, environmental enrichment, social and separation stress, and other forms of mild and manageable stress inoculation. The experimental resilience intervention introduced in this thesis had encouraging - although not definitive - trends towards promoting persistence. It is recommended that, in parallel with exploring other forms of intervention, this method should be explored further and adapted to increase the level of challenge before being applied to great apes in rehabilitation centres.

The lifting of lockdown restrictions was found to increase the probability of stress behaviours in orangutans but not gorillas. In addition, there were species-specific effects on a range of other behaviours, including posture, interaction with objects and enrichment, affiliative behaviours, head covering, and spatial use. For gorillas, the initial reopening of the zoo had effects on closed posture, object-holding, and spatial use, which were subsequently altered when the indoor visitor area reopened to the public. Another important finding is that, once the zoo had reopened, the three separate measures of visitor presence frequently contradicted one another, as well as contradicting some of the effects of lockdown restrictions lifting. In line with the existing literature on lockdowns and pre-Covid studies on zoo visitor presence, these results reflect the complex relationship between visitor presence and the behaviour of zoo-held animals. Even behaviours which may initially appear to be harmful, e.g. increased stress behaviours, may in the long term have an inoculating effect against future unexpected stressors. Therefore, although the lockdowns did undoubtably affect great apes in zoos, it is too simplified to categorise this effect as being ‘good’ or ‘bad’. It is likely that visitor presence can simultaneously have an enriching and a stressful effect on captive great apes. It is hoped that the results of this study will contribute to future research on this period of disruption, to help paint a clearer picture of how lockdowns impacted zoo-held animals.

The case study of Jiwa found that individual differences can impact wellbeing in great apes, e.g. in the domains of physical health and mental wellbeing. In addition, this study found that tailoring cognitive enrichment to an appropriate difficulty level for neurodivergent individuals like Jiwa can be a challenging and time-consuming process. It is important to establish how resilience interventions can be tailored to accommodate atypical individuals. One possibility is to apply alternative forms of resilience intervention which do not rely on specific cognitive or physical abilities, e.g. separation stress. However, particular care must be taken in applying resilience interventions to vulnerable individuals, whose wellbeing may already be impacted, to avoid causing further harm.

The research presented here has necessarily been exploratory in nature, in presenting a comprehensive overview of the current state of knowledge and providing practical suggestions for future efforts in developing appropriate and beneficial interventions for great apes. Therefore, it is essential that researchers take up the mantle in continuing to develop and refine appropriate resilience interventions, evaluating their benefit for great apes in rehabilitation centres and other captive environments. As well as determining the most effective forms, lengths, and combinations of interventions, it is also important to establish whether the age of an individual influences their responsiveness to a particular method. Ultimately, it is hoped that this field will progress to a sufficient degree that an extensive, long-term study can be carried out to measure the effectiveness of resilience interventions on the post-release success rate of orangutans, and the long-term wellbeing of great apes in other captive environments. This thesis represents a small step towards developing a programme of effective resilience interventions. However, it is hoped that a clear case has been made here for the potential value of promoting resilience, in helping to maximise the wellbeing of great apes in captivity, and in contributing towards efforts to return great apes back to the wild.

References

Abraham, A., & Gruss, M. (2010). Stress inoculation facilitates active avoidance learning of the semi-precocial rodent Octodon degus. *Behavioural Brain Research*, *213*(2), 293–303. https://doi.org/10.1016/j.bbr.2010.05.018

Adamec, R. E., & Shallow, T. (1993). Lasting effects on rodent anxiety of a single exposure to a cat. *Physiology and Behavior*, *54*(1), 101–109. https://doi.org/10.1016/0031-9384(93)90050-P

Agteren, J. Van, Iasiello, M., & Lo, L. (2018). Improving the wellbeing and resilience of health services staff via psychological skills training. *BMC Research Notes*, *11*(924), 1–5. https://doi.org/10.1186/s13104-018-4034-x

Aisa, B., Tordera, R., Lasheras, B., Del Río, J., & Ramírez, M. J. (2008). Effects of maternal separation on hypothalamic-pituitary-adrenal responses, cognition and vulnerability to stress in adult female rats. *Neuroscience*, *154*(4), 1218–1226. https://doi.org/10.1016/j.neuroscience.2008.05.011

Aisa, Bárbara, Tordera, R., Lasheras, B., Del Río, J., & Ramírez, M. J. (2007). Cognitive impairment associated to HPA axis hyperactivity after maternal separation in rats. *Psychoneuroendocrinology*, *32*(3), 256–266. https://doi.org/10.1016/j.psyneuen.2006.12.013

Akeman, E., Aupperle, R. L., Clausen, A. N., Cosgrove, K. T., Mcdermott, T. J., Cromer, L. D., … Aupperle, R. L. (2020). A pragmatic clinical trial examining the impact of a resilience program on college student mental health. *Depression and Anxiety*, *37*(3), 202–213. https://doi.org/10.1002/da.22969

Albert, J. (2020a). Bayesian Modeling Using Stan: Binomial Modeling. Retrieved 19 April 2023, from https://bayesball.github.io/BRMS/

Albert, J. (2020b). *ProbBayes: Probability and Bayesian Modeling*.

Amat, J., Aleksejev, R. M., Paul, E., Watkins, L. R., & Maier, S. F. (2010). Behavioral control over shock blocks behavioral and neurochemical effects of later social defeat. *Neuroscience*, *165*(4), 1031–1038. https://doi.org/10.1016/j.neuroscience.2009.11.005.

American Psychiatric Association. (2013). *Diagnostic and Statistical Manual of Mental Disorders: DSM-5*. https://doi.org/10.1176/appi.books.9780890425787

American Psychological Association. (2023). APA Dictionary of Psychology. Retrieved 23

June 2023, from www.dictionary.apa.org

Ancrenaz, M., Gumal, M., Marshall, A. J., Meijaard, E., Wich, S. A., & Husson, S. (2018). Pongo pygmaeus, Bornean orangutan. In *The IUCN Red List of Threatened Species 2016*. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T17975A17966347.en

Anderson, C. R. (1977). Locus of control, coping behaviors, and performance in a stress setting: A longitudinal study. *Journal of Applied Psychology*, *62*(4), 446–451. https://doi.org/10.1037/0021-9010.62.4.446

Andrews, M. W., & Rosenblum, L. A. (1993). Assessment of attachment in differentially reared infant monkeys (Macaca radiata): response to separation and a novel environment. *Journal of Comparative Psychology*, *107*(1), 84–90. https://doi.org/10.1037/0735-7036.107.1.84

Antilla, A., Clay, P., Geurts, T., Cossaboon, C., & Pietsch, R. (2013). *Allie's story: The road to recovery—a six year history of a neurological disease*. Great Ape Trust of Iowa.

Archard, G. A., & Braithwaite, V. A. (2011). Increased exposure to predators increases both exploration and activity level in Brachyrhaphis episcopi. *Journal of Fish Biology*, *78*(2), 593–601. https://doi.org/10.1111/j.1095-8649.2010.02880.x

Armstrong, A. R., Galligan, R. F., & Critchley, C. R. (2011). Emotional intelligence and psychological resilience to negative life events. *Personality and Individual Differences*, *51*(3), 331–336. https://doi.org/10.1016/j.paid.2011.03.025

Asa, C. S. (1997). The Development of Contraceptive Methods for Captive Wildlife. In *Technical Bulletin, Issue 1853* (pp. 235–238). United States Department of Agriculture.

ASAB Ethical Committee. (2023). Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching. *Animal Behaviour*, *195*, I–XI. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.09.006

Avital, A., Ram, E., Maayan, R., Weizman, A., & Richter-Levin, G. (2006). Effects of early-life stress on behavior and neurosteroid levels in the rat hypothalamus and entorhinal cortex. *Brain Research Bulletin*, *68*(6), 419–424. https://doi.org/10.1016/j.brainresbull.2005.09.015

Ayash, S., Schmitt, U., Lyons, D. M., & Müller, M. B. (2020). Stress inoculation in mice induces global resilience. *Translational Psychiatry*, *10*(1), 200. https://doi.org/10.1038/s41398-020-00889-0

Baer, R. A., Smith, G. T., Hopkins, J., Krietemeyer, J., & Toney, L. (2006). Using self-report assessment methods to explore facts of mindfulness. *Assessment*, *13*, 27–45.

Baratta, M. V., Leslie, N. R., Fallon, I. P., Dolzani, S. D., Chun, L. E., Tamalunas, A. M., … Maier, S. F. (2018). Behavioural and neural sequelae of stressor exposure are not modulated by controllability in females. *European Journal of Neuroscience*, *47*(8), 959–967. https://doi.org/10.1111/ejn.13833

Bardi, M., Rhone, A. P., Franssen, C. L., Hampton, J. E., Shea, E. A., Hyer, M. M., … Lambert, K. G. (2012). Behavioral training and predisposed coping strategies interact to influence resilience in male Long-Evans rats: Implications for depression. *Stress*, *15*(3), 306–317. https://doi.org/10.3109/10253890.2011.623739

Barrett, P. M., Lowry-Webster, H. M., Turner, C. M., & Johnson. (1998). The FRIENDS program integrity checklists and social validity measures.

Bartone, P. (1991). Development and validation of a short hardiness measure. *Annual Convention of the American Psychological Society*. Washington DC.

Basalamah, F., Atmoko, S. S. U., Perwitasari-Farajallah, D., Qayim, I., Abdullah, M., Singleton, I., & van Schaik, C. P. (2017). Preliminary result on ranging behavior of orangutans reintroduced into Jantho Sumatran Orangutan Reintroduction Station - Aceh Province. *International Journal of Basic Sciences & Applied Research*, *6*(3), 281–290.

Basalamah, F., Atmoko, S. S. U., Perwitasari-Farajallah, D., Qayim, I., Sihite, J., van Noordwijk, M., … Van Schaik, C. P. (2018). Monitoring orangutan reintroduction: Results of activity budgets, diets, vertical use and associations during the first year post-release in Kehje Sewen Forest, east Kalimantan, Indonesia. *Biodiversitas*, *19*(2), 609–620. https://doi.org/10.13057/biodiv/d190242

Bateson, M., & Matheson, S. M. (2007). Performance on a categorisation task suggests that removal of environmental enrichment induces ‘pessimism’ in captive European starlings (Sturnus vulgaris). *Animal Welfare*, *16*(S), 33–36. https://doi.org/10.1017/S0962728600031705

Bath, K. G., Nitenson, A. S., Lichtman, E., Lopez, C., Chen, W., Gallo, M., … Manzano-Nieves, G. (2017). Early life stress leads to developmental and sex selective effects on performance in a novel object placement task. *Neurobiology of Stress*, *7*, 57–67. https://doi.org/10.1016/j.ynstr.2017.04.001

Baudin, A., Blot, K., Verney, C., Estevez, L., Santamaria, J., Gressens, P., … Naudon, L. (2012). Maternal deprivation induces deficits in temporal memory and cognitive flexibility and exaggerates synaptic plasticity in the rat medial prefrontal cortex. *Neurobiology of Learning and Memory*, *98*(3), 207–214. https://doi.org/10.1016/j.nlm.2012.08.004

Baugher, B. J., & Sachs, B. D. (2022). Early life maternal separation induces sex-specific antidepressant-like responses but has minimal effects on adult stress susceptibility in mice. *Frontiers in Behavioral Neuroscience*, *16*, 941884. https://doi.org/10.3389/fnbeh.2022.941884

Bazak, N., Kozlovsky, N., Kaplan, Z., Matar, M., Golan, H., Zohar, J., … Cohen, H. (2009). Pre-pubertal stress exposure affects adult behavioral response in association with changes in circulating corticosterone and brain-derived neurotrophic factor. *Psychoneuroendocrinology*, *34*(6), 844–858. https://doi.org/10.1016/j.psyneuen.2008.12.018

Beamish, E. K., & O'Riain, M. J. (2014). The effects of permanent injury on the behavior and diet of commensal chacma baboons (Papio ursinus) in the Cape Peninsula, South Africa. *International Journal of Primatology*, *35*(5), 1004–1020. https://doi.org/10.1007/s10764-014-9779-z

Beck, A. T., Ward, C. H., Mendelson, M., Mock, J., & Erbaugh, J. (1961). An inventory for measuring depression. *Archives of General Psychiatry*, *4*(6), 561–571. https://doi.org/10.1001/ARCHPSYC.1961.01710120031004

Beck, B. B., Kleiman, D. G., Dietz, J. M., Castro, I., Carvalho, C., Martins, A., & Rettberg-Beck, B. (1991). Losses and reproduction in reintroduced golden lion tamarins, Leontopithecus rosalia. *Dodo, Journal of Jersey Wildlife Preservation Trust*, *27*, 50–61.

Beck, B. B., Walkup, K., Rodrigues, M., Unwin, S., Travis, D., & Stoinski, T. (2007). *Best practice guidelines for the reintroduction of great apes*. Gland, Switzerland: SSC Primate Specialist Group of the World Conservation Union.

Beck, K. D., & Luine, V. N. (2002). Sex differences in behavioral and neurochemical profiles after chronic stress: Role of housing conditions. *Physiology and Behavior*, *75*(5), 661–673. https://doi.org/10.1016/S0031-9384(02)00670-4

Benaroya-Milshtein, N., Hollander, N., Apter, A., Kukulansky, T., Raz, N., Wilf, A., … Pick, C. G. (2004). Environmental enrichment in mice decreases anxiety, attenuates stress responses and enhances natural killer cell activity. *European Journal of Neuroscience*, *20*(5), 1341–1347. https://doi.org/10.1111/j.1460-9568.2004.03587.x

Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. *Trends in Neurosciences*, *26*(9), 507–513. https://doi.org/10.1016/S0166-2236(03)00233-9

Bian, Y., Yang, L., Wang, Z., Wang, Q., Zeng, L., & Xu, G. (2015). Repeated three-hour maternal separation induces depression-like behavior and affects the expression of hippocampal plasticity-related proteins in C57BL/6N mice. *Neural Plasticity*, *2015*, 627837. https://doi.org/10.1155/2015/627837

Birke, L. (2002). Effects of browse, human visitors and noise on the behaviour of captive orang utans. *Animal Welfare*, *11*(2), 189–202. https://doi.org/10.1017/S0962728600028141

Blaney, E. C., & Wells, D. L. (2004). The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal Welfare*, *13*(2), 111–118. https://doi.org/10.1017/s0962728600026841

Block, J. H., & Block, J. (1980). The role of ego-control and ego resiliency in the organization of behavior. In W. A. Collins (Ed.), *Minnesota symposium on child psychology* (pp. 39–101). Hillsdale, NJ: Erlbaum.

Bloomfield, R. C., Gillespie, G. R., Kerswell, K. J., Butler, K. L., & Hemsworth, P. H. (2015). Effect of partial covering of the visitor viewing area window on positioning and orientation of zoo orangutans: A preference test. *Zoo Biology*, *34*(3), 223–229. https://doi.org/https://doi.org/10.1002/zoo.21207

Bloomsmith, M. A., Brent, L. Y., & Schapiro, S. J. (1991). Guidelines for developing and managing an environmental enrichment program for nonhuman primates. *Laboratory Animal Science*, *41*(4), 372–377.

Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W., & Wiegant, V. M. (2006). Effects of rearing and housing environment on behaviour and performance of pigs with different coping characteristics. *Applied Animal Behaviour Science*, *101*(1–2), 68–85. https://doi.org/10.1016/j.applanim.2006.01.001

Bonanno, G. A., Galea, S., Bucciarelli, A., & Vlahov, D. (2007). What predicts psychological resilience after disaster? The role of demographics, resources, and life stress. *Journal of Consulting and Clinical Psychology*, *75*(5), 671–682. https://doi.org/10.1037/0022-006X.75.5.671

Bondi, C. O., Rodriguez, G., Gould, G. G., Frazer, A., & Morilak, D. A. (2008). Chronic unpredictable stress induces a cognitive deficit and anxiety-like behavior in rats that is prevented by chronic antidepressant drug treatment. *Neuropsychopharmacology*, *33*(2), 320–331. https://doi.org/10.1038/sj.npp.1301410

Bonnie, K. E., Ang, M. Y. L., & Ross, S. R. (2016). Effects of crowd size on exhibit use by and behavior of chimpanzees (Pan troglodytes) and Western lowland gorillas (Gorilla gorilla) at a zoo. *Applied Animal Behaviour Science*, *178*, 102–110. https://doi.org/10.1016/j.applanim.2016.03.003

BOSF. (2023a). Orangutan reintroduction. Retrieved 15 June 2023, from https://www.orangutan.or.id/orangutan-reintroduction

BOSF. (2023b). Sanctuary care. Retrieved 15 June 2023, from www.orangutan.or.id/sanctuary-care

Bouchet, C. A., Lloyd, B. A., Loetz, E. C., Farmer, C. E., Ostrovskyy, M., Haddad, N., … Greenwood, B. N. (2017). Acute exercise enhances the consolidation of fear extinction memory and reduces conditioned fear relapse in a sex-dependent manner. *Learning and Memory*, *24*(8), 358–368. https://doi.org/10.1101/lm.045195.117

Bourke, C. H., & Neigh, G. N. (2011). Behavioral effects of chronic adolescent stress are sustained and sexually dimorphic. *Hormones and Behavior*, *60*(1), 112–120. https://doi.org/10.1016/j.yhbeh.2011.03.011

Bowman, R. E., Zrull, M. C., & Luine, V. N. (2001a). Chronic restraint stress enhances radial arm maze performance in female rats. *Brain Research*, *904*(2), 279–289. https://doi.org/10.1016/s0006-8993(01)02474-x.

Bowman, R. E., Zrull, M. C., & Luine, V. N. (2001b). Chronic stress effects on physiology and cognition in female rats. *Brain Research*, *904*, 279–280. https://doi.org/10.1016/s0006-8993(01)02474-x.

Brand, C. M., Boose, K. J., Squires, E. C., Marchant, L. F., White, F. J., Meinelt, A., & Snodgrass, J. J. (2016). Hair plucking, stress, and urinary cortisol among captive bonobos (Pan paniscus). *Zoo Biology*, *35*(5), 415–422. https://doi.org/10.1002/zoo.21320

Bravo-Tobar, I. D., Fernández, P., Sáez, J. C., & Dagnino-Subiabre, A. (2021). Long-term effects of stress resilience: Hippocampal neuroinflammation and behavioral approach in male rats. *Journal of Neuroscience Research*, *99*(10), 2493–2510. https://doi.org/10.1002/jnr.24902

Brereton, J. E., Perkins, K., Jones, E. M. L., & Mcmillan, C. (2023). Visitors and observers otter-ly influence the behavior and enclosure use of zoo-housed giant otters. *Zoo*

Biology, 1–13. https://doi.org/10.1002/zoo.21755

Breuer, T., Ndoundou-Hockemba, M., & Fishlock, V. (2005). First observation of tool use in wild gorillas. *PLoS Biology*, *3*(11), e380. https://doi.org/https://doi.org/10.1371/journal.pbio.0030380

Bridgeland, M. (1971). *Pioneer Work with Maladjusted Children: A Study of the Development of Therapeutic Education*. London: Staples Press.

Brimmell, J., Parker, J., Wilson, M., Vine, S., & Moore, L. (2019). Challenge and threat states, performance, and attentional control during a pressurized soccer penalty task. *Sport, Exercise, and Performance Psychology*, *8*(1), 63–79. https://doi.org/10.1037/spy0000147

Brockhurst, J., Cheleuitte-Nieves, C., Buckmaster, C. L., Schatzberg, A. F., & Lyons, D. M. (2015). Stress inoculation modeled in mice. *Translational Psychiatry*, *5*(3), 1–5. https://doi.org/10.1038/tp.2015.34

Brody, G. H., Beach, S. R. H., Philibert, R. A., Chen, Y., & Murry, V. M. (2009). Prevention effects moderate the association of 5-HTTLPR and youth risk behavior initiation: Gene × environment hypotheses tested via a randomized prevention design. *Child Development*, *80*(3), 645–661. https://doi.org/10.1111/j.1467-8624.2009.01288.x

Brown, P. L., Hurley, C., Repucci, N., & Drugan, R. C. (2001). Behavioral analysis of stress controllability effects in a new swim stress paradigm. *Pharmacology Biochemistry and Behavior*, *68*(2), 263–272. https://doi.org/10.1016/S0091-3057(00)00460-3

Brown, R. (2015). Building children and young people's resilience: Lessons from psychology. *International Journal of Disaster Risk Reduction*, *14*(2), 115–124. https://doi.org/10.1016/j.ijdrr.2015.06.007

Brüne, M., Brüne-Cohrs, U., McGrew, W. C., & Preuschoft, S. (2006). Psychopathology in great apes: Concepts, treatment options and possible homologies to human psychiatric disorders. *Neuroscience and Biobehavioral Reviews*, *30*(8), 1246–1259. https://doi.org/10.1016/j.neubiorev.2006.09.002

Brunson, K. L., Kramár, E., Lin, B., Chen, Y., Colgin, L. L., Yanagihara, T. K., … Baram, T. Z. (2005). Mechanisms of late-onset cognitive decline after early-life stress. *Journal of Neuroscience*, *25*(41), 9328–9338. https://doi.org/10.1523/JNEUROSCI.2281-05.2005

Buchheld, N., Grossman, P., & Walach, H. (2001). Measuring Mindfulness in Insight Meditation (Vipassana) and Meditation-Based Psychotherapy: The Development of the

Freiburg Mindfulness Inventory (FMI). *Journal for Meditation and Meditation Research*, *1*, 11–34.

Burgdorf, J., Kroes, R. A., & Moskal, J. R. (2017). Rough-and-tumble play induces resilience to stress in rats. *NeuroReport*, *28*(17), 1122–1126. https://doi.org/10.1097/WNR.0000000000000864

Butler, J., & Kern, M. L. (2016). The PERMA-profiler: A brief multidimensional measure of flourishing. *International Journal of Wellbeing*, *6*(3), 1–48.

Calandreau, L., Bertin, A., Boissy, A., Arnould, C., Constantin, P., Desmedt, A., … Leterrier, C. (2011). Effect of one week of stress on emotional reactivity and learning and memory performances in Japanese quail. *Behavioural Brain Research*, *217*(1), 104–110. https://doi.org/10.1016/j.bbr.2010.10.004

Calapai, A., Cabrera-Moreno, J., Moser, T., & Jeschke, M. (2022). Flexible auditory training, psychophysics, and enrichment of common marmosets with an automated, touchscreen-based system. *Nature Communications*, *13*(1), 1648. https://doi.org/https://doi.org/10.1038/s41467-022-29185-9

Caldji, C., Francis, D., Sharma, S., Plotsky, P. M., & Meaney, M. J. (2000). The effects of early rearing environment on the development of GABA(A) and central benzodiazepine receptor levels and novelty-induced fearfulness in the rat. *Neuropsychopharmacology*, *22*(3), 219–229. https://doi.org/10.1016/S0893-133X(99)00110-4

Calpe-López, C., Martínez-Caballero, M. A., García-Pardo, M. P., & Aguilar, M. A. (2022). Intermittent voluntary wheel running promotes resilience to the negative consequences of repeated social defeat in mice. *Physiology and Behavior*, *254*, 113916. https://doi.org/10.1016/j.physbeh.2022.113916

Campbell-Smith, G., Campbell-Smith, M., Singleton, I., & Linkie, M. (2011). Apes in space: Saving an imperilled orangutan population in Sumatra. *PLoS ONE*, *6*(2). https://doi.org/10.1371/JOURNAL.PONE.0017210

Campos-Cardoso, R., Novaes, L. S., Godoy, L. D., dos Santos, N. B., Perfetto, J. G., Lazarini-Lopes, W., … Munhoz, C. D. (2023). The resilience of adolescent male rats to acute stress-induced delayed anxiety is age-related and glucocorticoid release-dependent. *Neuropharmacology*, *226*, 109385. https://doi.org/10.1016/j.neuropharm.2022.109385

Canon. (2020). *Digital Photo Professional 4 2014-2020.*

Cant, J. G. H. (1992). Positional behavior and body size of arboreal primates: A theoretical framework for field studies and an illustration of its application. *American Journal of Physical Anthropology*, *88*(3), 273–283. https://doi.org/10.1002/ajpa.1330880302

Capitanio, J. P. (2011). Individual differences in emotionality: Social temperament and health. *American Journal of Primatology*, *73*(6), 507–515. https://doi.org/10.1002/ajp.20870

Carver, C. S., Scheier, M. F., & Weintraub, J. K. (1989). Assessing coping strategies: A theoretically based approach. *Journal of Personality and Social Psychology*, *5*, 267–283.

Castro, J. E., Diessler, S., Varea, E., Márquez, C., Larsen, M. H., Cordero, M. I., & Sandi, C. (2012). Personality traits in rats predict vulnerability and resilience to developing stress-induced depression-like behaviors, HPA axis hyper-reactivity and brain changes in pERK1/2 activity. *Psychoneuroendocrinology*, *37*(8), 1209–1223. https://doi.org/10.1016/j.psyneuen.2011.12.014

Celli, M. L., Tomonaga, M., Udono, T., Teramoto, M., & Nagano, K. (2003). Tool use task as environmental enrichment for captive chimpanzees. *Applied Animal Behaviour Science*, *81*(2), 171–182. https://doi.org/https://doi.org/10.1016/S0168-1591(02)00257-5

Chaby, L. E., Cavigelli, S. A., Hirrlinger, A. M., Caruso, M. J., & Braithwaite, V. A. (2015). Chronic unpredictable stress during adolescence causes long-term anxiety. *Behavioural Brain Research*, *278*, 492–495. https://doi.org/10.1016/j.bbr.2014.09.003

Chaby, L. E., Cavigelli, S. A., White, A., Wang, K., & Braithwaite, V. A. (2013). Long-term changes in cognitive bias and coping response as a result of chronic unpredictable stress during adolescence. *Frontiers in Human Neuroscience*, *7*, 328. https://doi.org/10.3389/fnhum.2013.00328

Chaby, L. E., Sheriff, M. J., Hirrlinger, A. M., & Braithwaite, V. A. (2015). Does early stress prepare individuals for a stressful future? Stress during adolescence improves foraging under threat. *Animal Behaviour*, *105*, 37–45. https://doi.org/10.1016/j.anbehav.2015.03.028

Chamove, A., Hosey, G. R., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo Biology*, *7*(4), 359–369. https://doi.org/10.1002/zoo.1430070407

Chandler, G., & Roberts, S. (2015). Resilience intervention for young adults with adverse childhood experiences. *Journal of the American Psychiatric Nurses Association*, *21*(6), 406–416. https://doi.org/10.1177/1078390315620609

Chant, L. (2014). Damian Aspinall's heartbreak as five gorillas raised at Howletts in Bekesbourne near Canterbury and Port Lympne in Hythe are found dead in the wild.

Retrieved 2 June 2023, from KentOnline website: https://www.kentonline.co.uk/canterbury/news/five-gorillas-raised-in-kent-23035/

Chappell, J., & Thorpe, S. K. S. (2022). The role of great ape behavioral ecology in One Health: Implications for captive welfare and re-habilitation success. *American Journal of Primatology*, *84*(4–5). https://doi.org/10.1002/ajp.23328

Chen, C. V., Chaby, L. E., Nazeer, S., & Liberzon, I. (2018). Effects of trauma in adulthood and adolescence on fear extinction and extinction retention: Advancing animal models of posttraumatic stress disorder. *Frontiers in Behavioral Neuroscience*, *12*, 247. https://doi.org/10.3389/fnbeh.2018.00247

Chesney, M. A., Neilands, T. B., Chambers, D. B., Taylor, J. M., & Folkman, S. (2006). A validity and reliability study of the coping self-efficacy scale. *British Journal of Health Psychology*, *11*, 421–437.

Chester Zoo. (2018). The road to recovery. Retrieved from https://www.chesterzoo.org/news/the-road-to-recovery/

Chiba, S., Numakawa, T., Ninomiya, M., Richards, M. C., Wakabayashi, C., & Kunugi, H. (2012). Chronic restraint stress causes anxiety- and depression-like behaviors, downregulates glucocorticoid receptor expression, and attenuates glutamate release induced by brain-derived neurotrophic factor in the prefrontal cortex. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *39*(1), 112–119. https://doi.org/10.1016/j.pnpbp.2012.05.018

Choo, Y., Todd, P. A., & Li, D. (2011). Visitor effects on zoo orangutans in two novel, naturalistic enclosures. *Applied Animal Behaviour Science*, *133*(1–2), 78–86. https://doi.org/10.1016/j.applanim.2011.05.007

Christianson, J. P., Paul, E. D., Irani, M., Thompson, B. M., Kubala, K. H., Yirmiya, R., … Maier, S. F. (2008). The role of prior stressor controllability and the dorsal raphé nucleus in sucrose preference and social exploration. *Behavioural Brain Research*, *193*(1), 87–93. https://doi.org/10.1016/j.bbr.2008.04.024

Cipolletta, C. (2004). Effects of group dynamics and diet on the ranging patterns of a western gorilla group (Gorilla gorilla gorilla) at Bai Hokou, Central African Republic. *American Journal of Primatology*, *64*(2), 193–205. https://doi.org/10.1002/ajp.20072

Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, *135*(1–2), 1–12.

https://doi.org/10.1016/j.applanim.2011.10.010

Clark, F. E. (2022). Bridging pure cognitive research and cognitive enrichment. *Animal Cognition*, *25*(6), 1671–1678. https://doi.org/10.1007/s10071-022-01636-2

Clark, F. E. (2023). In the zone: Towards a comparative study of flow state in primates. *Animal Behaviour and Cognition*, *10*(1), 62–88. https://doi.org/10.26451/abc.10.01.04.2023

Clark, F. E., Fitzpatrick, M., Hartley, A., King, A. J., Lee, T., Routh, A., … George, K. (2012). Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (Gorilla gorilla gorilla). *Zoo Biology*, *31*(3), 306–321. https://doi.org/10.1002/zoo.20396

Cohen, S., Kamarck, T., & Mermelstein, R. (1983). A Global Measure of Perceived Stress. *Journal of Health and Social Behavior*, *24*(4), 385–396.

Cohen, S., Memelstein, R., Kamarck, T., & Hoberman, H. (1985). Measuring the functional components of social support. In I. G. Sarason & B. Sarason (Eds.), *Social support: Theory, research, and application* (pp. 73–94). The Hague: Martinus Nijhoff.

Colditz, I. G., & Hine, B. C. (2016). Resilience in farm animals: Biology, management, breeding and implications for animal welfare. *Animal Production Science*, *56*(12), 1961–1983. https://doi.org/10.1071/AN15297

Cole, E. F., & Quinn, J. L. (2014). Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild. *Biology Letters*, *10*(5), 20140178. https://doi.org/10.1098/rsbl.2014.0178

Cole, N. (1989). *Mozu the Snow Monkey: Nature*. Toronto, ON: E1 Entertainment.

Colorado, R. A., Shumake, J., Conejo, N. M., Gonzalez-Pardo, H., & Gonzalez-Lima, F. (2006). Effects of maternal separation, early handling, and standard facility rearing on orienting and impulsive behavior of adolescent rats. *Behavioural Processes*, *71*(1), 51–58. https://doi.org/10.1016/j.beproc.2005.09.007

Commitante, R. (2005). *Orang-Utan Stress : Behaviour and Cortisol Responses in Rehabilitation*. University of Cambridge.

Connor, K. M., & Davidson, J. R. T. (2003). Development of a new resilience scale: the Connor-Davidson Resilience Scale (CD-RISC). *Depression and Anxiety*, *18*(2), 76–82. https://doi.org/10.1002/DA.10113

Cooke, C. M., & Schillaci, M. A. (2007). Behavioral responses to the zoo environment by white handed gibbons. *Applied Animal Behaviour Science*, *106*(1–3), 125–133. https://doi.org/10.1016/j.applanim.2006.06.016

Coopersmith, S. (1981). *SEI Self-Esteem Inventories Manual*. Redwood City, California: Mind Garden.

Coppel, D. B. (1980). *The Relationship of Perceived Social Support and Self-Efficacy to Major and Minor Stressors*. University of Washington.

Corcoran, C. A., Pierre, P. J., Haddad, T., Bice, C., Suomi, S. J., Grant, K. A., … Bennett, A. J. (2012). Long-term effects of differential early rearing in rhesus macaques: Behavioral reactivity in adulthood. *Developmental Psychobiology*, *54*(5), 546–555. https://doi.org/10.1002/dev.20613

Costa, P. T., & McCrae. (2008). The Revised NEO Personality Inventory (NEO-PI-R). In *The SAGE Handbook of Personality Theory and Assessment, Vol. 2. Personality Measurement and Testing* (pp. 179–198). https://doi.org/https://doi.org/10.4135/9781849200479.n9

Costa, P. T., & McCrae, R. R. (1984). Personality as a lifelong determinant of well-being. In C. Malatesta & C. Izard (Eds.), *Affective Process in Adult Development and Aging* (pp. 141–157). Beverly Hill, CA: Sage.

Costa, Paul T., & McCrae, R. R. (1980). Influence of extraversion and neuroticism on subjective well-being: Happy and unhappy people. *Journal of Personality and Social Psychology*, *38*(4), 668–678. https://doi.org/10.1037/0022-3514.38.4.668

Cotella, E. M., Gómez, A. S., Lemen, P., Chen, C., Fernández, G., Hansen, C., … Paglini, M. G. (2019). Long-term impact of chronic variable stress in adolescence versus adulthood. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *88*, 303–310. https://doi.org/10.1016/j.pnpbp.2018.08.003

Crawford, L. E., Knouse, L. E., Kent, M., Vavra, D., Harding, O., LeServe, D., … Lambert, K. G. (2020). Enriched environment exposure accelerates rodent driving skills. *Behavioural Brain Research*, *378*, 12309. https://doi.org/10.1016/j.bbr.2019.112309

Csikszentmihalyi, M. (1988). The flow experience and human psychology. In M. Csikszentmihalyi & I. S. Csikszentmihalyi (Eds.), *Optimal Experience: Psychological Studies of Flow in Consciousness* (pp. 15–35). New York: Cambridge University Press.

Cui, M., Yang, Y., Yang, J., Zhang, J., Han, H., Ma, W., … Cao, J. (2006). Enriched environment experience overcomes the memory deficits and depressive-like behavior induced by early life stress. *Neuroscience Letters*, *404*(1–2), 208–212. https://doi.org/10.1016/j.neulet.2006.05.048

Dalle Molle, R., Portella, A. K., Goldani, M. Z., Kapczinski, F. P., Leistner-Segala, S., Salum, G. A., … Silveira, P. P. (2012). Associations between parenting behavior and anxiety in a rodent model and a clinical sample: Relationship to peripheral BDNF levels. *Translational Psychiatry*, *2*(11), e195. https://doi.org/10.1038/tp.2012.126

Damerius, L. A. (2017). *What makes orangutans intelligent? The role of experience and learning in the development of problem-solving abilities in orangutans* (University of Zurich). https://doi.org/10.5167/uzh-146580

Daniels, W. M. U., Pietersen, C. Y., Carstens, M. E., & Stein, D. J. (2004). Maternal separation in rats leads to anxiety-like behavior and a blunted ACTH response and altered neurotransmitter levels in response to a subsequent stressor. *Metabolic Brain Disease*, *19*(1–2), 3–14. https://doi.org/10.1023/B:MEBR.0000027412.19664.b3

Davis, J. T., Mengersen, K., Abram, N. K., Ancrenaz, M., Wells, J. A., & Meijaard, E. (2013). It's not just conflict that motivates killing of orangutans. *PLoS ONE*, *8*(10), e75373. https://doi.org/10.1371/journal.pone.0075373

Davis, N., Schaffner, C. M., & Smith, T. E. (2005). Evidence that zoo visitors influence HPA activity in spider monkeys (Ateles geoffroyii rufiventris). *Applied Animal Behaviour Science*, *90*(2), 131–141. https://doi.org/10.1016/j.applanim.2004.08.020

De Jong, I. C., Prelle, I. T., van De Burgwal, J. A., Lambooij, E., Korte, S. M., Blokhuis, H. J., & Koolhaas, J. M. (2000). Effects of environmental enrichment on behavioral responses to novelty, learning, and memory, and the circadian rhythm in cortisol in growing pigs. *Physiology and Behavior*, *68*(4), 571–578. https://doi.org/10.1016/S0031-9384(99)00212-7

Delaney, C., Barrere, C., Robertson, S., Zahourek, R., Diaz, D., & Lachapelle, L. (2016). Pilot testing of the NURSE stress management intervention. *Journal of Holistic Nursing*, *34*(4), 369–389. https://doi.org/10.1177/0898010115622295

Delgado, R. A., & Van Schaik, C. P. (2000). The behavioral ecology and conservation of the orangutan (Pongo pygmaeus): A tale of two islands. *Evolutionary Anthropology*, *9*(5), 201–218. https://doi.org/10.1002/1520-6505(2000)9:5<201::AID-EVAN2>3.0.CO;2-Y

Denny, R. R., Connelly, K. L., Ghilotti, M. G., Meissler, J. J., Yu, D., Eisenstein, T. K., & Unterwald, E. M. (2021). Artificial intelligence identified resilient and vulnerable female rats after traumatic stress and ethanol exposure: Investigation of neuropeptide Y pathway regulation. *Frontiers in Neuroscience*, *15*, 772946. https://doi.org/10.3389/fnins.2021.772946

Derogatis, L. R. (2001). *Brief Symptom Inventory 18: Administration, scoring and procedures manual*. Minneapolis, Minnesota: NCS Pearson.

Digiorgio, A. L., Ma, Y., Upton, E. M., Gopal, S., Robinson, N. J., Susanto, T., & Knott, C. D. (2023). Famished frugivores or choosy consumers: A generalist frugivore (wild Bornean orangutans, Pongo pygmaeus wurmbii) leaves available fruit for nonfruit foods. *International Journal of Primatology*, *44*(2), 377–398. https://doi.org/10.1007/s10764-022-00347-2

Dishman, R. K., Renner, K. J., Youngstedt, S. D., Reigle, T. G., Bunnell, B. N., Burke, K. A., … Meyerhoff, J. L. (1997). Activity wheel running reduces escape latency and alters brain monoamine levels after footshock. *Brain Research Bulletin*, *42*(5), 399–406. https://doi.org/10.1016/S0361-9230(96)00329-2

Doremus-Fitzwater, T. L., Varlinskaya, E. I., & Spear, L. P. (2009). Social and non-social anxiety in adolescent and adult rats after repeated restraint. *Physiology and Behavior*, *97*(3–4), 484–494. https://doi.org/10.1016/j.physbeh.2009.03.025.Social

dos Santos Guilherme, M., Tsoutsouli, T., Chongtham, M. C., Winter, J., Gerber, S., Müller, M. B., & Endres, K. (2022). Selective targeting of chronic social stress-induced activated neurons identifies neurogenesis-related genes to be associated with resilience in female mice. *Psychoneuroendocrinology*, *139*, 105700. https://doi.org/10.1016/j.psyneuen.2022.105700

Douglas, C., Bateson, M., Walsh, C., Bédué, A., & Edwards, S. A. (2012). Environmental enrichment induces optimistic cognitive biases in pigs. *Applied Animal Behaviour Science*, *139*(1–2), 65–73. https://doi.org/10.1016/j.applanim.2012.02.018

Doyle, R. E., Fisher, A. D., Hinch, G. N., Boissy, A., & Lee, C. (2010). Release from restraint generates a positive judgement bias in sheep. *Applied Animal Behaviour Science*, *122*(1), 28–34. https://doi.org/10.1016/j.applanim.2009.11.003

Ducottet, C., & Belzung, C. (2004). Behaviour in the elevated plus-maze predicts coping after subchronic mild stress in mice. *Physiology and Behavior*, *81*(3), 417–426. https://doi.org/10.1016/j.physbeh.2004.01.013

Duttweiler, P. C. (2016). The Internal Control Index: A Newly Developed Measure of Locus of Control. *Educational and Psychological Measurement*, *44*(2), 209–221. https://doi.org/10.1177/0013164484442004

Dweck, C. S. (1975). The role of expectations and attributions in the alleviation of learned helplessness. *Journal of Personality and Social Psychology*, *31*(4), 674–685. https://doi.org/10.1037/h0077149

Eagle, A. L., Fitzpatrick, C. J., & Perrine, S. A. (2013). Single prolonged stress impairs social and object novelty recognition in rats. *Behavioural Brain Research*, *256*, 591–597. https://doi.org/10.1016/j.bbr.2013.09.014.

Edwards, C., & Imrie, R. (2008). Disability and the implications of the wellbeing agenda: Some reflections from the United Kingdom. *Journal of Social Policy*, *37*(3), 337–355. https://doi.org/10.1017/S0047279408001943

Egeland, B., Carlson, E., & Sroufe, L. A. (1993). Resilience as process. *Development and Psychopathology*, *5*(4), 517–528. https://doi.org/10.1017/S0954579400006131

Eiland, L., & McEwen, B. S. (2012). Early life stress followed by subsequent adult chronic stress potentiates anxiety and blunts hippocampal structural remodeling. *Hippocampus*, *22*(1), 82–91. https://doi.org/10.1002/hipo.20862

Elliot, A. J., & Church, M. A. (1997). A hierarchical model of approach and avoidance achievement motivation. *Journal of Personality and Social Psychology*, *72*, 218–232.

Endler, N. S., & Parker, J. D. A. (1990). *Coping Inventory for Stressful Situations (CISS): Manual*. Toronto: Multi-Health Systems.

Epstein, J. M., & Reed, J. (2019). Tree climbing methodology for orangutan conservation. *Primate Conservation*, (33), 59–64.

Ernst, K., Puppe, B., Schon, P. C., & Manteuffel, G. (2005). A complex automatic feeding system for pigs aimed to induce successful behavioural coping by cognitive adaptation. *Applied Animal Behaviour Science*, *91*(3–4), 205–281. https://doi.org/https://doi.org/10.1016/j.applanim.2004.10.010

Fabrega, H. (2002). *The origins of psychopathology: The phylogenetic and cultural basis of mental illness*. New Brunswick, NJ: Rutgers University Press.

Fagot, J., & Paleressompoulle, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior Research Methods*, *41*(2), 396–404. https://doi.org/10.3758/BRM.41.2.396

Farkas, D., & Orosz, G. (2015). Ego-resiliency reloaded: A three-component model of general resiliency. *PLoS ONE*, *10*(3), e0120883. https://doi.org/10.14755/MTAKIK.2014.0001

Farmer, K. H., & Courage, A. (2008). Sanctuaries and reintroduction: A role in gorilla conservation? In T. S. Stoinski, H. D. Steklis, & P. T. Mehlman (Eds.), *Conservation in the 21st Century: Gorillas as a Case Study* (pp. 79–106). https://doi.org/https://doi.org/10.1007/978-0-387-70721-1

Farrell, M. R., Holland, F. H., Shansky, R. M., & Brenhouse, H. C. (2016). Sex-specific effects of early life stress on social interaction and prefrontal cortex dendritic morphology in young rats. *Behavioural Brain Research*, *310*, 119–125. https://doi.org/10.1016/j.bbr.2016.05.009

FAWC. (1992). *The Five Freedoms*. London: Farm Animal Welfare Council.

