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ENABLING WILD-TYPE BEHAVIOURAL ECOLOGY IN CAPTIVE PARROT SPECIES

By

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GENERAL ABSTRACT

Earth is facing an accelerating biodiversity loss and potential sixth mass extinction. The integration of *ex situ* conservations efforts (i.e. where conservation occurs outside natural habitat), such as captive breeding and reintroduction, with *in situ* actions (e.g. habitat protection and restoration), can help to slow biodiversity loss. However, the potential of *ex situ* conservation is limited by the challenges of reintroducing captive-bred animals into their natural habitat, as they often lack the necessary behaviours and skills to survive in the wild. Parrots (order Psittaciformes) are a highly threatened avian taxon that are, however, commonly kept in captive settings, including zoo breeding programmes. They are cognitively advanced and prone to poor welfare in captivity, often exhibiting loss and alteration of wild-type behaviours, which may jeopardise present and future participation in reintroduction programmes. In this thesis, a multi-step methodology was applied to: (1) assess the activity budgets and space use, as well as cognition, locomotion, and social behaviours of three captive parrot species (grey parrot *Psittacus erithacus*; scarlet macaw *Ara macao*; swift parrot *Lathamus discolor*) in two zoos; (2) compare those data with *in situ* data; (3) propose and apply enclosure modifications, including an increase and re-organisation of structural complexity and new hanging feeders that partially conceal the food, to enable the wild-type behaviours found missing or under-represented; and (4) assess the post-modification behaviour to evaluate the effects of the modifications. Behavioural data were collected on free-living scarlet macaws in Costa Rica, as well as eight scarlet macaws, two groups of grey parrots, and two juvenile swift parrots in two zoos. Significant changes in the behaviour of the captive parrots were detected between the baseline and post-modification periods of observations, but these varied within and

across species. The modifications in the enclosures and changes in the social environment that occurred between periods (i.e. addition and/or death of parrots in the enclosure), likely affected these results. Increases in activity and natural behaviours such as locomotion and foraging were detected in some parrots, as well as improvements in space use and higher use of more challenging and diverse supports. The methodology and outcomes of this thesis have the potential to assist in improving the *ex situ* management of parrots, with applications to animal welfare and *ex situ* conservation.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. Biodiversity under threat

Biodiversity loss is accelerating, and the world may be facing a sixth mass extinction (Ceballos et al., 2015). The estimated vertebrate extinction rate over the last century is up to 100 times higher than the estimated pre-human background rate, as suggested by conservative estimates based on the number of confirmed extinctions of species (Ceballos et al., 2015). Anthropogenic factors such as habitat destruction, over-exploitation of resources, invasive species, and climate change, are the main drivers of species extinction (Ducatez & Shine, 2017). Figures from the latest assessment by the IUCN (International Union for the Conservation of Nature) Red List of Threatened Species show that over 40,000 (28%) of all assessed species are threatened with extinction, including 13% of the 11,188 bird species that were assessed (IUCN, 2023).

1.2. *Ex situ* conservation: Benefits and challenges

Ex situ conservation efforts (i.e. those outside natural habitat), such as captive breeding, reintroduction of captive-bred individuals to re-establish or boost wild populations, and translocation of individuals between populations, have played a major role in preventing the extinction of numerous species. Bolam et al., (2021) estimated that, globally, *ex situ* measures were taken in 63% and 56% of the 32 bird and 16 mammal species whose extinction was prevented. Furthermore, out of a global number of 95 (plant and animal) species that went extinct in the wild but remained in *ex situ* settings, since 1950, 11 have been lost while in human care but 12 have been returned to the wild (Smith et al., 2023). The Przewalski's horse (*Equus ferus)*, the Guam rail (*Hypotaenidia owstoni;* Bolam et al., 2021), and the European bison (*Bison bonasus;* Smith et al., 2023) are examples of species that were successfully returned to the wild,

after having been extirpated in the wild, and that would have gone permanently extinct if it was not for *ex situ* conservation measures.

Captivity can affect the behavioural repertoire (i.e. total range of behaviours exhibited) of animals, with the loss and modification of natural/wild-type behaviours, an effect that is more pronounced as the number of generations in captivity increases (McPhee, 2004). Evidence of loss of wild-type behaviours and/or development of maladaptive behaviours due to captivity has been reported in multiple taxa, including bank voles (*Clethrionomys glareolus;* Mathews et al., 2005), golden-lion tamarins (*Leontopithecus rosalia;* Stoinski et al., 2003), Atlantic salmon (*Salmo salar;* Roberts et al., 2011), northern water snakes (*Nerodia sipedon sipedon;* Roe et al., 2010), and grey partridges (*Perdix perdix;* Rantanen et al., 2010). This captivity-induced modification of the natural behavioural repertoire can jeopardise the success of reintroduction programmes. A review of the reintroduction success of carnivores showed that programmes involving captive-bred animals are less likely to succeed than those using wild-born animals, partly due to the decreased preparedness (i.e. lack of wild-type behavioural skills) of captive-bred animals to survive in the wild (Jule et al., 2008).

The morphology of muscles, organs and the skeleton of captive animals also changes in long-term captivity (O'Regan & Kitchener, 2005). Problems such as osteoarthritis (Rothschild, 2003) and reduced muscle strength (Hämäläinen et al., 2015) have been found to be higher in captive mammals than in their wild counterparts, due to reduced physical activity in constrained environments. Reports of captivity-induced

morphological alterations in birds include a decrease in gut length (Moss, 1972), a reduction in liver, heart and gut mass (AL-Mansour, 2005), increased body mass (Thompson et al., 2015), and a decrease in hippocampus size (Day et al., 2008). Pectoral muscle loss/atrophy due to disuse in captivity (i.e. flight restrictions in constrained environments) has been reported in Attwater's prairie chickens (*Tympanuchus cupido attwateri;* Hess et al., 2005), but not in sanderlings (*Calidris alba;* AL-Mansour, 2005) or red knots (*Calidris canutus;* Dietz et al., 1999). It was suggested that pectoral muscle building might be regulated endogenously in migratory bird species, with seasonal changes that occur in preparation for migration and that are less reliant on muscle use or disuse (Dietz et al., 1999). Even though Rothschild and Panza (2006) found no differences in incidence of osteoarthritis between captive and free-living pigeons (Columbiformes) or hawks (Accipitridae), this has not been investigated across avian taxa and it could still be an issue in other species. The effect of captivity on avian taxa can also be seen in species that have been selectively bred for generations in human care, resulting in substantial deviations from their wild counterparts, in both morphology (e.g. feather structure and arrangement; Bartels, 2003) and behaviour (e.g. song complexity and aggressiveness; Suzuki & Okanoya, 2021).

As a result, the IUCN recommends that captive animals selected for reintroduction programmes have comparable behavioural repertoires to the original or remaining animals in wild populations (IUCN, 2013). It is therefore of great importance to maintain the natural behavioural repertoire of wild animal populations while in captivity, in order

to secure their conservation potential (i.e. their suitability for participation in *ex situ* conservation efforts) and facilitate future reintroduction programmes.

The IUCN also recommends that reintroduction programmes include rigorous assessments and mitigation strategies for the risks free-living wild animals and the wider ecosystem face when animals are released from captivity into the wild (IUCN, 2013). These risks include the transmission of diseases (Viggers et al., 1993) and parasites (Van Oosterhout et al., 2007), predation, competition and/or inter-specific hybridization (IUCN, 2013). There is also a risk of intra-specific hybridization, if the released animals are genetically divergent from the wild population (e.g. different subspecies), which can have a negative effect on the fitness of the individuals within the population (i.e. outbreeding depression; Banes et al., 2016). Finally, maladaptive behaviours developed by animals in captivity can spread to their wild counterparts through social learning (Whitehead, 2010). Due to the risks mentioned above and the historical low success rate of reintroduction programmes (Armstrong & Seddon, 2008), skepticism about the overall benefits of reintroduction programmes has been previously reported among field biologists and conservationists (Sarrazin & Barbault, 1996).

Nevertheless, release programmes have been moving towards a more scientific, evidence-based, approach (Armstrong & Seddon, 2008; Taylor et al., 2017), and the risks involved for both the released and the wild animals can be minimised by following the IUCN guidelines for reintroductions (IUCN, 2013). Furthermore, the “One Plan

Approach to Conservation Planning" recommended by the IUCN Conservation Planning Specialist Group (CPSG) supports the integration of *in situ* and *ex situ* conservation efforts, and collaborative actions across all stakeholders, to manage and conserve species more effectively (IUCN CPSG, 2023).

1.3. The roles of zoos and aquariums

Zoos and aquariums can play an important role in conservation breeding programmes, as they collectively house multiple threatened species and generate vast knowledge on their *ex situ* husbandry and management, behaviour and health (Conde et al., 2013). Zoo members of the European Association of Zoos and Aquaria (EAZA) alone had made 637 contributions to reintroduction programmes by 2016, including animals for release, financial and human resources, equipment and project management (Gilbert et al., 2017). Zoo populations are often managed under collection plans, at the regional level, such as the European *ex situ* programme (EEP; EAZA, 2022) and the Species Survival Plan (SSP, managed by the American Association of Zoos and Aquariums; AZA, n.d.), and globally, such as the International Studbooks, managed by the World Association of Zoos and Aquariums (WAZA, 2022). These programmes aim to keep demographically and genetically healthy zoo-housed populations (WAZA, 2022), which work as insurance against extinction, and can be used to repopulate or boost the number of animals in wild populations.

In addition to their contributions to *ex situ* conservation, modern zoos and aquariums are also involved with *in situ* conservation, by managing and/or supporting field

conservation efforts (Wilson et al., 2019), and scientific research, both applied and fundamental (Rose et al., 2019). Furthermore, despite contention about the role of zoos in education (Fennell, 2013), zoo visits have been found to improve knowledge of nature and actions to protect it (Moss et al., 2015). Recreation is also a prominent role of zoos and aquariums (Greenwell et al., 2023), as they may have restorative effects on visitors similar to experiences in natural environments (Cracknell et al., 2017), and can have positive effects on human health (Coolman et al., 2020). Through their conservation, research, education, and recreation/engagement roles, zoos directly and indirectly benefit human societies, by improving people's health and survival (e.g. by helping to preserve ecosystem services and providing opportunities for immersion in nature), promoting their education and a more ethical co-existence with nature, and enhancing their socio-economic conditions (Greenwell et al., 2023). Despite these demonstrable benefits, keeping animals in zoos and aquariums raises ethical questions, often associated with concerns for the welfare of the animals (Minteer & Collins, 2013). Zoos and aquariums must therefore prioritise the welfare of their animals as well as their contributions to conservation, as stated in the World Zoo and Aquarium Conservation Strategy (Barongi et al., 2015). Animal behaviour research can assist them in those goals, by facilitating welfare assessments and interventions, and the evaluation of their animals' behavioural preparedness for reintroduction into the wild (Swaisgood, 2007).

1.4. Animal behaviour and welfare

Animal behaviour research can be a useful tool with multiple applications. First, it can be used in *in situ* conservation, facilitating the assessment of animal responses to

human impacts and changes in the environment, while also informing the implementation and management of conservation actions (Greggor et al., 2016). Secondly, behavioural research can also aid *ex situ* conservation, by helping to improve captive breeding programmes, evaluating and preparing animals for release into the wild, and monitoring their post-release adaptation to the natural environment (Lemos de Figueiredo & Díez-León, 2022). Finally, it can be used to assess and improve animal husbandry and welfare in captivity (Lemos de Figueiredo & Díez-León, 2022).

Inferring welfare states in non-human animals is a difficult task, due to the challenges of accurately assessing what an animal is feeling or experiencing (Ward et al., 2018). Behaviour is one of the indicators that is often used in animal welfare assessments, alongside others such as physical health and physiology (Mellor et al., 2015). One of the most prominent animal welfare frameworks, the Five Domains model, is composed of four physical/functional domains (nutrition, environment, health, and behaviour), and a fifth, affective experience, domain: mental state (Mellor, 2016). Under this model, positive welfare is encouraged by opportunities for the expression of rewarding behaviours (e.g. exploring and interacting with the environment) that are associated with positive affective states (e.g. comfort, pleasure; Mellor, 2016). On the other hand, negative welfare is associated with behavioural restrictions, which enable negative affective states (e.g. anxiety, frustration, boredom; Mellor, 2016).