Feng, X., Wang, L., Yang, S., Qin, D., Wang, J., Li, C., … Hu, X. (2011). Maternal separation produces lasting changes in cortisol and behavior in rhesus monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(34), 14312–14317. https://doi.org/10.1073/pnas.1010943108

Ferdowsian, H. R., Durham, D. L., Johnson, C. M., Brü Ne C, M., Kimwele, C., Kranendonk, G., … Ajarova, L. (2012). Signs of generalized anxiety and compulsive disorders in chimpanzees. *Journal of Veterinary Behavior: Clinical Applications and Research*, *7*(6), 353–361. https://doi.org/10.1016/j.jveb.2012.01.006

Fernandez, C. A., Choi, K. W., Marshall, B. D. L., Vicente, B., Saldivia, S., Kohn, R., … Buka, S. L. (2020). Assessing the relationship between psychosocial stressors and psychiatric resilience among Chilean disaster survivors. *British Journal of Psychiatry*, *217*(5), 630–637. https://doi.org/10.1192/bjp.2020.88.

Fletcher, D., & Sarkar, M. (2013). Psychological resilience: A review and critique of definitions, concepts, and theory. *European Psychologist*, *18*(1), 12–23. https://doi.org/10.1027/1016-9040/a000124

Foa, E. B., Riggs, D. S., Dancu, C. V., & Rothbaum, B. O. (1993). Reliability and validity of a brief instrument for assessing post-traumatic stress disorder. *Journal of Traumatic Stress*, *6*(4), 459–473. https://doi.org/10.1002/JTS.2490060405

Fooden, J., & Izor, R. J. (1983). Growth curves, dental emergence norms, and supplementary morphological observations in known-age captive orangutans. *American Journal of Primatology*, *5*(4), 285–301. https://doi.org/10.1002/ajp.1350050402

Forgeard, M. J. C., & Seligman, M. E. P. (2012). Seeing the glass half full: A review of the causes and consequences of optimism. *Pratiques Psychologiques*, *18*(2), 107–120. https://doi.org/10.1016/j.prps.2012.02.002

Foster, K., Cuzzillo, C., & Furness, T. (2018). Strengthening mental health nurses' resilience through a workplace resilience programme: A qualitative inquiry. *Journal of Psychiatric and Mental Health Nursing*, *25*(5–6), 338–348. https://doi.org/10.1111/jpm.12467

Francis, D. D., Diorio, J., Plotsky, P. M., & Meaney, M. J. (2002). Environmental enrichment reverses the effects of maternal separation on stress reactivity. *Journal of Neuroscience*, *22*(18), 7840–7843. https://doi.org/10.1523/jneurosci.22-18-07840.2002

Friborg, O., Hjemdal, O., Rosenvinge, J. H., & Martinussen, M. (2003). A new rating scale for adult resilience: What are the central protective resources behind healthy adjustment? *International Journal of Methods in Psychiatric Research*, *12*(2), 65–76. https://doi.org/10.1002/mpr.143

Fulk, L. J., Stock, H. S., Lynn, A., Marshall, J., Wilson, M. A., & Hand, G. A. (2004). Chronic physical exercise reduces anxiety-like behavior in rats. *International Journal of Sports Medicine*, *25*(1), 78–82. https://doi.org/10.1055/s-2003-45235

Fuss, J., Ben Abdallah, N. M. B., Vogt, M. A., Touma, C., Pacifici, P. G., Palme, R., … Gass, P. (2010). Voluntary exercise induces anxiety-like behavior in adult C57BL/6J mice correlating with hippocampal neurogenesis. *Hippocampus*, *20*(3), 364–376. https://doi.org/10.1002/hipo.20634

Galdikas, B. M. F. (1982). Orang-utan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo (Kalimantan Tengah). *Journal of Human Evolution*, *11*(1), 19–33. https://doi.org/10.1016/S0047-2484(82)80028-6

Galdikas, B. M. F. (1985). Orangutan sociality at Tanjung-Puting. *American Journal of Primatology*, *9*(2), 101–119. https://doi.org/doi:10.1002/ajp.1350090204

Gallegos-guajardo, J., Ruvalcaba-romero, N. A., Langley, A., & Villegas-guinea, D. (2015). Selective prevention for anxiety and resilience promotion: Outcomes of an anxiety prevention and resilience program with girls at risk. *Pensando Psicología*, *11*(18), 11–23. https://doi.org/https://doi.org/10.16925/pe.v11i18.1001

García-Capdevila, S., Portell-Cortés, I., Torras-Garcia, M., Coll-Andreu, M., & Costa-Miserachs, D. (2009). Effects of long-term voluntary exercise on learning and memory processes: dependency of the task and level of exercise. *Behavioural Brain Research*, *202*(2), 162–170. https://doi.org/10.1016/j.bbr.2009.03.020

Garcia-Marquez, C., & Armario, A. (1987). Chronic stress depresses exploratory activity and behavioral performance in the forced swimming test without altering ACTH response to a novel acute stressor. *Physiology and Behavior*, *40*(1), 33–38. https://doi.org/10.1016/0031-9384(87)90182-X

Gardner, K. L., Thrivikraman, K. V., Lightman, S. L., Plotsky, P. M., & Lowry, C. A. (2005). Early life experience alters behavior during social defeat: Focus on serotonergic systems. *Neuroscience*, *136*(1), 181–191. https://doi.org/10.1016/j.neuroscience.2005.07.042

Garmezy, N. (1993). Vulnerability and resilience. In D. C. Funder, R. D. Parke, C. Tomlinson-Keesey, & K. Widaman (Eds.), *Studying lives through time: Approaches to personality and development* (pp. 377–298). Washington DC: American Psychological Association.

Garnefski, N. ;, & Kraaij, V. (2006). Cognitive emotion regulation questionnaire-development of a short 18-item version (CERQ-short). *Personality and Individual Differences*, *41*, 1045–1053. https://doi.org/10.1016/j.paid.2006.04.010

Gelman, A., & Rubin, D. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511.

Gerber, M. M., Frankfurt, S. B., Contractor, A. A., Oudshoorn, K., Dranger, P., & Brown, L. A. (2018). Influence of multiple traumatic event types on mental health outcomes: Does count matter? *Journal of Psychopathology and Behavioral Assessment*, *40*, 645–654. https://doi.org/10.1007/s10862-018-9682-6

Gillanders, D., Bolderston, H., Bond, F. W., Dempster, M., Flaxman, P. E., Campbell, L., … Remington, B. (2014). The development and initial validation of The Cognitive Fusion Questionnaire. *Behavior Therapy*, *45*(1), 83–101. https://doi.org/10.1016/j.beth.2013.09.001

Gillen, H. B., & Gibala, M. J. (2014). Is high-intensity interval training a time-efficient exercise strategy to improve health and fitness? *Interval Training*, *39*(3), 409–412. https://doi.org/https://doi.org/10.1139/apnm-2013-0187@apnm-it.issue01

Gold, K. C., & Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology*, *13*(5), 509–522. https://doi.org/10.1002/zoo.1430130513

Gonzalez, S. T., Marty, V., Spigelman, I., Reise, S. P., & Fanselow, M. S. (2021). Impact of stress resilience and susceptibility on fear learning, anxiety, and alcohol intake. *Neurobiology of Stress*, *15*, 100335. https://doi.org/10.1016/j.ynstr.2021.100335

Goodman, R. (1997). The strengths and difficulties questionnaire: A research note. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *38*(5), 581–586. https://doi.org/10.1111/J.1469-7610.1997.TB01545.X

Goodwill, H. L., Manzano-Nieves, G., Gallo, M., Lee, H. I., Oyerinde, E., Serre, T., & Bath, K. G. (2019). Early life stress leads to sex differences in development of depressive-like outcomes in a mouse model. *Neuropsychopharmacology*, *44*(4), 711–720. https://doi.org/10.1038/s41386-018-0195-5

Gosling, S. D., Rentfrow, P. J., & Swann, W. B. (2003). A very brief measure of the Big-Five personality domains. *Journal of Research in Personality*, *37*(6), 504–528. https://doi.org/10.1016/S0092-6566(03)00046-1

Grassi-Oliveira, R., Honeycut, J., Holland, F. H., Ganguly, P., Brenhouse, H. C., Yang, G., … Li, W. (2016). Cognitive impairment effects of early life stress in adolescents can be predicted with early biomarkers: Impacts of sex, experience, and cytokines. *Psychoneuroendocrinology*, *71*, 19–30. https://doi.org/10.1016/j.psyneuen.2016.04.016.

Gratz, K. L., & Roemer, L. (2004). Multidimensional assessment of emotion regulation and dysregulation: development, factor structure, and initial validation of the difficulties in emotion regulation scale. *Journal of Psychopathology and Behavioral Assessment2*, *26*, 41–54. https://doi.org/10.1023/B:JOBA.0000007455.08539.94

Green, M. R., Barnes, B., & McCormick, C. M. (2013). Social instability stress in adolescence increases anxiety and reduces social interactions in adulthood in male long-evans rats. *Developmental Psychobiology*, *55*(8), 849–859. https://doi.org/10.1002/dev.21077

Greenberg, M. T. (2006). Promoting resilience in children and youth: preventive interventions and their interface with neuroscience. *Annual New York Academy of Science*, *1094*, 139–150. https://doi.org/10.1196/annals.1376.013

Greenwood, B. N., Foley, T. E., Burhans, D., Maier, S. F., & Fleshner, M. (2005). The consequences of uncontrollable stress are sensitive to duration of prior wheel running. *Brain Research*, *1033*(2), 164–178. https://doi.org/10.1016/j.brainres.2004.11.037

Greenwood, B. N., Foley, T. E., Day, H. E. W., Campisi, J., Hammack, S. H., Campeau, S., … Fleshner, M. (2003). Freewheel running prevents learned helplessness/behavioral depression: Role of dorsal raphe serotonergic neurons. *Journal of Neuroscience*, *23*(7), 2889–2898. https://doi.org/10.1523/jneurosci.23-07-02889.2003

Greenwood, B. N., Loughridge, A. B., Sadaoui, N., Christianson, J. P., & Fleshner, M. (2012). The protective effects of voluntary exercise against the behavioral consequences of uncontrollable stress persist despite an increase in anxiety following forced cessation of exercise. *Behavioural Brain Research*, *233*(2), 314–321. https://doi.org/10.1016/j.bbr.2012.05.017.The

Greenwood, B. N., Spence, K. G., Crevling, D. M., Clark, P. J., Craig, W. C., & Fleshner, M. (2013). Exercise-induced stress resistance is independent of exercise controllability and the medial prefrontal cortex. *European Journal of Neuroscience*, *37*(3), 469–478. https://doi.org/10.1111/ejn.12044

Greenwood, B. N., Strong, P. V., Dorey, A. A., & Fleshner, M. (2007). Therapeutic effects of exercise: Wheel running reverses stress-induced interference with shuttle box escape. *Behavioral Neuroscience*, *121*(5), 992–1000. https://doi.org/10.1037/0735-7044.121.5.992

Greiveldinger, L., Veissier, I., & Boissy, A. (2009). Behavioural and physiological responses of lambs to controllable vs. uncontrollable aversive events. *Psychoneuroendocrinology*, *34*(6), 805–814. https://doi.org/10.1016/j.psyneuen.2008.10.025

Greiveldinger, Lucile, Veissier, I., & Boissy, A. (2007). Emotional experience in sheep: Predictability of a sudden event lowers subsequent emotional responses. *Physiology and Behavior*, *92*(4), 675–683. https://doi.org/10.1016/j.physbeh.2007.05.012

Grippo, A. J., Gerena, D., Huang, J., Kumar, N., Shah, M., & Carter, C. S. (2007). Social isolation induces behavioral and neuroendocrine disturbances relevant to depression in female and male prarie voles. *Psychoneuroendocrinology*, *32*(8–10), 966–980.

Grippo, A. J., Wu, K. D., Hassan, I., & Carter, C. S. (2008). Social isolation in prairie voles induces behaviors relevant to negative affect: toward the development of a rodent model focused. *Depression and Anxiety*, *25*(6), E17–E26. https://doi.org/10.1002/da.20375.Social

Gross, J. J., & John, O. P. (2003). Individual differences in two emotion regulation processes: implications for affect, relationships, and well-being. *Journal of Personality and Social Psychology*, *85*(2), 348–362. https://doi.org/10.1037/0022-3514.85.2.348

Grotberg, E. (1995). A guide to promoting resilience in children: strengthening the human spirit. *Early Childhood Development: Practice and Reflections*, *8*, 1–39.

Gunawan, A. (2019). Blind orangutan found with 24 pellets his body now in stable condition.

Retrieved 16 June 2023, from The Jakarta Post website: https://www.thejakartapost.com/news/2019/11/28/blind-orangutan-found-with-24-pellets-his-body-now-in-stable-condition.html

Halsey, L. G., Coward, S. R. L., Crompton, R. H., & Thorpe, S. K. S. (2017). Practice makes perfect: Performance optimisation in 'arboreal' parkour athletes illuminates the evolutionary ecology of great ape anatomy. *Journal of Human Evolution*, *103*, 45–52. https://doi.org/10.1016/j.jhevol.2016.11.005

Han, X., Wang, W., Xue, X., Shao, F., & Li, N. (2011). Brief social isolation in early adolescence affects reversal learning and forebrain BDNF expression in adult rats. *Brain Research Bulletin*, *86*(3–4), 173–178. https://doi.org/10.1016/j.brainresbull.2011.07.008

Harati, H., Barbelivien, A., Herbeaux, K., Muller, M. A., Engeln, M., Kelche, C., … Majchrzak, M. (2013). Lifelong environmental enrichment in rats: Impact on emotional behavior, spatial memory vividness, and cholinergic neurons over the lifespan. *Age*, *35*(4), 1027–1043. https://doi.org/10.1007/s11357-012-9424-8

Harlow, H. F. (1958). The nature of love. *American Psychologist*, *13*, 673–685.

Hashmi, A., & Sullivan, M. (2020). The visitor effect in zoo-housed apes: the variable effect on behaviour of visitor number and noise. *Journal of Zoo and Aquarium Research*, *8*(4), 268–282. https://doi.org/10.19227/jzar.v8i4.523

Hattori, S., Hashimoto, R., Miyakawa, T., Yamanaka, H., Maeno, H., Wada, K., & Kunugi, H. (2007). Enriched environments influence depression-related behavior in adult mice and the survival of newborn cells in their hippocampi. *Behavioural Brain Research*, *180*(1), 69–76. https://doi.org/10.1016/j.bbr.2007.02.036

Hayes, S. C., Strosahl, K., Wilson, K. G., Bissett, R. T., Pistorello, J., Toarmino, D., … Mccurry, S. M. (2004). Measuring experiential avoidance: A preliminary test of a working model. *The Psychological Record*, *54*(4), 553–578. https://doi.org/10.1007/BF03395492

Heatherton, T. F., & Polivy, J. (1991). Development and validation of a scale for measuring state selfesteem. *Journal of Personality and Social Psychology*, *60*, 895–910.

Henshall, C., Davey, Z., & Jackson, D. (2020). The implementation and evaluation of a resilience enhancement programme for nurses working in the forensic setting. *International Journal of Mental Health Nursing*, *29*(3), 508–520. https://doi.org/10.1111/inm.12689

Heyman, G. D., & Cain, K. M. (2016). Young children's vulnerability to self-blame and helplessness: relationship to beliefs about goodness. *Child Development*, *63*(2), 401–415. https://doi.org/10.2307/1131488

Hirata, S., Hirai, H., Nogami, E., & Morimura, N. (2017). Chimpanzee Down syndrome: a case study of trisomy 22 in a captive chimpanzee. *Primates*, *58*(2), 267–273. https://doi.org/10.1007/s10329-017-0597-8

Hiroto, D. S. (1974). Locus of control and learned helplessness. *Journal of Experimental Psychology*, *102*(2), 187–193. https://doi.org/10.1037/h0035910

Hjemdal, O., Friborg, O., Stiles, T. C., Martinussen, M., & Rosenvinge, J. H. (2006). A New Scale for Adolescent Resilience: Grasping the Central Protective Resources Behind Healthy Development. *Measurement and Evaluation in Counseling and Development*, *39*(2), 84–96.

Hobaiter, C., & Byrne, R. W. (2010). Able-bodied wild chimpanzees imitate a motor procedure used by a disabled individual to overcome handicap. *PLoS ONE*, *5*(8), e11959. https://doi.org/10.1371/journal.pone.0011959

Hobfoll, S. E., Dunahoo, C. L., Ben-Porath, Y., & Monnier, J. (1994). Gender and coping: The The dual-axis model of coping. *American Journal of Community Psychology*, *22*, 49–82.

Hobfoll, Stevan E. (2002). Social and psychological resources and adaptation. *Review of General Psychology*, *6*(4), 307–324. https://doi.org/10.1037/1089-2680.6.4.307

Hoffman, A. N., Krigbaum, A., Ortiz, J. B., Mika, A., Hutchinson, K. M., Bimonte-Nelson, H. A., & Conrad, C. D. (2011). Recovery after chronic stress within spatial reference and working memory domains: Correspondence with hippocampal morphology. *European Journal of Neuroscience*, *34*(6), 1023–1030. https://doi.org/10.1111/j.1460-9568.2011.07820.x

Hong, S., Flashner, B., Chiu, M., ver Hoeve, E., Luz, S., & Bhatnagar, S. (2012). Social isolation in adolescence alters behaviors in the forced swim and sucrose preference tests in female but not in male rats. *Physiology and Behavior*, *105*(2), 269–275. https://doi.org/10.1016/j.physbeh.2011.08.036

Hopper, L. M., Shender, M. A., & Ross, S. R. (2016). Behavioral research as physical enrichment for captive chimpanzees. *Zoo Biology*, *35*, 293–297. https://doi.org/10.1002/zoo.21297

Hornor, G. (2017). Resilience. *Journal of Pediatric Health Care*, *31*(3), 384–390. https://doi.org/10.1016/j.pedhc.2016.09.005

Hosey, G. R. (2000). Zoo animals and their human audiences: What is the visitor effect? *Animal Welfare*, *9*(4), 343–357. https://doi.org/10.1017/S0962728600022946

Hourani, L., Tueller, S., Kizakevich, P., Lewis, G., Strange, L., Weimer, B., … Spira, J. (2016). Toward preventing post-traumatic stress disorder: Development and testing of a pilot predeployment stress inoculation training program. *Military Medicine*, *181*(9), 1151–1160. https://doi.org/10.7205/MILMED-D-15-00192

Hulshof, H. J., Novati, A., Sgoifo, A., Luiten, P. G. M., Den Boer, J. A., & Meerlo, P. (2011). Maternal separation decreases adult hippocampal cell proliferation and impairs cognitive performance but has little effect on stress sensitivity and anxiety in adult Wistar rats. *Behavioural Brain Research*, *216*(2), 552–560. https://doi.org/10.1016/j.bbr.2010.08.038

Hunton, V., Rendle, J., & Carter, A. (2022). Communication from the Zoo : Reports from Zoological Facilities of the Impact of COVID-19 Closures on Animals. *Journal of Zoological and Botanical Gardens*, *3*(2), 271–288. https://doi.org/10.3390/jzbg3020022

Hurley, J., Barrett, P., & Reet, P. (2006). 'Let a hundred flowers blossom, let a hundred schools of thought contend': a case for therapeutic pluralism in mental health nursing. *Journal of Psychiatric and Mental Health Nursing2*, *13*(2), 173–179. https://doi.org/https://doi.org/10.1111/j.1365-2850.2006.00938.x

Ilin, Y., & Richter-Levin, G. (2009). Enriched environment experience overcomes learning deficits and depressive-like behavior induced by juvenile stress. *PLoS ONE*, *4*(1). https://doi.org/10.1371/journal.pone.0004329

Isen, A. M. (2001). An influence of positive affect on decision making in complex situations: Theroretical issues with practical implications. *Journal of Consumer Psychology*, *11*(2), 75–85. https://doi.org/10.1207/s15327663jcp1102_01

Jacobson-Pick, S., Audet, M. C., Nathoo, N., & Anisman, H. (2011). Stressor experiences during the juvenile period increase stressor responsivity in adulthood: Transmission of stressor experiences. *Behavioural Brain Research*, *216*(1), 365–374. https://doi.org/10.1016/j.bbr.2010.08.016

Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: Implications for culture. *American Journal of Primatology*, *72*(1), 62–71. https://doi.org/10.1002/ajp.20752

Janoff-Bulman, R., & Brickman, P. (1982). Expectations and what people learn from failure. In N. T. Feather (Ed.), *Expectations and Actions: Expectancy-Value Models in Psychology* (pp. 207–237). https://doi.org/https://doi.org/10.4324/9781003150879

Jensvold, M. L. (2022). A preliminary assessment of compassion fatigue in chimpanzee caregivers. *Animals*, *12*(24), 3506. https://doi.org/10.3390/ani12243506

Jing, X. Y., Wang, Y., Zou, H. W., Li, Z. L., Liu, Y. J., & Li, L. F. (2021). mGlu2/3 receptor in the prelimbic cortex is implicated in stress resilience and vulnerability in mice. *European Journal of Pharmacology*, *906*, 174231. https://doi.org/10.1016/j.ejphar.2021.174231

Jones, M., Gartland, K. N., & Fuller, G. (2021). Effects of Visitor Presence and Crowd Size on Zoo-Housed Red Kangaroos (Macropus Rufus) During and After a COVID-19 Closure. *Animal Behaviour and Cognition*, *8*(4), 521–537. https://doi.org/10.26451/abc.08.04.06.2021

Joyce, S., Hons, B. A., Shand, F., Bryant, R. A., Lal, T. J., & Harvey, S. B. (2018). Mindfulness-based resilience training in the workplace: Pilot study of the internet-based Resilience@Work (RAW) mindfulness program. *Journal of Medical Internet Research*, *20*(9), e10326. https://doi.org/10.2196/10326

Kalinichev, M., Easterling, K. W., Plotsky, P. M., & Holtzman, S. G. (2002). Long-lasting changes in stress-induced corticosterone response and anxiety-like behaviors as a consequence of neonatal maternal separation in Long-Evans rats. *Pharmacology Biochemistry and Behavior*, *73*(1), 131–140. https://doi.org/10.1016/S0091-3057(02)00781-5

Katz, R. J., Roth, K. A., & Carroll, B. J. (1981). Acute and chronic stress effects on open field activity in the rat: Implications for a model of depression. *Neuroscience and Biobehavioral Reviews*, *5*(2), 247–251. https://doi.org/10.1016/0149-7634(81)90005-1

Kaye, M. (2016). Orangutan refugees: Weighing when to rescue the apes. Retrieved 14 June 2023, from Mongabay website: https://news.mongabay.com/2016/03/orangutan-refugees- weighing-when-to-rescue-the-apes/

Kent, M., Kovalev, D., Hart, B., Leserve, D., Handford, G., Vavra, D., & Lambert, K. (2022). The emotional impact of disrupted environmental contexts: Enrichment loss and coping profiles influence stress response recovery in Long–Evans rats. *Journal of*

Neuroendocrinology, *34*(7), e13179. https://doi.org/10.1111/jne.13179

Kessler, R. C. (1997). The effects of stressful life events on depression. *Annual Review of Psychology*, *48*, 191–214. https://doi.org/10.1146/annurev.psych.48.1.191

Keyes, C. L. M. (2002). The Mental Health Continuum: From Languishing to Flourishing in Life. *Journal of Health and Social Behavior*, *43*(2), 207–222.

Kinani, J. F., & Zimmerman, D. (2015). Tool use for food acquisition in a wild mountain gorilla (Gorilla beringei beringei). *American Journal of Primatology*, *77*(3), 353–357. https://doi.org/https://doi.org/10.1002/ajp.22351

King, J. E., & Landau, V. I. (2003). Can chimpanzee (Pan troglodytes) happiness be estimated by human raters? *Journal of Research in Personality*, *37*(1), 1–15. https://doi.org/10.1016/S0092-6566(02)00527-5

King, T., Chamberlain, C., & Courage, A. (2005). Rehabilitation of orphan gorillas and bonobos in the Congo. *International Zoo News*, *52*(4), 198–209.

Knott, C. D. (1998). Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*, *19*(6), 1061–1079. https://doi.org/10.1023/A:1020330404983

Kochi, C., Liu, H., Zaidi, S., Atrooz, F., Dantoin, P., & Salim, S. (2017). Prior treatmill exercise promotes resilience to vicarious trauma in rats. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *77*, 216–221. https://doi.org/10.1016/j.pnpbp.2017.04.018

Kozina, A. (2012). The LAOM Multidimensional Anxiety Scale for Measuring Anxiety in Children and Adolescents: Addressing the Psychometric Properties of the Scale. *Journal of Psychoeducational Assessment*, *30*(3), 264–273. https://doi.org/10.1177/0734282911423362/ASSET/IMAGES/LARGE/10.1177_0734282911423362-FIG1.JPEG

Kozina, A. (2020). School-based prevention of anxiety using the ‘My FRIENDS’ emotional resilience program: Six-month follow-up. *International Journal of Psychology*, *55*(S1), 70–77. https://doi.org/10.1002/ijop.12553

Kralick, A. E., O’Connell, C. A., Bastian, M. L., Hoke, M. K., Zemel, B. S., Schurr, T. G., & Tocheri, M. W. (2023). Beyond dimorphism: Body size variation among adult orangutans is not dichotomous by sex. *Integrative and Comparative Biology*, icad015. https://doi.org/10.1093/icb/icad015

Krause, E. T., Honarmand, M., Wetzel, J., & Naguib, M. (2009). Early fasting is long lasting: Differences in early nutritional conditions reappear under stressful conditions in adult female zebra finches. *PLoS ONE*, *4*(3), e5015. https://doi.org/10.1371/journal.pone.0005015

Kriengwatana, B., Farrell, T. M., Aitken, S. D. T., Garcia, L., & MacDougall-Shackleton, S. A. (2015). Early-life nutritional stress affects associative learning and spatial memory but not performance on a novel object test. *Behaviour*, *152*(2), 195–218. https://doi.org/10.1163/1568539X-00003239

Kroenke, K., Spitzer, R. L., & Williams, J. B. W. (2001). The PHQ-9: Validity of a Brief Depression Severity Measure. *Journal of General Internal Medicine*, *16*(9), 606. https://doi.org/10.1046/J.1525-1497.2001.016009606.X

Kruschke, J. K. (2021). Bayesian analysis reporting guidelines. *Nature Human Behaviour*, *5*(10), 1282–1291. https://doi.org/10.1038/s41562-021-01177-7

Kubala, K. H., Christianson, J. P., Kaufman, R. D., Watkins, L. R., & Maier, S. F. (2012). Short- and long-term consequences of stressor controllability in adolescent rats. *Behavioural Brain Research*, *234*(2), 278–284. https://doi.org/10.1016/j.bbr.2012.06.027

Kuhar, C. W. (2008). Group differences in captive gorillas' reaction to large crowds. *Applied Animal Behaviour Science*, *110*(3–4), 377–385. https://doi.org/10.1016/j.applanim.2007.04.011

Kutsukake, N. (2003). Assessing relationship quality and social anxiety among wild chimpanzees using self-directed behaviour. *Behaviour*, *140*(8), 1153–1171. https://doi.org/10.1163/156853903322589687

Lalanza, J. F., Sanchez-Roige, S., Cigarroa, I., Gagliano, H., Fuentes, S., Armario, A., … Escorihuela, R. M. (2015). Long-term moderate treadmill exercise promotes stress-coping strategies in male and female rats. *Scientific Reports*, *5*, 16166. https://doi.org/10.1038/srep16166

Lambert, K. G., Hyer, M. M., Rzucidlo, A. A., Bergeron, T., Landis, T., & Bardi, M. (2014). Contingency-based emotional resilience: Effort-based reward training and flexible coping lead to adaptive responses to uncertainty in male rats. *Frontiers in Behavioral Neuroscience*, *8*, 124. https://doi.org/10.3389/fnbeh.2014.00124

Lambert, K., Hyer, M., Bardi, M., Rzucidlo, A., Scott, S., Terhune-Cotter, B., … Kinsley, C. (2016). Natural-enriched environments lead to enhanced environmental engagement and altered neurobiological resilience. *Neuroscience*, *330*, 386–394. https://doi.org/10.1016/j.neuroscience.2016.05.037

Lameira, A. R., & Call, J. (2018). Time-space – displaced responses in the orangutan vocal system. *Science Advances*, *4*(11), eaau3401. https://doi.org/DOI: 10.1126/sciadv.aau3401

Langer, E. J. (1975). The illusion of control. *Journal of Personality and Social Psychology*, *32*(2), 311–328. https://doi.org/https://doi.org/10.1037/0022-3514.32.2.311

Las Hayas, C., Izco-Basurko, I., Fullaondo, A., Gabrielli, S., Zwiefka, A., Hjemdal, O., … Arnfjord, U. B. (2019). UPRIGHT, a resilience-based intervention to promote mental well-being in schools: Study rationale and methodology for a European randomized controlled trial. *BMC Public Health*, *19*(1), 1–10. https://doi.org/10.1186/S12889-019-7759-0/TABLES/2

Law, A., Logan, H., & Baron, R. S. (1994). Desire for control, felt control, and stress inoculation training during dental treatment. *Journal of Personality and Social Psychology*, *67*(5), 926–936. https://doi.org/10.1037//0022-3514.67.5.926.

Le Dorze, C., & Gisquet-Verrier, P. (2016). Effects of multiple brief exposures to trauma-associated cues on traumatized resilient and vulnerable rats. *Brain Research*, *1652*, 71–80. https://doi.org/10.1016/j.brainres.2016.10.002

Leasure, J. L., & Jones, M. (2008). Forced and voluntary exercise differentially affect brain and behavior. *Neuroscience*, *156*(3), 456–465. https://doi.org/10.1016/j.neuroscience.2008.07.041

Leckie, M. S. (1979). *Symptoms of Stress Inventory*. Seattle, Washington: University of Washington Press.

Lecrubier, Y., Sheehan, D. V., Weiller, E., Amorim, P., Bonora, I., Sheehan, K. H., … Dunbar, G. C. (1997). The Mini International Neuropsychiatric Interview (MINI). A short diagnostic structured interview: reliability and validity according to the CIDI. *European Psychiatry*, *12*(5), 224–231. https://doi.org/10.1016/S0924-9338(97)83296-8

Lee, C. W., Fang, Y. P., Chu, M. C., Chung, Y. J., Chi, H., Tang, C. W., … Lin, H. C. (2021). Differential mechanisms of synaptic plasticity for susceptibility and resilience to chronic social defeat stress in male mice. *Biochemical and Biophysical Research Communications*, *562*, 112–118. https://doi.org/10.1016/j.bbrc.2021.05.064

Lee, J. H., Kim, H. J., Kim, J. G., Ryu, V., Kim, B. T., Kang, D. W., & Jahng, J. W. (2007).

Depressive behaviors and decreased expression of serotonin reuptake transporter in rats that experienced neonatal maternal separation. *Neuroscience Research*, *58*(1), 32–39. https://doi.org/10.1016/j.neures.2007.01.008

Leggio, M. G., Mandolesi, L., Federico, F., Spirito, F., Ricci, B., Gelfo, F., & Petrosini, L. (2005). Environmental enrichment promotes improved spatial abilities and enhanced dendritic growth in the rat. *Behavioural Brain Research*, *163*(1), 78–90. https://doi.org/10.1016/j.bbr.2005.04.009

Lethmate, J. (1977a). Nest-building behavior of an isolated hand-reared young orangutan. *Primates*, *18*(3), 545–554. https://doi.org/10.1007/BF02383132

Lethmate, J. (1977b). Tool making by a young orangutan. *Behaviour*, *62*(1–2), 174–189. https://doi.org/https://doi.org/10.1163/156853977X00090

Leussis, M. P., Freund, N., Brenhouse, H. C., Thompson, B. S., & Andersen, S. L. (2012). Depressive-like behavior in adolescents after maternal separation: Sex differences, controllability, and GABA. *Developmental Neuroscience*, *34*(2–3), 210–217. https://doi.org/10.1159/000339162

Levenstein, S., Prantera, C., Varvo, V., Scribano, M. L., Berto, E., Luzi, C., & Andreoli, A. (1993). Development of the perceived stress questionnaire: A new tool for psychosomatic research. *Journal of Psychosomatic Research*, *37*(1), 19–32. https://doi.org/10.1016/0022-3999(93)90120-5

Lewis, R. N., Chang, Y. M., Ferguson, A., Lee, T., Clifforde, L., & Abeyesinghe, S. M. (2020). The effect of visitors on the behavior of zoo-housed western lowland gorillas (Gorilla gorilla gorilla). *Zoo Biology*, *39*(5), 283–296. https://doi.org/10.1002/zoo.21552

Li, B., Zhang, H., Cao, Y., Li, Z., Xu, X., Song, Z., & Wang, J. hui. (2022). Molecular changes in nucleus accumbens due to amelioration of depressive-like behavior by housing with companion. *Brain Research Bulletin*, *189*, 34–43. https://doi.org/10.1016/j.brainresbull.2022.08.010

Li, Z. L., Wang, Y., Zou, H. W., Jing, X. Y., Liu, Y. J., & Li, L. F. (2021). GABA(B) receptors within the lateral habenula modulate stress resilience and vulnerability in mice. *Physiology and Behavior*, *230*, 113311. https://doi.org/10.1016/j.physbeh.2021.113311

Litchholt, B. (2021). *Chimpanzees, conservation, and community: an analysis of the Jane Goodall Institute's Triangle Approach*. John Hopkins University.

Liu, H., Atrooz, F., Salvi, A., & Salim, S. (2017). Behavioral and cognitive impact of early life stress: insights from an animal model. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *78*, 88–95. https://doi.org/10.1002/dev.20449.Challenges

Lo, L., Iasiello, M., Carey, M., & Agteren, J. Van. (2020). Improving the wellbeing of female prisoners via psychological skills training: A feasability study. *International Journal of Offender Therapy and Comparative Criminology*, *64*(15), 1571–1586. https://doi.org/10.1177/0306624X20928029

Long, B. C. (1984). Aerobic conditioning and stress inoculation: A comparison of stress-management interventions. *Cognitive Therapy and Research*, *8*(5), 517–541. https://doi.org/https://doi.org/10.1007/BF01173289

Lonsdorf, E. V, Ross, S. R., Linick, S. A., Milstein, M. S., & Melber, T. N. (2009). An experimental , comparative investigation of tool use in chimpanzees and gorillas. *Animal Behaviour*, *77*(5), 1119–1126. https://doi.org/10.1016/j.anbehav.2009.01.020

Lovibond, S. H., & Lovibond, P. F. (1995). *Manual for the Depression Anxiety & Stress Scales* (2nd Editio). Sydney: Psychology Foundation.

Lu, J., Gong, X., Yao, X., Guang, Y., Yang, H., Ji, R., … Xie, P. (2021). Prolonged chronic social defeat stress promotes less resilience and higher uniformity in depression-like behaviors in adult male mice. *Biochemical and Biophysical Research Communications*, *553*, 107–113. https://doi.org/10.1016/j.bbrc.2021.03.058

Lu, S., Wei, F., & Li, G. (2021). The evolution of the concept of stress and the framework of the stress system. *Cell Stress*, *5*(6), 76–85. https://doi.org/10.15698/cst2021.06.250

Lucas, M., Ilin, Y., Anunu, R., Kehat, O., Xu, L., Desmedt, A., & Richter-Levin, G. (2014). Long-term effects of controllability or the lack of it on coping abilities and stress resilience in the rat. *Stress*, *17*(5), 423–430. https://doi.org/10.3109/10253890.2014.930430

Luine, V. (2002). Sex differences in chronic stress effects on memory in rats. *Stress*, *5*(3), 205–216. https://doi.org/10.1080/1025389021000010549

Luine, V., Martinez, C., Villegas, M., Magariños, A. M., & Mcewen, B. S. (1996). Restraint stress reversibly enhances spatial memory performance. *Physiology and Behavior*, *59*(1), 27–32. https://doi.org/10.1016/0031-9384(95)02016-0

Luine, V., Villegas, M., Martinez, C., & McEwen, B. S. (1994). Repeated stress causes reversible impairments of spatial memory performance. *Brain Research*, *639*(1), 167–170. https://doi.org/10.1016/0006-8993(94)91778-7

Lukas, K. E. (1999). A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (Gorilla gorilla gorilla). *Applied Animal Behaviour Science*, *63*(3), 237–249. https://doi.org/10.1016/S0168-1591(98)00239-1

Luo, L., Zande, L. E. va. der, Marwijk, M. A. va., Knol, E. F., Rodenburg, T. B., Bolhuis, J. E., & Parois, S. P. (2022). Impact of enrichment and repeated mixing on resilience in pigs. *Frontiers in Veterinary Science*, *9*, 829060. https://doi.org/10.3389/fvets.2022.829060

Luthar, S. S., & Zelazo, L. B. (2003). Research on resilience: An integrative review. In S. S. Luthar (Ed.), *Resilience and Vulnerability: Adaptation in the Context of childhood Adversities*. Cambridge: Cambridge University Press.

Lutz, A., Slagter, H. A., Dunne, J. D., & Davidson, R. J. (2008). Attention regulation and monitoring in meditation. *Trends in Cognitive Sciences*, *12*(4), 163–169. https://doi.org/10.1016/j.tics.2008.01.005

Lykken, D., & Tellegen, A. (1996). Happiness is a stochastic phenomenon. *Psychological Science*, *7*(3), 186–189. https://doi.org/10.1111/j.1467-9280.1996.tb00355.x

Lyons, D. M., Buckmaster, C. L., & Schatzberg, A. F. (2018). Learning to actively cope with stress in female mice. *Psychoneuroendocrinology*, *96*, 78–83. https://doi.org/10.1016/j.psyneuen.2018.06.010

Lyons, D. M., & Parker, K. J. (2007). Stress inoculation-induced indications of resilience in monkeys. *Journal of Traumatic Stress*, *20*(4), 423–433. https://doi.org/10.1002/jts.

Lyte, J. M., Koester, L. R., Daniels, K. M., & Lyte, M. (2022). Distinct cecal and fecal microbiome responses to stress are accompanied by sex- and diet-dependent changes in behavior and gut serotonin. *Frontiers in Neuroscience*, *16*, 827343. https://doi.org/10.3389/fnins.2022.827343

Machado, T. D., Dalle Molle, R., Laureano, D. P., Portella, A. K., Werlang, I. C. R., Benetti, C. D. S., … Silveira, P. P. (2013). Early life stress is associated with anxiety, increased stress responsivity and preference for ‘comfort foods’ in adult female rats. *Stress*, *16*(5), 549–556. https://doi.org/10.3109/10253890.2013.816841

Mackrain, M. (2008). *Deveraux Adult Resilience Scale*. Lewisville, North Carolina: Kaplan Early Learning Company Publishing.

Maddi, S. R. (2006). Hardiness: the courage to grow from stresses. *Journal of Positive*

Psychology, *1*(160–168).

Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, *44*(5), 967–979. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80592-5

Maggioncalda, A. (1995). *The socioendocrinology of orangutan growth, development, and reproduction—an analysis of endocrine profiles of juvenile, developing adolescent, developmentally arrested adolescent, adult, and aged captive male orangutans*. Duke University, North Carolina.

Mahoney, M. J., & Thoresen, C. E. (1974). *Self-Control: Power to the Person*. Monterey, California: Brooks-Cole.

Maier, S. F. (2001). Exposure to the stressor environment prevents the temporal dissipation of behavioral depression/learned helplessness. *Biological Psychiatry*, *49*(9), 763–773. https://doi.org/10.1016/S0006-3223(00)01095-7

Maisels, F., Bergl, R. A., & Williamson, E. A. (2018). Gorilla gorilla, Western gorilla. *The IUCN Red List of Threatened Species*, e.T9404A136250858. https://doi.org/http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T9404A136250858.en

Mällo, T., Matrov, D., Kõiv, K., & Harro, J. (2009). Effect of chronic stress on behavior and cerebral oxidative metabolism in rats with high or low positive affect. *Neuroscience*, *164*(3), 963–974. https://doi.org/10.1016/j.neuroscience.2009.08.041

Malone, N., Fuentes, A., & White, F. J. (2012). Variation in the social systems of extant hominoids: Comparative insight into the social behavior of early hominins. *International Journal of Primatology*, *33*, 1251–1277. https://doi.org/10.1007/s10764-012-9617-0

Mandleco, B. L., & Peery, J. C. (2000). An organizational framework for conceptualising resilience in children. *Journal of Child and Adolescent Psychiatric Nursing*, *13*(3), 99–111. https://doi.org/10.1111/j.1744-6171.2000.tb00086.x

Marais, L., van Rensburg, S. J., van Zyl, J. M., Stein, D. J., & Daniels, W. M. U. (2008). Maternal separation of rat pups increases the risk of developing depressive-like behavior after subsequent chronic stress by altering corticosterone and neurotrophin levels in the hippocampus. *Neuroscience Research*, *61*(1), 106–112. https://doi.org/10.1016/j.neures.2008.01.011

Marco, E. M., Valero, M., De La Serna, O., Aisa, B., Borcel, E., Ramirez, M. J., & Viveros, M. P. (2013). Maternal deprivation effects on brain plasticity and recognition memory in adolescent male and female rats. *Neuropharmacology*, *68*, 223–231. https://doi.org/10.1016/j.neuropharm.2012.08.014

Marino, J. (2023). Measuring burnout in zoo & aquarium professionals: A case for equity and justice. *Animal Keepers' Forum*, *50*(4), 103–108. https://doi.org/10.22541/au.167959485.55767921/v1

Markham, R., & Groves, C. P. (1990). Brief communication: weights of wild orang utans. *American Journal of Physical Anthropology*, *81*, 1–3. https://doi.org/https://doi.org/10.1002/ajpa.1330810102

Martland, R., Korman, N., Firth, J., Vancampfort, D., Thompson, T., & Stubbs, B. (2022). Can high-intensity interval training improve mental health outcomes in the general population and those with physical illnesses? A systematic review and meta-analysis of 53 randomized controlled trials. *British Journal of Sports Medicine*, *56*(5), 279–291. https://doi.org/10.1136/bjsports-2021-103984

Masman, M., Scarpace, C., Liriano, A., & Margulis, S. W. (2022). Does the absence of zoo visitors during the COVID-19 pandemic impact gorilla behavior. *Journal of Zoological and Botanical Gardens*, *3*(3), 349–356. https://doi.org/doi.org/10.3390/jzbg3030027

Mason, G. J. (1991). Stereotypies : a critical review. *Animal Behaviour*, *41*(6), 1015–1037. https://doi.org/https://doi.org/10.1016/S0003-3472(05)80640-2

Masten, A. S., Best, K. M., & Garmezy, N. (1990). Resilience and development: Contributions from the study of children who overcome adversity. *Development and Psychopathology*, *2*(4), 425–444. https://doi.org/10.1017/S0954579400005812

Masten, A. S., Morison, P., Pellegrini, D., & Tellegen, A. (1990). Competence under stress: risk and protective factors. In J. E. Rolf, A. S. Masten, D. Cicchetti, K. H. Nuechterlein, & S. Weintraub (Eds.), *Risk and Protective Factors in the Development of Psychopathology1* (pp. 236–256). Cambridge: Cambridge University Press.