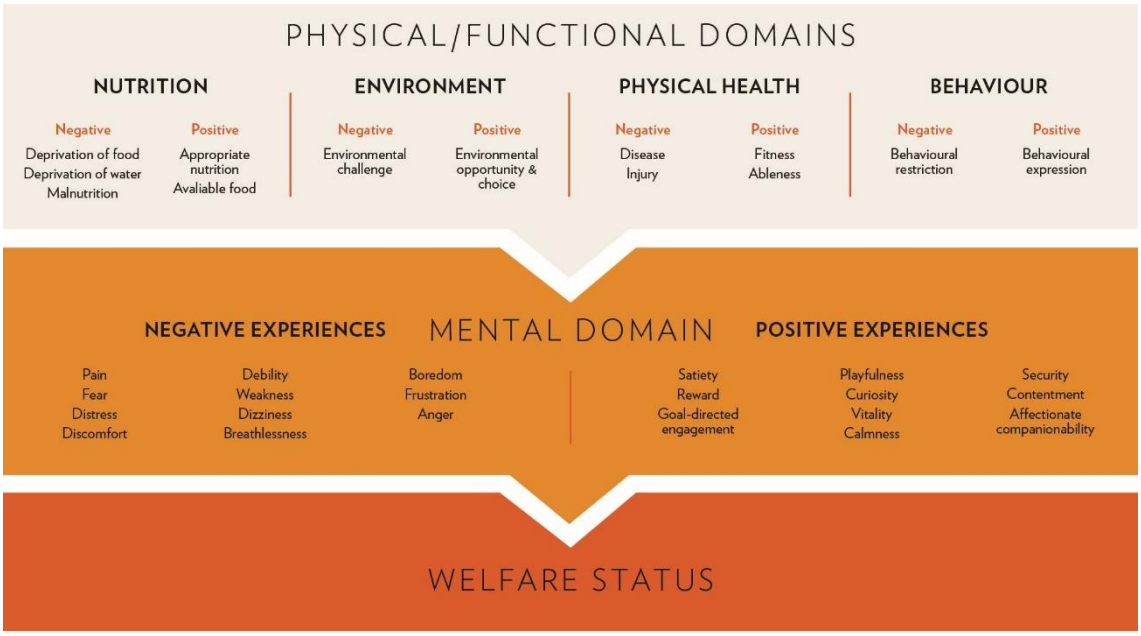


Figure 1.1. Schematic representation of the "Five Domains" model of animal welfare.
The overall welfare state of an animal is influenced by the combination of negative and/or positive experiences in its physical and mental domains. Taken from Mellor et al., (2015).

The Five Domains model was proposed as a replacement for the Five Freedoms paradigm, which despite being highly influential in animal welfare science, it focussed on minimising negative welfare experiences (i.e. it states animals should be free from pain, discomfort, hunger, fear, distress, and free to perform natural behaviours) with limited consideration for positive experiences or the overall mental state of the animal (Mellor, 2016). Therefore, WAZA encourages the use of the Five Domains model to facilitate animal welfare assessments in zoo animals, and states that welfare is negative or positive when negative or positive experiences are predominant, respectively, and neutral when there is an overall balance of positive and negative experiences (Mellor et al., 2015).

1.4.1. Wild-type behaviours and animal welfare

The natural/wild conditions in which species live influence the evolution of their behavioural needs and coping mechanisms (Broom, 2011), and the expression of those behaviours may therefore be rewarding to the animal (Veasey et al., 1996). Animals under human care should therefore be provided with an environment that takes into consideration, and fulfils, those behavioural needs (Broom, 2011), with the WAZA Animal Welfare Strategy also highlighting the importance of providing captive animals with the opportunity to express species-specific behaviours (Mellor et al., 2015).

The association between the expression of wild-type behaviours and positive animal welfare has, however, been disputed (Browning, 2020). Animals in the wild also experience suboptimal welfare, due to aversive experiences such as predation, hunger, and thirst (Veasey et al., 1996). Replicating these natural but aversive experiences in captivity would likely be detrimental to animal welfare (Mellor et al., 2020; Veasey et al., 1996), especially considering that captive animals have reduced control and opportunities to respond to those experiences (e.g. search for food if hungry, evade a predator). Similarly, behaviours such as fighting, or avoiding predators, are natural to many species, but are likely to have a negative effect on welfare in captivity (Browning, 2020). Furthermore, captive animals may experience improved welfare from expressing behaviours that, despite not having been observed in their wild counterparts (i.e. not natural to the species), are still rewarding for the animal (Browning, 2020; Veasey et al., 1996). However, if an animal has evolved to express a behaviour to fulfil a need in the natural environment (e.g. vigilance, explore

a food resource), and in captivity that need is readily fulfilled (e.g. no exposure to predators, food readily available), the non-expression of that behaviour may create a void in the daily activity of the animal that is detrimental to welfare (Veasey et al., 1996). The response to that void is often the development of abnormal behaviours (e.g. stereotypies: repetitive and seemingly functionless behaviours), which are often associated with poor welfare (Manteca et al., 2016; Wolfensohn et al., 2018).

Therefore, in this thesis, animal welfare is defined as a combination of three conceptions: natural living, basic health and functioning, and affective states, as proposed by Fraser (2008). The expression of natural behaviours, associated with opportunities for a more natural living, will be the primary measure of welfare, but the potential associations of those behaviours with health and affective states of the parrots (Psittaciformes; the focus taxon in this thesis) will also be discussed.

1.5. Parrots: Psittaciformes

The avian order Psittaciformes, which includes all the birds commonly known as parrots, includes three superfamilies: Strigopoidea (New Zealand parrots, genera Nestor and Strigops), Cacatuoidea (cockatoos, family Cacatuidae) and Psittacoidea (three families: Psittacidae, Psittrichasidae and Psittaculidae) (Figure 1.2; Joseph et al., 2012). Even though they can be found in a wide range of habitats and latitudes, they are most common in forest, tropical environments and in the southern hemisphere (Olah et al., 2016). Among their most distinguishable features are the zygodactyl feet (two forward and two backward toes), which they use for foraging (including grasping

food to manipulate it) and for perching and climbing (Sustaita et al., 2013), and powerful mandibles and curved bills, unique among birds, evolved for crushing hard objects (Tokita, 2003).

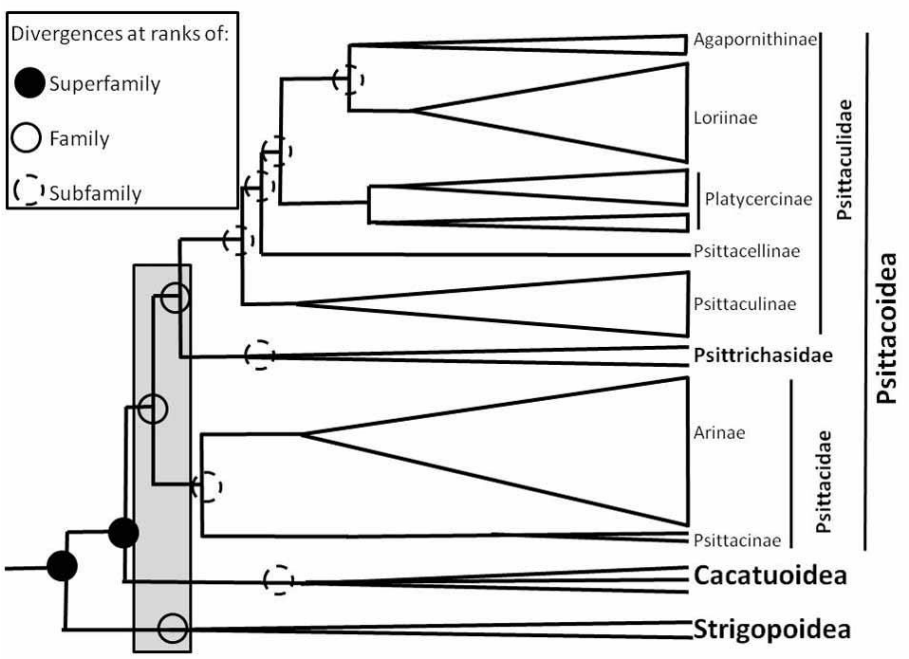


Figure 1.2. The phylogeny of parrots (order Psittaciformes).
Schematic representation of the relationships among parrot taxa (order Psittaciformes), taken from Joseph et al., (2012).

There are 398 known extant parrot species and 16 that have gone extinct. Of those 398, 111 (28%) are threatened ("Vulnerable", "Endangered" or "Critically Endangered" in the IUCN Red List of Threatened Species) and 60 (15%) are "Near Threatened" (Olah et al., 2016). Agriculture, associated with habitat loss, and hunting and trapping (fuelled by the illegal pet trade) are the most common threats to parrot populations, but logging, climate change and invasive species are also significant threats to parrots worldwide (Olah et al., 2016). An investigation into the global pet trade between 2006 and 2012 found a higher number of birds in the trade than other taxonomic groups,

and parrots were found to be the most commonly trafficked avian taxon (Bush et al., 2014).

Among the most important conservation actions for parrot species across different regions, *ex situ* efforts were identified as required for the conservation of over 10% of the targeted species in each region (Olah et al., 2016). The IUCN recommends that *ex situ* conservation programmes should be started for species that are vulnerable to human activities and/or at risk of becoming critically endangered or extinct in a short period of time (IUCN SSC, 2002), which is, as discussed above, the case for a high number of parrot species. Furthermore, as captive parrots are estimated to be as numerous as their wild counterparts, each around 50 million (Mellor et al., 2021), they have the potential to have a significant role in wildlife conservation. Records from the Zoological Information Management System (ZIMS) alone showed over 60,000 individuals in over 700 institutions across six regions (Species360, 2018). Consequently, out of the approximately 50 million parrots that are estimated to be in captivity, most are pets or in animal collections that are not part of the ZIMS database (Mellor et al., 2021).

Even though birds outnumber mammals in zoos, most of the published zoo-based research has been on mammalian taxa (Rose et al., 2019). A review of zoo-based research between 2009 and 2018 found that 69% of the papers published in that period focused on mammals. There was, however, a positive trend in bird-focused publication

numbers in that period, showing a potential shift in research focus to include a higher diversity of taxonomic groups (Rose et al., 2019).

1.5.1. Parrot welfare in captivity

Parrots in captivity often exhibit abnormal behaviours (i.e. not exhibited by the species in the natural habitat), which may be indicate of poor welfare (Engebretson, 2006). Feather plucking, which consists of a parrot removing its own feathers, is frequently observed (Jayson et al., 2014; van Zeeland et al., 2009), and stereotypic behaviours have also been reported across parrot taxa (e.g. Garner et al., 2003; Williams et al., 2017). Even parrot species that are thought to adapt relatively well to captivity, like the budgerigar *Melopsittacus undulatus*, exhibit stereotypic behaviours (Polverino et al., 2012, 2015). Stereotypic behaviours are commonly used as an animal welfare indicator and are in most cases associated with poor welfare (Mason & Latham, 2004). There are exceptions, however, as animals may also engage in stereotypic behaviour as a coping mechanism in sub-optimal environments, and in those circumstances, stereotyping animals may experience better welfare than their low-stereotyping counterparts that are less able to cope with the environment. Furthermore, some stereotypies may persist even after improvements in the environment, and may be a result of habit rather than a reflection of current welfare conditions (Mason & Latham, 2004).

The incidence of stereotypic behaviours varies across parrot species in captivity, with those with larger brains more likely to develop stereotypic behaviours (Mellor et al.,

2021). It has been suggested that animals with bigger brains in relation to their body size tend to have increased cognitive function (Deaner et al., 2007), including foraging (Edmunds et al., 2016) and problem-solving abilities (Benson-Amram et al., 2016). This association between brain size and cognitive abilities has been questioned, due to confounding ecological and life-history variables in cross-taxa comparisons, as well as challenges in accurately measuring and comparing brains with diverse morphologies (Logan et al., 2018). However, Sayol et al., (2016) showed that birds with larger brains in relation to their body size also have disproportionately larger pallial areas within their brains, regions that are associated with general cognition. Therefore, it is possible that the welfare issues frequently reported for captive parrots, especially in species with larger brains, are associated with their advanced cognitive abilities. Furthermore, the welfare of captive parrots has been found to be negatively affected by space restrictions, inadequate social environments (Polverino et al., 2012), and impoverished enclosures (Meehan et al., 2004) that fail to provide physical and mental stimulation to the animals (Mellor et al., 2021).