Matsumoto, T., Itoh, N., Inoue, S., & Nakamura, M. (2016). An observation of a severely disabled infant chimpanzee in the wild and her interactions with her mother. *Primates*, *57*(1), 3–7. https://doi.org/10.1007/s10329-015-0499-6

McCormick, C. M., Smith, C., & Mathews, I. Z. (2008). Effects of chronic social stress in adolescence on anxiety and neuroendocrine response to mild stress in male and female rats. *Behavioural Brain Research*, *187*(2), 228–238. https://doi.org/10.1016/j.bbr.2007.09.005

McCubbin, M. (2023). Chapter 1: Orangutans. In *An Atlas of Endangered Species*. London: Two Roads Books.

McElreath, R. (2020). *Statistical Rethinking: A Bayesian Course with Examples in R and Stan* (2nd ed.). Florida: CRC Press.

McElreath, R. (2021). *Rethinking: Statistical Rethinking book package*.

McIntosh, J., Anisman, H., & Merali, Z. (1999). Short- and long-periods of neonatal maternal separation differentially affect anxiety and feeding in adult rats: Gender-dependent effects. *Developmental Brain Research*, *113*(1–2), 97–106. https://doi.org/10.1016/S0165-3806(99)00005-X

Mcloughlin, E., Arnold, R., Freeman, P., Turner, J. E., Roberts, G. A., Fletcher, D., … Moore, L. J. (2022). Lifetime stressor exposure and psychophysiological reactivity and habituation to repeated acute social stressors. *Journal of Sport and Exercise Psychology*, *44*(6), 427–438. https://doi.org/10.1123/jsep.2022-0196

Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, *102*, 246–261. https://doi.org/10.1016/j.applanim.2006.05.031

Meichenbaum, D. (1985). *Stress Inoculation Training*. Elmsford, New York: Pergamon Press.

Meichenbaum, D., & Cameron, R. (1983). Stress inoculation training: Toward a general paradigm for training coping skills. In D. Meichenbaum & M. Jaremko (Eds.), *Stress Reduction and Prevention* (pp. 115–154). New York: Plenum.

Meijaard, E., Buchori, D., Hadiprakarsa, Y., Utami-Atmoko, S. S., Nurcahyo, A., Tjiu, A., … Mengersen, K. (2011). Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. *PLoS ONE*, *6*(11), e27491. https://doi.org/10.1371/JOURNAL.PONE.0027491

Mellor, D. J., & Beausoleil, N. J. (2015). Extending the ‘Five Domains’ model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*, *24*(3), 241–253. https://doi.org/10.7120/09627286.24.3.241

Mellor, D. J., & Reid, C. S. W. (1994). Concepts of animal well-being and predicting the impact of procedures on experimental animals. In B. R, G. Jenkin, & M. DJ (Eds.), *Improving the Well-being of Animals in the Research Environment* (pp. 3–18). Glen Osmond, SA, Australia: Australian and New Zealand Council for the Care of Animals in Research and Teaching.

Mellor, David J., Beausoleil, N. J., Littlewood, K. E., McLean, A. N., McGreevy, P. D., Jones, B., & Wilkins, C. (2020). The 2020 Five Domains Model: Including human–animal interactions in assessments of animal welfare. *Animals*, *10*(10), 1870. https://doi.org/10.3390/ani10101870

Meyers, D. G., & Diener, E. (1995). Who is happy? *Psychological Science*, *6*(1), 10–19. https://doi.org/doi.org/10.1111/j.1467-9280.1995.tb00298.x

Miles, H. L. W. (1990). The cognitive foundations for reference in a signing orangutan. In S. T. Parker & K. R. Gibson (Eds.), *'Language' and Intelligence in Monkeys and Apes* (pp. 511–539). Cambridge: Cambridge University Press.

Miller, L. C., & Nadler, R. D. (1981). Mother-infant relations and infant development in captive chimpanzees and orang-utans. *International Journal of Primatology*, *2*(3), 247–261. https://doi.org/10.1007/BF02739333

Mineur, Y. S., Belzung, C., & Crusio, W. E. (2007). Functional implications of decreases in neurogenesis following chronic mild stress in mice. *Neuroscience*, *150*(2), 251–259. https://doi.org/10.1016/j.neuroscience.2007.09.045

Minulescu, M. (2008). ABCD-M Scales Description. In *ABCD-M Technical Manual (in Romanian)* (pp. 87–116). Sinapsis Publishing.

Moos, R. H. (1993). *Coping Responses Inventory: CRI from Adults*. Odessa, Texas: Psychological Assessment Resources.

Morales Picard, A., Mundry, R., Auersperg, A. M., Boeving, E. R., Boucherie, P. H., Bugnyar, T., … Slocombe, K. E. (2020). Why preen others? Predictors of allopreening in parrots and corvids and comparisons to grooming in great apes. *Ethology*, *126*(2), 207–228. https://doi.org/10.1111/eth.12999

Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, *102*(3–4), 262–302. https://doi.org/10.1016/J.APPLANIM.2006.05.032

Mourlon, V., Baudin, A., Blanc, O., Lauber, A., Giros, B., Naudon, L., & Daugé, V. (2010). Maternal deprivation induces depressive-like behaviours only in female rats. *Behavioural Brain Research*, *213*(2), 278–287. https://doi.org/10.1016/j.bbr.2010.05.017

Mrdalj, J., Murison, R., Soulé, J., Kinn Rød, A. M., Milde, A. M., Pallesen, S., & Grønli, J. (2016). Mild daily stressors in adulthood may counteract behavioural effects after constant presence of mother during early life. *Physiology and Behavior*, *165*, 313–321.

https://doi.org/10.1016/j.physbeh.2016.08.018

Muhammad, A., & Kolb, B. (2011). Maternal separation altered behavior and neuronal spine density without influencing amphetamine sensitization. *Behavioural Brain Research*, *223*(1), 7–16. https://doi.org/10.1016/j.bbr.2011.04.015

Mul, J. D., Soto, M., Cahill, M. E., Ryan, R. E., Takahashi, H., So, K., … Goodyear, L. J. (2018). Voluntary wheel running promotes resilience to chronic social defeat stress in mice: A role for nucleus accumbens ΔfosB. *Neuropsychopharmacology*, *43*(9), 1934–1942. https://doi.org/10.1038/s41386-018-0103-z

Nahvi, R. J., Tanelian, A., Nwokafor, C., Godino, A., Parise, E., Estill, M., … Sabban, E. L. (2023). Transcriptome profiles associated with resilience and susceptibility to single prolonged stress in the locus coeruleus and nucleus accumbens in male sprague-dawley rats. *Behavioural Brain Research*, *439*, 114162. https://doi.org/10.1016/j.bbr.2022.114162

Nair, S., Sagar, M., Sollers, J., Consedine, N., & Broadbent, E. (2015). Do slumped and upright postures affect stress responses? A randomized trial. *Health Psychology*, *34*(6), 632–641. https://doi.org/10.1037/hea0000146

Nakamichi, M. (2004). Tool-use and tool-making by captive, group-living orangutans (Pongo pygmaeus abelii) at an artificial termite mound. *Behavioural Processes*, *65*(1), 87–93. https://doi.org/10.1016/j.beproc.2003.07.002

Nakamichi, M., Fujii, H., & Koyama, T. (1983). Behavioral development of a malformed infant in a free-ranging group of Japanese monkeys. *Primates*, *24*(1), 52–66. https://doi.org/10.1007/BF02381453

Nakano, K. (1991). The Role of Coping Strategies on Psychological and Physical Well-being. *Japanese Psychological Research*, *33*(4), 160–167. https://doi.org/10.4992/PSYCHOLRES1954.33.160

NASA. (2003). Fires on Borneo and Sumatra. Retrieved 15 June 2023, from https://earthobservatory.nasa.gov/images/13664/fires-on-borneo-and-sumatra

Navaee, M., & Kaykha, H. (2019). The effects of stress inoculation training on coping strategies among midwives in primary health-care centers. *Nursing and Midwifery Studies*, *8*(4), 176–182. https://doi.org/10.4103/nms.nms_71_18

NCTSN. (2023). About child trauma. Retrieved 15 June 2023, from https://www.nctsn.org/what-is-child-trauma/about-child-trauma

Neff, K. D. (2003). Development and validation of a scale to measure self-compassion. *Self and Identity*, *2*, 223–250.

Neme, L. (2010). Teaching orangutans to be wild - orangutan rehabilitation. Retrieved 15 June 2023, from Mongabay website: https://news.mongabay.com/2010/12/teaching-orangutans-to-be-wild-orangutan-rehabilitation/

Neme, L. (2016). Leuser's legacy: how rescued orangutans help assure species survival. Retrieved 16 June 2023, from Mongabay website: https://news.mongabay.com/2016/03/leusers-legacy-how-rescued-orangutans-help-assure-species-survival/

Nijman, V. (2005). *In Full Swing: An Assessment of Trade in Orang-utans and Gibbons on Java and Bali, Indonesia*. Selangor: TRAFFIC Southeast Asia.

Nolen-Hoekseme, S., Fredrickson, B. L., Loftus, G. R., & Lutz, C. (2014). *Atkinson & Hilgard's Introduction to Psychology* (16th ed.). Boston: Cengage Learning.

Novaco, R. W. (1975). *Anger Control: The Development and Evaluation of an Experimental Treatment*. Lexington: Lexington Books.

Novak, M. A., & Harlow, H. F. (1975). Social recovery of monkeys isolated for the first year of life: I. Rehabilitation and therapy. *Developmental Psychology*, *11*(4), 453–465. https://doi.org/10.1037/h0076661

Núñez, Juan F., Ferré, P., García, E., Escorihuela, R. M., Fernández-Teruel, A., & Tobeña, A. (1995). Postnatal handling reduces emotionality ratings and accelerates two-way active avoidance in female rats. *Physiology and Behavior*, *57*(5), 831–835. https://doi.org/10.1016/0031-9384(94)00308-R

Núñez, Juan Francisco, Ferré, P., Escorihuela, R. M., Tobeña, A., & Fernández-Teruel, A. (1996). Effects of postnatal handling of rats on emotional, HPA-Axis, and prolactin reactivity to novelty and conflict. *Physiology and Behavior*, *60*(5), 1355–1359. https://doi.org/10.1016/S0031-9384(96)00225-9

Ogawa, T., Mikuni, M., Kuroda, Y., Muneoka, K., Mori, K. J., & Takahashi, K. (1994). Periodic maternal deprivation alters stress response in adult offspring: Potentiates the negative feedback regulation of restraint stress-induced adrenocortical response and reduces the frequencies of open field-induced behaviors. *Pharmacology, Biochemistry and Behavior*, *49*(4), 961–967. https://doi.org/10.1016/0091-3057(94)90250-X

Otsu, N. (1979). A threshold selection method from gray-level histograms. *IEEE*

Transactions on Systems, Man, and Cybernetics, *9*(1), 62–66. https://doi.org/10.1109/TSMC.1979.4310076

Overmier, J. B., & Seligman, M. E. (1967). Effects of inescapable shock upon subsequent escape and avoidance responding. *Journal of Comparative and Physiological Psychology*, *63*(1), 28–33. https://doi.org/10.1037/h0024166

Palmer, A. (2018). Kill, incarcerate, or liberate? Ethics and alternatives to orangutan rehabilitation. *Biological Conservation*, *227*, 181–188. https://doi.org/10.1016/j.biocon.2018.09.012

Parihar, V., Hattiangady, B., Kuruba, R., Shuai, B., & Shetty, A. (2011). Predictable chronic mild stress improves mood, hippocampal neurogenesis and memory. *Physiology and Behavior*, *16*(2), 171–183. https://doi.org/10.1038/mp.2009.130

Parker, K. J., Buckmaster, C. L., Hyde, S. A., Schatzberg, A. F., & Lyons, D. M. (2019). Nonlinear relationship between early life stress exposure and subsequent resilience in monkeys. *Scientific Reports*, *9*(1), 1–8. https://doi.org/10.1038/s41598-019-52810-5

Parker, K. J., Buckmaster, C. L., Justus, K. R., Schatzberg, A. F., & Lyons, D. M. (2005). Mild early life stress enhances prefrontal-dependent response inhibition in monkeys. *Biological Psychiatry*, *57*(8), 848–855. https://doi.org/10.1016/j.biopsych.2004.12.024

Parker, K. J., Buckmaster, C. L., Lindley, S. E., Schatzberg, A. F., & Lyons, D. M. (2012). Hypothalamic-pituitary-adrenal axis physiology and cognitive control of behavior in stress inoculated monkeys. *International Journal of Behavioral Development*, *36*(1), 543–562. https://doi.org/10.1177/0165025411406864.

Parker, K. J., Buckmaster, C. L., Schatzberg, A. F., & Lyons, D. M. (2004). Prospective investigation of stress inoculation in young monkeys. *Archives of General Psychiatry*, *61*(9), 933–941. https://doi.org/10.1001/archpsyc.61.9.933

Parker, K. J., Rainwater, K. L., Buckmaster, C. L., Schatzberg, A. F., Lindley, S. E., & Lyons, D. M. (2007). Early life stress and novelty seeking behavior in adolescent monkeys. *Psychoneuroendocrinology*, *32*(7), 785–792. https://doi.org/10.1016/j.psyneuen.2007.05.008

Patki, G., Solanki, N., & Salim, S. (2014). Witnessing traumatic events causes severe behavioral impairments in rats. *International Journal of Neuropsychopharmacology*, *17*(12), 2017–2029. https://doi.org/10.1017/S1461145714000923

Peleg-Raibstein, D., & Feldon, J. (2011). Differential effects of post-weaning juvenile stress on the behaviour of C57BL/6 mice in adolescence and adulthood. *Psychopharmacology*, *214*(1), 339–351. https://doi.org/10.1007/s00213-010-1991-8

Pellegrini, A. D., & Smith, P. K. (Eds.). (2005). *The Nature of Play: Great Apes and Humans*. New York: The Guildford Press.

Pelsker, R., & Mayer, V. (2008). Nonhuman primates mask signs of pain. *Laboratory Primate Newsletter*, *47*(1), 1–3.

Peng, L., Li, M., Zuo, X., Miao, Y., Chen, L., Yu, Y., … Wang, T. (2014). Application of the Pennsylvania resilience training program on medical students. *Personality and Individual Differences*, *61–62*, 47–51. https://doi.org/10.1016/j.paid.2014.01.006

Penke, Z., Felszeghy, K., Fernette, B., Sage, D., Nyakas, C., & Burlet, A. (2001). Postnatal maternal deprivation produces long-lasting modifications of the stress response, feeding and stress-related behaviour in the rat. *European Journal of Neuroscience*, *14*(4), 747–755. https://doi.org/10.1046/j.0953-816X.2001.01691.x

Perrine, S. A., Eagle, A. L., George, S. A., Mulo, K., Kohler, R. J., Gerard, J., … Conti, A. C. (2016). Severe, multimodal stress exposure induces PTSD-like characteristics in a mouse model of single prolonged stress. *Behavioural Brain Research*, *303*, 228–237. https://doi.org/10.1016/j.bbr.2016.01.056

Pietrelli, A., Di Nardo, M., Masucci, A., Brusco, A., Basso, N., & Matkovic, L. (2018). Lifelong aerobic exercise reduces the stress response in rats. *Neuroscience*, *376*, 94–107. https://doi.org/10.1016/j.neuroscience.2018.02.019

Pilkonis, P. A., Choi, S. W., Reise, S. P., Stover, A. M., Riley, W. T., & Cella, D. (2011). Item Banks for Measuring Emotional Distress From the Patient-Reported Outcomes Measurement Information System (PROMIS®): Depression, Anxiety, and Anger. *Assessment*, *18*(3), 263–283. https://doi.org/10.1177/1073191111411667

Pluess, M., Boniwell, I., Hefferon, K., & Tunariu, A. (2017). Preliminary evaluation of a school-based resilience-promoting intervention in a high- risk population: Application of an exploratory two-cohort treatment/control design. *PLoS ONE*, *12*(5), 1–18. https://doi.org/10.1371/journal. pone.0177191

Plumptre, A. J., Nixon, S., Kujirakwinja, D. K., Vieilledent, G., Critchlow, R., Williamson, E. A., … Hall, S. (2016). Catastrophic decline of world’s largest primate: 80% loss of Grauer’s gorilla (Gorilla beringei graueri) population justifies critically endangered status. *PLoS ONE*, *11*(10), e0162697. https://doi.org/10.1371/journal.pone.0162697

Plumptre, A. J., Robbins, M. M., & Williamson, E. A. (2019). Gorilla beringei, Eastern gorilla. *The IUCN Red List of Threatened Species*, e.T39994A115576640. https://doi.org/http://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39994A115576640.en

Pohl, J., Olmstead, M. C., Wynne-Edwards, K. E., Harkness, K., & Menard, J. L. (2007). Repeated exposure to stress across the childhood-adolescent period alters rats' anxiety- and depression-like behaviors in adulthood: The importance of stressor type and gender. *Behavioral Neuroscience*, *121*(3), 462–474. https://doi.org/10.1037/0735-7044.121.3.462

Power, R. A., & Pluess, M. (2015). Heritability estimates of the Big Five personality traits based on common genetic variants. *Translational Psychiatry*, *5*(7), e604. https://doi.org/10.1038/tp.2015.96

Pradhan, G. R., Van Noordwijk, M. A., & van Schaik, C. P. (2012). A model for the evolution of developmental arrest in male orangutans. *American Journal of Physical Anthropology*, *149*(1), 18–25. https://doi.org/10.1002/ajpa.22079

Prasetyo, D. (2019). *Understanding bimaturism: the influence of social conditions, energy intake, and endocrinological status on flange development in Bornean orangutans (Pongo pygmaeus wurmbii)*. Rutgers, the State University of New Jersey.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, *1*, 515–526. https://doi.org/https://doi.org/10.1017/S0140525X00076512

Preuschoft, S., Yassir, I., Putri, A. I., Aoliya, N., Yuliani, E., Badriyah, S. N., … Kalcher-sommersguter, E. (2021). Learning to be an orangutan - implications of life history for orangutan rehabilitation. *Animals*, *11*(3), 1–23. https://doi.org/10.3390/ani11030767

Prince, C. R., & Anisman, H. (1984). Acute and chronic stress effects on performance in a forced-swim task. *Behavioral and Neural Biology*, *42*(2), 99–119. https://doi.org/10.1016/S0163-1047(84)90942-7

ProKal. (2017). Orangutan yang Masuki Kebun Warga Kembali Dilepasliarkan. Retrieved 14 June 2023, from ProKalteng website: http://kalteng.prokal.co/read/news/41643-orangutan- yang-masuki-kebun-warga-kembali-dilepasliarkan.html

Pryce, C. R., Dettling, A., Spengler, M., Spaete, C., & Feldon, J. (2004). Evidence for altered monoamine activity and emotional and cognitive disturbance in marmoset monkeys exposed to early life stress. *Annals of the New York Academy of Sciences*, *1032*, 245–249. https://doi.org/10.1196/annals.1314.030

Puppe, B., Ernst, K., Schön, P. C., & Manteuffel, G. (2007). Cognitive enrichment affects behavioural reactivity in domestic pigs. *Applied Animal Behaviour Science*, *105*(1–3), 75–86. https://doi.org/10.1016/j.applanim.2006.05.016

R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Radloff, L. S. (1977). The CES-D Scale: A self-report depression scale for research in the general population. *Applied Psychological Measurement*, *1*(3), 385–401. https://doi.org/https://doi.org/10.1177/014662167700100306

Reimers, M., Schwarzenberger, F., & Preuschoft, S. (2007). Rehabilitation of research chimpanzees: Stress and coping after long-term isolation. *Hormones and Behavior*, *51*(3), 428–435. https://doi.org/10.1016/j.yhbeh.2006.12.011

Remus, J. L., Jamison, D., & Johnson, J. D. (2013). An animal model of recurrent depression: Sensitized depression-like behavior when rats are re-exposed to chronic mild stress. *Brain, Behavior, and Immunity*, *32*(S), e4–e5. https://doi.org/10.1016/j.bbi.2013.07.026

Reynolds, W. M. (1987). *Reynolds Adolescent Depression Scale: Professional Manual*. Odessa, Florida: Psychological Assessment Resources.

Riskind, J. H., & Gotay, C. C. (1982). Physical posture: Could it have regulatory or feedback effects on motivation and emotion? *Motivation and Emotion*, *6*, 273–298.

Riskind, John H., & Gotay, C. C. (1982). Physical posture: Could it have regulatory or feedback effects on motivation and emotion? *Motivation and Emotion*, *6*(3), 273–298. https://doi.org/10.1007/BF00992249/METRICS

Robinson, S., Christ, C. C., Cahill, M. M., Aldrich, S. J., & Taylor-Yeremeeva, E. (2019). Voluntary exercise or systemic propranolol ameliorates stress-related maladaptive behaviors in female rats. *Physiology and Behavior*, *198*, 120–133. https://doi.org/10.1016/j.physbeh.2018.10.012

Röder, E. L., Timmermans, P. J. A. A., & Vossen, J. M. H. H. (1989). Effects of rearing and exposure condition upon the acquisition of phobic behaviour in cynomolgus monkeys. *Behaviour Research and Therapy*, *27*(3), 221–231. https://doi.org/10.1016/0005-7967(89)90040-5

Rogerson, S., Meir, R., Crowley-mchattan, Z., Mcewen, K., & Pastoors, R. (2016). A randomized controlled pilot trial investigating the impact of a workplace resilience program during a time of significant organizational change. *Journal of Occupational and Environmental Medicine*, *58*(4), 329–334. https://doi.org/10.1097/JOM.0000000000000677

Romeo, R. D., Mueller, A., Sisti, H. M., Ogawa, S., McEwen, B. S., & Brake, W. G. (2003). Anxiety and fear behaviors in adult male and female C57BL/6 mice are modulated by maternal separation. *Hormones and Behavior*, *43*(5), 561–567. https://doi.org/10.1016/S0018-506X(03)00063-1

Rosenberg, M. (1965). *Society and the Adolescent Self-Image*. Princeton, New Jersey: Princeton University Press.

Roth, T. S., Rianti, P., Fredriksson, G. M., Wich, S. A., & Nowak, M. G. (2020). Grouping behavior of Sumatran orangutans (Pongo abelii) and Tapanuli orangutans (Pongo tapanuliensis) living in forest with low fruit abundance. *American Journal of Primatology*, *82*(5), e23123. https://doi.org/10.1002/ajp.23123

Russon. (2009). Orangutan rehabilitation and reintroduction. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 327–350). New York: Oxford University Press.

Russon, A. E. (2008). Orangutan rehabilitation and reintroduction: Successes, failures, and role in conservation. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 327–350). https://doi.org/10.1093/acprof:oso/9780199213276.001.0001

Rutter, M. (2012). Resilience as a dynamic concept. *Development and Psychopathology*, *24*(2), 335–344. https://doi.org/10.1017/S0954579412000028

Ryan, E. B., Proudfoot, K. L., & Fraser, D. (2012). The effect of feeding enrichment methods on the behavior of captive Western lowland gorillas. *Zoo Biology*, *31*(2), 235–241. https://doi.org/10.1002/zoo.20403

Ryff, C. D. (1989). Happiness is everything, or is it? Explorations on the meaning of psychological well-being. *Journal of Personality and Social Psychology*, *57*, 1069–1081.

Sackett, G. P. (1972). Exploratory behavior of rhesus monkeys as a function of rearing experiences and sex. *Developmental Psychology*, *6*(2), 260–270.

https://doi.org/10.1037/h0032081

Sakuraba, Y., Tomonaga, M., & Hayashi, M. (2016). A new method of walking rehabilitation using cognitive tasks in an adult chimpanzee (Pan troglodytes) with a disability: a case study. *Primates*, *57*(3), 403–412. https://doi.org/10.1007/S10329-016-0541-3/FIGURES/5

Sampedro-Piquero, P., Castilla-Ortega, E., Zancada-Menendez, C., Santín, L. J., & Begega, A. (2016). Environmental enrichment as a therapeutic avenue for anxiety in aged Wistar rats: Effect on cat odor exposition and GABAergic interneurons. *Neuroscience*, *330*, 17–25. https://doi.org/10.1016/j.neuroscience.2016.05.032

Santarelli, S., Zimmermann, C., Kalideris, G., Lesuis, S. L., Arloth, J., Uribe, A., … Schmidt, M. V. (2017). An adverse early life environment can enhance stress resilience in adulthood. *Psychoneuroendocrinology*, *78*, 213–221. https://doi.org/10.1016/j.psyneuen.2017.01.021

Savage, A., & Snowdon, C. T. (1982). Mental retardation and neurological deficits in a twin orangutan. *American Journal of Primatology*, *3*(1–4), 239–251. https://doi.org/10.1002/ajp.1350030121

Scheier, M., & Carver, C. (2001). Optimism, pessimism, and self-regulation. In E. C. Chang (Ed.), *Optimism and Pessimism: Implications for theory, research, and practice*. Washington, DC: American Psychological Association.

Scheier, M. F., & Carver, C. S. (1985). Optimism, coping, and health: Assessment and implications of generalized outcome expectancies. *Health Psychology*, *4*, 219–247.

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., … Cardona, A. (2012). Fiji: an open-source platform for biological-image analysis. *Nature Methods*, *9*(7), 676–682. https://doi.org/doi:10.1038/nmeth.2019

Schmidt, D. A. (2004). Nutrition. In *Orangutan Husbandry Manual*. Orangutan Species Survival Plan.

Schreurs, P. J. G., van de Willige, G., Tellegen, B., & Brosschot, J. F. (1993). *Herziene handleiding Utrechtse Coping Lijst (UCL)*. Lisse: Swets & Zeitlinger B.V.

Schrijver, N. C. A., Bahr, N. I., Weiss, I. C., & Würbel, H. (2002). Dissociable effects of isolation rearing and environmental enrichment on exploration, spatial learning and HPA activity in adult rats. *Pharmacology Biochemistry and Behavior*, *73*(1), 209–224. https://doi.org/10.1016/S0091-3057(02)00790-6

Schubert, T., Friedmann, F., & Regenbrecht, H. (2001). The experience of presence: Factor analystic insights. *Presence: Teleoperators and Virtual Environments*, *10*(3), 266–281.

Schuppli, C., Forss, S., Meulman, E., Atmoko, S. U., & van Noordwijk, M. (2017). The effects of sociability on exploratory tendency and innovation repertoires in wild Sumatran and Bornean orangutans. *Scientific Reports*, *7*(1), 15464. https://doi.org/10.1038/s41598-017-15640-x

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/10.1016/j.anbehav.2016.06.014

Schwartz, G. E., Davidson, R. J., & Goleman, D. J. (1978). Patterning of cognitive and somatic processes in the self-regulation of anxiety: Effects of meditation versus exercise. *Psychosomatic Medicine*, *40*(4), 321–328. https://doi.org/10.1097/00006842-197806000-00004

Schwarzer, R., & Jerusalem, M. (1995). Generalized Self-Efficacy Scale. In J. Weinman, S. Wright, & M. Johnston (Eds.), *Measures in health psychology: A user's portfolio. Causal and control beliefs* (pp. 35–37). Windsor, England: NFER-NELSON.

Seery, M. D., Leo, R. J., Lupien, S. P., Kondrak, C. L., & Almonte, J. L. (2013). An upside to adversity? Moderate cumulative lifetime adversity is associated with resilient responses in the face of controlled stressors. *Psychological Science*, *24*(7), 1181–1189. https://doi.org/10.1177/0956797612469210

Seery, Mark D., Holman, E. A., & Silver, R. C. (2010). Whatever does not kill us: Cumulative lifetime adversity, vulnerability, and resilience. *Journal of Personality and Social Psychology*, *99*(6), 1025–1041. https://doi.org/10.1037/a0021344

Seligman, M. E., Maier, S. F., & Geer, J. H. (1968). Alleviation of learned helpless in the dog. *Journal of Abnormal Psychology*, *73*(3), 256–262. https://doi.org/10.1037/h0025831

Seligman, M. E. P. (1975). *Helplessness: On depression, development, and death*. San Francisco: Freeman.

Seligman, M. E. P., & Csikszentmihalyi, M. (2000). Positive psychology: An introduction. *American Psychologist*, *55*(1), 5–14. https://doi.org/https://doi.org/10.1037/0003-066X.55.1.5

Seligman, M. E., Rosellini, R. A., & Kozak, M. J. (1975). Learned helplessness in the rat:

Time course, immunization, and reversibility. *Journal of Comparative and Physiological Psychology*, *88*(2), 542–547. https://doi.org/10.1037/h0076431

Seligman, Martin E. P., Kaslow, N. J., Alloy, L. B., Peterson, C., Tanenbaum, R. L., & Abramson, L. Y. (1984). Attributional style and depressive symptoms among children. *Journal of Abnormal Psychology*, *93*(2), 235–238. https://doi.org/10.1037/0021-843X.93.2.235

Shatté, A., Perlman, A., Smith, B., & Lynch, W. D. (2017). The Positive Effect of Resilience on Stress and Business Outcomes in Difficult Work Environments. *Journal of Occupational and Environmental Medicine*, *59*(2), 135–140. https://doi.org/10.1097/JOM.0000000000000914

Sherman, J., Ancrenaz, M., & Meijaard, E. (2020). Shifting apes: Conservation and welfare outcomes of Bornean orangutan rescue and release in Kalimantan, Indonesia. *Journal for Nature Conservation*, *55*, 125807. https://doi.org/10.1016/J.JNC.2020.125807

Sherwen, S. L., Harvey, T. J., Magrath, M. J. L., Butler, K. L., Fanson, K. V, & Hemsworth, P. H. (2015). Effects of visual contact with zoo visitors on black-capped capuchin welfare. *Applied Animal Behaviour Science*, *167*, 65–73. https://doi.org/10.1016/j.applanim.2015.03.004

Sherwen, S. L., & Hemsworth, P. H. (2019). The visitor effect on zoo animals: Implications and opportunities for zoo animal welfare. *Animals*, *9*(6), 366. https://doi.org/10.3390/ANI9060366

Shi, D. D., Zhang, Y. D., Ren, Y. Y., Peng, S. Y., Yuan, T. F., & Wang, Z. (2021). Predictable maternal separation confers adult stress resilience via the medial prefrontal cortex oxytocin signaling pathway in rats. *Molecular Psychiatry*, *26*(12), 7296–7307. https://doi.org/10.1038/s41380-021-01293-w

Shi, P., Hu, L., Ren, H., & Dai, Q. (2023). Reward enhances resilience to chronic social defeat stress in mice: Neural ECs and mGluR5 mechanism via neuroprotection in VTA and DRN. *Frontiers in Psychiatry*, *14*, 1084367. https://doi.org/10.3389/fpsyt.2023.1084367

Shu, C., Xiao, L., Tang, J., Wang, G., Zhang, X., & Wang, X. (2015). Blunted behavioral and molecular responses to chronic mild stress in adult rats with experience of infancy maternal separation. *Tohoku Journal of Experimental Medicine*, *235*(2), 18–87. https://doi.org/10.1620/tjem.235.81

Shure, M. B., Spivack, G., & Jaeger, M. (1971). Problem-solving thinking and adjustment among disadvantaged preschool children. *Child Development*, *42*(6), 1791. https://doi.org/10.2307/1127585

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Simons, J., & Gaher, R. (2005). The Distress Tolerance Scale: development and validation of a self-report measure. *Motivation and Emotion*, *29*, 83–102.

Singleton, I., Wich, S. A., Nowak, M., Usher, G., Utami-Atmoko, S. S., & -. (2018). Pongo abelii, Sumatran Orangutan. In *The IUCN Red List of Threatened Species 2017*. https://doi.org/10.1016/j.cub.2017.09.047.Taxonomic

Siviy, S. M., & Harrison, K. A. (2008). Effects of neonatal handling on play behavior and fear towards a predator odor in juvenile rats (Rattus norvegicus). *Journal of Comparative Psychology*, *122*(1), 1–8. https://doi.org/10.1037/0735-7036.122.1.1

Skynner, L. A., Amory, J. R., & Hosey, G. (2004). The effect of visitors on the self-injurious behaviour of a male pileated gibbon (Hylobates pileatus). *Zoologische Garten*, *74*(1), 38–41.

Smith, B., Shatté, A., Perlman, A., Siers, M., & Lynch, W. D. (2018). Improvements in resilience, stress, and somatic symptoms following online resilience training: A dose-response effect. *Journal of Occupational and Environmental Medicine*, *60*(1), 1–5. https://doi.org/10.1097/JOM.0000000000001142

Smith, B. W., Dalen, J., Wiggins, K., Tooley, E., Christopher, P., & Bernard, J. (2008). The brief resilience scale: assessing the ability to bounce back. *International Hournal of Behavioral Medicine*, *15*(3), 194–200.

Smith, R. J., & Jungers, W. L. (1997). Body mass in comparative primatology. *Journal of Human Evolution*, *32*(6), 523–559. https://doi.org/https://doi.org/10.1006/jhev.1996.0122

Smith, T. E., McGreer-Whitworth, B., & French, J. A. (1998). Close proximity of the heterosexual partner reduces the physiological and behavioral consequences of novel-cage housing in black tufted-ear marmosets (Callithrix kuhli). *Hormones and Behavior*, *34*(3), 211–222. https://doi.org/10.1006/hbeh.1998.1469

SOCP. (2023a). Orangutan confiscation. Retrieved 15 June 2023, from https://www.sumatranorangutan.org/our-work/creating-new-wild-populations/confiscation/

SOCP. (2023b). Rehabilitation. Retrieved 15 June 2023, from https://www.sumatranorangutan.org/our-work/creating-new-wild-populations/rehabilitation/

SOCP. (2023c). Why is Orangutan Haven needed? Retrieved 15 June 2023, from https://orangutanhaven.com/why-is-orangutan-haven-needed/

Spielberger, C. D. (1988). *Manual for the State-Trait Anger Expression Inventory (STAXI)*. Odessa, Florida: Psychological Assessment Resources.

Spielberger, C. D., Gorsuch, R. L., & Lushene, R. E. (1970). *STAI Manual for the State-Trait Anxiety Inventory*. Palo Alto: Consulting Psychologists Press.

Špinka, M., & Wemelsfelder, F. (2011). Environmental Challenge and Animal Agency. In *Animal Welfare* (pp. 27–44). Wallingford, UK: CAB International.

Spitzer, R. L., Kroenke, K., Williams, J. B. W., & Löwe, B. (2006). A brief measure for assessing generalized anxiety disorder: the GAD-7. *Archives of Internal Medicine*, *166*(10), 1092–1097. https://doi.org/10.1001/ARCHINTE.166.10.1092

Stamatakis, A., Pondiki, S., Kitraki, E., Diamantopoulou, A., Panagiotaropoulos, T., Raftogianni, A., & Stylianopoulou, F. (2008). Effect of neonatal handling on adult rat spatial learning and memory following acute stress. *Stress*, *11*(2), 148–159. https://doi.org/10.1080/10253890701653039

Steinhardt, M., & Doblier, C. (2010). Evaluation of a resilience intervention to enhance coping strategies and protective factors and decrease symptomatology. *Journal of American College Health*, *56*(4), 445–453. https://doi.org/10.3200/JACH.56.44.445-454

Sterlemann, V., Ganea, K., Liebl, C., Harbich, D., Alam, S., Holsboer, F., … Schmidt, M. V. (2008). Long-term behavioral and neuroendocrine alterations following chronic social stress in mice: Implications for stress-related disorders. *Hormones and Behavior*, *53*(2), 386–394. https://doi.org/10.1016/j.yhbeh.2007.11.001

Stoinski, Tara S, Jaicks, Ã. H. F., Drayton, L. A., Atlanta, Z., Dian, T., Gorilla, F., & International, F. (2012). Visitor effects on the behavior of captive western lowland gorillas: The importance of individual differences in examining welfare. *Zoo Biology*, *31*(5), 586–599. https://doi.org/10.1002/zoo.20425

Strekalova, T., Pavlov, D., Trofimov, A., Anthony, D. C., Svistunov, A., Proshin, A., …

Cespuglio, R. (2022). Hippocampal over-expression of cyclooxygenase-2 (COX-2) is associated with susceptibility to stress-induced anhedonia in mice. *International Journal of Molecular Sciences*, *23*(4), 2061. https://doi.org/10.3390/ijms23042061

Strelau, J., & Zawadzki. (1993). The Formal Characteristics of Behavior - Temperament Inventory (FCB-TI): theoretical assumptions and scale construction. *European Journal of Personality*, *7*, 313–336.

Strindberg, S., Maisels, F., Williamson, E. A., Blake, S., Stokes, E. J., Aba, R., … Wilkie, D. S. (2018). Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Science Advances*, *4*(4), eaar2964. https://doi.org/10.1126/sciadv.aar2964

Strzelewicz, A. R., Ordoñes Sanchez, E., Rondón-Ortiz, A. N., Raneri, A., Famularo, S. T., Bangasser, D. A., & Kentner, A. C. (2019). Access to a high resource environment protects against accelerated maturation following early life stress: A translational animal model of high, medium and low security settings. *Hormones and Behavior*, *111*, 46–59. https://doi.org/10.1016/j.yhbeh.2019.01.003

Sun, X. M., Tu, W. Q., Shi, Y. W., Xue, L., & Zhao, H. (2014). Female-dependent impaired fear memory of adult rats induced by maternal separation, and screening of possible related genes in the hippocampal CA1. *Behavioural Brain Research*, *267*, 111–118. https://doi.org/10.1016/j.bbr.2014.03.022

Suo, L., Zhao, L., Si, J., Liu, J., Zhu, W., Chai, B., … Lu, L. (2013). Predictable chronic mild stress in adolescence increases resilience in adulthood. *Neuropsychopharmacology*, *38*(8), 1387–1400. https://doi.org/10.1038/npp.2013.67

Suomi, S. J., & Harlow, H. F. (1972). Social rehabilitation of isolate-reared monkeys. *Developmental Psychology*, *6*(3), 487–496. https://doi.org/10.1037/h0032545

Suomi, S. J., Harlow, H. F., & Domek, C. J. (1970). Effect of repetitive infant-infant separation of young monkeys. *Journal of Abnormal Psychology*, *76*(2), 161–172. https://doi.org/10.1037/h0029809

Sussman, R. W., Garber, P. A., & Cheverud, J. M. (2005). News and views: Importance of cooperation and affiliation in the evolution of primate sociality. *American Journal of Physical Anthropology*, *128*(1), 84–97. https://doi.org/10.1002/ajpa.20196

Swiergiel, A. H., Zhou, Y., & Dunn, A. J. (2007). Effects of chronic footshock, restraint and corticotropin-releasing factor on freezing, ultrasonic vocalization and forced swim behavior in rats. *Behavioural Brain Research*, *183*(2), 178–187. https://doi.org/10.1016/j.bbr.2007.06.006

Szabo, Z., & Marian, M. (2012). Stress inoculation training in adolescents: Classroom intervention benefits. *Journal of Cognitive and Behavioral Psychotherapies*, *12*(2), 175–188.

Tamir, M., John, O. P., Srivastava, S., & Gross, J. J. (2007). Implicit Theories of Emotion: Affective and Social Outcomes Across a Major Life Transition. *Journal of Personality and Social Psychology*, *92*(4), 731–744. https://doi.org/10.1037/0022-3514.92.4.731

Tanner, M. K., Fallon, I. P., Baratta, M. V., & Greenwood, B. N. (2019). Voluntary exercise enables stress resistance in females. *Behavioural Brain Research*, *369*, 111923. https://doi.org/10.1016/j.bbr.2019.111923.

Taylor, J. (2022). *Sexy but Psycho*. London: Constable.

Taylor, S. (2020). Animal crips. In S. Jenkins, K. S. Montford, & C. Taylor (Eds.), *Disability and Animality: Crip Perspectives in Critical Animal Studies* (pp. 13–34). Abingdon: Routledge.

Tecwyn, Emma C., Thorpe, S. K. S., & Chappell, J. (2013). A novel test of planning ability: Great apes can plan step-by-step but not in advance of action. *Behavioural Processes*, *100*, 174–184. https://doi.org/10.1016/j.beproc.2013.09.016

Tecwyn, Emma Carolan. (2013). *Physical Cognition in Great Apes : Planning & Object Compliance*. University of Birmingham.

Tennant, R., Hiller, L., Fishwick, R., Platt, S., Joseph, S., Weich, S., … Stewart-Brown, S. (2007). The Warwick-Edinburgh Mental Wellbeing Scale (WEMWBS): development and UK validation. *Health and Quality of Life Outcomes*, *5*(63). https://doi.org/https://doi.org/10.1186/1477-7525-5-63

Thompson, M. E., Zhou, A., & Knott, C. D. (2012). Low testosterone correlates with delayed development in male orangutans. *PLoS ONE*, *7*(10), 1–7. https://doi.org/10.1371/journal.pone.0047282

Thorpe, S. K. S., Neufuss, J., Myatt, J., Tarrega, E., Wamba, G., Sulistyo, F., … Chappell, J. (2022). The EDT: An evidence-based framework for improving captive great ape well-being. In S. Unwin, A. White, & A. Landiouw (Eds.), *State of the Apes Volume V: Health and Disease at the Human-Ape Interface*. ARCUS Foundation.