1.5.2. Parrot cognition

The cognitive abilities of parrots and corvids (Corvidae), surpass those of other avian taxa, and are often compared to those of primates and even great apes (Lambert et al., 2019). Parrots have similar, and sometimes greater, number of neurons in their forebrain than primates, despite having smaller absolute brain sizes (Olkowicz et al., 2016), which may be the basis for their advanced cognitive abilities.

Parrots exhibit cognitive abilities such as motor self-regulation (e.g. delaying the consumption of a low-value reward while waiting for a higher-value reward), behavioural flexibility and innovation (e.g. quickly adjust their behavioural repertoire in response to the environment), and the ability to track and retrieve objects that have been concealed or displaced (i.e. object permanence; Lambert et al., 2019). Furthermore, some parrot species are also capable of complex tool use, including the use of multiple tools at the same time as well as manufacturing tools with different characteristics for specific needs (Rössler & Auersperg, 2023). Social learning (i.e. behavioural development by observing and copying the behaviour of other animals) has also been observed across parrot species (Lambert et al., 2019), with some species also showing cooperative and prosocial behaviour (Rössler & Auersperg, 2023).

Research on parrot cognition has often relied on small sample sizes and has been mostly focused on a small number of species, with over half the papers published on just three species: African grey parrot (*Psittacus erithacus*), the orange-winged amazon (*Amazona amazonica*) and the kea (*Nestor notabilis*; Cussen, 2017). Despite evidence of increased research into parrot cognition in recent years, featuring a higher diversity of species (Rössler & Auersperg, 2023), intra- and inter-specific variations in parrot cognitive abilities are still understudied (Cussen, 2017; Cussen & Mench, 2014). They have, however, been detected. For example, Brucks et al. (2021) observed individual, sex and species differences in a delayed gratification task used to test self-control in three macaw species (Arinae) and the grey parrot. These intra- and inter-specific differences in parrot cognition should be considered when assessing parrot

welfare in captivity, and when planning interventions to their *ex situ* environment (Clark et al., 2019). Even though behaviour and welfare issues have been observed across parrot taxa (Engebretson, 2006), it is possible that the augmented cognitive abilities of some species may exacerbate the challenges they face in captivity (Mellor et al., 2021). As they likely evolved those abilities in response to the challenges and complexity of their natural environment, those abilities should be appropriately stimulated in captivity (Mellor et al., 2021). Similarly, the parrot species with relatively lower cognitive function than their larger-brained counterparts (Mellor et al., 2021) require cognitive stimulation that is appropriate for their abilities (Clark et al., 2009) and associated with their natural behavioural ecology.

1.6. Target species

The selection of parrot species for my research was based on: (1) how common they are in captivity, (2) how likely they are to benefit from *ex situ* conservation actions in the short- or long-term, (3) whether they are threatened in the wild, and (4) their geographic distribution (i.e. inclusion of species from different geographic locations).

1.6.1. Grey parrot

The grey parrot is in the superfamily Psittacoidea, family Psittacidae, and subfamily Psittacinae (Joseph et al., 2012), and is native to the forests and savannahs of Central Africa, from Ghana to Kenya (BirdLife International, 2018a). They are listed as “Endangered” in the IUCN Red List of Threatened Species and subject to *ex situ* conservation (BirdLife International, 2018a).

Table 1.1. Summary of conservation variables for parrot species included in this study, based on the IUCN Red List of Threatened Species.
↑, =, ↓: increasing, stable, decreasing population trend.

Species	Geographic range	Habitat	Number of mature individuals	Threat status	Population trend
Grey parrot (P*sittacus erithacus*)	Central Africa (multiple countries)	Forest, savannah	0.56-12.7 million	Endangered	↓
Scarlet macaw (*Ara macao*)	Central and South America (multiple countries)	Forest	20,000-49,999	Least Concern	↓
Green-winged macaw (*A. chloropterus*)	South America (multiple countries)	Forest, savannah	50,000-499,999	Least Concern	↓
Great green macaw (*A. ambiguus*)	Central and South America (multiple countries)	Forest	500-1,000	Critically Endangered	↓
Red-fronted macaw (*A. rubrogenys*)	South America (Bolivia)	Forest, shrubland	134-272	Critically Endangered	↓
Hyacinth macaw (*Anodorhynchus hyacinthinus*)	South America (Bolivia, Brazil, Paraguay).	Forest, savannah, grassland	4,300	Vulnerable	↓
Swift parrot (*Lathamus discolor*)	Australia	Forest	1,000-2,499	Critically Endangered	↓

They are also one of the most popular avian pets (BirdLife International, 2018a) and very common in zoos (1,894 animals in 262 zoos across six regions; Species360, 2018). They are also already part of an European Studbook (officially-managed breeding programme in European zoos and aquariums; EAZA Parrot TAG, 2016).

1.6.2. Scarlet macaw

Scarlet macaws (Psittacoidea, Psittacidae, subfamily Arinae) are a neotropical widespread species that can be found in Central and South America (Nemeth & Vaughan, 2004). They are not globally threatened ("Least Concern" in the IUCN Red List of Threatened Species), but their population is declining (BirdLife International, 2016a). Even though they are not subject to *ex situ* conservation by the IUCN (BirdLife International, 2016a), there are active reintroduction programmes for this species (e.g. Costa Rica; Rescate Wildlife Rescue Center, n.d.). They are very common in zoos (1,661 animals in 244 zoos across six regions; Species360, 2018) and a species be maintained as part of an European breeding programme (EAZA Parrot TAG, 2016).

1.6.3. Other macaws

The green-winged or red-and-green macaw (*A. chloropterus*), like the scarlet macaw, is also a widespread South American species that is not globally threatened, but that is facing population declines (BirdLife International, 2021a). The great green macaw (*A. ambiguus*) is native to multiple Central and South American countries, but fewer individuals remain in the wild in comparison to their scarlet and green-winged counterparts, and it is listed as "Critically Endangered" (BirdLife International, 2020). Even rarer is the red-fronted macaw (*A. rubrogenys*), which can only be found in Bolivia, and with no more than 272 mature individuals estimated to remain in the wild (BirdLife International, 2021b). The largest of the macaws, the hyacinth macaw (*Anodorhynchus hyacinthinus*) can be found in Bolivia, Brazil and Paraguay, and is listed as "Vulnerable" (BirdLife International, 2016b). All these macaw species share a

decreasing population trend as a result of habitat loss and the illegal pet trade, among other threats (Table 1.1).