Thorpe, S. K.S., Crompton, R. H., & Alexander, R. M. N. (2007). Orangutans use compliant branches to lower the energetic cost of locomotion. *Biology Letters*, *3*(3), 253–256. https://doi.org/10.1098/rsbl.2007.0049

Thorpe, Susannah K.S., & Crompton, R. H. (2005). Locomotor ecology of wild orangutans (Pongo pygmaeus abelii) in the Gunung Leuser ecosystem, Sumatra, Indonesia: A multivariate analysis using log-linear modelling. *American Journal of Physical Anthropology*, *127*(1), 58–78. https://doi.org/10.1002/ajpa.20151

Thorpe, Susannah K.S., Holder, R., & Crompton, R. H. (2009). Orangutans employ unique strategies to control branch flexibility. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(31), 12646–12651. https://doi.org/10.1073/pnas.0811537106

Toledo-Rodriguez, M., & Sandi, C. (2007). Stress before puberty exerts a sex- and age-related impact on auditory and contextual fear conditioning in the rat. *Neural Plasticity*, *2007*, 71203. https://doi.org/10.1155/2007/71203

Torrisi, S. A., Lavanco, G., Maurel, O. M., Gulisano, W., Laudani, S., Geraci, F., … Leggio, G. M. (2021). A novel arousal-based individual screening reveals susceptibility and resilience to PTSD-like phenotypes in mice. *Neurobiology of Stress*, *14*, 100286. https://doi.org/10.1016/j.ynstr.2020.100286

Toth, E., Gersner, R., Wilf-Yarkoni, A., Raizel, H., Dar, D. E., Richter-Levin, G., … Zangen, A. (2008). Age-dependent effects of chronic stress on brain plasticity and depressive behavior. *Journal of Neurochemistry*, *107*(2), 522–532. https://doi.org/10.1111/j.1471-4159.2008.05642.x

Tsoory, M., Cohen, H., & Richter-Levin, G. (2007). Juvenile stress induces a predisposition to either anxiety or depressive-like symptoms following stress in adulthood. *European Neuropsychopharmacology*, *17*(4), 245–256. https://doi.org/10.1016/j.euroneuro.2006.06.007

Tsoory, M., & Richter-Levin, G. (2006). Learning under stress in the adult rat is differentially affected by ‘juvenile’ or ‘adolescent’ stress. *International Journal of Neuropsychopharmacology*, *9*(6), 713–728. https://doi.org/10.1017/S1461145705006255

Turner, S. E., Fedigan, L. M., Matthews, H. D., & Nakamichi, M. (2014). Social consequences of disability in a nonhuman primate. *Journal of Human Evolution*, *68*(1), 47–57. https://doi.org/10.1016/J.JHEVOL.2014.01.002

Uher, J., Asendorpf, J. B., & Call, J. (2008). Personality in the behaviour of great apes:

temporal stability, cross-situational consistency and coherence in response. *Animal Behaviour*, *75*(1), 99–112. https://doi.org/10.1016/j.anbehav.2007.04.018

Ungur, M., & Liebenberg, L. (2011). Assessing Resilience Across Cultures Using Mixed Methods: Construction of the Child and Youth Resilience Measure. *Journal of Mixed Methods Research*, *5*(2), 126–149.

Utami-Atmoko, S., Traylor-Holzer, K., Rifqi, M. A., Siregar, P. G., Achmad, B., Priadjati, A., … Lees, C. M. (2017). *Orangutan Population and Habitat Viability Assessment: Final Report*. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

Utami, S. S., Goossens, B., Bruford, M. W., De Ruiter, J. R., & Van Hooff, J. A. R. A. M. (2002). Male bimaturism and reproductive success in Sumatran orang-utans. *Behavioral Ecology*, *13*(5), 643–652. https://doi.org/10.1093/BEHECO/13.5.643

Uysal, N., Ozdemir, D., Yalaz, G., & Bediz, C. S. (2005). Effects of maternal deprivation on melatonin production and cognition in adolescent male and female rats. *Neuroendocrinology Letters*, *26*(5), 555–560.

van Adrichem, G. G. J., Utami, S. S., Wich, S. A., van Hooff, J. A. R. A. M., & Sterck, E. H. M. (2006). The development of wild immature Sumatran orangutans (Pongo abelii) at Ketambe. *Primates*, *47*(4), 300–309. https://doi.org/10.1007/S10329-006-0193-9/FIGURES/6

van Casteren, A., Sellers, W. I., Thorpe, S. K. S., Coward, S., Crompton, R. H., Myatt, J. P., & Ennos, A. R. (2012). Nest-building orangutans demonstrate engineering know-how to produce safe, comfortable beds. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(18), 6873–6877. https://doi.org/10.1073/pnas.1200902109

van Doeselaar, L., Yang, H., Bordes, J., Brix, L., Engelhardt, C., Tang, F., & Schmidt, M. V. (2021). Chronic social defeat stress in female mice leads to sex-specific behavioral and neuroendocrine effects. *Stress*, *24*(2), 168–180. https://doi.org/10.1080/10253890.2020.1864319

van Noordwijk, M A, Sauren, S. E. B., Abham, A. A., Morrogh-Bernard, H. C., Atmoko, S. S. U., & van Schaik, C. P. (2009). Development of independence: Sumatran and Bornean orangutans compared. In S. A. Wich, S. S. U. Atmoko, R. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (pp. 189–203). https://doi.org/10.1093/acprof:oso/9780199213276.001.0001

van Noordwijk, Maria A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, *127*(1), 79–94. https://doi.org/10.1002/AJPA.10426

Van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution*, *36*(6), 719–741. https://doi.org/10.1006/jhev.1999.0304

Varker, T., & Devilly, G. J. (2012). An analogue trial of inoculation/resilience training for emergency services personnel: Proof of concept. *Journal of Anxiety Disorders*, *26*(6), 696–701. https://doi.org/10.1016/j.janxdis.2012.01.009

Videan, E. N. (2006). Bed-building in captive chimpanzees (Pan troglodytes): the importance of early rearing. *American Journal of Physical Anthropology*, *68*(7), 745–751.

Völter, C. J., & Call, J. (2012). Problem solving in great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo abelii): The effect of visual feedback. *Animal Cognition*, *15*(5), 923–936. https://doi.org/10.1007/s10071-012-0519-5

von Bernhardi, R., Eugenín-von Bernhardi, L., & Eugenín, J. (2017). What is neural plasticity? *Advances in Experimental Medicine and Biology*, *1015*, 1–15. https://doi.org/10.1007/978-3-319-62817-2_1

Wagnild, G. M., & Young, H. (1993). Development and psychometric evaluation of the resilience scale. *Journal of Nursing Measurement*, *1*(2), 165–178.

Walker, S. C., Cavieres, A., Peñaloza-Sancho, V., El-Deredy, W., McGlone, F. P., & Dagnino-Subiabre, A. (2022). C-low threshold mechanoafferent targeted dynamic touch modulates stress resilience in rats exposed to chronic mild stress. *European Journal of Neuroscience*, *55*, 2925–2938. https://doi.org/10.1111/ejn.14951

Walsh, P. D., Abernethy, K. A., Bermejo, M., Beyers, R., Wachter, P. De, Akou, M. E., & Huijbregts, B. (2003). Catastrophic ape decline in western equatorial Africa. *Nature*, *422*, 611–614. https://doi.org/10.1038/nature01472.1.

Wang, Y., Jiang, Y., Song, B. L., Zou, H. W., Li, Z. L., Li, L. F., & Liu, Y. J. (2022). mGlu2/3 receptors within the ventral part of the lateral septal nuclei modulate stress resilience and vulnerability in mice. *Brain Research*, *1779*, 147783. https://doi.org/10.1016/j.brainres.2022.147783

Watanabe, S. (2010). Asymptotic equivalence of Bayes cross validation and Widely Applicable Information Criterion in singular learning theory. *Journal of Machine Learning Research*, *11*, 3571–3594.

https://doi.org/https://doi.org/10.48550/arXiv.1004.2316

Watson, D., Clark, L. A., & Tellegen, A. . (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality and Social Psychology*, *54*(6), 1063–1070. https://doi.org/https://doi.org/10.1037/0022-3514.54.6.1063

Weathers, F. W., Litz, B. T., Keane, T. M., Palmieri, P. A., Marx, B. P., & Schnurr, P. P. (2013). The PTSD Checklist for DSM-5 (PCL-5). Retrieved from National Center for PTSD website: www.ptsd.va.gov

Wei, Y., Wang, G., Wang, H., He, J., Zhang, N., Wu, Z., … Yang, C. (2018). Sex-dependent impact of different degrees of maternal separation experience on OFT behavioral performances after adult chronic unpredictable mild stress exposure in rats. *Physiology and Behavior*, *194*, 153–161. https://doi.org/10.1016/j.physbeh.2018.04.034

Weintraub, A., Singaravelu, J., & Bhatnagar, S. (2010). Enduring and sex-specific effects of adolescent social isolation in rats on adult stress reactivity. *Brain Research*, *1343*, 83–92. https://doi.org/10.1016/j.brainres.2010.04.068

Weiss, A., Gartner, M. C., Gold, K. C., & Stoinski, T. S. (2013). Extraversion predicts longer survival in gorillas: An 18-year longitudinal study. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1752), 20122231. https://doi.org/10.1098/rspb.2012.2231

Weissman, M. M., & Paykel, E. S. (1974). *The Depressed Woman: A Study of Social Relationships*. Chicago: Universities Press.

Wells, D. L. (2005). A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, *93*(1–2), 13–17. https://doi.org/10.1016/J.APPLANIM.2005.06.019

Wemelsfelder, F., Haskell, M., Mendl, M. T., Calvert, S., & Lawrence, A. B. (2000). Diversity of behaviour during novel object tests is reduced in pigs housed in substrate-impoverished conditions. *Animal Behaviour*, *60*(3), 385–394. https://doi.org/10.1006/anbe.2000.1466

Wesner, J. S., & Pomeranz, J. P. F. (2021). Choosing priors in Bayesian ecological models by simulating from the prior predictive distribution. *Ecosphere*, *12*(9), e03739. https://doi.org/10.1002/ecs2.3739

Whiten, A., & Mesoudi, A. (2008). Establishing an experimental science of culture: Animal social diffusion experiments. *Philosophical Transactions of the Royal Society B:*

Biological Sciences, *363*(1509), 3477–3488. https://doi.org/10.1098/rstb.2008.0134

Wich, S. A., Meijaard, E., Marshall, A., Husson, S., Ancrenaz, M., Lacy, R., … Singleton, I. (2008). Distribution and conservation status of the orangutan (Pongo spp.) on Borneo and Sumatra: how many remain? *Oryx*, *42*(3), 329–339. https://doi.org/doi:10.1017/S003060530800197X

Wich, S. A., Singleton, I., Nowak, M. G., Utami Atmoko, S. S., Nisam, G., Arif, S. M., … Kühl, H. S. (2016). Land-cover changes predict steep declines for the Sumatran orangutan (Pongo abelii). *Science Advances*, *2*(3), e1500789. https://doi.org/doi:10.1126/sciadv.1500789

Wich, S. A., Struebig, M., Refisch, J., Wilting, A., Kramer-Schadt, S., & Meijaard, E. (2015). *The Future of the Bornean Orangutan: Impacts of Change in Land Cover and Climate*. Nairobi: UNEP/GRASP.

Wich, S. A., Vogel, E. R., Larsen, M. D., Fredriksson, G., Leighton, M., Yeager, C. P., … Marshall, A. J. (2011). Forest fruit production is higher on Sumatra than on Borneo. *PLoS One*, *6*(6), e21279. https://doi.org/doi: 10.1371/journal.pone.0021278

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Wickham, H., & Bryan, J. (2022). *readxl: Read Excel Files*.

Wilkin, M., Waters, P., McCormick, C., & Menard, J. (2012). Intermittent physical stress during early- and mid-adolescence differentially alters rats' anxiety- and depression-like behaviors in adulthood. *Behavioral Neuroscience*, *126*(2), 344–360. https://doi.org/10.1037/a0027258

Williams, E., Carter, A., Rendle, J., Fontani, S., Walsh, N. D., Armstrong, S., … Ward, S. J. (2022). The impact of COVID-19 zoo closures on behavioural and physiological parameters of welfare in primates. *Animals*, *12*(13), 1622. https://doi.org/doi: 10.3390/ani12131622

Williams, E., Carter, A., Rendle, J., & Ward, S. J. (2021a). Impacts of COVID-19 on animals in zoos: A longitudinal multi-species analysis. *Journal of Zoological and Botanical Gardens*, *2*, 130–145. https://doi.org/10.3390/jzbg2020010

Williams, E., Carter, A., Rendle, J., & Ward, S. J. (2021b). Understanding impacts of zoo visitors: Quantifying behavioural changes of two popular zoo species during COVID-19 closures. *Applied Animal Behaviour Science*, *236*, 105253. https://doi.org/10.1016/j.applanim.2021.105253

Willmore, L., Cameron, C., Yang, J., Witten, I. B., & Falkner, A. L. (2022). Behavioural and dopaminergic signatures of resilience. *Nature*, *611*(7934), 124–132. https://doi.org/10.1038/s41586-022-05328-2

Winwood, P. C., Colon, R., Psych, O., & Mcewen, K. (2013). *A Practical Measure of Workplace Resilience Developing the Resilience at Work Scale*. https://doi.org/10.1097/JOM.0b013e3182a2a60a

Wisløff, U., Ellingsen, Ø., & Kemi, O. J. (2009). High-intensity interval training to maximize cardiac benefits of exercise training? *Exercise and Sport Sciences Reviews*, *37*(3), 139–146. https://doi.org/10.1097/JES.0b013e3181aa65fc

Wolpe, J., & Lang, P. J. (1964). A fear survey schedule for use in behaviour therapy. *Behavior Research and Therapy*, *2*(1), 27–30.

Wommack, J. C., Salinas, A., Melloni, R. H., & Delville, Y. (2004). Behavioural and neuroendocrine adaptations to repeated stress during puberty in male golden hamsters. *Journal of Neuroendocrinology*, *16*(9), 767–775. https://doi.org/10.1111/j.1365-2826.2004.01233.x

Wood, G. E., Norris, E. H., Waters, E., Stoldt, J. T., & McEwen, B. S. (2008). Chronic immobilization stress alters aspects of emotionality and associative learning in the rat. *Behavioral Neuroscience*, *122*(2), 282–292. https://doi.org/10.1037/0735-7044.122.2.282

Wood, W. (1998). Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (Pan troglodytes). *Zoo Biology*, *17*(3), 211–230. https://doi.org/10.1002/(SICI)1098-2361(1998)17:3<211::AID-ZOO5>3.0.CO;2-C

Yan, L., Wang, M., Yang, F., Wang, Y., Wang, S., So, K. F., & Zhang, L. (2023). Physical exercise mediates a cortical FMRP–mTOR pathway to improve resilience against chronic stress in adolescent mice. *Translational Psychiatry*, *13*(1), 16. https://doi.org/10.1038/s41398-023-02311-x

Yang, Y., Cao, J., Xiong, W., Zhang, J., Zhou, Q., Wei, H., … Xu, L. (2003). Both stress experience and age determine the impairment or enhancement effect of stress on spatial memory retrieval. *Journal of Endocrinology*, *178*(1), 45–54. https://doi.org/10.1677/joe.0.1780045

Yohn, N. L., & Blendy, J. A. (2017). Adolescent chronic unpredictable stress exposure is a sensitive window for long-term changes in adult behavior in mice. *Neuropsychopharmacology*, *42*(8), 1670–1678. https://doi.org/10.1038/npp.2017.11

Zalosnik, M. I., Pollano, A., Trujillo, V., Suárez, M. M., & Durando, P. E. (2014). Effect of maternal separation and chronic stress on hippocampal-dependent memory in young adult rats: Evidence for the match-mismatch hypothesis. *Stress*, *17*(5), 445–450. https://doi.org/10.3109/10253890.2014.936005

Zambrana, C., Marco, E. M., Arranz, L., De Castro, N. M., Viveros, M. P., & De La Fuente, M. (2007). Influence of aging and enriched environment on motor activity and emotional responses in mice. *Annals of the New York Academy of Sciences*, *1100*, 543–552. https://doi.org/10.1196/annals.1395.060

Zandberg, L., Quinn, J. L., Naguib, M., & van Oers, K. (2017). Personality-dependent differences in problem-solving performance in a social context reflect foraging strategies. *Behavioural Processes*, *134*, 95–102. https://doi.org/10.1016/j.beproc.2016.09.007

Zhang, J., He, Z. xiong, Qu, Y. shan, Li, L. fu, Wang, L. min, Yuan, W., … Tai, F. dao. (2021). Different baseline physical activity predicts susceptibility and resilience to chronic social defeat stress in mice: Involvement of dopamine neurons. *European Neuropsychopharmacology*, *45*, 15–28. https://doi.org/10.1016/j.euroneuro.2021.02.011

Zimmerman, P. H., & Koene, P. (1998). The effect of loss of predictability and controllability of reward during frustration on behaviour in two strains of laying hens, Gallus gallus domesticus. *Netherlands Journal of Zoology*, *48*(3), 255–265. https://doi.org/10.1163/156854298x00101

Appendix A: Overview of common tools to measure resilience in humans

Category	**Name of measure**	**Citation**
Resilience	Adult Resilience Scale	(Mackrain, 2008)
	Adult Resilience Social Acceptability Measure	(Barrett, Lowry-Webster, Turner, & Johnson, 1998)
	Brief Resilience Scale	(B. W. Smith et al., 2008)
	Child and Youth Resilience Measure	(Ungur & Liebenberg, 2011)
	Connor-Davidson Resilience Scale	(Connor & Davidson, 2003)
	Coping Inventory for Stressful Situations	(Endler & Parker, 1990)
	Coping Orientations to Problems Experienced (COPE) Scale	(Carver, Scheier, & Weintraub, 1989)
	Coping Responses Inventory	(Moos, 1993)
	Dispositional Resilience Scale	(Bartone, 1991)
	Distress Tolerance Scale	(Simons & Gaher, 2005)
	MeQuilibrium Resilience Measure	(Shatté, Perlman, Smith, & Lynch, 2017)
	Resilience at Work (R@W) Scale	(Winwood, Colon, Psych, & Mcewen, 2013)
	Resilience Scale	(Wagnild & Young, 1993)
	Resilience Scale for Adolescents (READ-28)	(Hjemdal, Friborg, Stiles, Martinussen, & Rosenvinge, 2006)
	Resilience Scale for Adults	(Friborg, Hjemdal, Rosenvinge, & Martinussen, 2003)
	Strategic Approach to Coping Scale	(S. E. Hobfoll, Dunahoo, Ben-Porath, & Monnier, 1994)
	Utrecht Coping List	(Schreurs, van de Willige, Tellegen, & Brosschot, 1993)
	Ways of Coping Checklist	(Nakano, 1991)
Stress	Brief Symptom Inventory (Global Distress)	(Derogatis, 2001)
	Depression, Anxiety, and Stress Scale	(Lovibond & Lovibond, 1995)
	Perceived Stress Questionnaire	(Levenstein et al., 1993)

Category	Name of measure	Citation
	Perceived Stress Scale	(Cohen, Kamarck, & Mermelstein, 1983)
	PTSD Checklist	(Weathers et al., 2013)
	PTSD Symptom Scale - Self-Report	(Foa, Riggs, Dancu, & Rothbaum, 1993)
	Symptoms of Stress Inventory	(Leckie, 1979)
	Tension Thermometer	(Long, 1984)
Emotional regulation	Cognitive Emotion Regulation Questionnaire	(Garnefski & Kraaij, 2006)
	Difficulties in Emotion Regulation Scale	(Gratz & Roemer, 2004)
	Emotion Regulation Questionnaire	(Gross & John, 2003)
	Implicit Theories of Emotion Scale	(Tamir, John, Srivastava, & Gross, 2007)
	Proneness to Provocation	(Novaco, 1975)
	Strengths and Difficulties Questionnaire - Emotional Problems Score	(Goodman, 1997)
	Self-monitoring of anger reactions	(Mahoney & Thoresen, 1974)
	State-Trait Anger Expression Inventory	(Spielberger, 1988)
Depression	Beck Depression Inventory	(A. T. Beck, Ward, Mendelson, Mock, & Erbaugh, 1961)
	Center for Epidemiologic Studies Depression Scale	(Radloff, 1977)
	Depression, Anxiety, and Stress Scale	(Lovibond & Lovibond, 1995)
	Mini International Neuropsychiatric Interview (MINI) Depression Scale	(Lecrubier et al., 1997)
	Patient Health Questionnaire (for depression)	(Kroenke, Spitzer, & Williams, 2001)
	Patient-Reported Outcomes Measurement Information System (PROMIS) Depression and Anxiety symptom measures	(Pilkonis et al., 2011)
	Reynolds Adolescent Depression Scale	(Reynolds, 1987)
Anxiety	AN-UD Anxiety Scale	(Kozina, 2012)
	Cognitive-Somatic Anxiety Questionnaire	(Schwartz, Davidson, & Goleman, 1978)

Category	**Name of measure**	**Citation**
	Depression, Anxiety, and Stress Scale	(Lovibond & Lovibond, 1995)
	Generalised Anxiety Disorder Scale	(Spitzer, Kroenke, Williams, & Löwe, 2006)
	Patient-Reported Outcomes Measurement Information System (PROMIS) Depression and Anxiety symptom measures	(Pilkonis et al., 2011)
	State-Trait Anxiety Inventory Trait Anxiety Scale (STAI A-TRAIT)	(Spielberger, Gorsuch, & Lushene, 1970)
Psychological wellbeing	Mental Health Continuum	(Keyes, 2002)
	PERMA Profiler	(Butler & Kern, 2016)
	Positive and Negative Affect Scale (PANAS)	(Watson, Clark, & Tellegen, 1988)
	Psychological Well-Being Scale	(Ryff, 1989)
	Warwick-Edinburgh Mental Wellbeing Scale	(Tennant et al., 2007)
Personality	ABCD-M personality test	(Minulescu, 2008)
	Formal Characteristics of Behaviour - Temperament Inventory	(Strelau & Zawadzki, 1993)
	Revised NEO Personality Inventory	(P. T. Costa & McCrae, 2008)
	Ten-Item Personality Inventory	(Gosling, Rentfrow, & Swann, 2003)
Self-efficacy	Coping Self-Efficacy	(Chesney, Neilands, Chambers, Taylor, & Folkman, 2006)
	General Self-Efficacy Scale	(Schwarzer & Jerusalem, 1995)
	Internal Control Index	(Duttweiler, 2016)
	Self-Efficacy Scale	(Coppel, 1980)
Self-esteem	Coopersmith Self-Esteem Inventory	(Coopersmith, 1981)
	Rosenberg Self-Esteem Scale	(Rosenberg, 1965)
	State Self-Esteem Scale - Current Thoughts	(Heatherton & Polivy, 1991)
Mindfulness	Five Facet Mindfulness Questionnaire	(Baer, Smith, Hopkins, Krietemeyer, & Toney, 2006)
	Freiburg Mindfulness Inventory	(Buchheld, Grossman, & Walach, 2001)
Other	Acceptance and Action Questionnaire	(Hayes et al., 2004)

Category	Name of measure	Citation
	Achievement Goal Scale	(Elliot & Church, 1997)
	Cognitive Fusion Questionnaire	(Gillanders et al., 2014)
	Fear Survey Schedule	(Wolpe & Lang, 1964)
	Igroup Presence Questionnaire	(Schubert, Friedmann, & Regenbrecht, 2001)
	Interpersonal Support Evaluation List	(Cohen, Memelstein, Kamarck, & Hoberman, 1985)
	Life Orientation Test (for optimism)	(M. F. Scheier & Carver, 1985)
	Self-Compassion Scale	(Neff, 2003)
	Social Adjustment Scale	(Weissman & Paykel, 1974)

Appendix B: Overview of common types of nonhuman animal behavioural measurements relevant to resilience

Attribute	Relevance	Name of measure	Taxonomic groups
Anxiety	Stress indicator	Elevated plus maze/elevated zero maze	Rodents
		Open field test	Rodents/ agricultural
		Light/dark test	Rodents/birds
		Novelty suppressed feeding test	Rodents
		Behavioural observations	Any
		‘Behaviourally anchored’ criteria for generalized anxiety disorder.	Primates
Depression	Stress indicator	Porsolt forced swim test	Rodents
		Social interaction test (with stranger)	Rodents
		Tail suspension	Rodents
		Latency to escape electric shock.	Rodents/dogs
		Sucrose consumption test (quantity).	Rodents
		Sucrose preference test (over water).	Rodents
		Body weight.	Rodents
Memory and spatial learning	Problem-solving/ planning	Radial arm maze (win-shift tasks)	Rodents
		Fear conditioning	Rodents
		Two-way shuttle-box	Rodents/dogs
		Morris water maze/Dry Morris water maze (on land)	Rodents
		Spatial foraging task	Birds
		Associative learning task	Birds
		Novel odor recognition memory test	Rodents
		Barnes maze	Rodents
		Y-maze	Rodents
Fear & emotional reactivity	Low emotional reactivity	Acoustic startle	Rodents/ primates
		Two-way shuttle-box	Rodents/dogs
		Fear conditioning/extinction	Rodents
		Tonic immobility test	Birds
		Hole-in-the-wall test	Birds
		Novel object test	Any
Exploration	Curiosity and physical activity	Open field test / novel environment	Any
		Novel object	Any
		Novel odour	Rodents
		Novelty-suppressed feeding test	Rodents
		Social exploration/juvenile social exploration	Rodents
		Approach/avoidance test	Primates
		Behavioural observations	Any

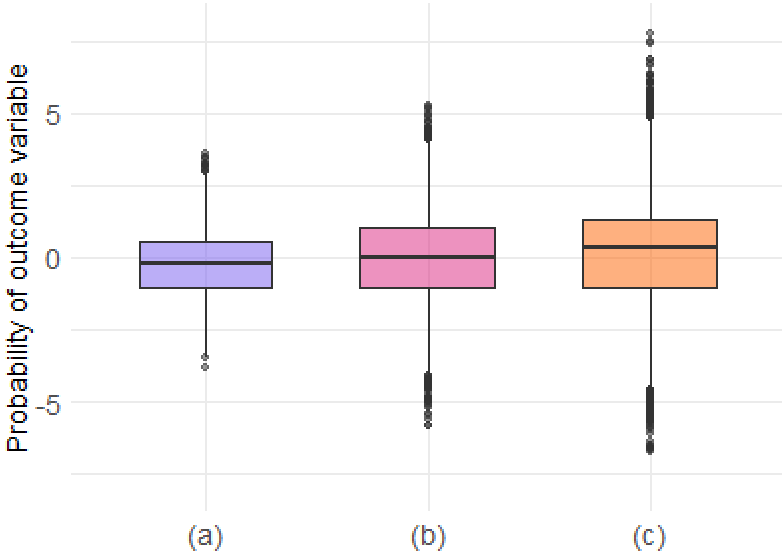
Attribute	**Relevance**	**Name of measure**	**Taxonomic groups**
Inhibition	Inhibitory control	Detour-reaching task	Primates
Other		Behavioural observations (e.g. aggression, vigilance)	Any
		Human-rated personality/behaviour assessments	Any
		Locomotion	Any
		Coping profile assessment	Rodents
		Condition of fur	Rodents
		Olfactory discrimination task.	Rodents
		Problem solving digging task.	Rodents
		Vocalisations	Any

Appendix C: Resilience experiment prior distributions

The table below lists the priors used for week and a_bar in each model. The priors different to dnorm(0,1.5) are shown in bold.

ID	Gorillas	Orangutans
1	dnorm(0,1.5)	**dnorm(0,1)**
2	dnorm(0,1.5)	dnorm(0,1.5)
3	dnorm(0,1.5)	dnorm(0,1.5)
4	**dnorm(0,1)**	dnorm(0,1.5)
5	dnorm(0,1.5)	dnorm(0,1.5)
6	dnorm(0,1.5)	**dnorm(0,1)**
7	**dnorm(0,1)**	**dnorm(0,1)**
8	dnorm(0,1.5)	dnorm(0,1.5)
9	dnorm(0,1.5)	N/A
10	dnorm(0,1.5)	**dnorm(0,2)**
11	dnorm(0,1.5)	N/A

The figure below shows a comparison of prior distributions for models with means of 0 and standard deviations of (a) 1, (b) 1.5, and (c) 2. This figure is based on 10,000 samples from the prior distribution of each model structure.



Appendix D: Resilience experiment MCMC diagnostics

Showing MCMC diagnostics for each species, including mean, standard deviation (sd), 89% credible intervals, number of effective samples (n_eff), and the Gelman-Rubin convergence diagnostic (Rhat4) (Gelman & Rubin, 1992).

Orangutans

Outcome variable	Treatment group	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Control	-0.23	0.73	-1.36	0.94	1137.40	1.00
	Treatment	-0.08	0.73	-1.23	1.07	1110.65	1.00
2	Control	-0.17	1.03	-1.86	1.42	716.11	1.01
	Treatment	-0.18	1.03	-1.87	1.39	727.97	1.01
3	Control	0.05	1.00	-1.53	1.64	1376.78	1.00
	Treatment	-0.13	1.00	-1.72	1.43	1440.69	1.01
4	Control	0.36	1.06	-1.31	2.08	1320.93	1.00
	Treatment	0.00	1.05	-1.68	1.67	1296.73	1.00
5	Control	0.47	1.07	-1.19	2.24	1315.57	1.00
	Treatment	-0.02	1.06	-1.70	1.68	1250.74	1.00
6	Control	0.55	0.69	-0.55	1.59	1296.37	1.00
	Treatment	0.21	0.69	-0.87	1.27	1345.31	1.00
7	Control	0.13	0.82	-1.16	1.46	1918.17	1.00
	Treatment	-0.14	0.83	-1.48	1.17	1792.09	1.00
8	Control	0.13	0.82	-1.16	1.46	1918.17	1.00
	Treatment	-0.14	0.83	-1.48	1.17	1792.09	1.00
10	Control	0.14	0.71	-0.97	1.24	1759.71	1.00
	Treatment	0.01	0.71	-1.12	1.12	1792.37	1.00

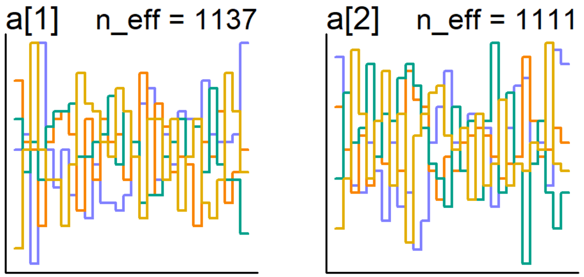
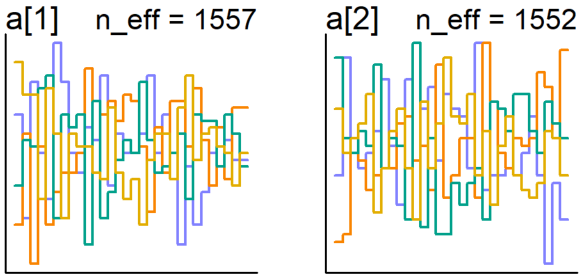
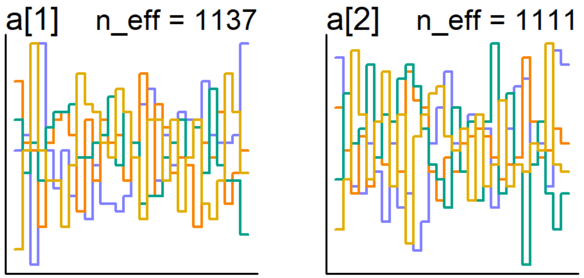
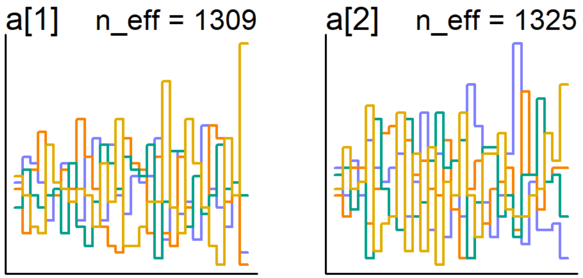
Gorillas

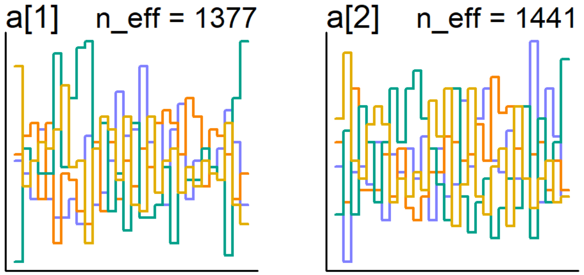
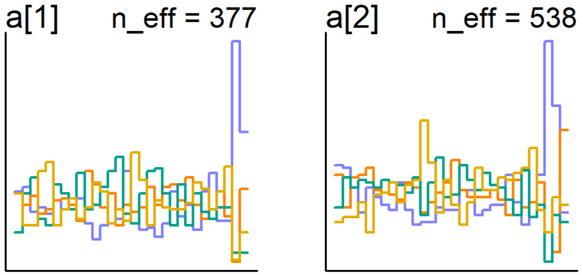
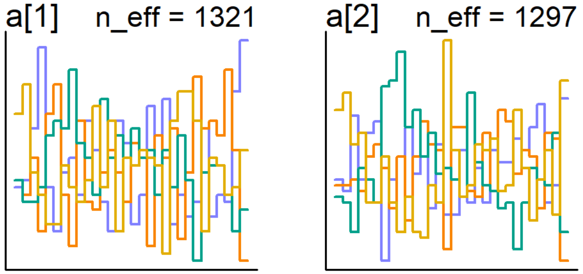
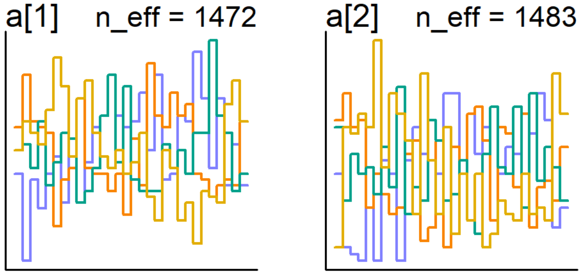
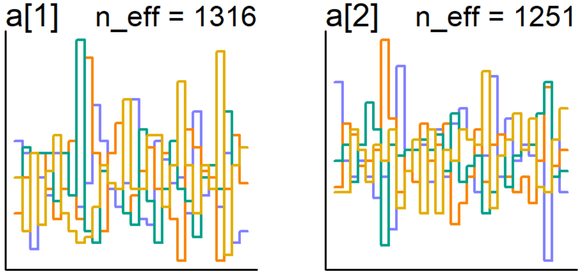
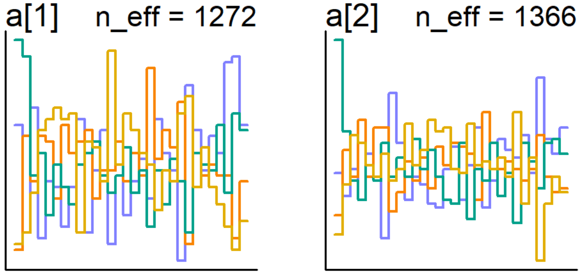
Outcome variable	Treatment group	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Control	-0.21	1.01	-1.81	1.40	1556.56	1.00
	Treatment	0.11	1.03	-1.50	1.73	1551.76	1.00
2	Control	-0.25	1.03	-1.87	1.45	1309.31	1.00
	Treatment	-0.02	1.03	-1.63	1.67	1325.14	1.00
3	Control	-0.12	1.04	-1.73	1.63	377.05	1.00
	Treatment	0.24	1.01	-1.36	1.81	537.82	1.00
4	Control	-0.14	0.73	-1.33	1.02	1471.91	1.00
	Treatment	-0.08	0.74	-1.25	1.08	1483.05	1.00
5	Control	-0.02	1.04	-1.66	1.68	1271.84	1.00
	Treatment	0.13	1.06	-1.49	1.87	1365.62	1.00
6	Control	-0.02	1.01	-1.65	1.61	1574.71	1.00
	Treatment	-0.40	1.02	-1.99	1.23	1700.62	1.00
7	Control	-0.13	0.73	-1.29	1.02	1533.14	1.00
	Treatment	0.12	0.75	-1.06	1.33	1560.16	1.00

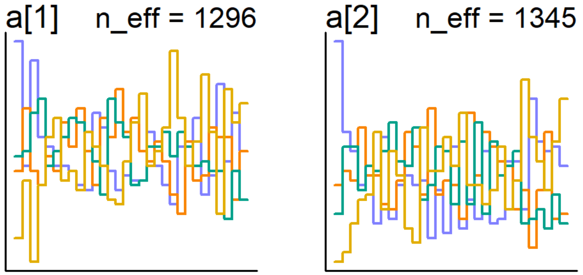
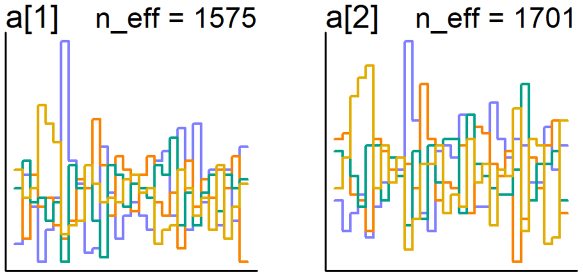
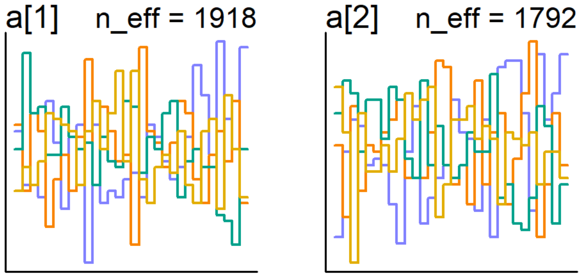
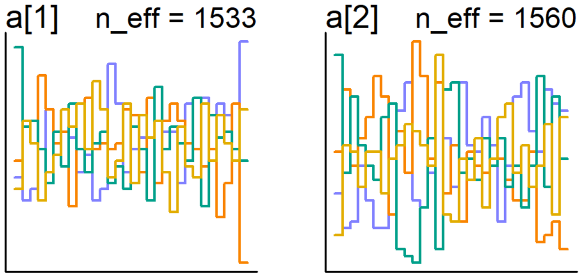
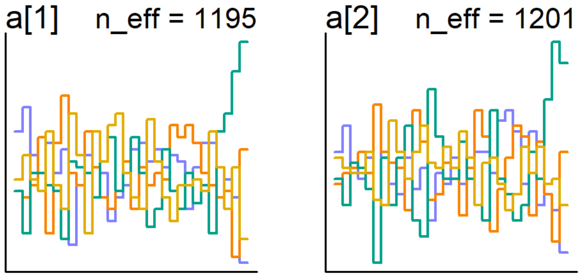
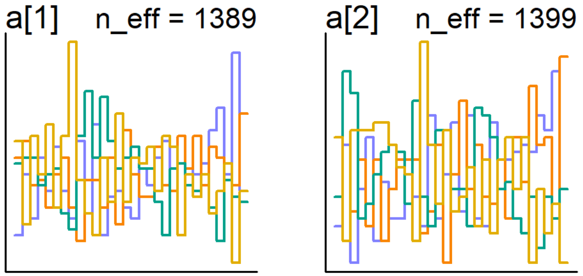
Outcome variable	Treatment group	mean	sd	5.5%	94.5%	n_eff	Rhat4
8	Control	0.00	1.01	-1.56	1.63	1014.30	1.00
	Treatment	0.01	1.02	-1.59	1.66	1273.37	1.00
9	Control	0.06	1.03	-1.54	1.69	1388.78	1.00
	Treatment	0.12	1.03	-1.51	1.75	1398.84	1.00
10	Control	-0.17	0.99	-1.73	1.42	1512.23	1.00
	Treatment	0.13	0.99	-1.40	1.73	1481.78	1.00
11	Control	0.15	1.02	-1.76	1.48	1373.14	1.00
	Treatment	0.03	1.01	-1.57	1.66	1402.11	1.00

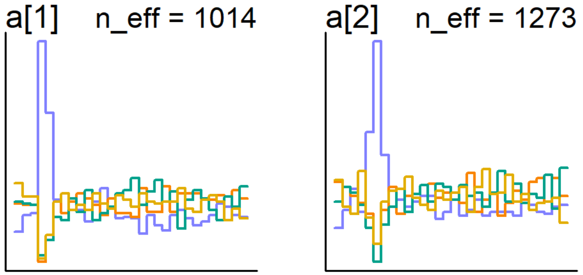
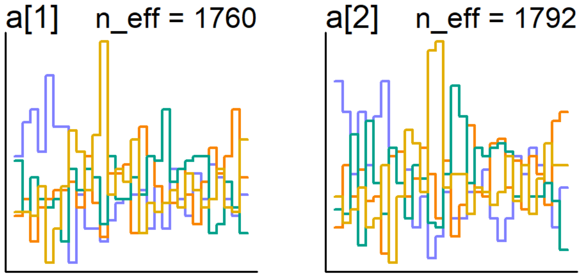
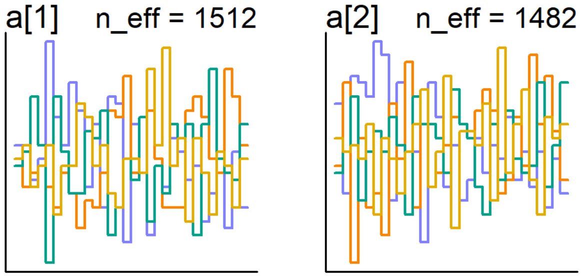
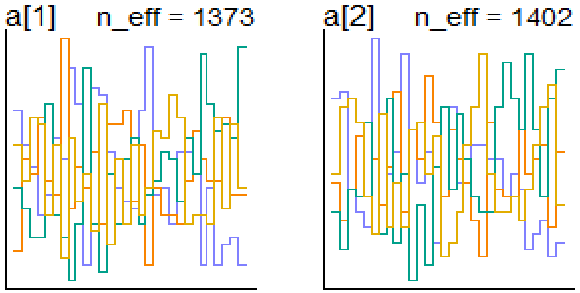
Appendix E: Resilience experiment MCMC chain convergence

Trankplots for each species and outcome variable (#), showing chain convergence and number of effective samples (n_eff) for control (a[1]) and treatment (a[2]) groups. 'N/A' indicates outcome variables not measured for that species.