1.6.4. Swift parrot

Swift parrots are an Australian migrant species (Psittacoidea, Psittaculidae, subfamily Platycercinae*;* Joseph et al., 2012) that breed in Tasmania and overwinter in mainland Australia (Saunders & Heinsohn, 2008). Their population is declining and they are "Critically Endangered" in the IUCN Red List of Threatened Species (BirdLife International, 2018b), mainly due to habitat loss and nest predation by the introduced sugar glider (*Petaurus breviceps;* BirdLife International, 2018b). They are uncommon in zoos (131 animals in 22 zoos across three regions; Species360, 2018), but common among private breeders (BirdLife International, 2018b). They are one of the priority species for European *ex situ* programmes (EAZA Parrot TAG, 2016) and subject to *ex situ* conservation (BirdLife International, 2018b).

1.7. Enclosure modifications and environmental enrichment

The studies in this thesis were developed to inform the *ex situ* management of parrots, and help to address the limitations of *ex situ* conservation (section 1.2) and welfare issues (section 1.4.1) in this taxon. It combines behavioural assessments of zoo-housed parrots, comparisons with free-living parrots, and evidence-based enclosure modifications.

Environmental enrichment is broadly defined as modifications to captive environments with the goal of providing increased physical and mental stimulation to captive animals, and consequently improve their behaviour and welfare (de Azevedo et al., 2007). Enrichment can fall into one or more of the following categories: cognitive (focuses on cognitive challenges such as puzzle feeders), food-based (e.g. food presentation, aims to encourage foraging behaviours), sensory (e.g. olfactory, auditory and visual stimuli), social (i.e. opportunities for social interactions with conspecifics and heterospecifics), and physical/structural (increasing structural complexity within the enclosure; de Azevedo et al., 2007).

By enriching the *ex situ* environment with modifications that increase its complexity, captive animals have increased opportunities for behavioural expression, which positively affects their welfare (section 1.4). Enrichment has been shown to improve welfare in captive parrots by decreasing stereotypies (Meehan et al., 2004), reducing feather-picking behaviour (van Hoek & King, 1997), and increasing natural behaviours such as foraging and locomotion (Clyvia et al., 2015; van Hoek et al., 1997). Enrichment can also help captive-bred animals to develop the necessary behaviours for survival in the wild, thereby increasing the success of reintroduction programmes (Reading et al., 2013).

1.7.1. Enclosure Design Tool (EDT)

This research was developed under the wider Enclosure Design Tool (EDT) project. The EDT is a web application that facilitates behavioural assessments of captive

animals and evidence-based modifications to their *ex situ* environment (University of Birmingham, 2022). Baseline data are collected on captive animals, which are then uploaded into the web application to be automatically compared with the available data on wild individuals (Figure 1.3).

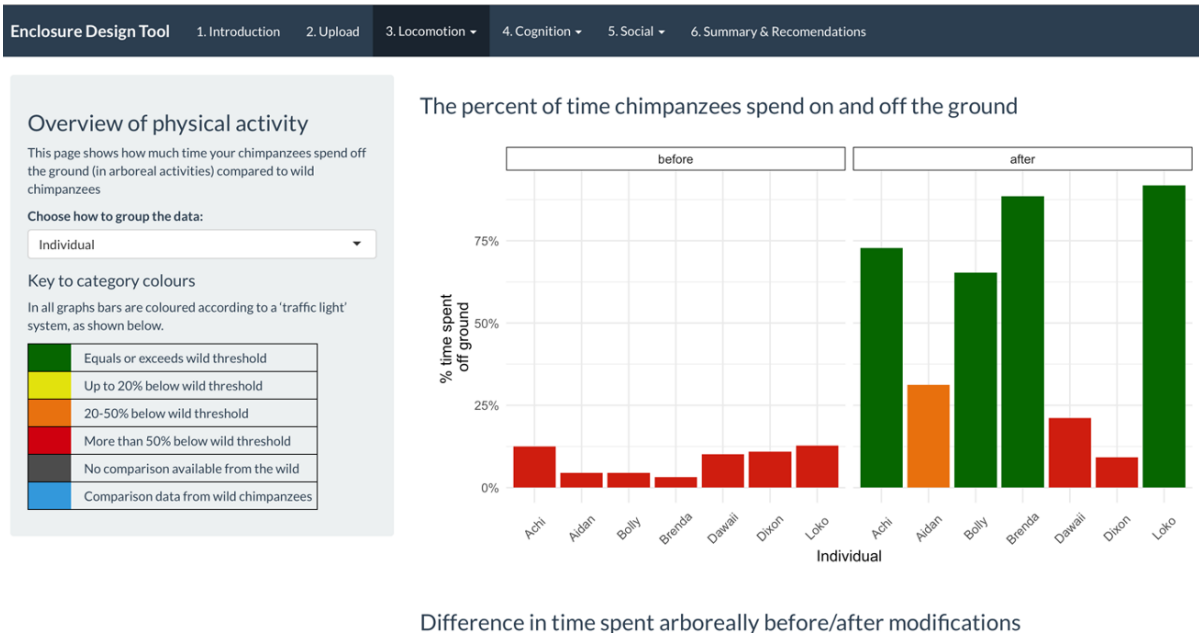


Figure 1.3. The Enclosure Design Tool (EDT).
Screenshot of the EDT developed for chimpanzees *Pan troglodytes.* The coloured bars represent percentage of time each individual chimpanzee spent off the ground, with the different colours highlighting how much those behaviours deviate from available data from wild animals. Image: Jackie Chappell.