#	Orangutans	Gorillas
1		
2		

#	Orangutans	Gorillas
3		
4		
5		

#	**Orangutans**	**Gorillas**
6		
7		
8		

#	Orangutans	Gorillas
9	N/A	
10		
11	N/A	

Appendix F: Resilience experiment WAIC scores

Orangutans

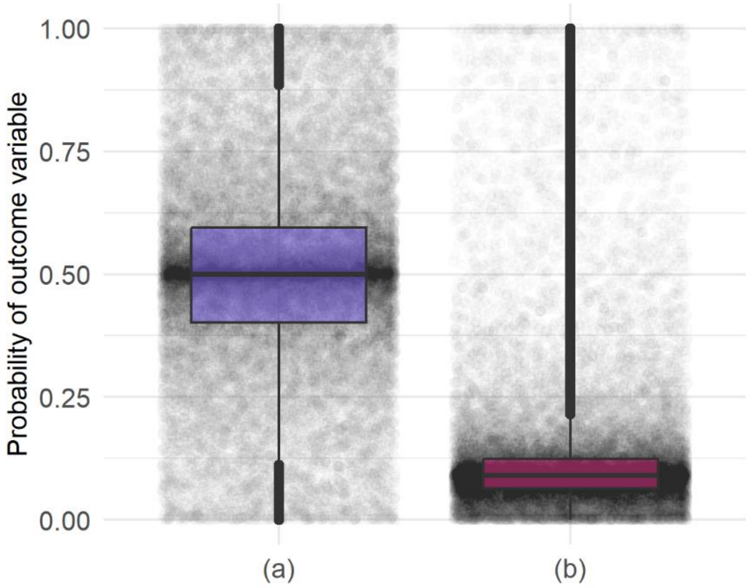
Model	WAIC	lppd	penalty	std_err
1	42.9	-16.1	5.3	7.9
2	29.3	-9.4	5.3	3.7
3	42.8	-15.9	5.6	8
4	44.6	-16.6	5.7	4
5	51.4	-20	5.7	4.2
6	38.3	-14	5.2	5.1
7	47.9	-17.5	6.4	13.3
8	31.4	-10.9	4.8	6.3
9	27.6	-6.8	7	4.3

Gorillas

Model	WAIC	lppd	penalty	std_err
1	34.9	-11.4	6	3.9
2	33.9	-11.9	5.1	3.9
3	44.6	-17.4	4.9	3.6
4	35.7	-12.5	5.4	5.1
5	47.9	-18.6	5.3	4.2
6	30.3	-10.2	5	4.5
7	24.3	-5.8	6.4	2.8
8	48.1	-19	5.1	7
9	44.8	-17.9	4.5	3.3
10	49.7	-19.9	4.9	6.6
11	49.9	-19.6	5.3	8.7

Appendix G: Lockdown study prior distributions

A sample of 10,000 observations was extracted from the prior distributions of both model types and converted to the outcome scale, in order to demonstrate the difference in prior distribution between the broad priors and informed priors used in these models, as recommended by Wesner & Pomeranz (2021).



Appendix H: Lockdown study MCMC diagnostics

Showing MCMC diagnostics for each species, including mean, standard deviation (sd), 89% credible intervals, number of effective samples (n_eff), and the Gelman-Rubin convergence diagnostic (Rhat4).

Orangutans: Lockdown status

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Lockdown	-3.14	0.88	-4.76	-2.12	737.11	1.01
	Post-lockdown	-2.36	0.86	-3.94	-1.35	748.53	1.01
2	Lockdown	0.25	0.52	-0.50	1.10	1475.11	1.00
	Post-lockdown	-0.15	0.52	-0.91	0.69	1490.25	1.00
3	Lockdown	0.17	0.50	-0.57	0.86	1316.66	1.00
	Post-lockdown	-0.22	0.50	-0.97	0.47	1303.33	1.00
4	Lockdown	-0.20	0.52	-1.17	0.22	396.58	1.01
	Post-lockdown	-0.12	0.52	-1.09	0.32	394.71	1.01
5	Lockdown	-0.15	0.43	-0.84	0.38	616.64	1.00
	Post-lockdown	0.03	0.43	-0.65	0.56	607.66	1.00
6	Lockdown	-0.17	0.59	-1.26	0.31	442.85	1.01
	Post-lockdown	-0.27	0.60	-1.40	0.19	438.71	1.01
7	Lockdown	-0.52	1.11	-2.87	0.31	380.04	1.01
	Post-lockdown	-0.59	1.12	-2.97	0.24	375.30	1.01
8	Lockdown	-2.47	0.46	-3.18	-1.79	891.59	1.01
	Post-lockdown	-2.19	0.46	-2.91	-1.52	893.44	1.01
9	Lockdown	-1.45	0.95	-3.15	-0.08	1145.98	1.00
	Post-lockdown	0.49	0.95	-1.21	1.86	1147.17	1.00
12	Lockdown	-2.33	0.39	-2.92	-1.89	460.54	1.01
	Post-lockdown	-2.42	0.40	-3.03	-2.02	453.32	1.01
13	Lockdown	-2.31	0.50	-3.15	-1.72	579.38	1.00
	Post-lockdown	-2.55	0.51	-3.45	-2.00	572.80	1.00

Gorillas: Lockdown status

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Lockdown	-2.13	0.33	-2.55	-1.61	1049.62	1.00
	Semi-lockdown	-2.39	0.32	-2.90	-1.96	1054.62	1.00
	Post-lockdown	-2.56	0.38	-3.24	-2.14	1161.06	1.00
2	Lockdown	-0.03	0.35	-0.52	0.43	653.07	1.00
	Semi-lockdown	0.24	0.35	-0.25	0.71	661.41	1.00
	Post-lockdown	-0.28	0.35	-0.77	0.18	658.89	1.00
3	Lockdown	0.12	0.25	-0.22	0.47	1005.97	1.01
	Semi-lockdown	-0.20	0.25	-0.55	0.15	1007.40	1.01

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
	Post-lockdown	0.06	0.25	-0.29	0.41	1000.23	1.01
4	Lockdown	0.03	0.17	-0.18	0.24	840.59	1.01
	Semi-lockdown	-0.05	0.16	-0.30	0.11	795.27	1.01
	Post-lockdown	-0.01	0.17	-0.26	0.18	832.79	1.01
5	Lockdown	-0.09	0.25	-0.45	0.24	674.90	1.00
	Semi-lockdown	0.16	0.25	-0.18	0.50	656.67	1.00
	Post-lockdown	-0.07	0.25	-0.41	0.28	664.54	1.00
6	Lockdown	-1.45	0.86	-2.99	-0.43	723.39	1.01
	Semi-lockdown	-0.15	0.83	-1.64	0.85	719.46	1.01
	Post-lockdown	-0.04	0.83	-1.53	0.96	735.94	1.01
7	Lockdown	-1.27	1.79	-4.84	0.52	424.84	1.02
	Semi-lockdown	1.64	1.96	-5.49	0.29	367.10	1.02
	Post-lockdown	-2.29	2.83	-7.83	0.28	432.60	1.02
8	Lockdown	-2.40	0.24	-2.75	-2.11	683.75	1.01
	Semi-lockdown	-2.21	0.23	-2.51	-1.89	621.39	1.01
	Post-lockdown	-2.39	0.24	-2.73	-2.09	687.41	1.01
10	Lockdown	-0.70	0.23	-1.03	-0.35	519.89	1.01
	Semi-lockdown	-0.98	0.23	-1.31	-0.62	529.73	1.01
	Post-lockdown	-0.75	0.23	-1.07	-0.39	514.22	1.01
11	Lockdown	-3.69	0.89	-4.79	-2.32	824.32	1.00
	Semi-lockdown	-5.61	0.93	-6.82	-4.17	894.97	1.00
	Post-lockdown	-9.79	2.65	-14.28	-6.64	1209.80	1.00
12	Lockdown	-1.84	0.50	-2.62	-1.08	1307.94	1.00
	Semi-lockdown	-2.49	0.49	-3.31	-1.79	1179.56	1.00
	Post-lockdown	-2.87	0.51	-3.75	-2.18	1203.90	1.00
13	Lockdown	-2.16	0.35	-2.60	-1.70	424.28	1.01
	Semi-lockdown	-2.47	0.35	-2.96	-2.07	366.46	1.01
	Post-lockdown	-2.47	0.38	-3.05	-2.07	384.72	1.01

Orangutans: Total visitors

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Low	-2.08	0.64	-3.10	-1.19	805.60	1.00
	Normal	-3.23	0.74	-4.53	-2.31	796.37	1.00
	Busy	-2.31	0.65	-3.34	-1.40	835.46	1.00
2	Low	0.30	0.41	-0.32	0.93	1505.01	1.00
	Normal	-0.44	0.41	-1.06	0.18	1540.78	1.00
	Busy	0.23	0.42	-0.38	0.90	1547.16	1.00
3	Low	-0.06	0.20	-0.31	0.19	716.06	1.00
	Normal	0.06	0.20	-0.17	0.34	736.73	1.00
	Busy	-0.01	0.21	-0.29	0.27	756.45	1.00
5	Low	0.25	0.44	0.44	0.86	973.40	1.00
	Normal	0.03	0.44	0.44	0.65	979.41	1.00

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
	Busy	-0.51	0.45	0.45	0.09	1023.43	1.00
6	Low	0.34	0.70	-0.872	1.34	1067.55	1.00
	Normal	-0.05	0.71	-1.28	0.92	1097.18	1.00
	Busy	-1.29	0.88	-2.84	-0.16	1240.66	1.00
8	Low	-2.92	0.49	-3.66	-2.17	1421.93	1.00
	Normal	-1.83	0.49	-2.57	-1.07	1420.60	1.00
	Busy	-2.21	0.50	-2.96	-1.46	1472.60	1.00
9	Low	0.94	1.08	-0.90	2.57	1366.95	1.00
	Normal	-0.75	1.08	-2.58	0.86	1367.75	1.00
	Busy	-3.30	1.92	-6.83	-0.93	1763.53	1.00

Gorillas: Total visitors

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Low	-1.90	0.69	-2.98	-0.85	1501.55	1.01
	Normal	-2.68	0.70	-3.85	-1.69	1436.39	1.00
	Busy	-3.27	1.21	-5.53	-2.00	1735.47	1.00
2	Low	0.12	0.24	-0.24	0.47	1391.50	1.00
	Normal	0.08	0.25	-0.27	0.44	1404.21	1.00
	Busy	-0.23	0.25	-0.62	0.11	1414.97	1.00
3	Low	0.00	0.42	-0.63	0.62	1175.19	1.00
	Normal	-0.41	0.42	-1.04	0.21	1173.91	1.00
	Busy	0.39	0.42	-0.25	1.02	1174.63	1.00
5	Low	0.43	0.46	-0.29	1.11	1751.56	1.00
	Normal	-0.57	0.46	-1.30	0.11	1767.76	1.00
	Busy	-0.01	0.48	-0.75	0.70	1872.42	1.00
6	Low	-0.82	1.05	-2.61	0.70	1683.68	1.00
	Normal	1.10	1.05	-0.64	2.68	1799.15	1.00
	Busy	-2.313	1.81	-5.44	-0.14	2028.74	1.00
8	Low	-2.08	0.51	-2.83	-1.32	1740.42	1.00
	Normal	-2.55	0.51	-3.33	-1.82	1790.64	1.00
	Busy	-2.58	0.82	-3.88	-1.66	1607.16	1.00
10	Low	-0.84	0.51	-1.57	0.03	982.64	1.00
	Normal	-0.48	0.51	-1.22	0.39	986.26	1.00
	Busy	-0.94	0.51	-1.68	-0.09	996.60	1.00
11	Low	-5.72	3.31	-11.22	-1.08	855.69	1.01
	Normal	-1.42	2.13	-4.40	2.10	771.24	1.01
	Busy	-4.87	3.26	-10.41	-0.44	1043.93	1.00

Orangutans: Visitor noise

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Quiet	-2.39	0.45	-3.07	-1.89	730.66	1.00
	Some noise	-2.57	0.46	-3.28	-2.14	706.71	1.00
	Loud noise	-2.21	0.46	-2.81	-1.54	897.14	1.00
2	Quiet	0.11	0.37	-0.40	0.69	1061.92	1.00
	Some noise	0.23	0.37	-0.27	0.82	1039.06	1.00
	Loud noise	-0.32	0.41	-0.97	0.21	1253.48	1.00
3	Quiet	-0.01	0.20	-0.19	0.18	320.05	1.00
	Some noise	-0.02	0.19	-0.20	0.16	326.11	1.00
	Loud noise	-0.02	0.21	-0.24	0.19	365.25	1.00
5	Quiet	0.05	0.24	-0.24	0.39	820.57	1.01
	Some noise	0.04	0.24	-0.27	0.36	811.45	1.01
	Loud noise	-0.19	0.29	-0.69	0.09	853.12	1.00
6	Quiet	0.84	0.91	-0.67	2.168	1202.05	1.00
	Some noise	-0.67	0.91	-2.21	0.66	1194.55	1.00
	Loud noise	-1.75	1.20	-3.88	-0.19	1500.50	1.00
8	Quiet	-2.39	0.30	-2.84	-1.99	1184.93	1.00
	Some noise	-2.46	0.30	-2.91	-2.08	1166.93	1.00
	Loud noise	-2.09	0.32	-2.46	-1.56	1244.43	1.00
9	Quiet	-0.11	0.58	-1.12	0.65	815.24	1.00
	Some noise	0.23	0.57	-0.76	1.01	822.46	1.00
	Loud noise	-0.85	0.67	-2.05	-0.04	883.23	1.00

Gorillas: Visitor noise

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	Quiet	-2.77	0.52	-3.66	-2.21	1430.44	1.00
	Some noise	-2.32	0.46	-3.04	-1.72	1468.45	1.00
	Loud noise	-2.10	0.47	-2.76	-1.40	1674.24	1.00
2	Quiet	0.08	0.18	-0.12	0.30	734.65	1.01
	Some noise	-0.04	0.18	-0.27	0.16	734.29	1.01
	Loud noise	-0.07	0.18	-0.30	0.13	744.72	1.01
3	Quiet	0.12	0.40	-0.50	0.74	1494.26	1.00
	Some noise	0.33	0.40	-0.31	0.94	1473.27	1.00
	Loud noise	-0.49	0.40	-1.13	0.12	1464.33	1.00
5	Quiet	0.43	0.47	-0.26	1.08	1091.97	1.00
	Some noise	-0.26	0.47	-0.95	0.38	1105.2	1.00
	Loud noise	-0.33	0.48	-1.04	0.32	1242.63	1.00
6	Quiet	0.04	0.41	-0.54	0.64	1029.38	1.00
	Some noise	0.06	0.40	-0.52	0.66	1081.56	1.00
	Loud noise	-0.35	0.56	-1.38	0.18	887.72	1.00
8	Quiet	-2.02	0.41	-2.64	-1.43	1116.12	1.00
	Some noise	-2.74	0.42	-3.38	-2.18	1104.61	1.00

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
	Loud noise	-2.33	0.43	-2.98	-1.74	1149.08	1.00
10	Quiet	-0.77	0.48	-1.45	0.05	609.09	1.01
	Some noise	-0.81	0.48	-1.49	0.01	610.16	1.01
	Loud noise	-0.81	0.48	-1.50	0.02	605.34	1.01
11	Quiet	-1.33	1.40	-3.64	0.71	1166.15	1.00
	Some noise	-0.97	1.35	-3.19	1.04	1259.49	1.00
	Loud noise	-1.59	1.79	-4.63	0.66	1084.15	1.00

Orangutans: Visitor presence

Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	None	-2.19	0.55	-3.11	-1.44	1464.27	1.00
	<20	-2.71	0.56	-3.73	-2.02	1347.99	1.00
	20+	-2.63	0.88	-4.19	-1.67	1557.23	1.00
2	None	0.21	0.40	-0.25	0.88	1160.43	1.00
	<20	0.10	0.39	-0.37	0.78	1175.15	1.00
	20+	-0.32	0.49	-1.20	0.19	1306.61	1.01
3	None	-0.06	0.29	-0.41	0.20	476.09	1.01
	<20	-0.04	0.29	-0.38	0.22	481.71	1.01
	20+	0.04	0.31	-0.25	0.46	683.18	1.01
5	None	-0.35	0.39	-0.95	0.17	1238.33	1.01
	<20	0.13	0.39	-0.45	0.66	1090.82	1.01
	20+	0.12	0.43	-0.48	0.75	1068.34	1.00
6	None	0.45	0.85	-0.951	1.63	1009.38	1.00
	<20	-0.37	0.85	-1.80	0.82	1016.44	1.00
	20+	-1.75	1.64	-4.72	0.01	1196.00	1.00
8	None	-2.19	0.30	-2.64	-1.76	1140.17	1.00
	<20	-2.50	0.30	-2.96	-2.09	1165.02	1.00
	20+	-2.24	0.34	-2.72	-1.70	1537.64	1.00
9	None	0.21	0.96	-1.47	1.51	880.20	1.01
	<20	-0.10	0.96	-1.81	1.21	857.32	1.01
	20+	-2.46	1.94	-5.89	-0.28	1042.88	1.01

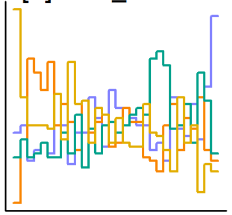
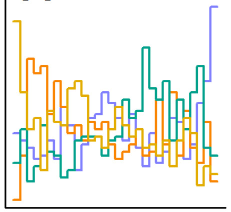
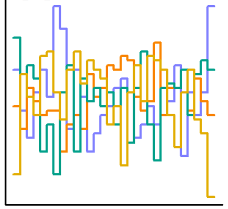
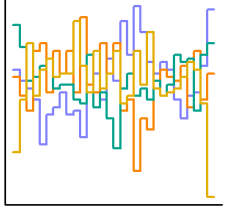
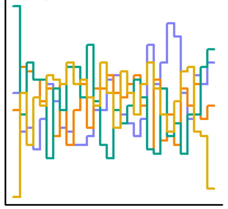
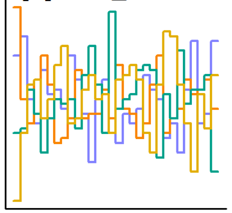
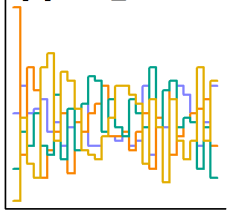
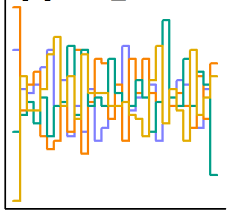
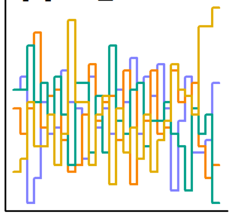
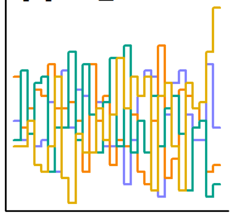
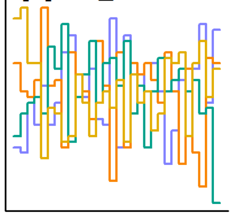
Gorillas: Visitor presence

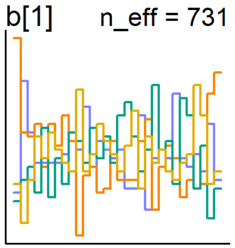
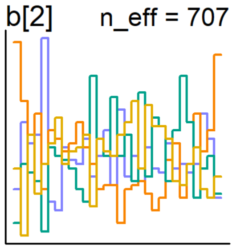
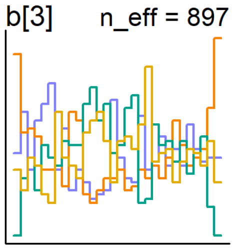
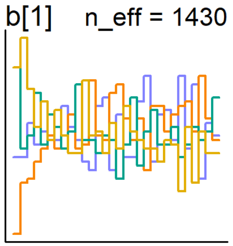
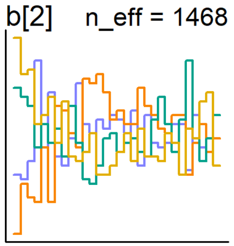
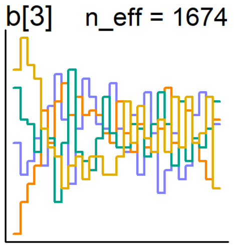
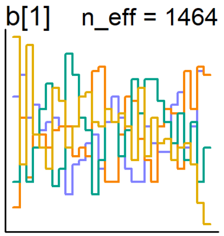
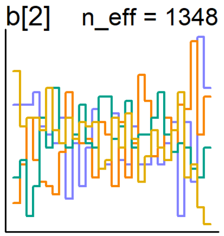
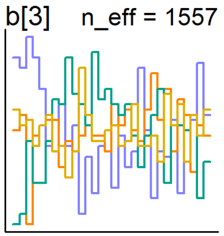
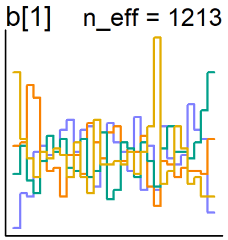
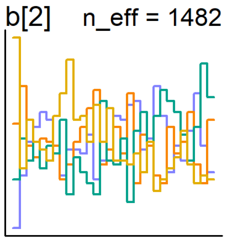
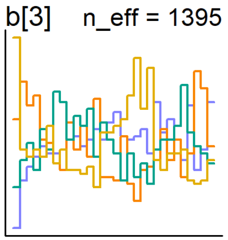
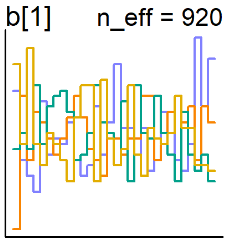
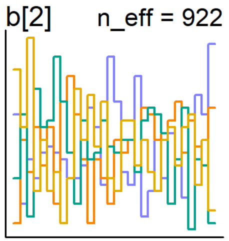
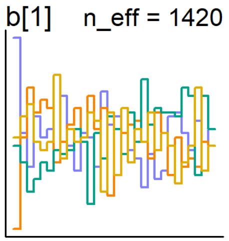
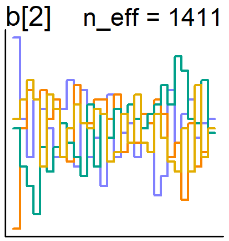
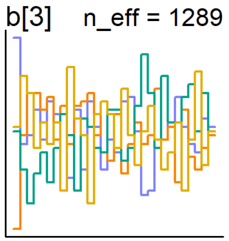
Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
1	None	-2.535	0.47	-3.34	-1.96	1213.152	1.00
	<20	-2.13	0.44	-2.73	-1.44	1481.580	1.01
	20+	-2.48	0.49	-3.31	-1.85	1395.196	1.00
2	None	0.05	0.16	-0.12	0.25	683.66	1.00
	<20	-0.00	0.17	-0.20	0.19	677.13	1.00
	20+	-0.06	0.17	-0.28	0.11	677.17	1.00

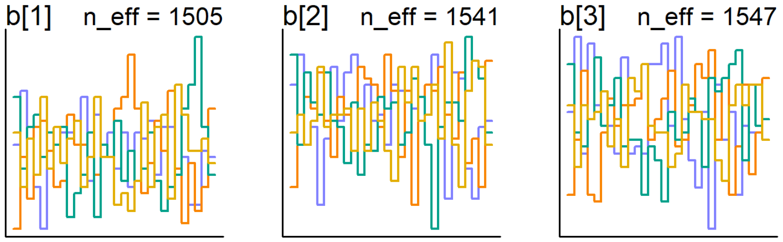
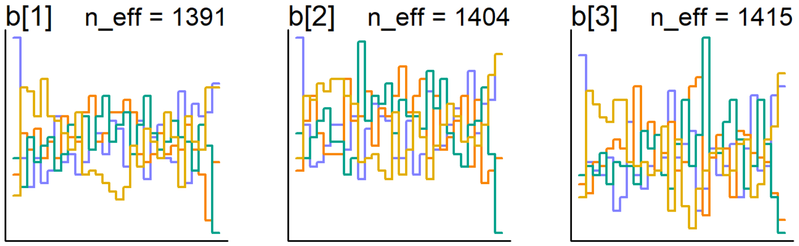
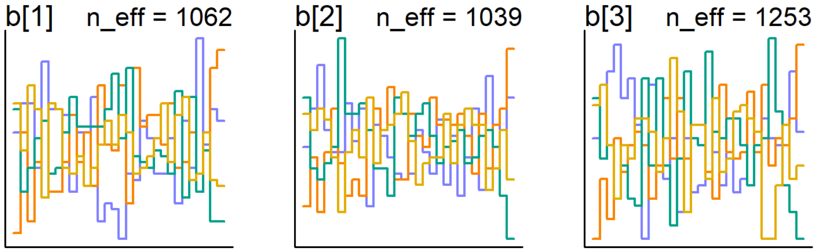
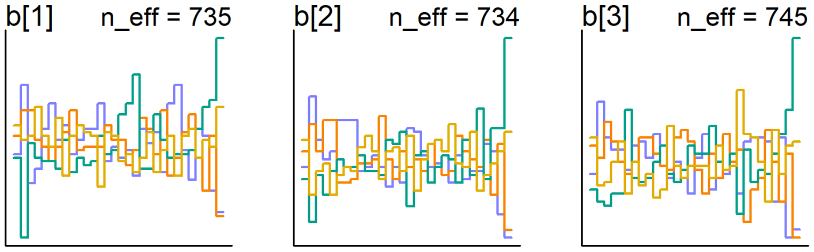
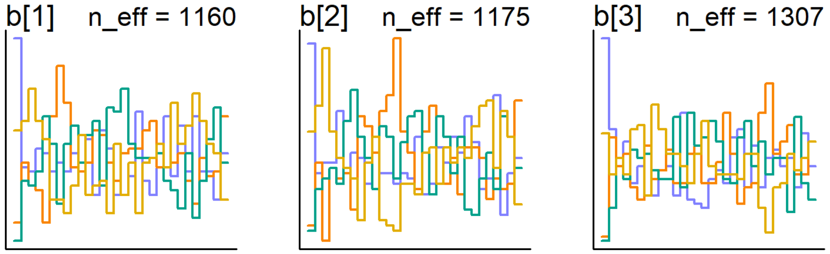
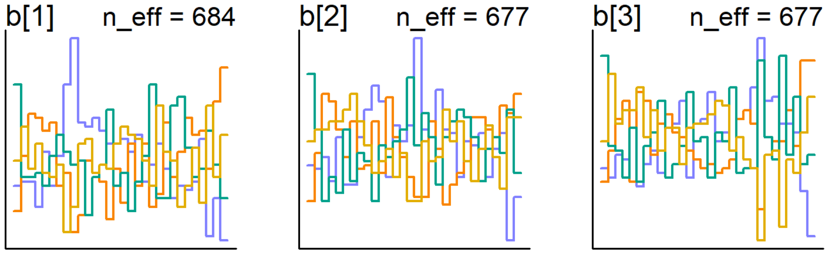
Outcome variable	Lockdown status	mean	sd	5.5%	94.5%	n_eff	Rhat4
3	None	0.14	0.27	-0.25	0.55	1305.33	1.00
	<20	0.11	0.27	-0.30	0.53	1399.30	1.00
	20+	-0.24	0.27	-0.66	0.173	1366.66	1.00
5	None	0.10	0.27	-0.28	0.46	1233.94	1.00
	<20	-0.17	0.27	-0.58	0.16	1232.51	1.00
	20+	0.03	0.27	-0.35	0.42	1286.15	1.00
6	None	0.04	0.67	-1.14	0.97	1467.53	1.00
	<20	-0.99	0.69	-2.25	-0.10	1265.16	1.00
	20+	0.28	0.66	-0.83	1.23	1659.34	1.00
8	None	-2.25	0.23	-2.53	-1.92	1439.75	1.00
	<20	-2.38	0.22	-2.72	-2.12	1638.13	1.00
	20+	-2.35	0.22	-2.70	-2.05	1568.04	1.00
10	None	-0.65	0.56	-1.39	0.31	869.99	1.00
	<20	-0.75	0.56	-1.50	0.20	877.19	1.00
	20+	-1.03	0.60	-1.89	-0.04	976.13	1.00
11	None	-1.71	1.78	-4.87	0.80	1292.82	1.00
	<20	-2.07	2.50	-6.77	0.84	1149.52	1.00
	20+	-1.28	2.00	-4.62	1.34	1895.33	1.00

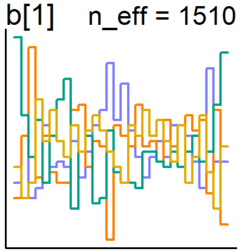
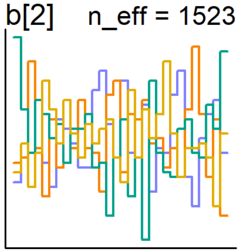
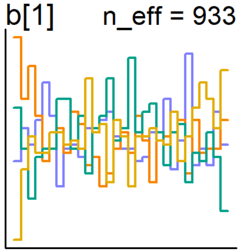
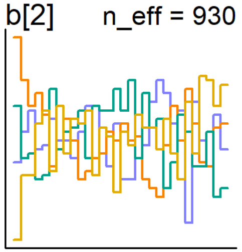
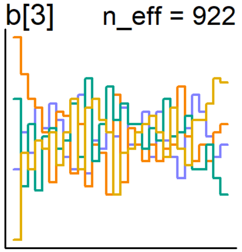
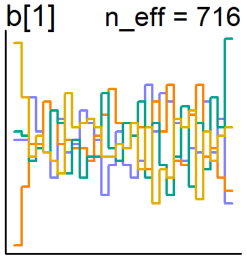
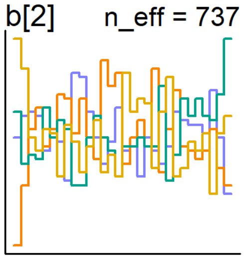
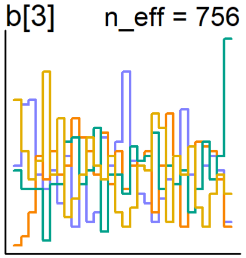
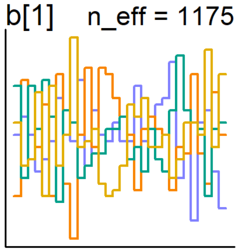
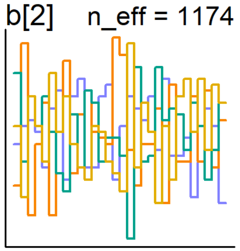
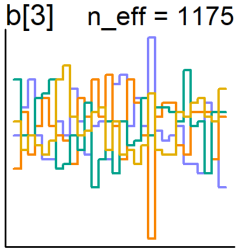
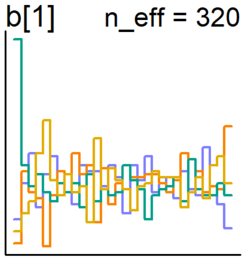
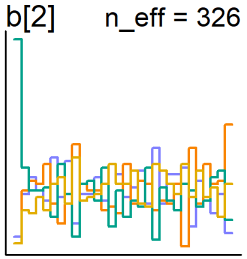
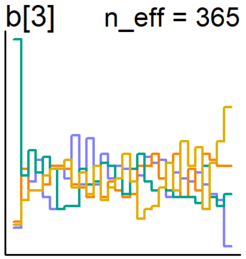
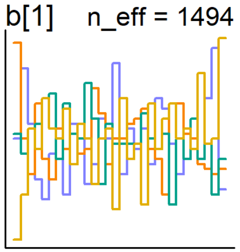
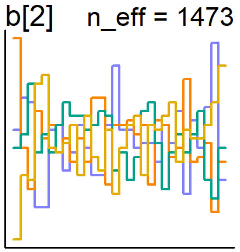
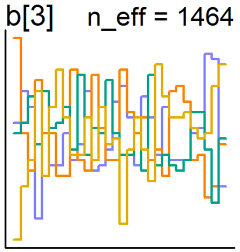
Appendix I: Lockdown study MCMC chain resolution

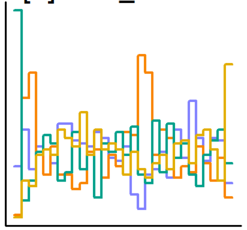
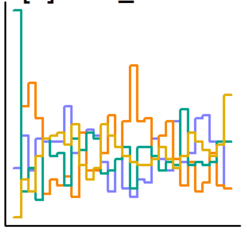
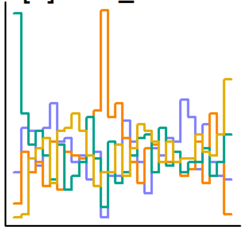
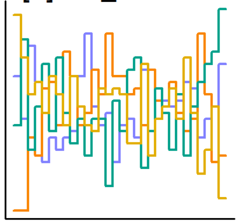
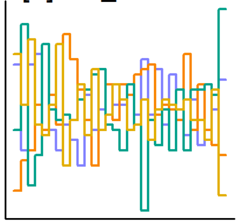
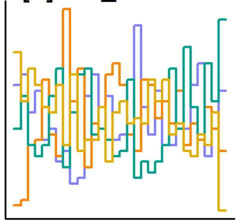
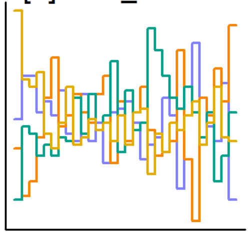
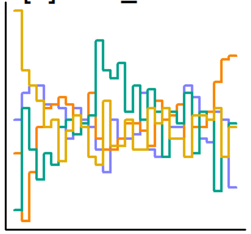
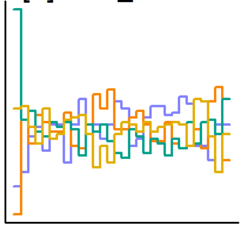
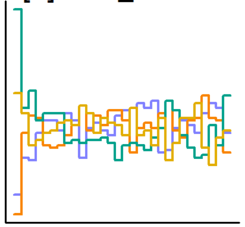
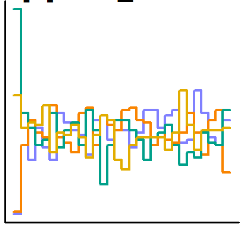
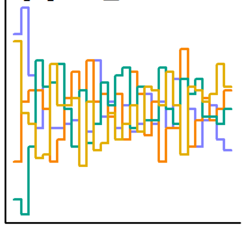
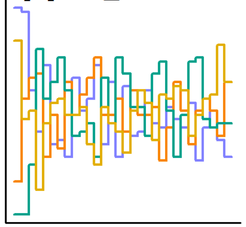
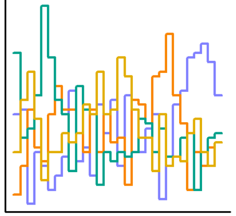
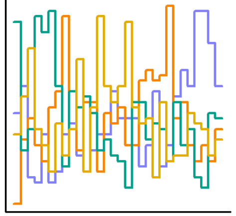
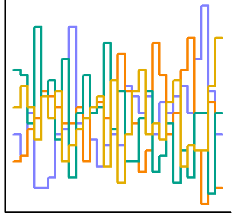
Trankplots for each species and outcome variable (#), showing chain convergence and number of effective samples (n_eff). ‘b[1]’ = lockdown/low visitor levels/quiet noise/no visitor presence; ‘b[2]’ = semi-lockdown/medium visitor levels/some noise/<20 visitors; ‘b[3]’ post-lockdown/high visitor levels, loud noise, 20+ visitors. ‘N/A’ indicates outcome variables not measured for that species.

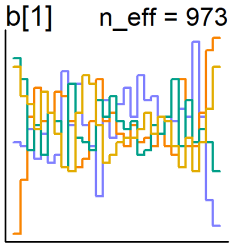
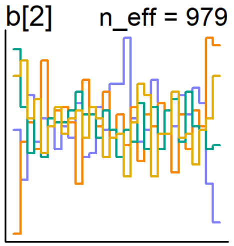
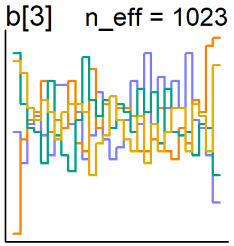
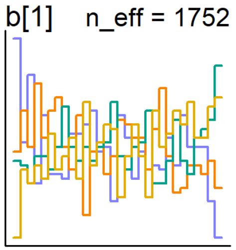
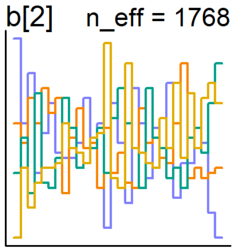
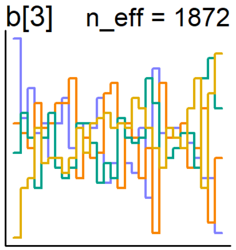
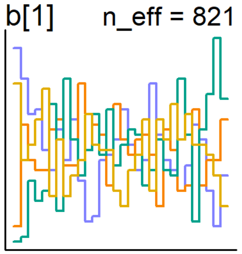
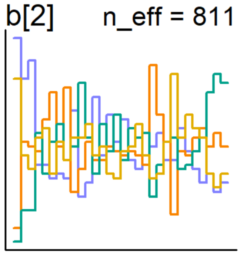
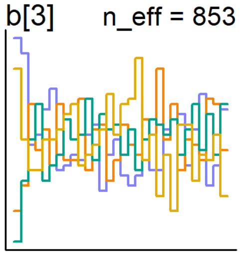
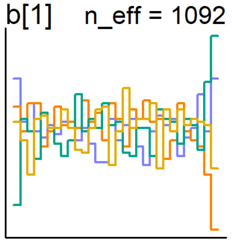
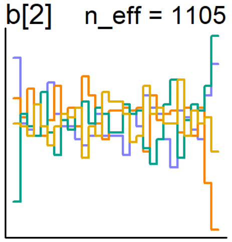
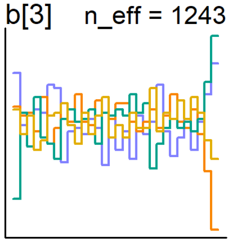
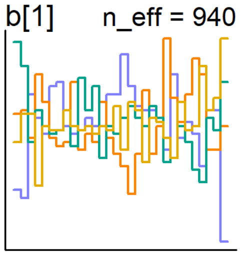
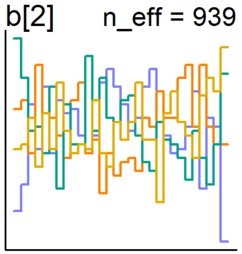
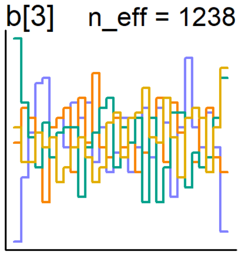
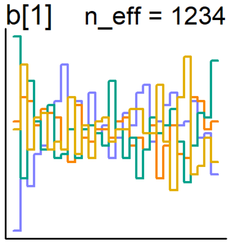
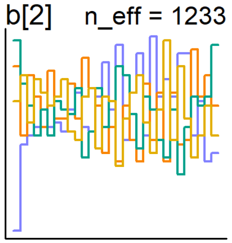
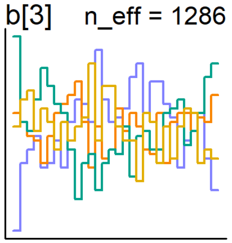
#	Predictor	Orangutans	Gorillas
1	Lockdown status	b[1] n_eff = 737  b[2] n_eff = 749 	b[1] n_eff = 1050  b[2] n_eff = 1055  b[3] n_eff = 1161 
	Total visitors	b[1] n_eff = 806  b[2] n_eff = 796  b[3] n_eff = 835 	b[1] n_eff = 1502  b[2] n_eff = 1436  b[3] n_eff = 1735 

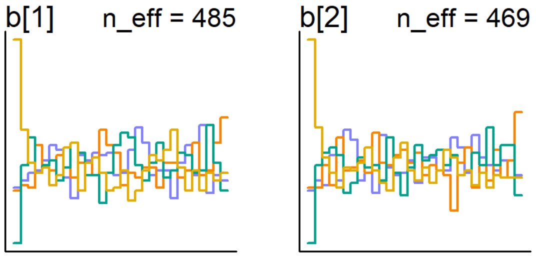
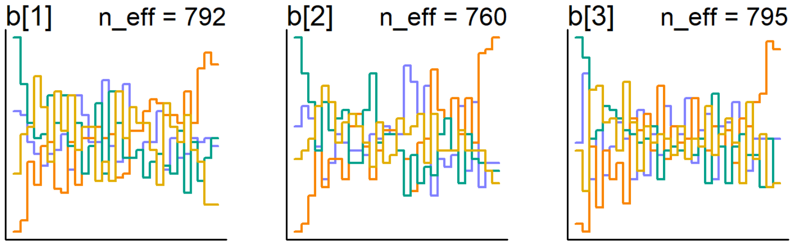
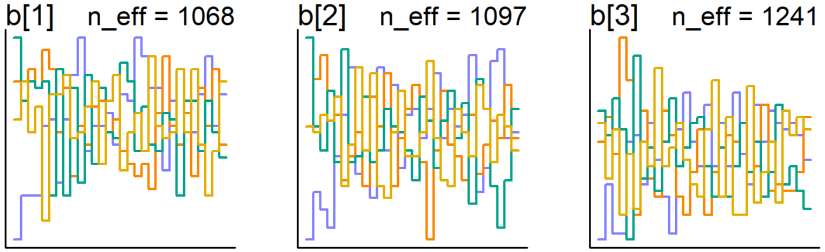
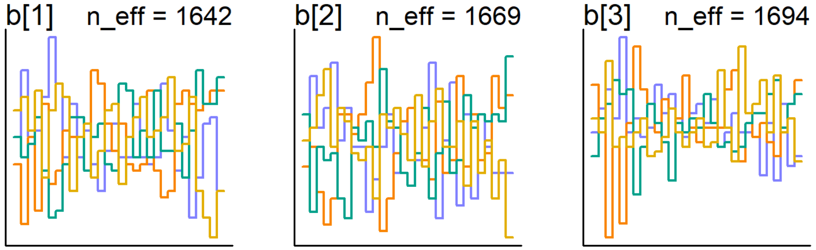
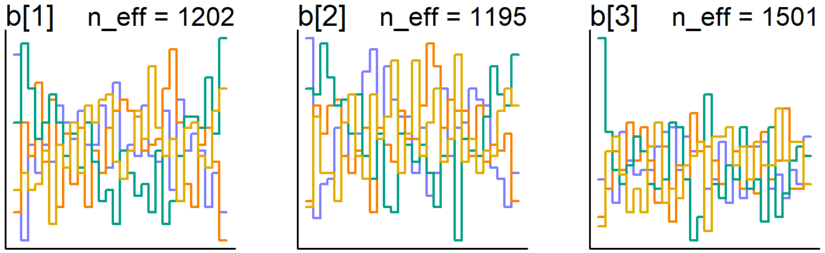
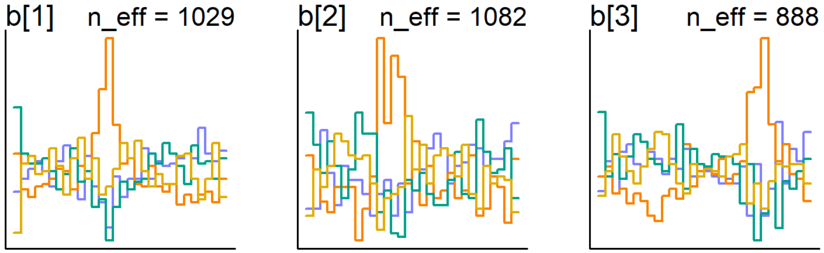
#	Predictor	Orangutans	Gorillas
	Visitor noise	 b[1] n_eff = 731  b[2] n_eff = 707  b[3] n_eff = 897	 b[1] n_eff = 1430  b[2] n_eff = 1468  b[3] n_eff = 1674
	Visitor presence	 b[1] n_eff = 1464  b[2] n_eff = 1348  b[3] n_eff = 1557	 b[1] n_eff = 1213  b[2] n_eff = 1482  b[3] n_eff = 1395
2	Lockdown status	 b[1] n_eff = 920  b[2] n_eff = 922	 b[1] n_eff = 1420  b[2] n_eff = 1411  b[3] n_eff = 1289

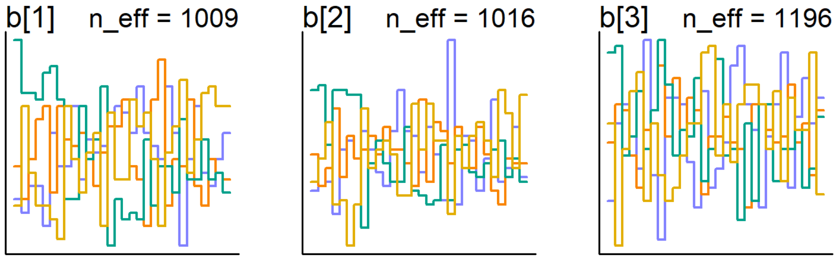
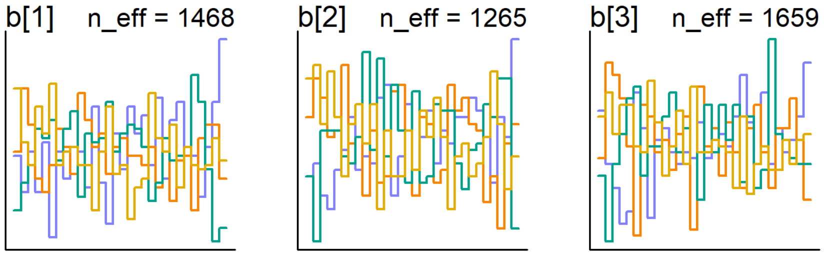
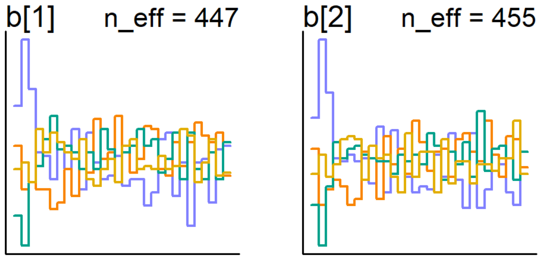
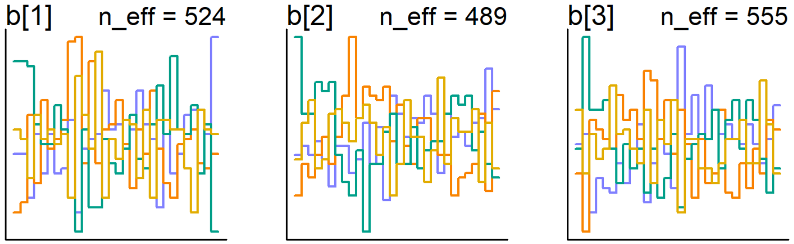
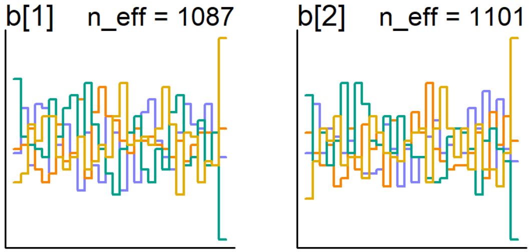
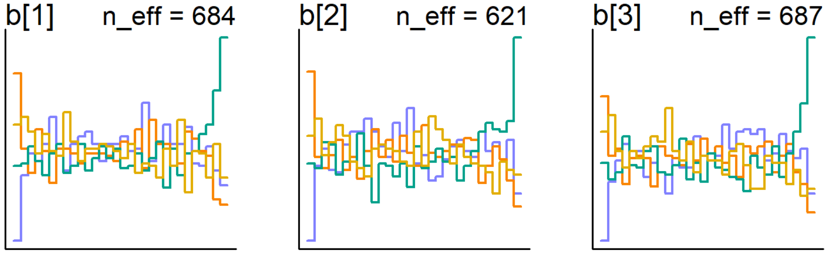
#	**Predictor**	**Orangutans**	**Gorillas**
	Total visitors		
	Visitor noise		
	Visitor presence		

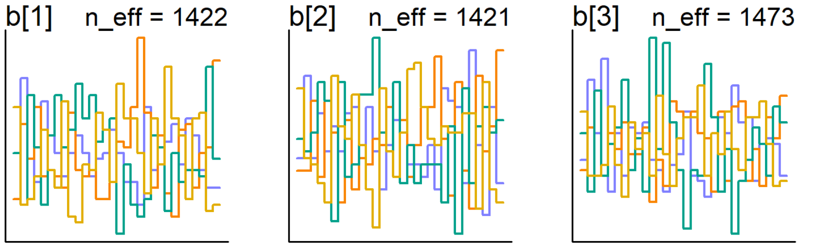
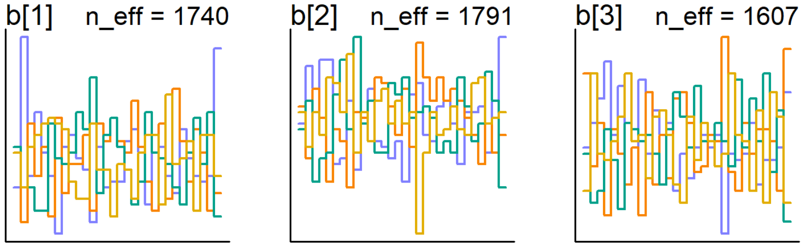
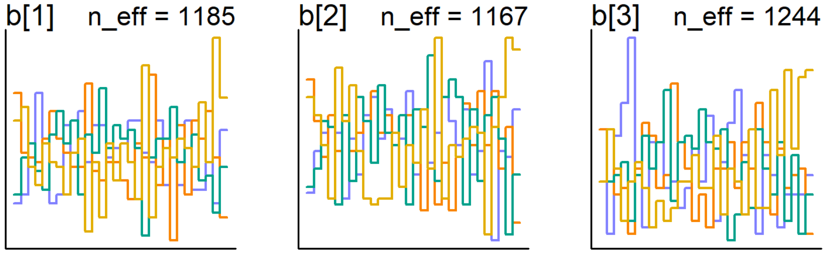
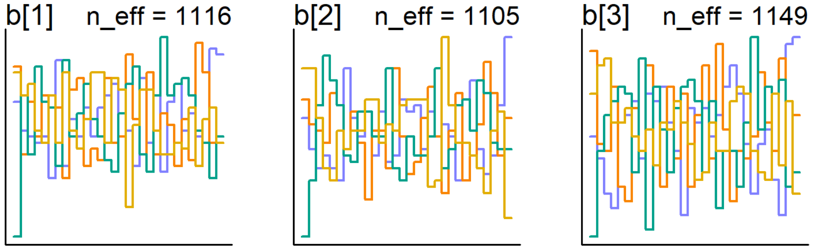
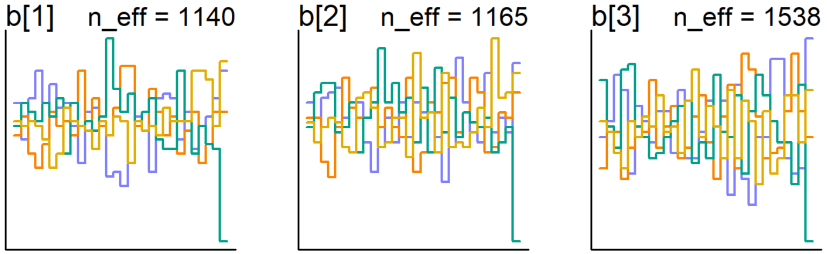
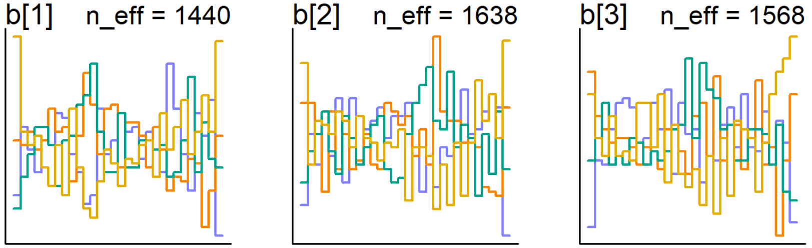
#	Predictor	Orangutans	Gorillas
3	Lockdown status	 	  
	Total visitors	  	  
	Visitor noise	  	  

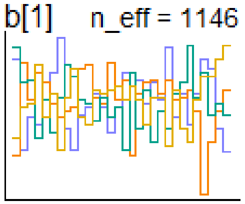
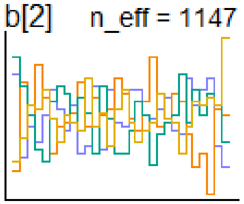
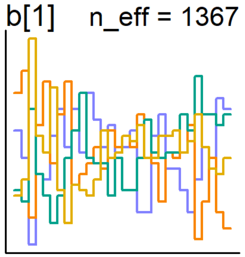
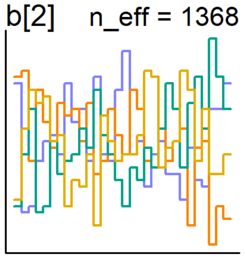
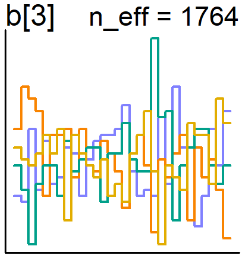
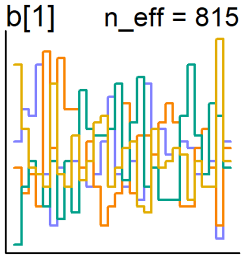
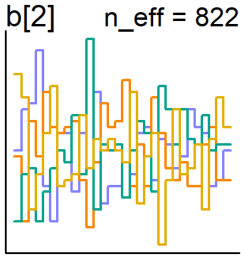
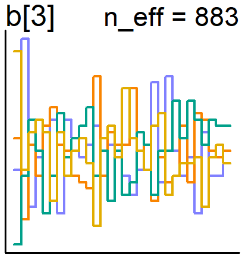
#	Predictor	Orangutans	Gorillas
	Visitor presence	 b[1] n_eff = 476  b[2] n_eff = 482  b[3] n_eff = 683	 b[1] n_eff = 1305  b[2] n_eff = 1399  b[3] n_eff = 1367
4	Lockdown status	 b[1] n_eff = 324  b[2] n_eff = 330	 b[1] n_eff = 443  b[2] n_eff = 378  b[3] n_eff = 410
5	Lockdown status	 b[1] n_eff = 1165  b[2] n_eff = 1159	 b[1] n_eff = 1230  b[2] n_eff = 1233  b[3] n_eff = 1590

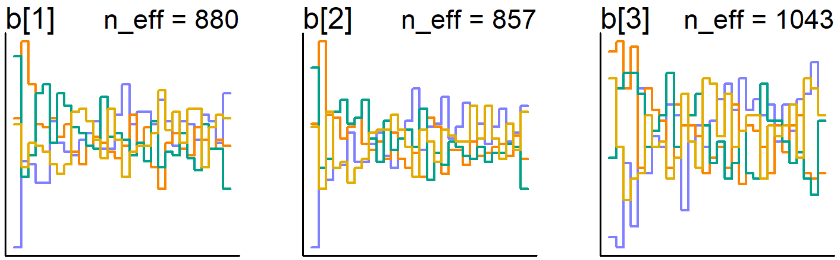
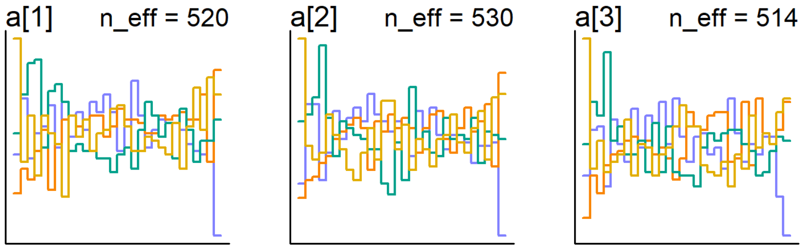
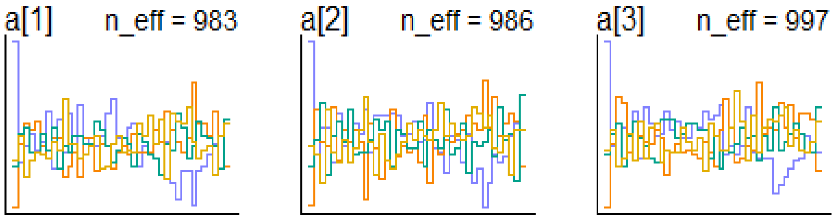
#	Predictor	Orangutans			Gorillas		
	Total visitors						
	Visitor noise						
	Visitor presence						

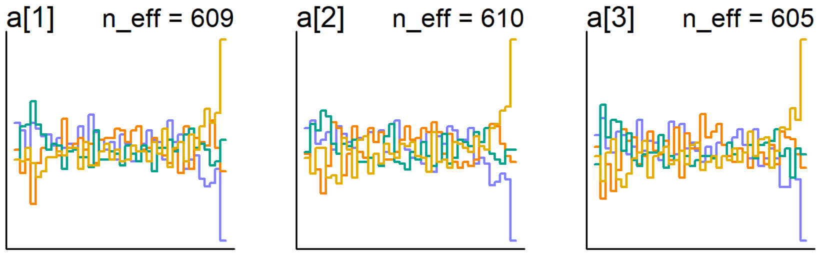
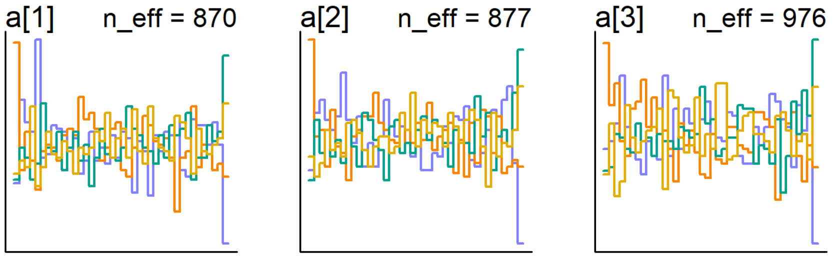
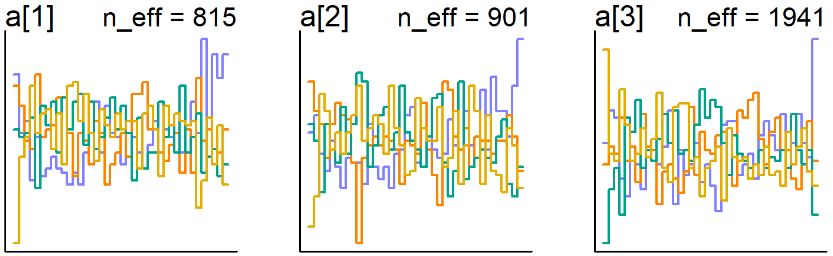
#	Predictor	Orangutans	Gorillas
6	Lockdown status		
	Total visitors		
	Visitor noise		

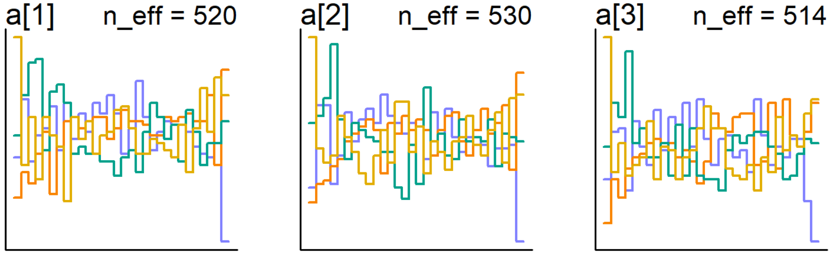
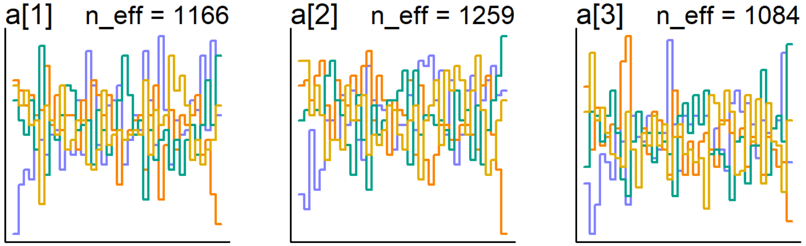
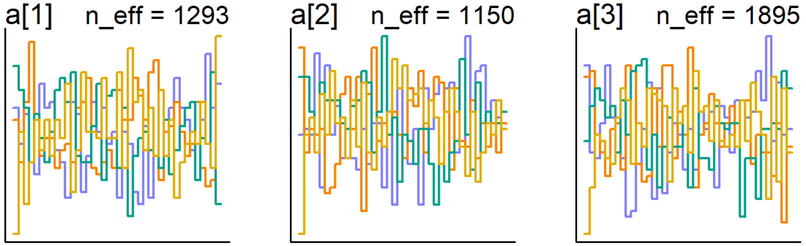
#	Predictor	Orangutans	Gorillas
	Visitor presence		
7	Lockdown status		
8	Lockdown status		

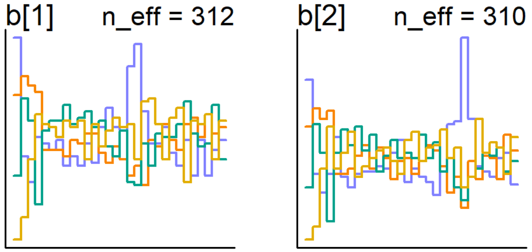
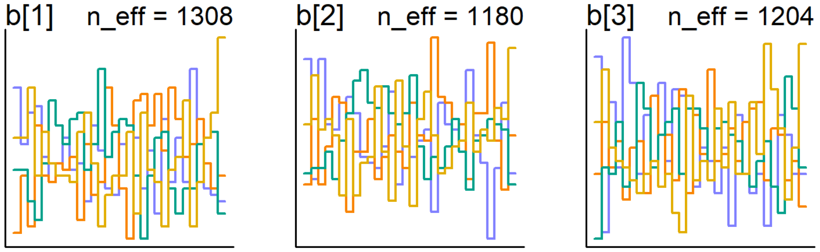
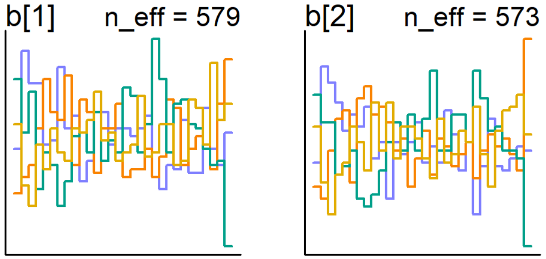
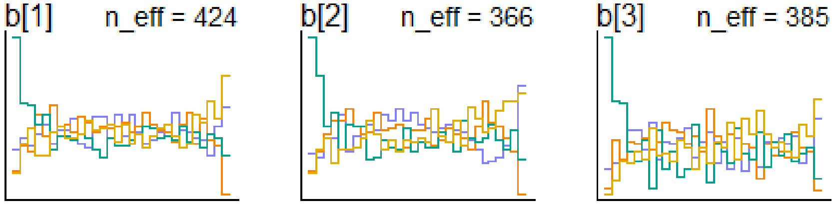
#	Predictor	Orangutans	Gorillas
	Total visitors		
	Visitor noise		
	Visitor presence		

#	Predictor	Orangutans	Gorillas
9	Lockdown status	 	N/A
	Total visitors	  	N/A
	Visitor noise	  	N/A

#	Predictor	Orangutans	Gorillas
	Visitor presence		N/A
10	Lockdown status	N/A	
	Total visitors	N/A	

#	Predictor	Orangutans	Gorillas
	Visitor noise	N/A	
	Visitor presence	N/A	
11	Lockdown status	N/A	

#	Predictor	Orangutans	Gorillas
	Total visitors	N/A	
	Visitor noise	N/A	
	Visitor presence	N/A	

#	Predictor	Orangutans	Gorillas
12	Focus on keeper		
13	Focus on researcher		

Appendix J: Lockdown study WAIC scores

Predictor: Lockdown status

Model	Species	WAIC	lppd	penalty	std_error
1	Orangutan	1345.9	-664.4	8.5	82.0
	Gorilla	2032.5	-1005.8	10.4	97.8
2	Orangutan	10464.4	-5221.1	11.1	90.2
	Gorilla	19666.6	-9822.1	11.2	151.7
3	Orangutan	10499.4	-5238.7	10.9	84.4
	Gorilla	20454.0	-10215.7	11.3	142.3
4	Orangutan	4248.3	-2115.4	8.8	113.6
	Gorilla	5388.4	-2683.9	10.3	120.1
5	Orangutan	8840.3	-4411.1	9.1	82.4
	Gorilla	10006.3	-4992.3	10.9	81.1
6	Orangutan	3207.8	-1596.2	7.7	106.5
	Gorilla	1793.4	-885.3	11.4	94.5
7	Orangutan	534.9	-261.3	6.1	50.1
	Gorilla	94.8	-43.1	4.4	29.6
8	Orangutan	6734.9	-3359.3	8.1	94.1
	Gorilla	3552.2	-1765.6	10.5	107.8
9	Orangutan	2365.8	-1175.3	7.6	76.9
10	Gorilla	9602.7	-4793.3	8.0	69.6
11	Gorilla	682.7	-335.1	6.3	63.7
12	Orangutan	2247.9	-1116.5	7.5	105.1
	Gorilla	2478.4	-1228.7	10.5	111
13	Orangutan	1981.6	-982.1	8.7	97.7
	Gorilla	2532.8	-1255.6	10.8	106.3

Predictor: Total visitors

Model	Species	WAIC	lppd	penalty	std_error
1	Orangutan	631.7	-307.5	8.4	56.0
	Gorilla	948.7	-464.8	9.6	68.7
2	Orangutan	4879.2	-2428.0	11.6	60.9
	Gorilla	12857.5	-6416.7	12.0	120.4
3	Orangutan	5122.8	-2550.3	11.1	57.1
	Gorilla	13140.9	-6558.4	12.1	113.9
5	Orangutan	4459.5	-2219.7	10.0	56.0
	Gorilla	5142.7	-2559.1	12.3	68.6
6	Orangutan	939.9	-461.8	8.2	33.3
	Gorilla	641.7	-310.6	10.3	39.0
8	Orangutan	3384.9	-1683.5	9.0	63.5

Model	Species	WAIC	lppd	penalty	std_error
	Gorilla	2085.1	-1032.4	10.1	79.9
9	Orangutan	2048.3	-1015.3	8.8	75.2
10	Gorilla	6207.9	-3095.0	8.9	61.4
11	Gorilla	101.4	-48.1	2.6	25.4

Predictor: Visitor noise

Model	Species	WAIC	lppd	penalty	std_error
1	Orangutan	638.3	-311.3	7.8	56.5
	Gorilla	955.7	-467.1	10.8	69.7
2	Orangutan	4920.3	-2448.3	11.8	60.8
	Gorilla	12872.8	-6424.5	11.9	119.9
3	Orangutan	5124.8	-2552.0	10.5	57.5
	Gorilla	13035.6	-6505.6	12.1	113.0
5	Orangutan	4485.7	-2233.1	9.7	55.4
	Gorilla	5182.0	-2579.2	11.8	69.1
6	Orangutan	876.7	-430.4	8.0	35.8
	Gorilla	686.8	-332.5	10.9	41.8
8	Orangutan	3472.5	-1727.4	8.8	63.2
	Gorilla	2072.9	-1025.3	11.1	80.2
9	Orangutan	2235.4	-1107.9	9.9	76.4
10	Gorilla	6234.1	-3108.8	8.2	60.4
11	Gorilla	116.8	-55.1	3.3	30.2

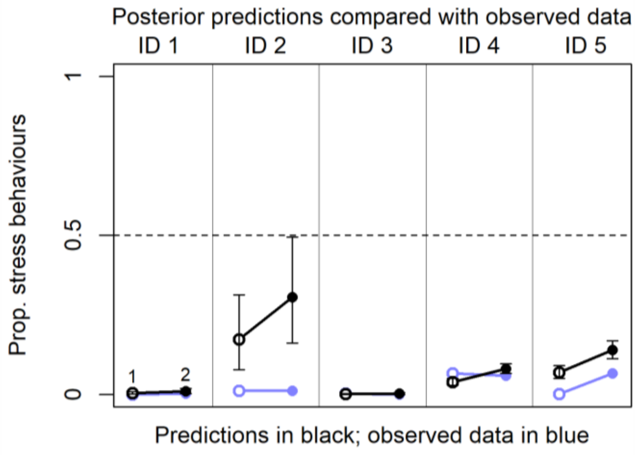
Predictor: Visitor presence

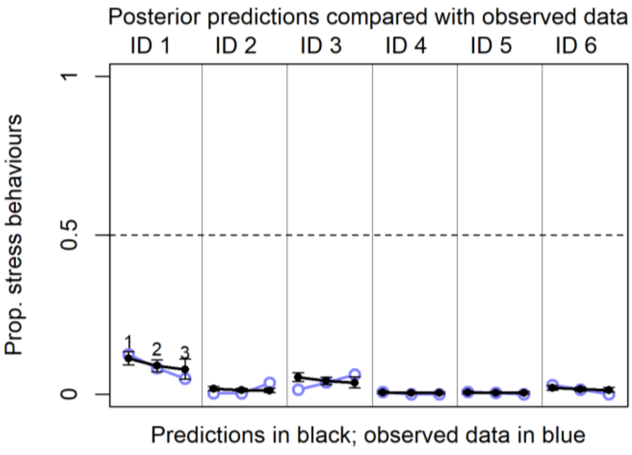
Model	Species	WAIC	lppd	penalty	std_error
1	Orangutan	633.1	-308.8	7.8	56.2
	Gorilla	956.2	-468.9	9.2	69.2
2	Orangutan	4924.4	-2450.6	11.6	60.8
	Gorilla	12876.8	-6426.5	11.9	120.1
3	Orangutan	5125.0	-2551.8	10.7	57.6
	Gorilla	13209.6	-6592.3	12.6	112.2
5	Orangutan	4445.4	-2213.1	9.6	56.2
	Gorilla	5249.8	-2613.3	11.6	67.7
6	Orangutan	926.5	-455.7	7.5	33.5
	Gorilla	673.3	-325.5	11.1	42.1
8	Orangutan	3467.1	-1725.0	8.6	63.1
	Gorilla	2096.7	-1038.2	10.1	80.1
9	Orangutan	2233.6	-1107.5	9.3	77.6
10	Gorilla	9602.7	-4793.3	8.0	69.6
11	Gorilla	116.2	-55.7	2.4	30.1

Appendix K: Lockdown study posterior predictive check

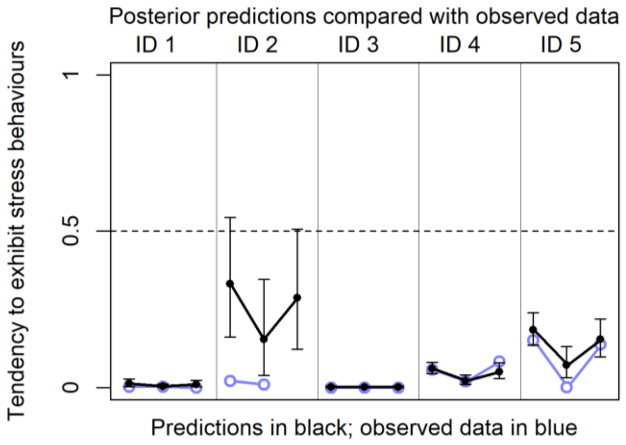
Orangutan IDs: ID 1 = Basuki, ID 2 = Batu, ID 3 = Kayan, ID 4 = Kibriah, ID 5 = Maliku.
Gorilla IDs: ID 1 = Asante, ID 2 = Biddy, ID 3 = Lope, ID 4 = Oumbi, ID 5 = Ozala, ID 6 = Shufai.

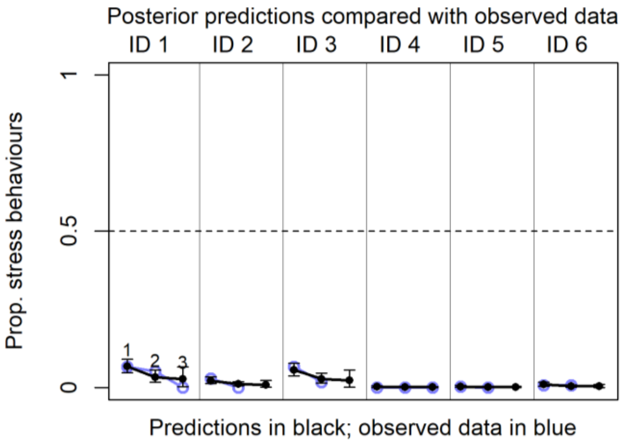
Model 1. Lockdown status v. stress behaviours orangutans left, gorillas right):



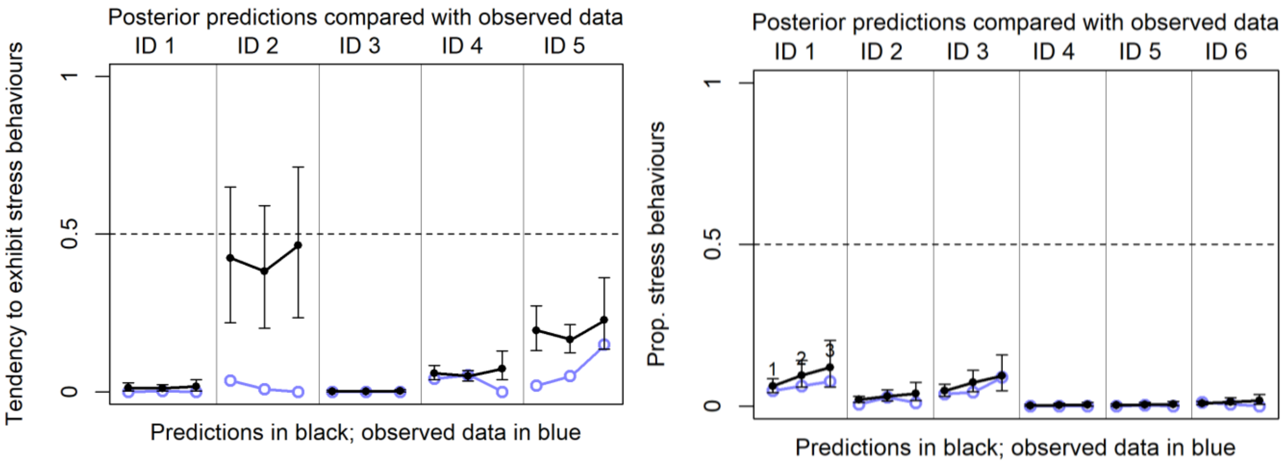


Model 1. Total visitors v. stress behaviours (orangutans left, gorillas right):

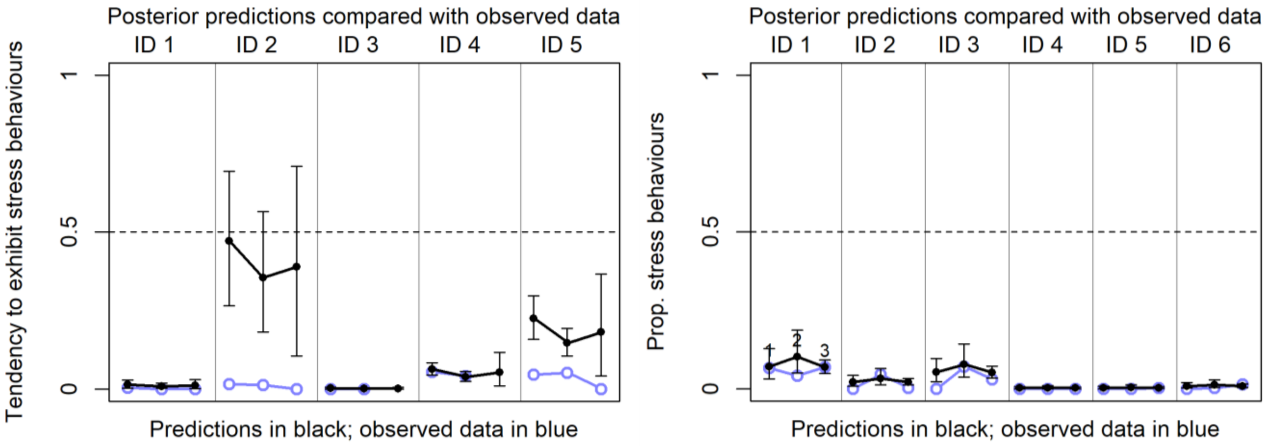




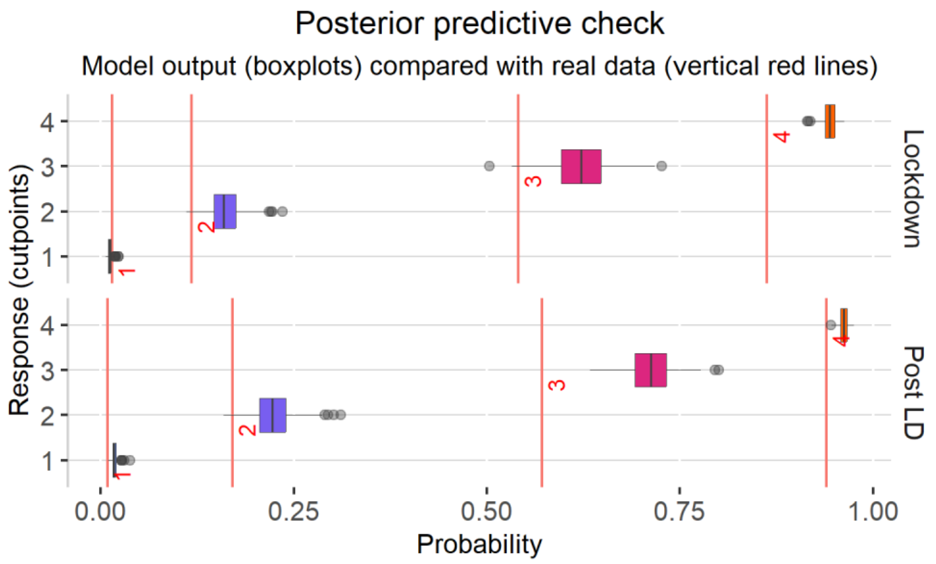
Model 1. Visitor noise v. stress behaviours (orangutans left, gorillas right):



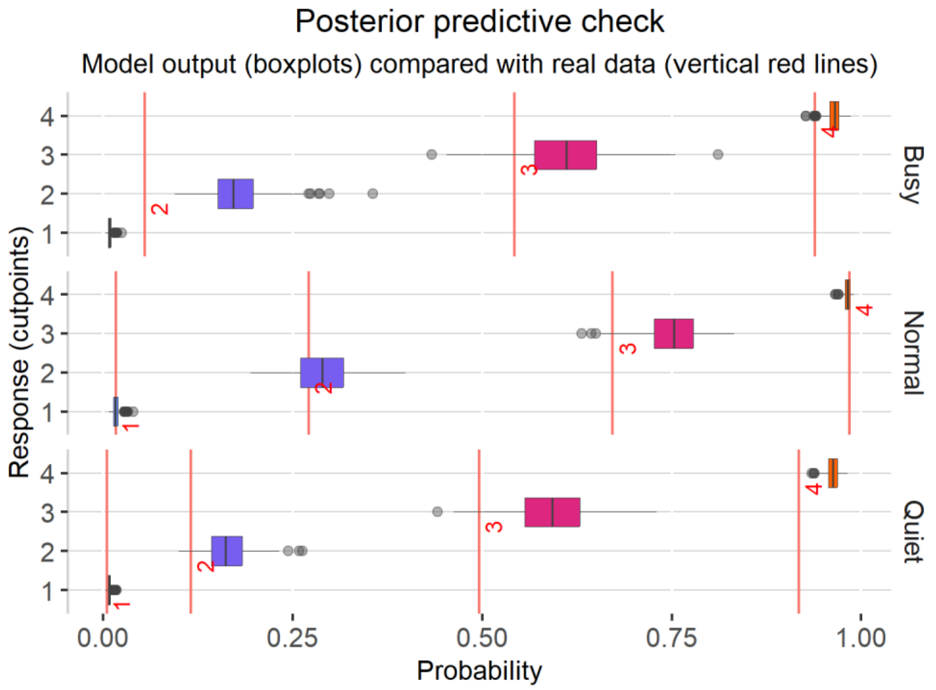
Model 1. Visitor presence v. stress behaviours (orangutans left, gorillas right):



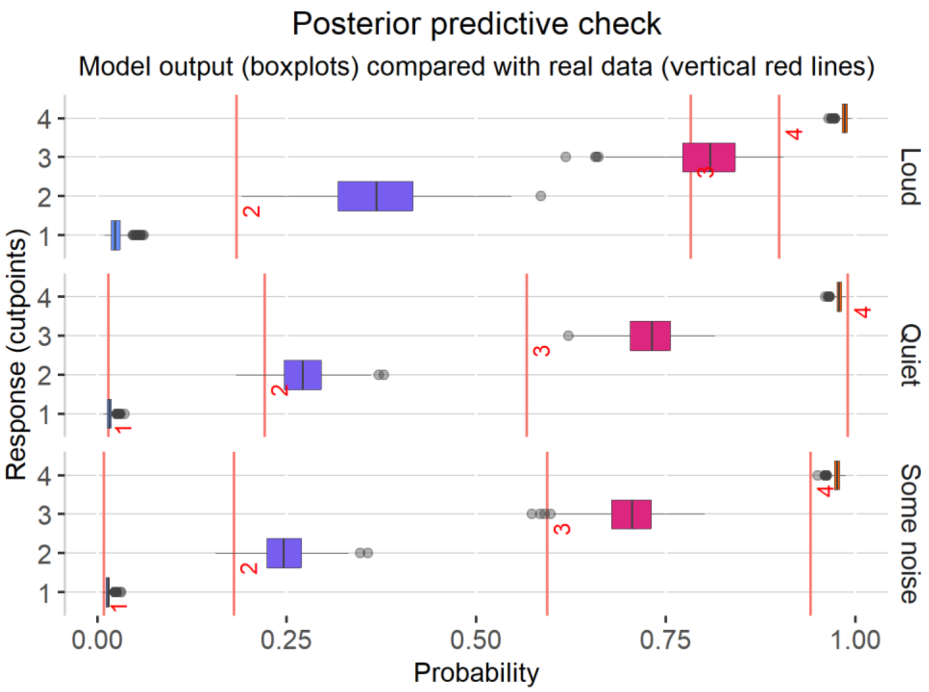
Model 2. Lockdown status v. hunched posture (orangutans):



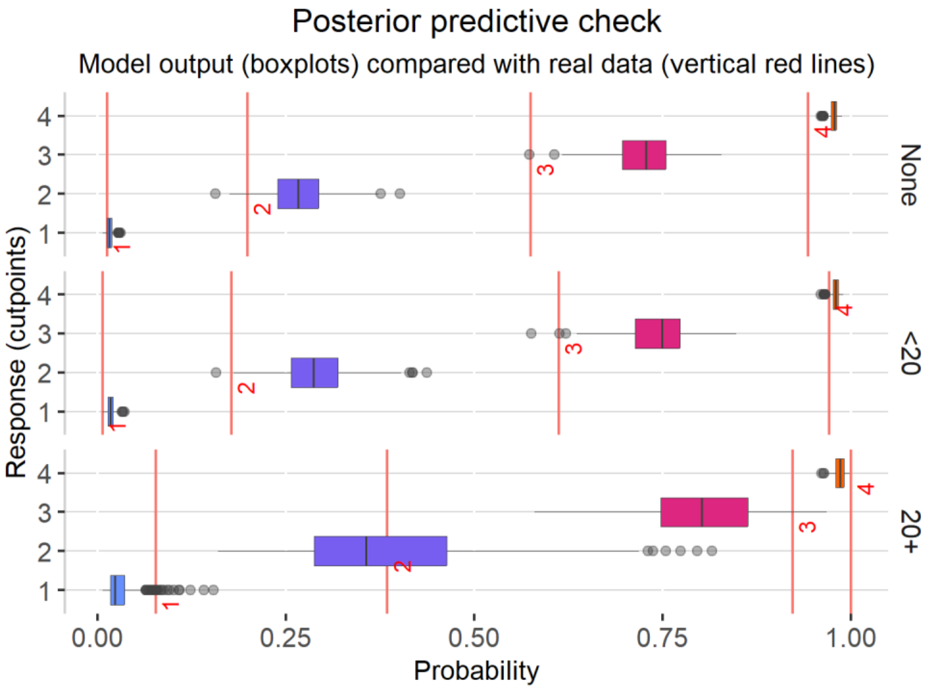
Model 2. Total visitors v. hunched posture (orangutans):



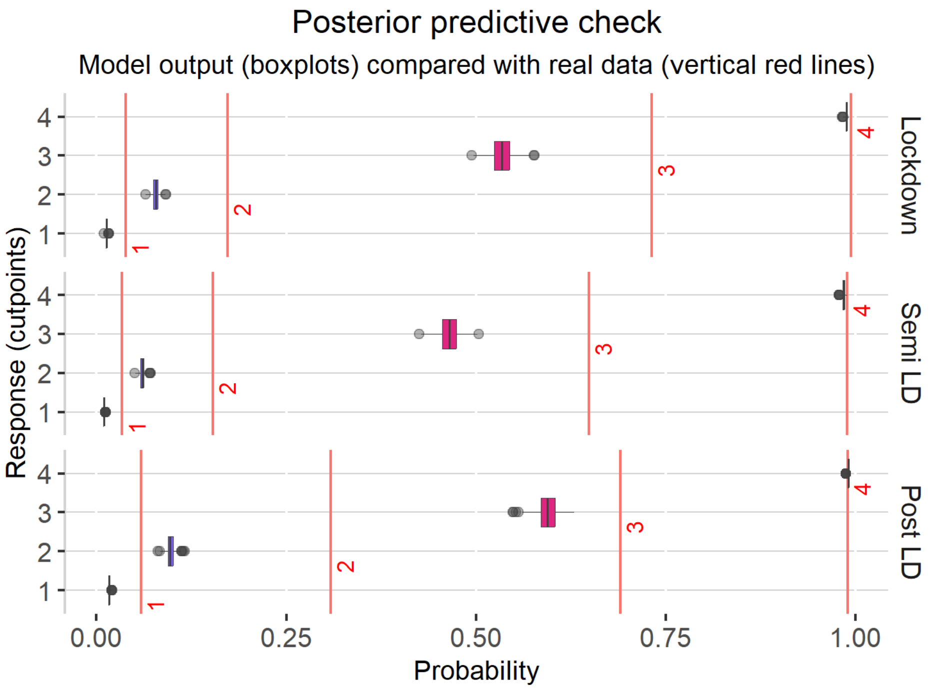
Model 2. Visitor noise v. hunched posture (orangutans):