Modifications to the enclosure, management and/or husbandry are then proposed with the goal of replicating, as close as possible, the complexity of the species' natural environment, and consequently enabling wild-type behaviours (Chappell & Thorpe, 2022; University of Birmingham, 2022). It can be used with animals in short-term (e.g. rehabilitation and release programmes) and long-term captivity (e.g. permanent care at zoos and sanctuaries; Chappell & Thorpe, 2022; University of Birmingham, 2022). The EDT has been developed for orangutans (*Pongo* spp.*)* and chimpanzees (*Pan troglodytes*), with successful interventions (i.e. positive impact on behaviour) reported

for animals housed in rehabilitation centres and sanctuaries (Chappell & Thorpe, 2022). However, long-term plans for the EDT involve the development of extensions to include as many other taxa as possible (University of Birmingham, 2022). Parrots were selected as a priority taxon in the EDT expansion plans, as they are highly threatened, common in *ex situ* settings, likely to benefit from *ex situ* conservation (section 1.5), and prone to experiencing poor welfare in human care (section 1.5.1).

1.8. Aims and objectives

The general aims of this thesis are to (1) improve knowledge of behavioural ecology of free-living scarlet macaws to facilitate comparisons with their captive counterparts, (2) identify missing and under-represented wild-type behaviours in captive parrots, (3) apply evidence-based (i.e. based on each species' natural history and behavioural ecology) enclosure and husbandry modifications to enable those behaviours, (4) evaluate the effectiveness of those modifications in enabling a wild-type behavioural repertoire, and (5) use findings to create a scientific foundation for a parrot-focussed EDT.

The behavioural observations of free-living scarlet macaws, featured in Chapter 2, supplement available literature on the behavioural ecology of this species, and aid comparisons with captive parrots (Figure 1.4). Chapter 3 includes assessments of activity budgets and enclosure use of grey parrots and scarlet macaws in two zoos, as well as comparisons with their wild counterparts (data from Chapter 2 and from the literature), and enclosure modifications to enable wild-type behaviours. The cognition,

locomotion and support use, and social behaviour and proximity of these captive parrots are assessed in Chapter 4, using the same methodology as Chapter 3 (i.e. comparisons with *in situ* data and evidence-based modifications). Finally, Chapter 5 covers the behavioural assessments of two zoo-housed swift parrots, as well as small-scale husbandry modifications applied to enable specific wild-type feeding behaviours (Figure 1.4).

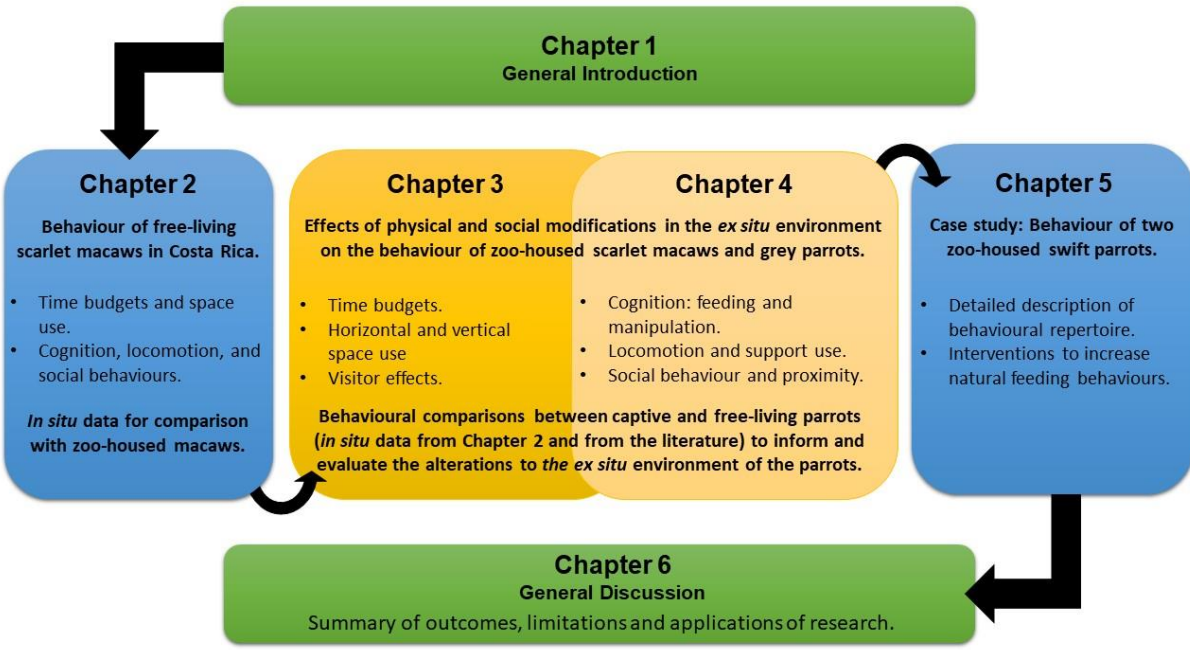


Figure 1.4. Diagram detailing the structure of this thesis.
Summary of the content in each chapter of this thesis. The arrows show the order of the chapters in the thesis. Chapters 3 and 4 overlap as they feature behavioural data collected on the same parrots.

CHAPTER 2

BEHAVIOURAL OBSERVATIONS OF FREE-LIVING SCARLET MACAWS IN COSTA RICA

Paper planned for publication:

Lemos de Figueiredo, R.[1], Chappell, J. (in prep). Behavioural observations of free-living scarlet macaws (*Ara macao*) in Costa Rica, with applications for *ex situ* management and husbandry. *Animals MDPI*.

[1] Collected and analysed all data.

ABSTRACT

Scarlet macaws are a popular parrot species that are native to Central and South America. There are gaps in knowledge about their behavioural ecology in the wild, which compromises both *in situ* and *ex situ* management and conservation efforts for this species. Seventeen days of behavioural observations were conducted on free-living scarlet macaws in two locations in Costa Rica, in February 2022, with the aims of (1) advancing our knowledge of this species' natural behavioural ecology, and (2) generating data for comparison with captive macaws to help to inform their *ex situ* management (e.g. enclosure design and enrichment). Line transects were walked within the two locations (Nicoya Peninsula - a release area for captive-bred reintroduced individuals and no extant wild population; Punta Leona (PL) - area of natural habitat within a resort inhabited by wild scarlet macaws), and focal interval sampling of multiple scarlet macaws in a group was used to record behaviour and space use. The macaws at both locations were generally active, mostly stayed high in the tree canopy, and relied on climbing to move within it, while using a high variety of supports. The macaws at PL exhibited significantly higher engagement in feeding and locomotion behaviours, and less perching, than those at Nicoya, possibly due to differences in resource availability (i.e. supplementary feeding at Nicoya), rearing conditions (captive-bred versus wild-hatched), and age (i.e. younger population at Nicoya). Furthermore, the wild scarlet macaws at PL exhibited a variety of foraging strategies to acquire and manipulate food items within the tree canopy, including common use of their feet during manipulation. Despite limitations caused by a small sample size and a short period of observations, this study provides insights into the

behavioural ecology of scarlet macaws in the wild, and can aid behaviour and welfare assessments of captive macaws while helping to inform their *ex situ* management.