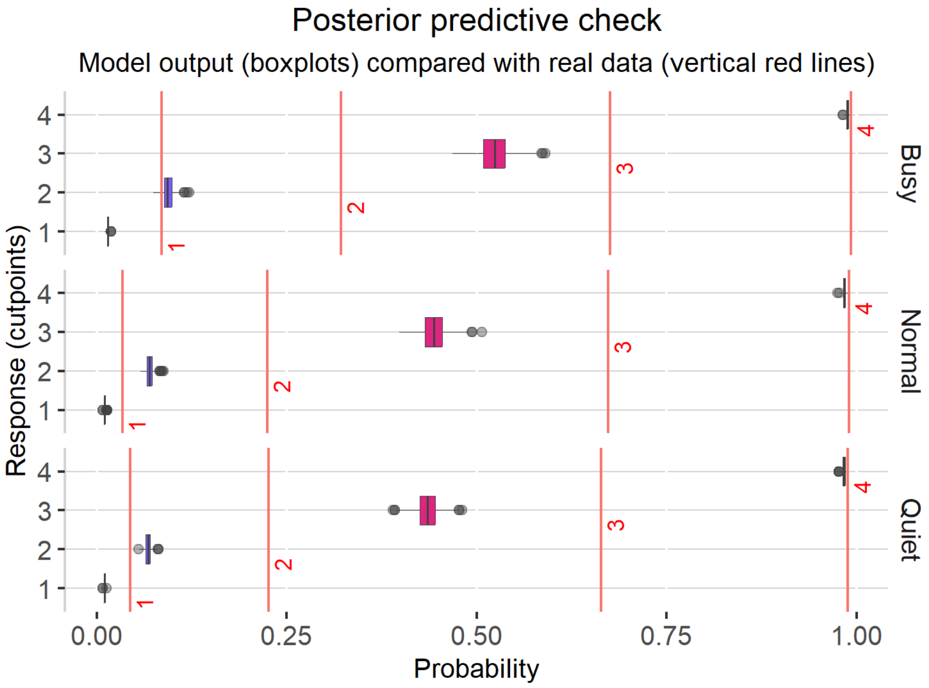
Model 2. Visitor presence v. hunched posture (orangutans):



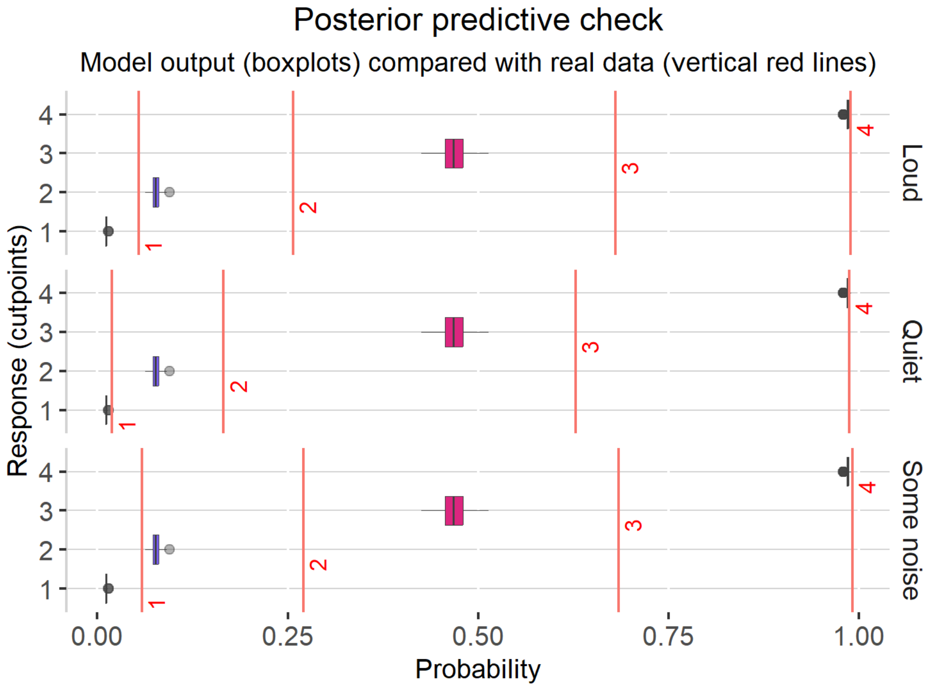
Model 2. Lockdown status v. hunched posture (gorillas):



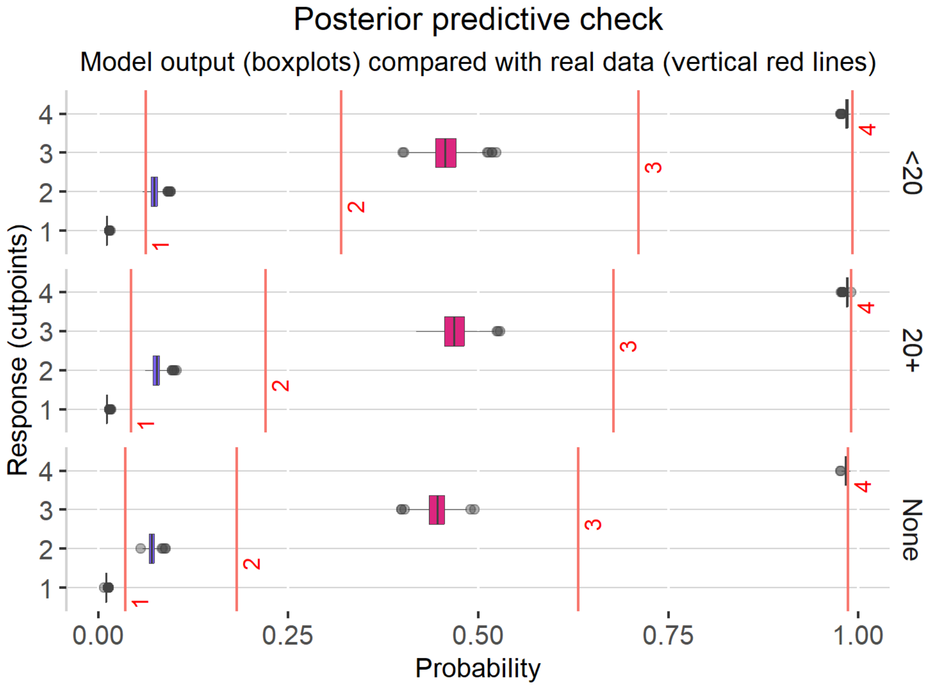
Model 2. Total visitors v. hunched posture (gorillas):



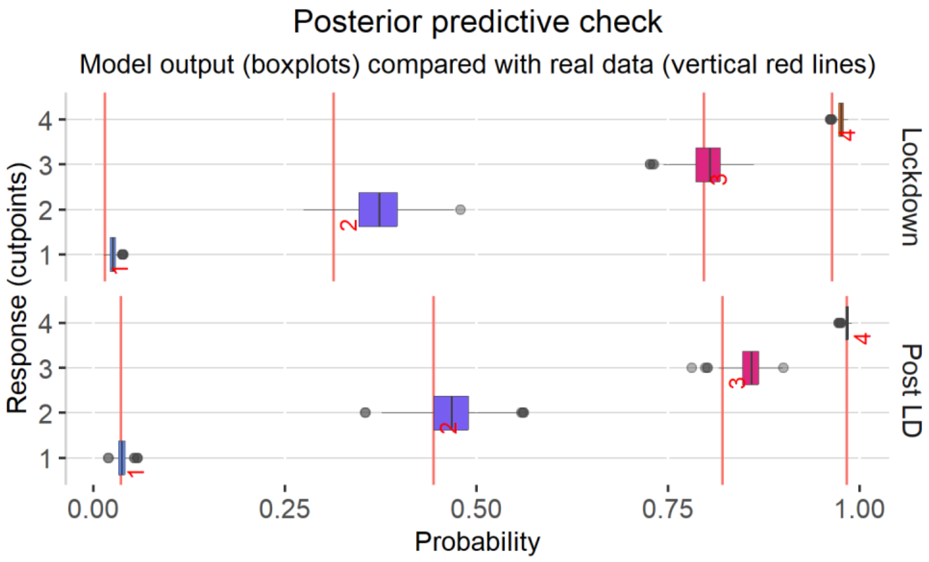
Model 2. Visitor noise v. hunched posture (gorillas):



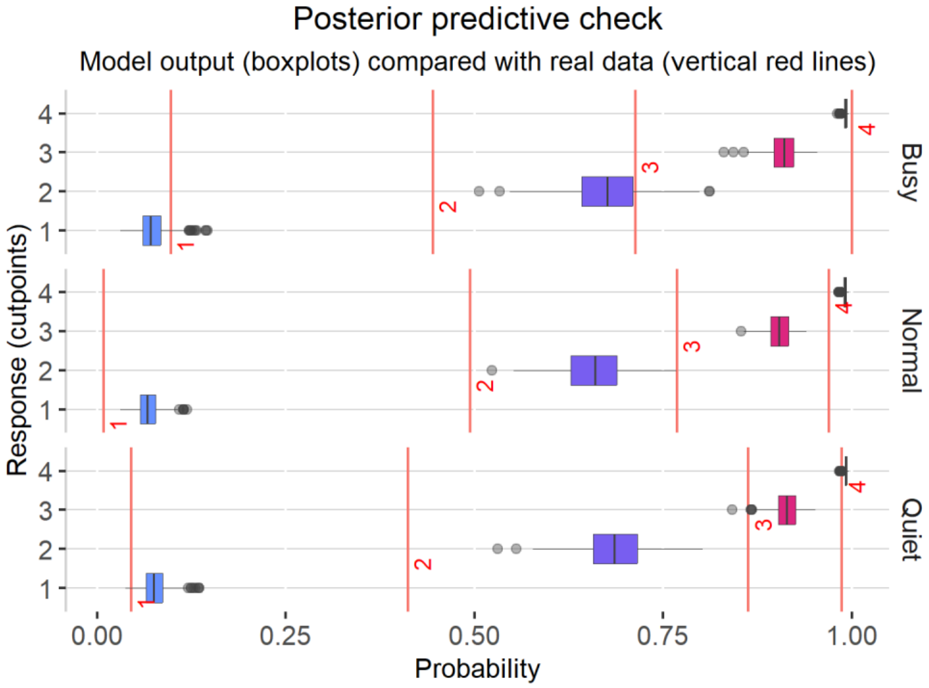
Model 2. Visitor presence v. hunched posture (gorillas):



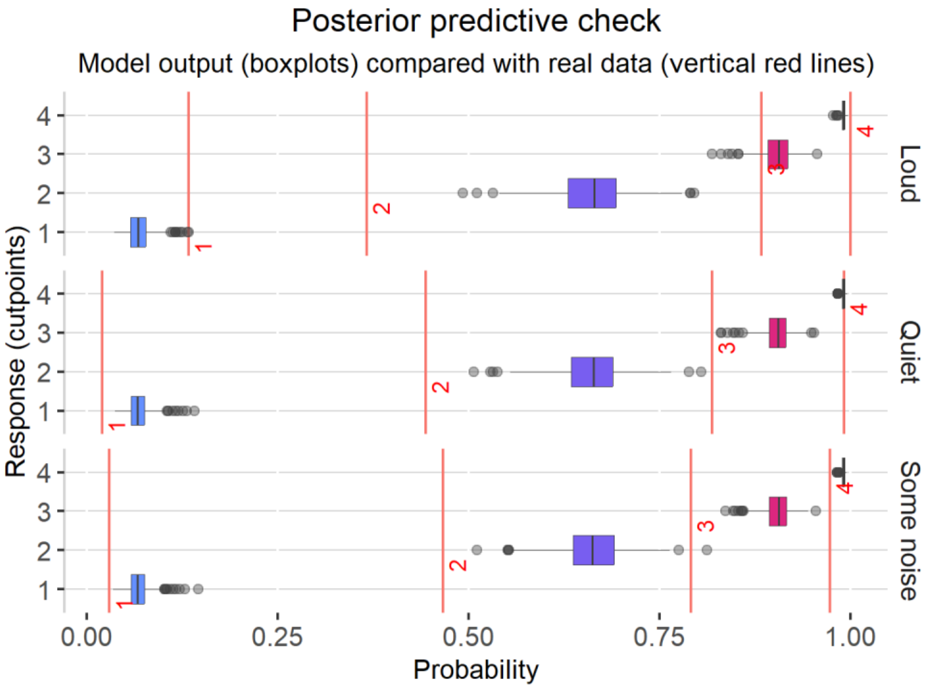
Model 3. Lockdown status v. closed posture (orangutans):



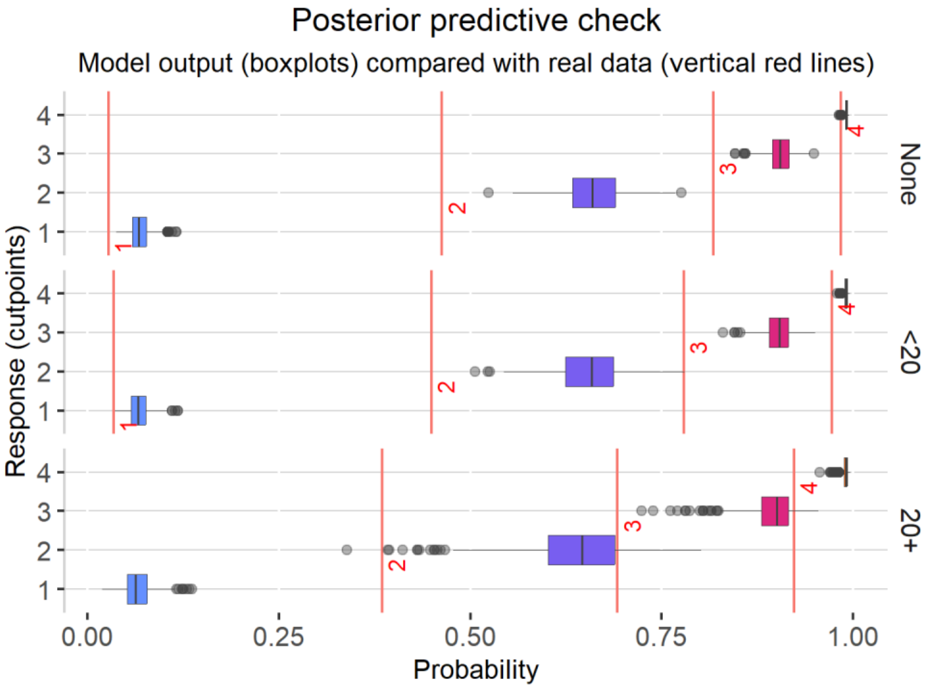
Model 3. Total visitors v. closed posture (orangutans):



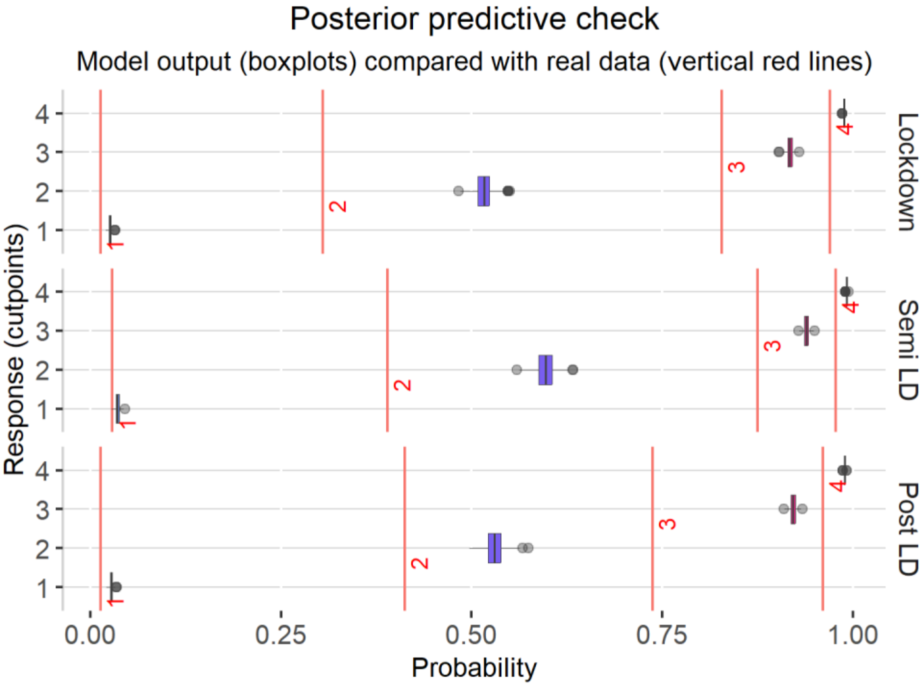
Model 3. Visitor noise v. closed posture (orangutans):



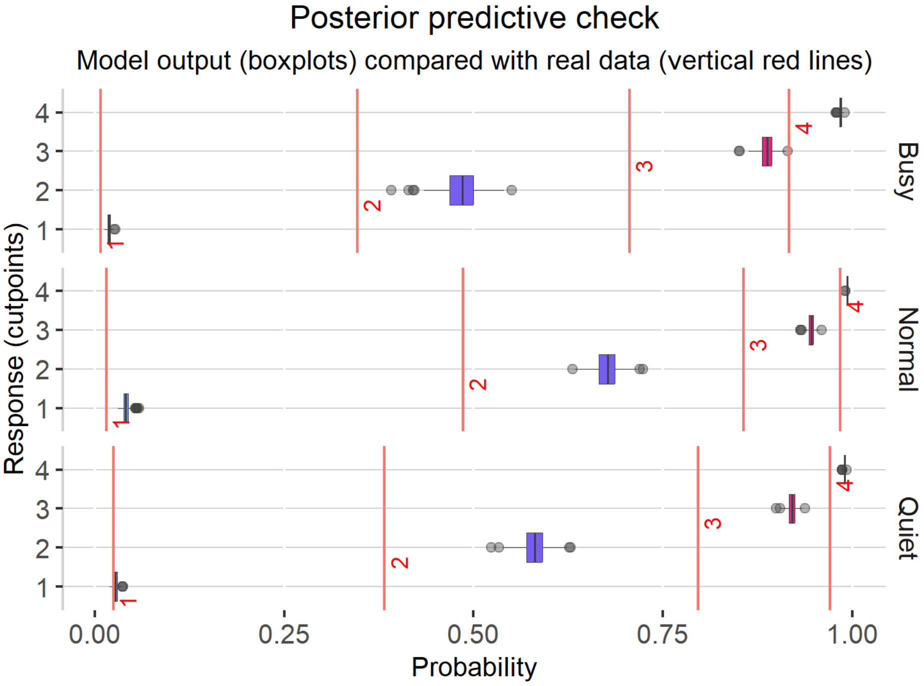
Model 3. Visitor presence v. closed posture (orangutans):



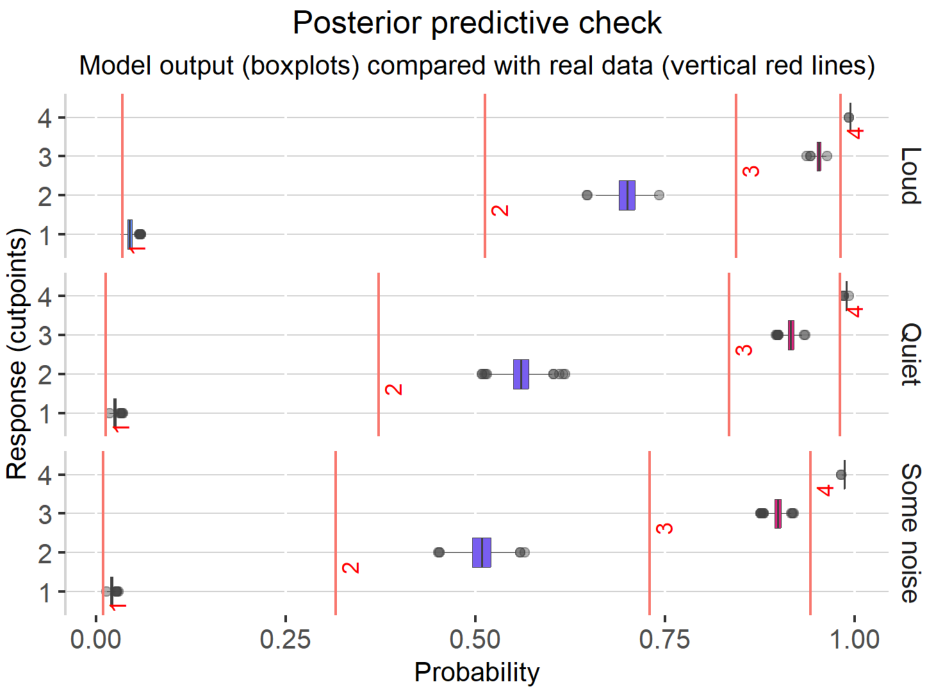
Model 3. Lockdown status v. closed posture (gorillas):



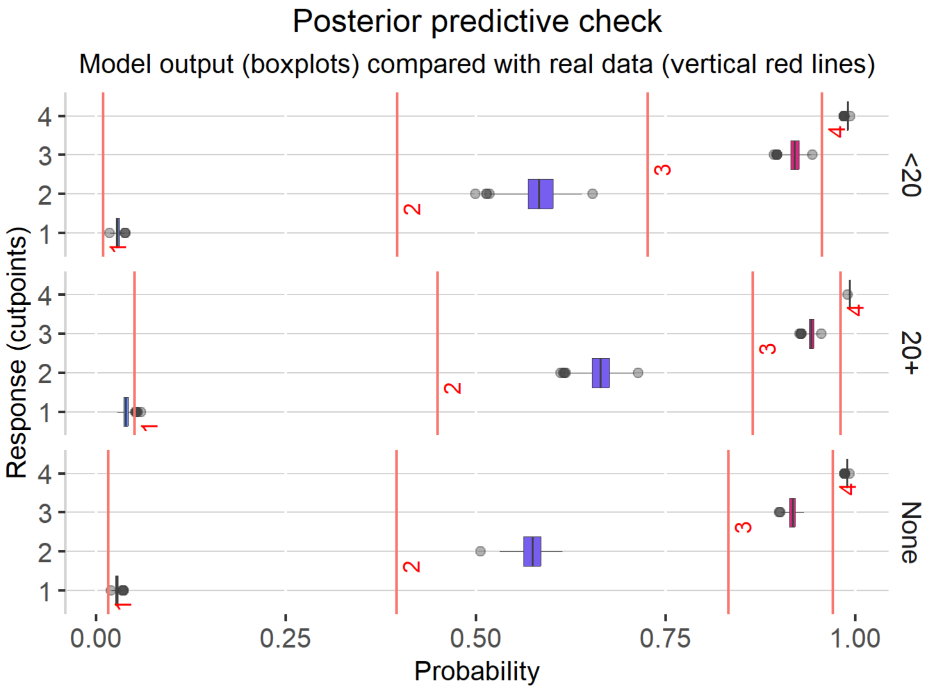
Model 3. Total visitors v. closed posture (gorillas):



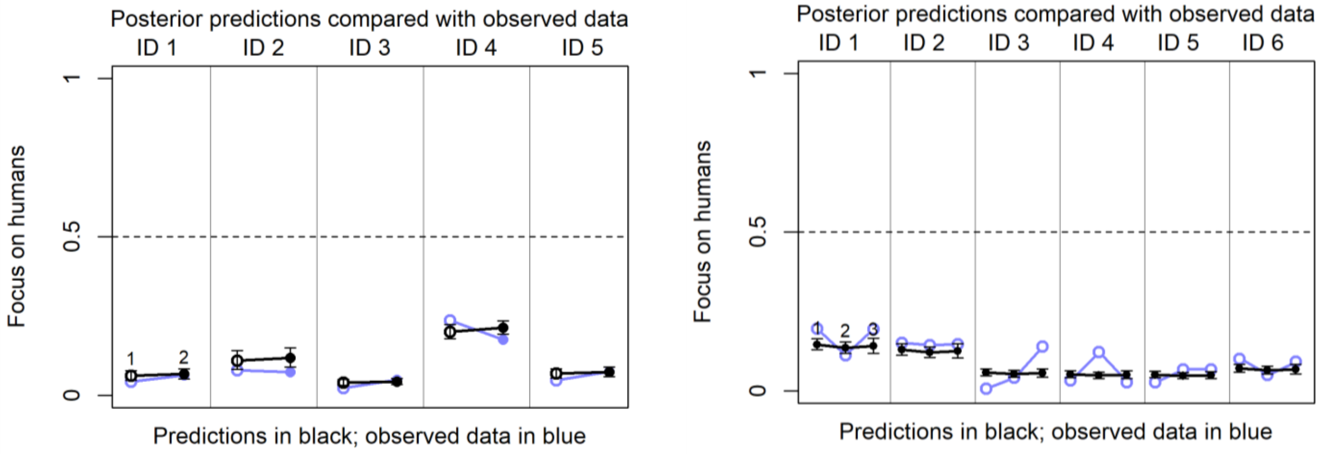
Model 3. Visitor noise v. closed posture (gorillas):



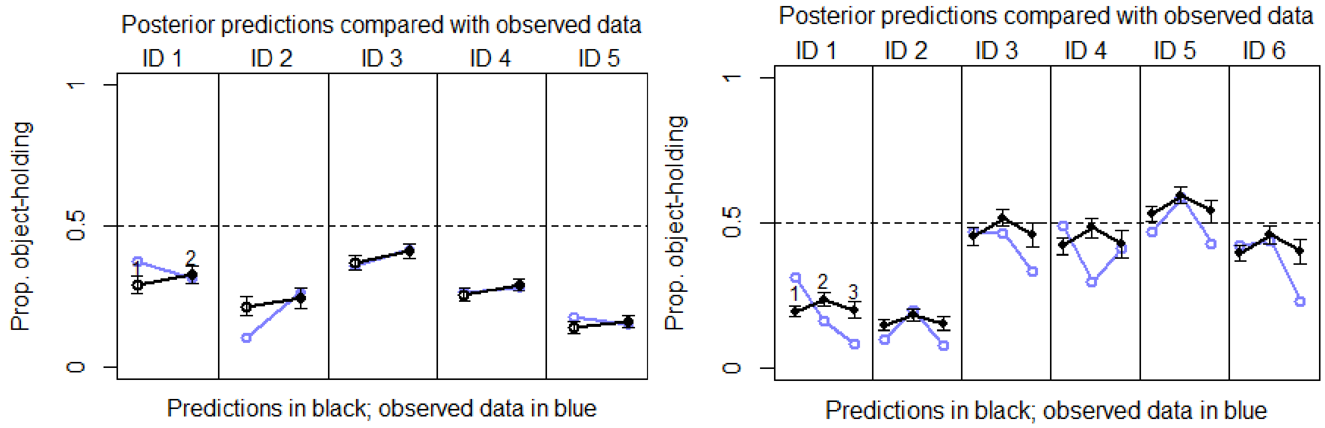
Model 3. Visitor presence v. closed posture (gorillas):



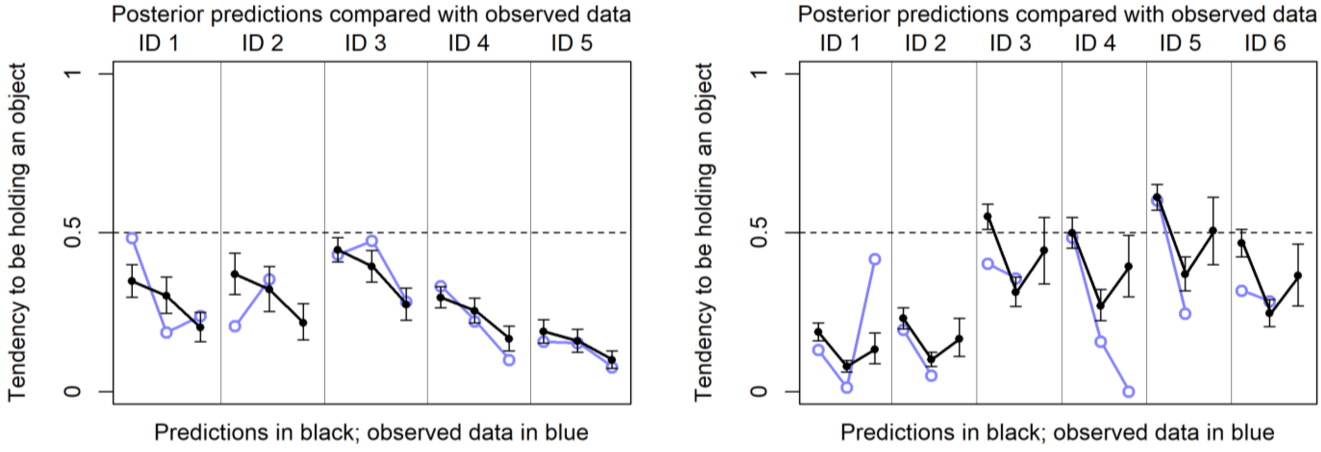
Model 4. Lockdown status v. focus on humans (orangutans left, gorillas right):



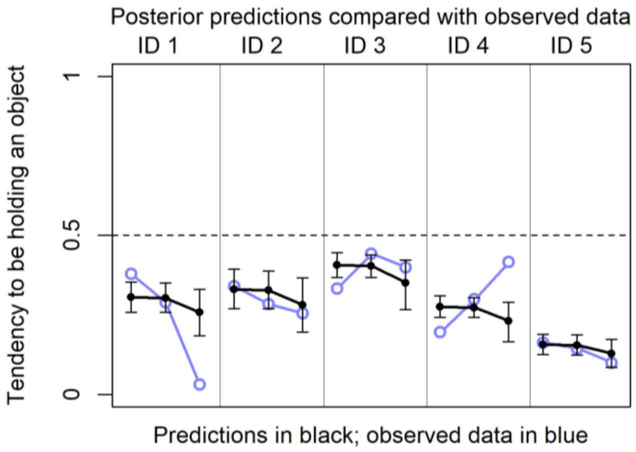
Model 5. Lockdown status v. object-holding (orangutans left, gorillas right):

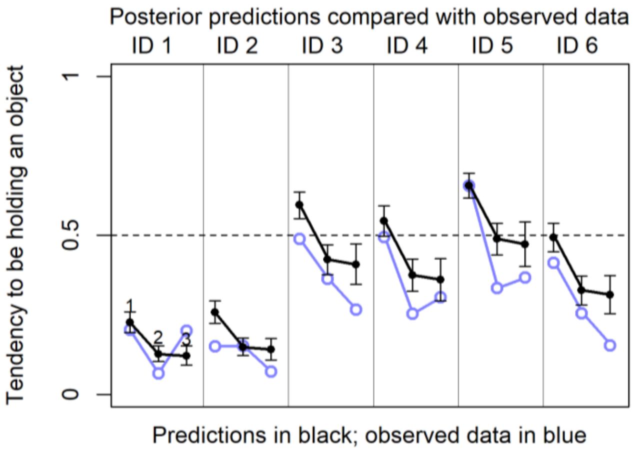


Model 5. Total visitors v. object-holding (orangutans left, gorillas right):

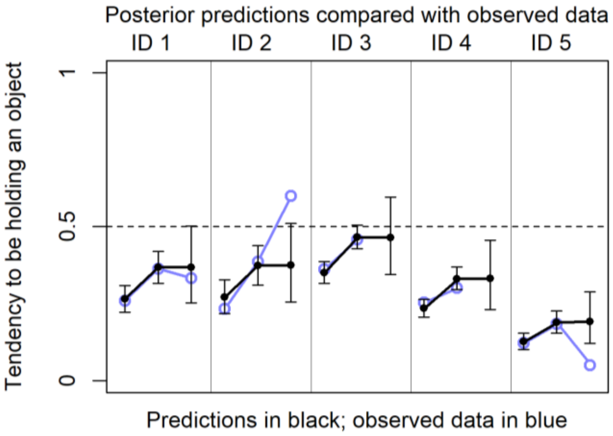


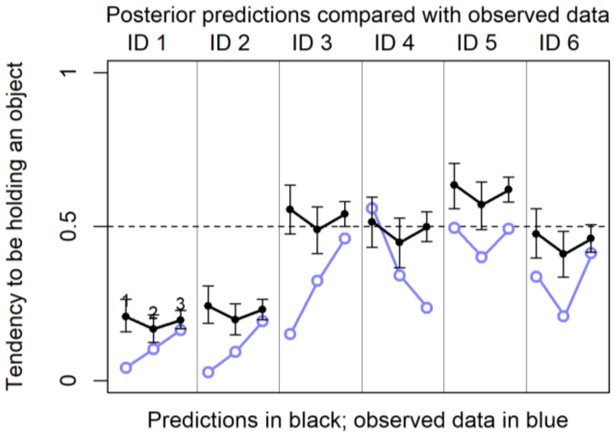
Model 5. Visitor noise v. object-holding (orangutans left, gorillas right):



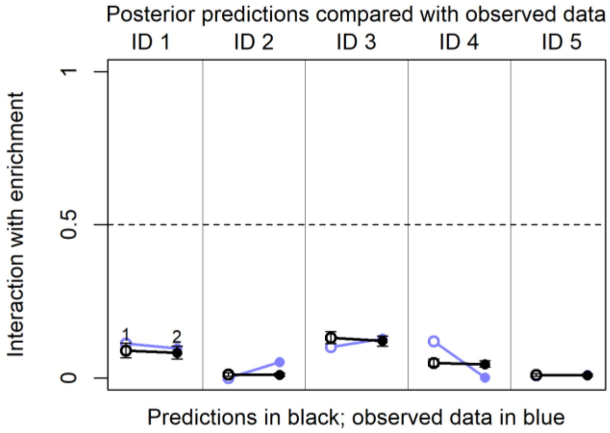


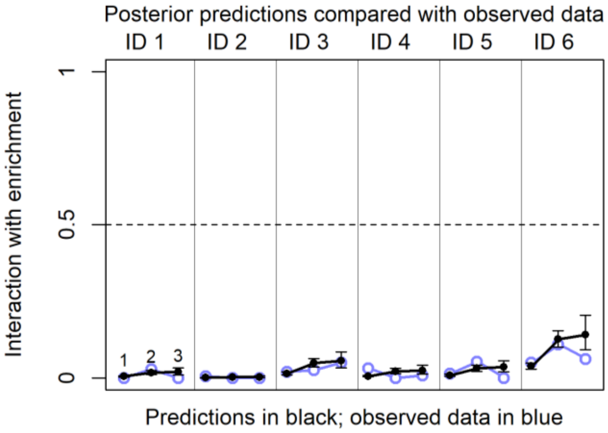
Model 5. Visitor presence v. object-holding (orangutans left, gorillas right):



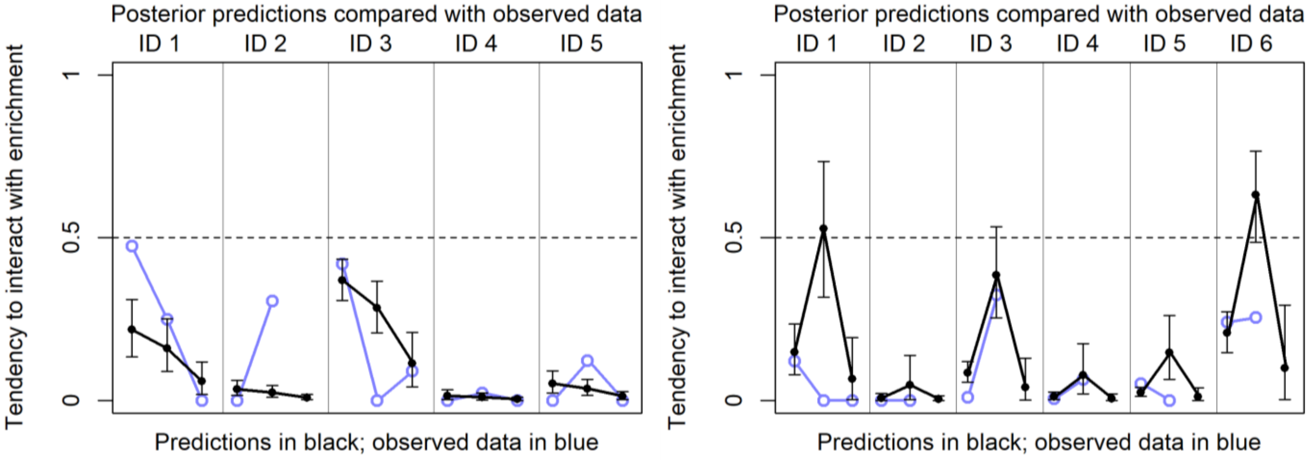


Model 6. Lockdown status v. interacting with enrichment (orangutans left, gorillas right):

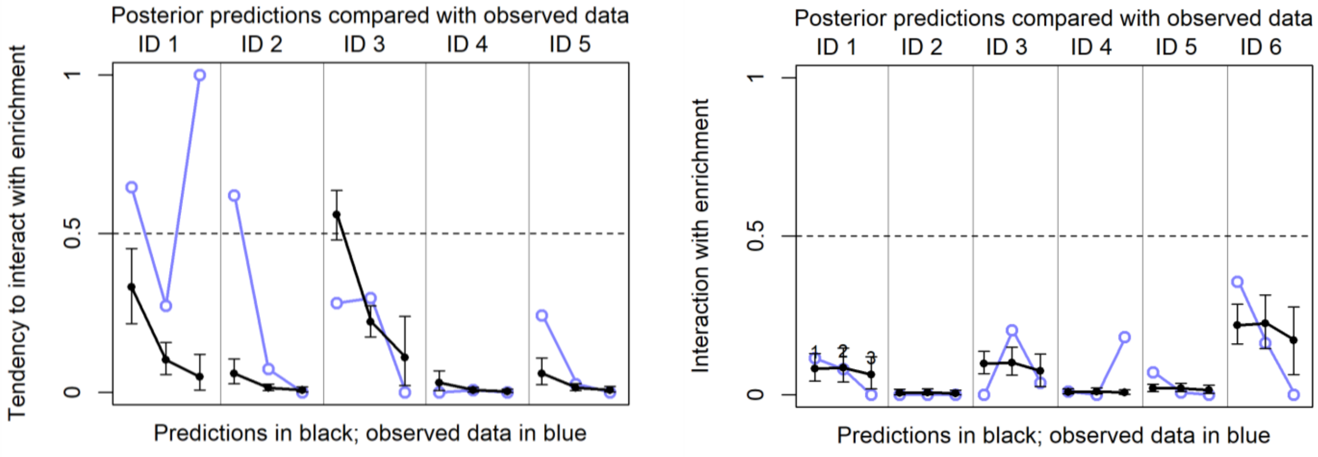




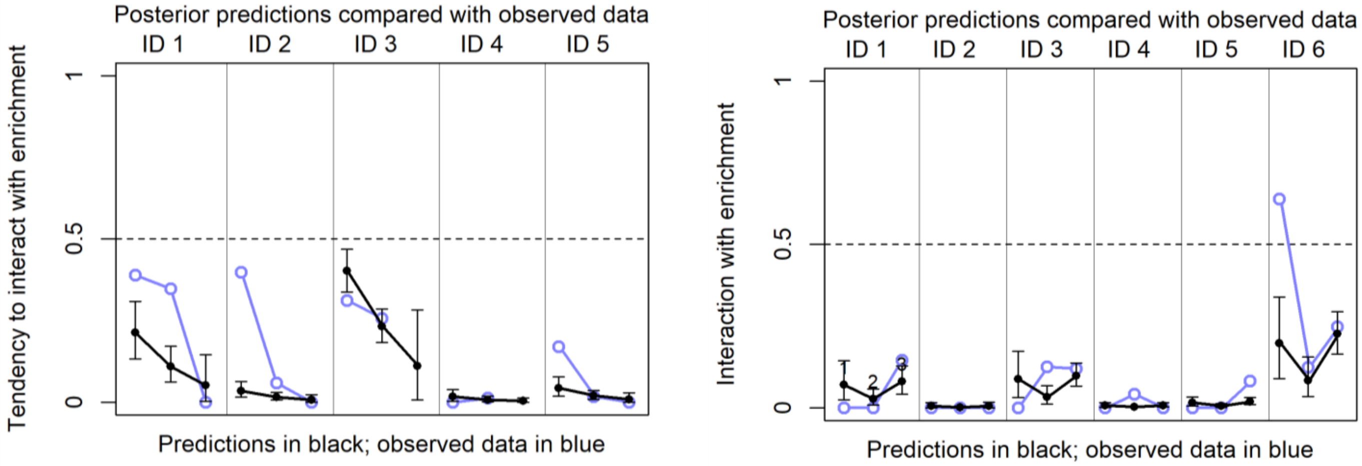
Model 6. Total visitors v. interacting with enrichment (orangutans left, gorillas right):



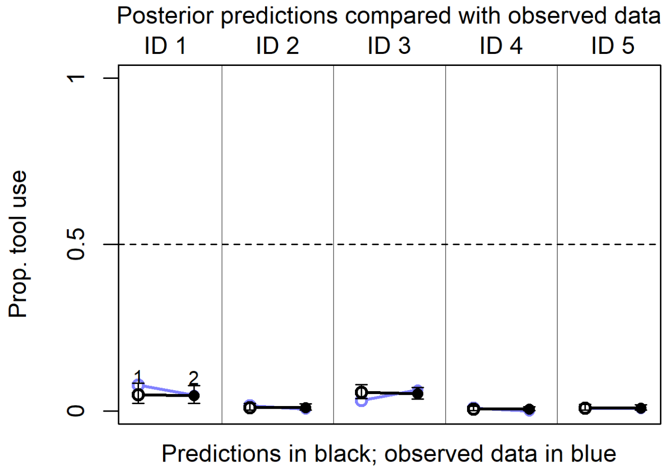
Model 6. Visitor noise v. interacting with enrichment (orangutans left, gorillas right):

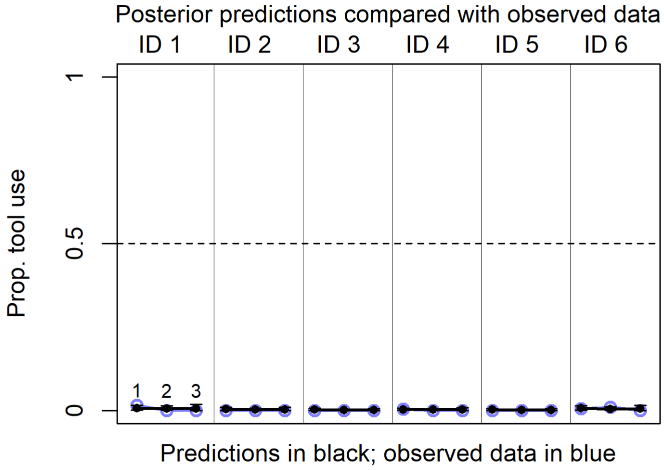


Model 6. Visitor presence v. interacting with enrichment (orangutans left, gorillas right):

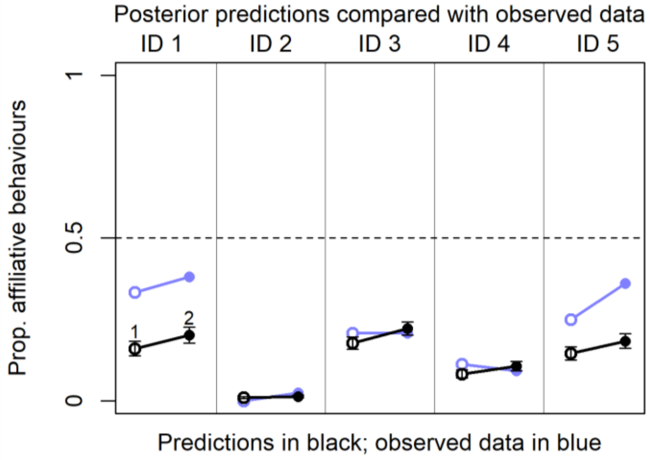


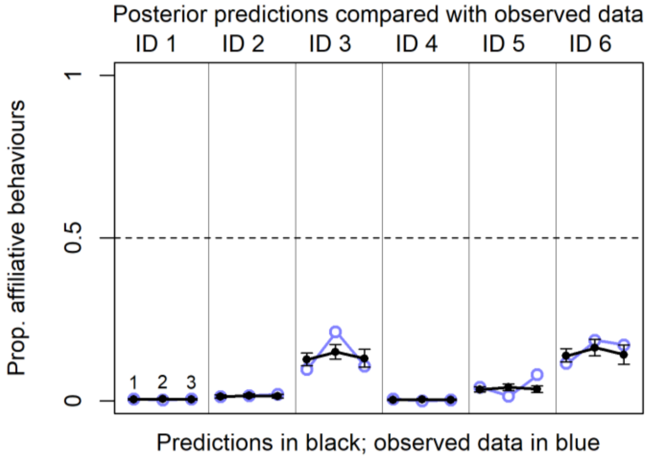
Model 7. Lockdown status v. using tools (orangutans left, gorillas right):



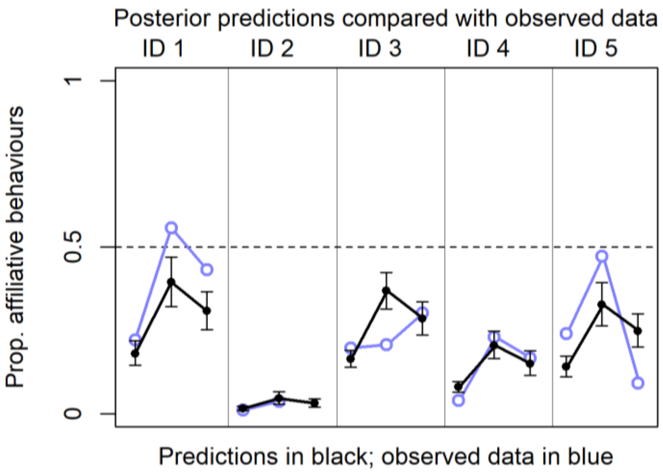


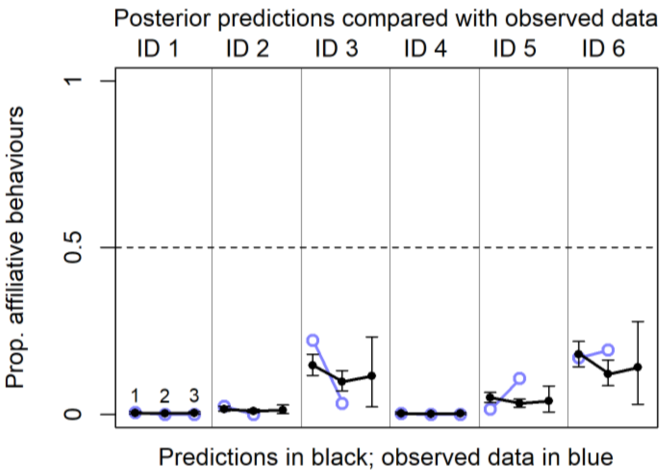
Model 8. Lockdown status v. affiliative behaviours (orangutans left, gorillas right):



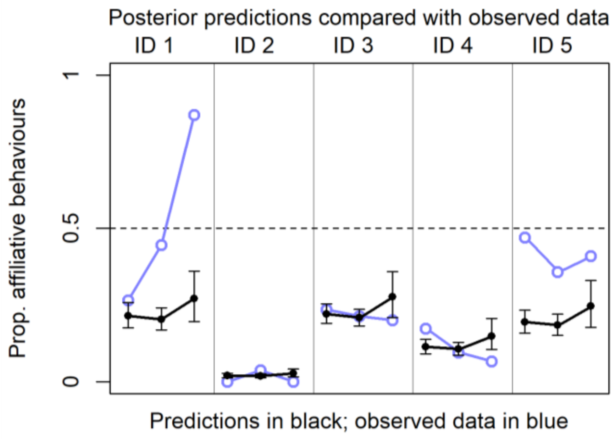


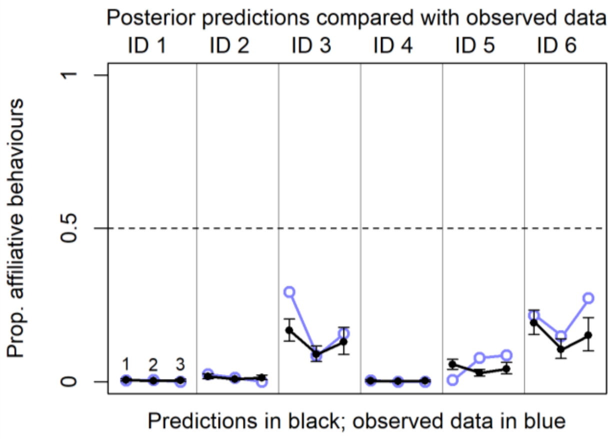
Model 8. Total visitors v. affiliative behaviours (orangutans left, gorillas right):



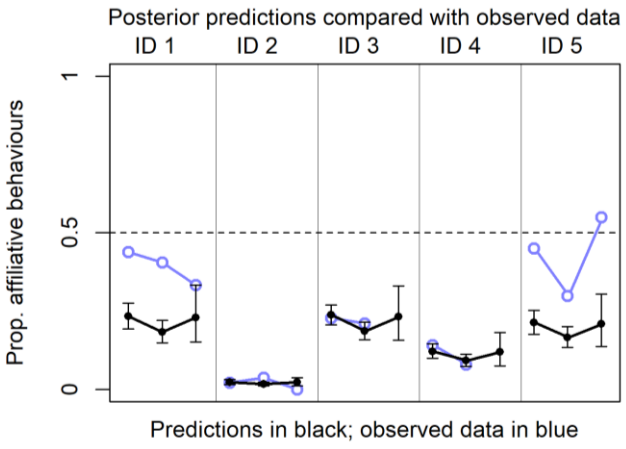


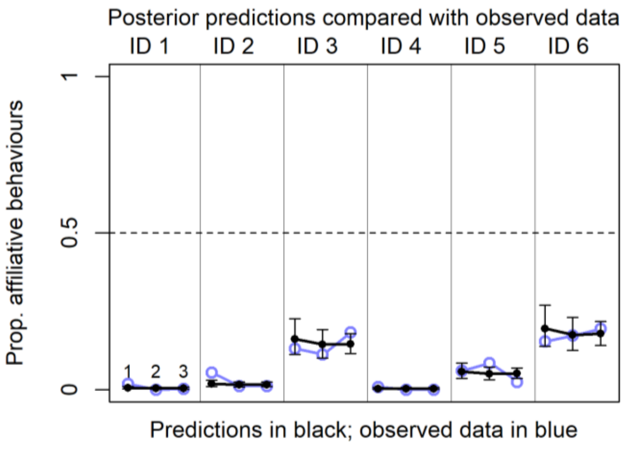
Model 8. Visitor noise v. affiliative behaviours (orangutans left, gorillas right):



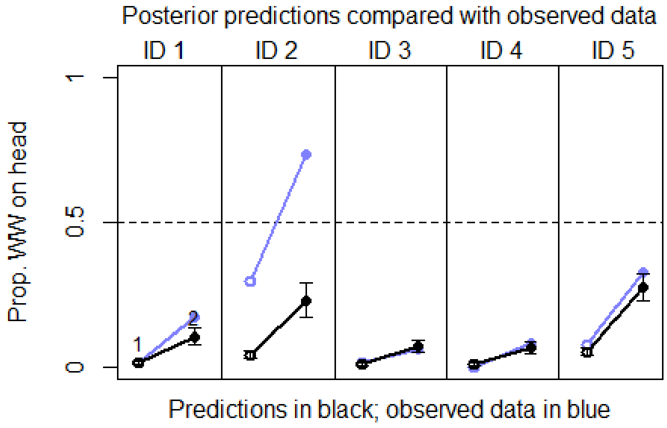


Model 8. Visitor presence v. affiliative behaviours (orangutans left, gorillas right):

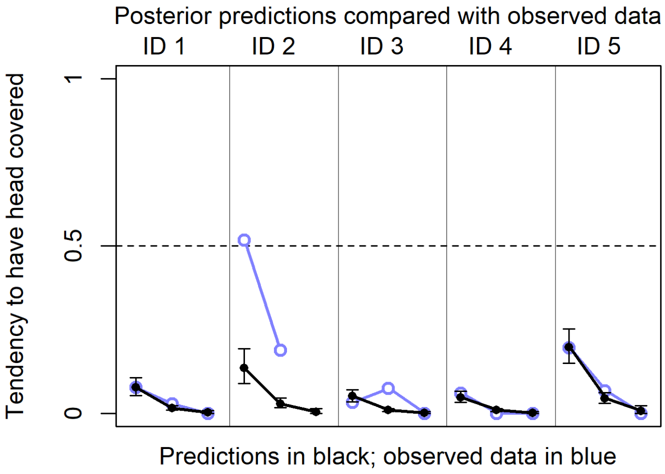




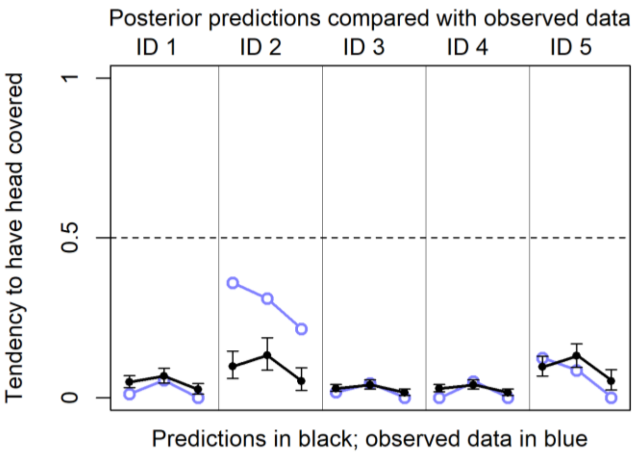
Model 9. Lockdown status v. head covering (orangutans):



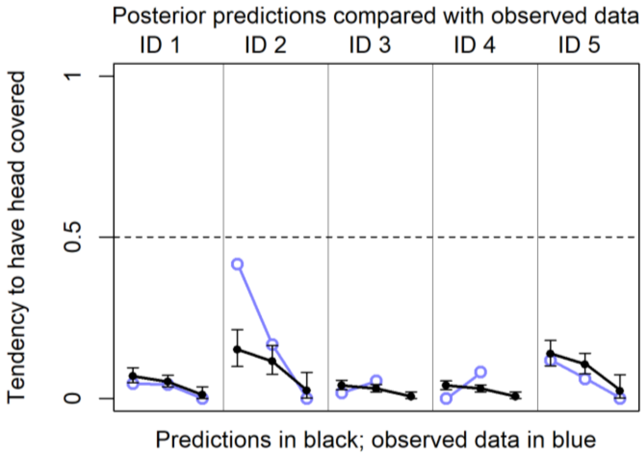
Model 9. Total visitors v. head covering (orangutans):



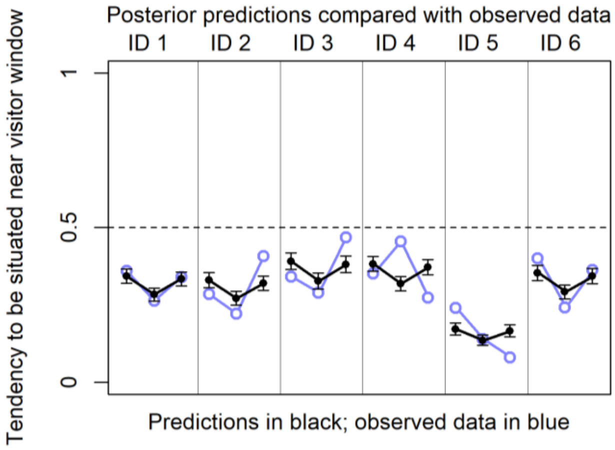
Model 9. Visitor noise v. head covering (orangutans):



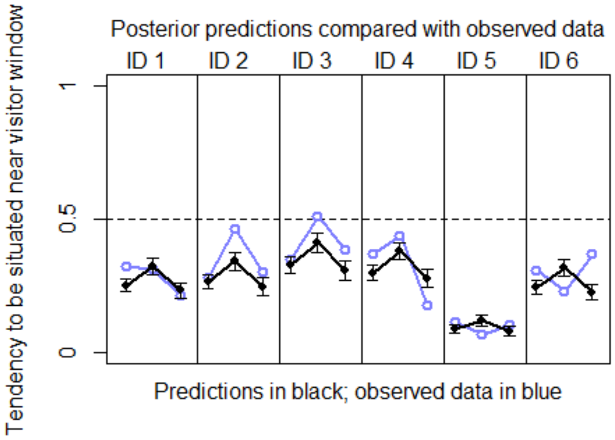
Model 9. Visitor presence v. head covering (orangutans):



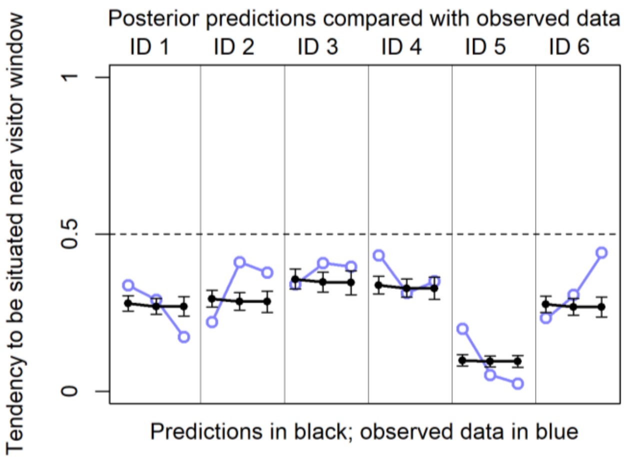
Model 10. Lockdown status v. proximity to visitor window (gorillas):



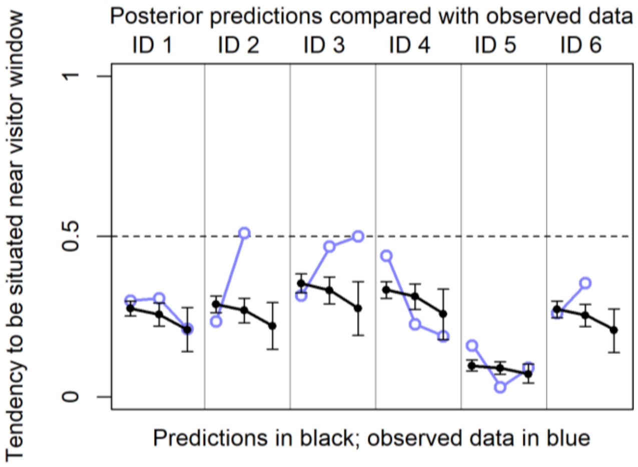
Model 10. Total visitors v. proximity to visitor window (gorillas):



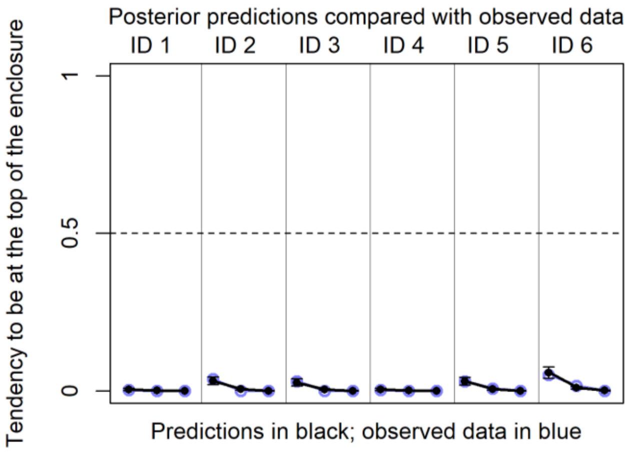
Model 10. Visitor noise v. proximity to visitor window (gorillas):



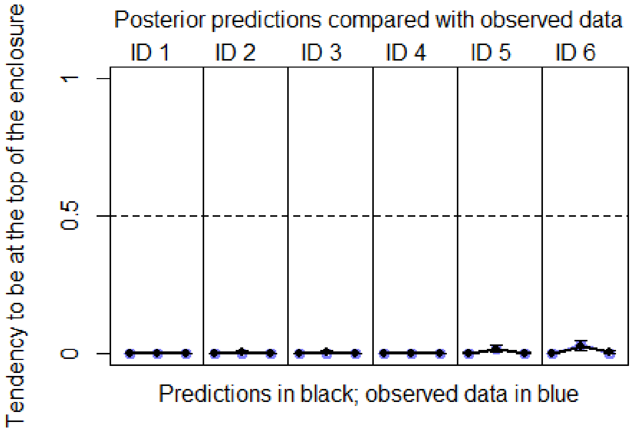
Model 10. Visitor presence v. proximity to visitor window (gorillas):



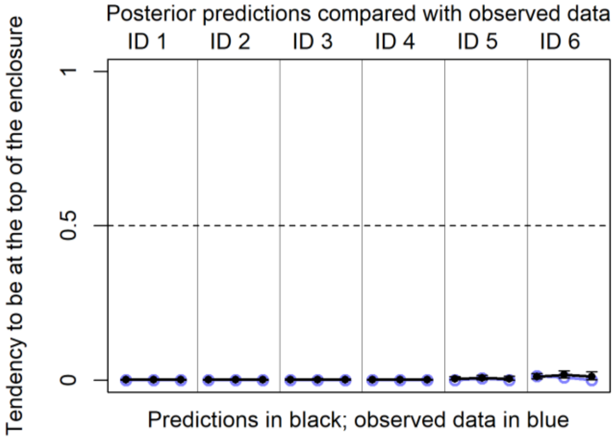
Model 11. Lockdown status v. height in enclosure (gorillas):



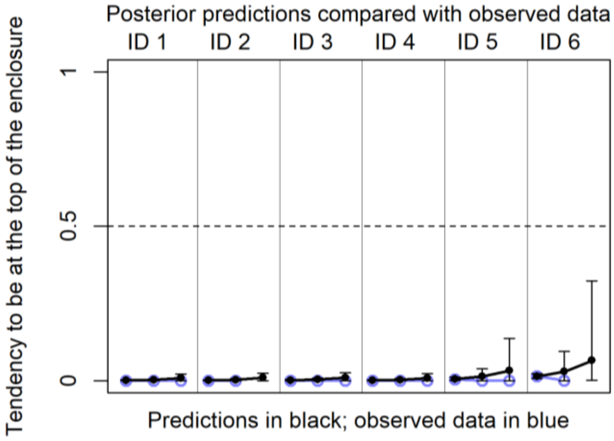
Model 11. Total visitors v. height in enclosure (gorillas):



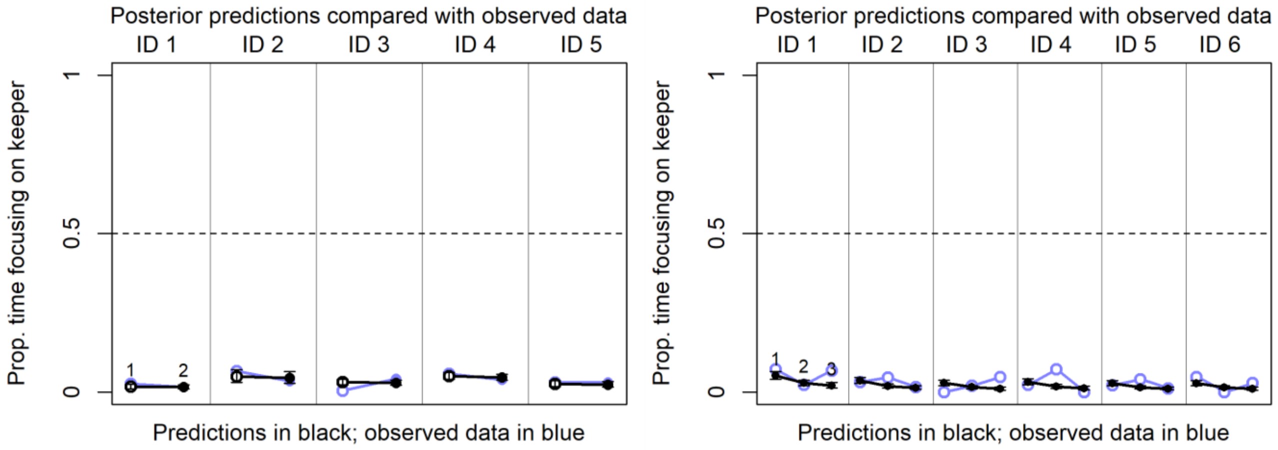
Model 11. Visitor noise v. height in enclosure (gorillas):



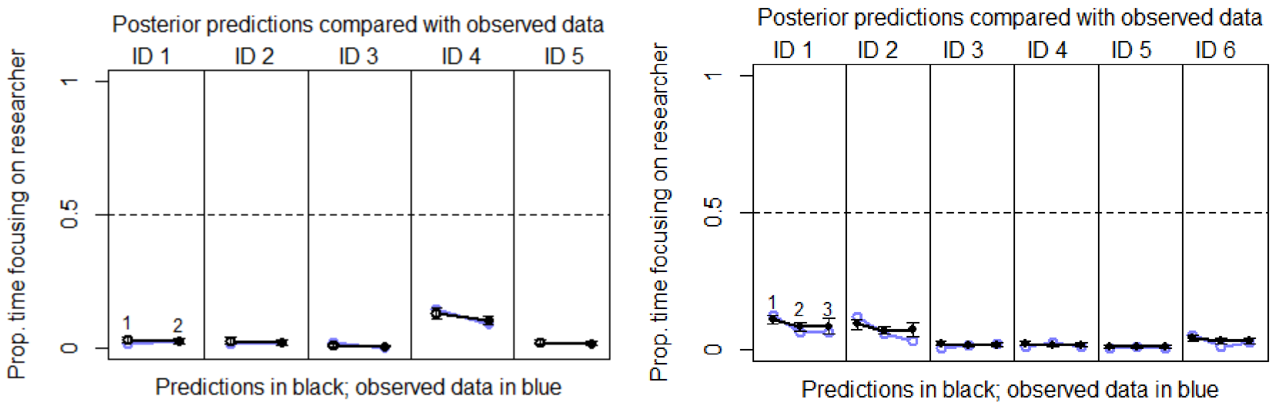
Model 11. Visitor presence v. height in enclosure (gorillas):



Model 12. Lockdown status v. focus on keeper (orangutans left, gorillas right):



Model 13. Lockdown status v. focus on researcher (orangutans left, gorillas right):



Appendix L: Lockdown study effect sizes

Includes mean and 89% credible intervals, indicating 5.5% to 94.5% of the probability distribution (McElreath, 2020). Notable effects, that do not span or include zero, are highlighted in bold.

<u>Orangutans: Lockdown status</u>

Model	Outcome variable	Mean	5.50%	94.50%
1	**Stress behaviours**	**0.05**	**0.01**	**0.11**
2	**Hunched posture**	**-0.09**	**-0.12**	**-0.07**
3	**Closed posture**	**-0.09**	**-0.12**	**-0.07**
4	Focus on humans	0.02	-0.01	0.05
5	**Object-holding**	**0.04**	**0.02**	**0.06**
6	Interacting with enrichment	-0.02	-0.06	0.01
7	Tool use	-0.01	-0.09	0.06
8	**Affiliative behaviours**	**0.02**	**0.01**	**0.04**
9	**Covered head**	**0.38**	**0.19**	**0.47**
12	Focus on keeper	-0.01	-0.02	0.01
13	Focus on researcher	-0.02	-0.04	0.00

<u>Gorillas: Lockdown status</u>

Model	Outcome variable	Mean	5.50%	94.50%	Model
1	Stress behaviours	Lockdown to semi-LD	-0.02	-0.05	0.00
1	Stress behaviours	Semi-LD to post-LD	-0.01	-0.04	0.01
1	Stress behaviours	Lockdown to post-LD	-0.04	-0.08	0.00
2	**Hunched posture**	**Lockdown to semi-LD**	**0.07**	**0.05**	**0.09**
2	**Hunched posture**	**Semi-LD to post-LD**	**-0.13**	**-0.15**	**-0.10**
2	**Hunched posture**	**Lockdown to post-LD**	**-0.06**	**-0.08**	**-0.04**
3	**Closed posture**	**Lockdown to semi-LD**	**-0.08**	**-0.10**	**-0.06**
3	**Closed posture**	**Semi-LD to post-LD**	**0.07**	**0.05**	**0.09**
3	Closed posture	Lockdown to post-LD	-0.01	-0.03	0.00
4	Focus on humans	Lockdown to semi-LD	-0.02	-0.06	0.01
4	Focus on humans	Semi-LD to post-LD	0.01	-0.02	0.05
4	Focus on humans	Lockdown to post-LD	-0.01	-0.06	0.03
5	**Object-holding**	**Lockdown to semi-LD**	**0.06**	**0.03**	**0.09**
5	**Object-holding**	**Semi-LD to post-LD**	**-0.06**	**-0.09**	**-0.02**
5	Object-holding	Lockdown to post-LD	0.01	-0.03	0.05
6	**Interacting with enrichment**	**Lockdown to semi-LD**	**0.26**	**0.11**	**0.35**
6	Interacting with enrichment	Semi-LD to post-LD	0.02	-0.06	0.11
6	**Interacting with enrichment**	**Lockdown to post-LD**	**0.28**	**0.12**	**0.41**
7	Tool use	Lockdown to semi-LD	-0.04	-0.26	0.12
7	Tool use	Semi-LD to post-LD	-0.02	-0.27	0.20
7	Tool use	Lockdown to post-LD	-0.07	-0.36	0.15

8	Affiliative behaviours	Lockdown to semi-LD	0.02	0.00	0.03
8	Affiliative behaviours	Semi-LD to post-LD	-0.01	-0.03	0.00
8	Affiliative behaviours	Lockdown to post-LD	0.00	-0.02	0.02
10	**Proximity to window**	**Lockdown to semi-LD**	**-0.12**	**-0.20**	**-0.07**
10	**Proximity to window**	**Semi-LD to post-LD**	**0.10**	**0.05**	**0.16**
10	Proximity to window	Lockdown to post-LD	-0.02	-0.07	0.02
11	**Height in enclosure**	**Lockdown to semi-LD**	**-0.28**	**-0.66**	**-0.07**
11	**Height in enclosure**	**Semi-LD to post-LD**	**-0.05**	**-0.12**	**-0.01**
11	**Height in enclosure**	**Lockdown to post-LD**	**-0.32**	**-0.77**	**-0.09**
12	**Focus on keeper**	**Lockdown to semi-LD**	**-0.06**	**-0.12**	**-0.02**
12	Focus on keeper	Semi-LD to post-LD	-0.02	-0.05	0.00
12	**Focus on keeper**	**Lockdown to post-LD**	**-0.09**	**-0.16**	**-0.03**
13	Focus on researcher	Lockdown to semi-LD	-0.03	-0.05	0.00
13	Focus on researcher	Semi-LD to post-LD	0.00	-0.02	0.02
13	Focus on researcher	Lockdown to post-LD	-0.03	-0.07	0.00

Orangutans: Total visitors

Model	Outcome variable	Mean	5.50%	94.50%	Model
1	Stress behaviours	Low to high	-0.02	-0.08	0.03
1	**Stress behaviours**	**Low to normal**	**-0.08**	**-0.17**	**-0.02**
1	Stress behaviours	Normal to high	0.06	0.00	0.14
2	Hunched posture	Low to high	-0.02	-0.08	0.05
2	**Hunched posture**	**Low to normal**	**-0.18**	**-0.22**	**-0.13**
2	**Hunched posture**	**Normal to high**	**0.16**	**0.09**	**0.23**
3	Closed posture	Low to high	0.01	-0.04	0.06
3	Closed posture	Low to normal	0.03	0.00	0.07
3	Closed posture	Normal to high	-0.02	-0.08	0.03
5	**Object-holding**	**Low to high**	**-0.05**	**-0.09**	**-0.02**
5	**Object-holding**	**Low to normal**	**-0.13**	**-0.20**	**-0.06**
5	**Object-holding**	**Normal to high**	**-0.18**	**-0.24**	**-0.12**
6	**Interacting with enrichment**	**Low to high**	**-0.33**	**-0.52**	**-0.15**
6	**Interacting with enrichment**	**Low to normal**	**-0.09**	**-0.17**	**-0.02**
6	**Interacting with enrichment**	**Normal to high**	**-0.24**	**-0.44**	**-0.06**
8	**Affiliative behaviours**	**Low to high**	**0.05**	**0.02**	**0.09**
8	**Affiliative behaviours**	**Low to normal**	**0.09**	**0.04**	**0.15**
8	**Affiliative behaviours**	**Normal to high**	**-0.04**	**-0.08**	**-0.01**
9	**Covered head**	**Low to high**	**-0.60**	**-0.85**	**-0.27**
9	**Covered head**	**Low to normal**	**-0.33**	**-0.42**	**-0.17**
9	**Covered head**	**Normal to high**	**-0.27**	**-0.58**	**-0.05**

Gorillas: Total visitors

Model	Outcome variable	Mean	5.50%	94.50%	Model
1	Stress behaviours	Low to high	-0.09	-0.24	0.00
1	**Stress behaviours**	**Low to normal**	**-0.07**	**-0.16**	**-0.02**
1	Stress behaviours	Normal to high	-0.02	-0.11	0.04
2	**Hunched posture**	**Low to high**	**-0.09**	**-0.12**	**-0.05**
2	Hunched posture	Low to normal	-0.01	-0.03	0.02
2	**Hunched posture**	**Normal to high**	**-0.08**	**-0.11**	**-0.04**
3	**Closed posture**	**Low to high**	**0.09**	**0.06**	**0.12**
3	**Closed posture**	**Low to normal**	**-0.10**	**-0.12**	**-0.07**
3	**Closed posture**	**Normal to high**	**0.19**	**0.15**	**0.22**
5	**Object-holding**	**Low to high**	**-0.23**	**-0.27**	**-0.19**
5	**Object-holding**	**Low to normal**	**0.13**	**0.04**	**0.22**
5	**Object-holding**	**Normal to high**	**-0.10**	**-0.20**	**-0.01**
6	Interacting with enrichment	Low to high	-0.17	-0.50	0.08
6	**Interacting with enrichment**	**Low to normal**	**0.38**	**0.20**	**0.51**
6	**Interacting with enrichment**	**Normal to high**	**-0.55**	**-0.83**	**-0.24**
8	Affiliative behaviours	Low to high	-0.04	-0.14	0.05
8	**Affiliative behaviours**	**Low to normal**	**-0.04**	**-0.08**	**-0.01**
8	Affiliative behaviours	Normal to high	0.00	-0.08	0.08
10	Proximity to window	Low to high	-0.05	-0.14	0.01
10	**Proximity to window**	**Low to normal**	**0.21**	**0.07**	**0.47**
10	**Proximity to window**	**Normal to high**	**-0.26**	**-0.57**	**-0.09**
11	Height in enclosure	Low to high	0.08	-0.09	0.43
11	**Height in enclosure**	**Low to normal**	**3.13**	**0.01**	**7.85**
11	**Height in enclosure**	**Normal to high**	**-3.05**	**-7.32**	**-0.01**

Orangutans: Visitor noise

Model	Outcome variable	Mean	5.50%	94.50%	Model
1	Stress behaviours	Quiet to loud	0.02	-0.03	0.08
1	Stress behaviours	Quiet to some noise	-0.01	-0.05	0.01
1	Stress behaviours	Some noise to loud	0.03	-0.01	0.10
2	Hunched posture	Quiet to loud	-0.10	-0.21	0.00
2	Hunched posture	Quiet to some noise	0.03	0.00	0.07
2	**Hunched posture**	**Some noise to loud**	**-0.13**	**-0.23**	**-0.02**
3	Closed posture	Quiet to loud	0.00	-0.06	0.05
3	Closed posture	Quiet to some noise	0.00	-0.03	0.03
3	Closed posture	Some noise to loud	0.00	-0.05	0.05
5	**Object-holding**	**Quiet to loud**	**-0.06**	**-0.15**	**0.01**
5	Object-holding	Quiet to some noise	0.00	-0.04	0.03
5	Object-holding	Some noise to loud	-0.06	-0.15	0.01

Model	Outcome variable	Mean	5.50%	94.50%	Model
6	**Interacting with enrichment**	**Quiet to loud**	**-0.48**	**-0.70**	**-0.24**
6	**Interacting with enrichment**	**Quiet to some noise**	**-0.31**	**-0.40**	**-0.18**
6	Interacting with enrichment	Some noise to loud	-0.17	-0.42	0.02
8	Affiliative behaviours	Quiet to loud	0.03	0.00	0.07
8	Affiliative behaviours	Quiet to some noise	-0.01	-0.02	0.01
8	Affiliative behaviours	Some noise to loud	0.03	0.00	0.07
9	**Covered head**	**Quiet to loud**	**-0.16**	**-0.29**	**-0.03**
9	**Covered head**	**Quiet to some noise**	**0.08**	**0.03**	**0.13**
9	**Covered head**	**Some noise to loud**	**-0.24**	**-0.37**	**-0.11**

Gorillas: Visitor noise

Model	Outcome variable	Mean	5.50%	94.50%	Model
1	Stress behaviours	Quiet to loud	0.05	0.00	0.12
1	Stress behaviours	Quiet to some noise	0.03	0.00	0.07
1	**Stress behaviours**	**Some noise to loud**	**0.02**	**0.02**	**0.08**
2	**Hunched posture**	**Quiet to loud**	**-0.04**	**-0.07**	**-0.01**
2	Hunched posture	Quiet to some noise	-0.03	-0.06	0.00
2	Hunched posture	Some noise to loud	-0.01	-0.03	0.01
3	**Closed posture**	**Quiet to loud**	**-0.15**	**-0.17**	**-0.12**
3	**Closed posture**	**Quiet to some noise**	**0.05**	**0.02**	**0.07**
3	**Closed posture**	**Some noise to loud**	**-0.19**	**-0.22**	**-0.16**
5	Object-holding	Quiet to loud	-0.06	-0.15	0.01
5	Object-holding	Quiet to some noise	0.00	-0.04	0.03
5	Object-holding	Some noise to loud	-0.06	-0.15	0.01
6	Interacting with enrichment	Quiet to loud	-0.09	-0.29	0.04
6	Interacting with enrichment	Quiet to some noise	0.00	-0.08	0.09
6	Interacting with enrichment	Some noise to loud	-0.09	-0.29	0.03
8	Affiliative behaviours	Quiet to loud	-0.03	-0.07	0.00
8	**Affiliative behaviours**	**Quiet to some noise**	**-0.06**	**-0.10**	**-0.03**
8	**Affiliative behaviours**	**Some noise to loud**	**0.03**	**0.01**	**0.06**
10	Proximity to window	Quiet to loud	-0.02	-0.11	0.03
10	Proximity to window	Quiet to some noise	-0.02	-0.09	0.02
10	Proximity to window	Some noise to loud	0.00	-0.06	0.06
11	Height in enclosure	Quiet to loud	-0.04	-0.64	0.48
11	Height in enclosure	Quiet to some noise	0.26	-0.16	1.13
11	Height in enclosure	Some noise to loud	-0.30	-1.38	0.26

Orangutans: Visitor presence

Model	Outcome variable	Mean	5.50%	94.50%	Model
1	Stress behaviours	None to 20+	-0.03	-0.13	0.06
1	**Stress behaviours**	**None to <20**	**-0.04**	**-0.09**	**-0.01**
1	Stress behaviours	<20 to 20+	0.01	-0.06	0.09
2	Hunched posture	None to 20+	-0.12	-0.32	0.01
2	Hunched posture	None to <20	-0.03	-0.06	0.01
2	Hunched posture	<20 to 20+	-0.10	-0.29	0.03
3	Closed posture	None to 20+	0.02	-0.05	0.15
3	Closed posture	None to <20	0.00	-0.02	0.03
3	Closed posture	<20 to 20+	0.02	-0.06	0.14
5	Object-holding	None to 20+	0.11	0.00	0.15
5	**Object-holding**	**None to <20**	**0.12**	**0.08**	**0.15**
5	Object-holding	<20 to 20+	0.00	-0.12	0.12
6	**Interacting with enrichment**	**None to 20+**	**-0.38**	**-0.68**	**-0.11**
6	**Interacting with enrichment**	**None to <20**	**-0.18**	**-0.25**	**-0.09**
6	Interacting with enrichment	<20 to 20+	-0.20	-0.51	0.05
8	Affiliative behaviours	None to 20+	0.00	-0.04	0.04
8	**Affiliative behaviours**	**None to <20**	**-0.03**	**-0.04**	**-0.01**
8	Affiliative behaviours	<20 to 20+	0.02	-0.01	0.07
9	**Covered head**	**None to 20+**	**-0.40**	**-0.69**	**-0.11**
9	**Covered head**	**None to <20**	**-0.07**	**-0.12**	**-0.02**
9	**Covered head**	**<20 to 20+**	**-0.33**	**-0.63**	**-0.06**

Gorillas: Visitor presence

Model	Outcome variable	Mean	5.50%	94.50%	Model
1	Stress behaviours	None to 20+	0.00	-0.04	0.05
1	Stress behaviours	None to <20	0.03	0.00	0.09
1	Stress behaviours	<20 to 20+	-0.03	-0.10	0.02
2	Hunched posture	None to 20+	-0.03	-0.06	0.00
2	Hunched posture	None to <20	-0.01	-0.04	0.01
2	Hunched posture	<20 to 20+	-0.01	-0.05	0.01
3	**Closed posture**	**None to 20+**	**-0.09**	**-0.12**	**-0.06**
3	Closed posture	None to <20	-0.01	-0.04	0.02
3	**Closed posture**	**<20 to 20+**	**-0.09**	**-0.12**	**-0.05**
5	Object-holding	None to 20+	-0.02	-0.08	0.05
5	**Object-holding**	**None to <20**	**-0.07**	**-0.11**	**-0.02**
5	Object-holding	<20 to 20+	0.05	-0.01	0.12
6	Interacting with enrichment	None to 20+	0.05	-0.12	0.23
6	**Interacting with enrichment**	**None to <20**	**-0.22**	**-0.36**	**-0.08**

Model	Outcome variable	Mean	5.50%	94.50%	Model
6	**Interacting with enrichment**	**<20 to 20+**	**0.27**	**0.10**	**0.44**
8	Affiliative behaviours	None to 20+	-0.01	-0.04	0.02
8	Affiliative behaviours	None to <20	-0.01	-0.04	0.01
8	Affiliative behaviours	<20 to 20+	0.00	-0.02	0.03
10	Proximity to window	None to 20+	-0.20	-0.48	0.00
10	Proximity to window	None to <20	-0.06	-0.18	0.02
10	Proximity to window	<20 to 20+	-0.14	-0.36	0.02
11	Height in enclosure	None to 20+	0.76	-0.74	2.72
11	Height in enclosure	None to <20	0.12	-0.92	1.02
11	Height in enclosure	<20 to 20+	0.64	-0.82	2.71

Appendix M: Jiwa experimental procedures

Session 1:

Probe feeder suspended from ceiling outside enclosure for 30 minutes, requiring subject to use a stick to obtain the food reward.

Session 2:

Tube part of the probe feeder is put inside enclosure for 30 minutes, with peanut butter inside each end of the tube within reach of the subject's fingers.

Sessions 3 and 4 (social learning):

1) Demonstrator sets up cameras, placing the tube along with sticks inside the subject's bed den. Demonstrator holds tube and stands outside bed den in keeper corridor. Once subject has entered bed den, the first demonstration starts.
2) During each demonstration, the researcher attracts attention by using vocalisations, pointing at apparatus inside bed den, and alternating gaze between subject and subject's apparatus, until the subject picks up apparatus.
3) Once the subject is holding apparatus, the demonstrator continues attracting attention and vocalising, but this time pointing at the demonstrator's apparatus and alternating gaze between subject and demonstrator's apparatus.
4) Once the subject's head is orientated towards researcher, researcher inserts stick into tube, before withdrawing it and allowing subject to see peanut butter on end of stick (out of reach), and then miming eating the peanut butter. This demonstration is repeated for as long as subject's gaze is orientated towards the demonstrator.
5) Each demonstration session ends after 2 minutes, after which time the researcher leaves the area for three minutes. This process is repeated 6 times over a 30-minute period.
6) If the subject loses interest within the 2-minute period, the demonstrator attempts to attract attention by vocalizing, pointing at apparatus, and alternating gaze between subject and apparatus.
7) If the subject starts to focus attention on their apparatus, for example trying to insert fingers inside tube, and is not already holding a stick, the demonstrator passes another stick through the wire mesh directly to the subject.

Sessions 5 to 8 (stick withdrawal):

1) Demonstrator sets up cameras during feeding time, and waits until the subject has finished eating, at which point the first demonstration will start.
2) During each demonstration, researcher holds a tube filled with a food reward and a stick already inside the tube. Demonstrator attracts attention by using vocalisations, pointing at apparatus, and alternating gaze between subject and apparatus, until subject approaches demonstrator.
3) Once subject has approached demonstrator, demonstrator holds tube near the wire mesh at head level, encouraging subject to withdraw the stick.
4) If the subject successfully withdraws the stick, the researcher continues drawing attention to the apparatus as in Step 2, while holding the tube at the subject's eye level.
5) If the stick is successfully withdrawn, the demonstrator replaces the stick so that the research subject can try again.
6) Each demonstration session ends after 2 minutes, after which time the researcher leaves the area for three minutes. This process is repeated 6 times over a 30-minute period.

Session 9:

The procedure is the same as sessions 5 to 8, but the stick is provided to the subject rather than being placed inside the probe feeder, which requires the subject to voluntarily insert the stick inside the feeder in order to obtain the food reward.