Keywords: behavioural ecology, *ex situ* conservation, *in situ* research, Neotropical parrots

2.1. Introduction

Scarlet macaws are a popular parrot species, as one of the most common in the pet trade (Weston & Memon, 2009), and with a significance to human culture that dates to the 10th century, when they were acquired as symbols of social status (Watson et al., 2015). Despite this popularity among humans, research on the behavioural ecology of this species is still limited, with the published *in situ* research focussing on feeding observations (Nemeth & Vaughan, 2004), nesting and parental behaviours (Vaughan et al., 2009; Vigo-Trauco et al., 2021), post-fledging movements (Myers & Vaughan, 2004), migratory patterns (Brightsmith et al., 2021), and feeding ecology (Brightsmith & Villalobos, 2011). Other studies have also investigated the behaviour of released captive-bred individuals, with the aim of assessing their adaptation to the natural environment (Cornejo et al., 2005; Estrada, 2014).

Animal behaviour research can be used to inform *in situ* and *ex situ* conservation, and the management and husbandry of captive animals (section 1.4). Captive birds can therefore benefit from research on their wild counterparts (Rose, 2021), as basing the *ex situ* management of a species on scientific evidence, generated from research on its natural history, rather than traditional practice, has been found to improve animal

husbandry and welfare (Loughman, 2020). Consequently, gaps in knowledge of the natural behaviour of a species hinder not only conservation efforts but also husbandry and welfare in human care. Furthermore, some of the existing behavioural research on wild macaws relies on qualitative observations alone (e.g. descriptions of food manipulation; Nemeth & Vaughan, 2004; Silva, 2018) which, although useful to inform *ex situ* management, are of limited use for *in situ* – *ex situ* comparative studies. On the other hand, quantification of behaviours of wild animals can be used for comparison with their captive counterparts and determine whether the latter exhibit similar frequencies of wild-type behaviours. These comparisons are helpful in conservation breeding programmes (e.g. when evaluating whether a captive animal is suitable for reintroduction into the wild, one of the main challenges of *ex situ* conservation; section 1.2), and although they can also be useful in animal welfare assessments, this approach has limitations and requires caution (Howell & Cheyne, 2019; Veasey et al., 1996). On the one hand, wild-captive comparisons can loosely inform what behaviours, and in what frequencies, a captive animal should be exhibiting (Howell & Cheyne, 2019). On the other hand, deviations from wild-type behaviours are not necessarily representative of poor welfare (section 1.4.1), and therefore, wild-captive comparisons should be used alongside other indicators (e.g. health and affective states; Fraser, 2008) to more accurately assess the welfare status of captive animals (Howell & Cheyne, 2019).

The scarlet macaw has disappeared from most of its historical range within Central America (Figure 2.1) and estimates suggest the Central American scarlet macaw

population is below 4,000 individuals, with 2,000 estimated to remain in Costa Rica (Macaw Recovery Network, n.d.).



Figure 2.1. Historical and current geographic range of scarlet macaws in Central America.
Striped, brown shapes show areas where scarlet macaws were formerly found but are now potentially extinct. Orange shapes show areas where scarlet macaws are extant. Image taken from BirdLife International (2016a).

The Central Pacific Conservation Area, located in western central Costa Rica, constitutes over 500,000 ha of varied habitat, and it is inhabited by 83.6% of the 892 bird species identified in the country (SINAC, n.d.). Despite having one of the two largest scarlet macaw populations in Costa Rica (the other is located further south at Osa Peninsula; Figure 2.2A), surveys from the early 1990s showed a declining

population in that region, which could have led to local extinction if there had been no intervention (Vaughan et al., 2005).

A



B



Figure 2.2. Map of study areas in Costa Rica, where free-living scarlet macaws were observed in February 2022.

(A) Locations of Bosque Escondido (in Nicoya Peninsula) and Hotel y Club Punta Leona (within Central Pacific Conservation Area), where data collection took place, Rescate Wildlife Rescue Center (organisation releasing captive-bred scarlet macaws into the wild in Nicoya), Barra Honda and Palo Verde National Parks, and Osa Peninsula (areas with extant wild scarlet macaw populations in Costa Rica). (B) Detail of Hotel y Club Punta Leona in Costa Rica. Observations took place within the area bounded by the white line. The coloured lines represent the three line transects walked during data collection in that location. Maps from Google Earth (2023).

Collaborative conservation efforts, which were set up in 1994 and included anti-poaching measures, placing artificial nests, natural nest protection, economic incentives to local communities, and environmental education, were successful at stabilising the population (Vaughan et al., 2005). The Hotel y Club Punta Leona, a resort and tourist attraction within the Central Pacific Conservation Area in Puntarenas (Figure 2.2A), and one of the main partners in the conservation efforts for the scarlet macaw in the region, protects over 100 ha of primary and secondary forest, beaches and trees within developed areas (Vaughan, 2019; Figure 2.2B). Between 1995 and 2018, 15 natural nests were found within that area and artificial nests have also been placed there and occupied by scarlet macaws (Vaughan, 2019).

Only small and fragmented scarlet macaw groups remain in the Nicoya Peninsula (northwest of Costa Rica; Figure 2.2A), as surveys conducted in 2016-2017 found only 14 individuals and seven nests, distributed across 800 km^2 in two national parks (Barra Honda National Park and Palo Verde National Park**;** Figure 2.2A; Artavia-Duran, 2018). In 2016, the Rescate Wildlife Rescue Centre, a non-profit wildlife rehabilitation organisation based at Alajuela (Figure 2.2A), started a scarlet macaw reintroduction project south of those national parks, at Pilas de Canjel, in their Bosque Escondido release site (Figure 2.2A), which consists of 1,800-acre dry tropical forest (J.M. Pittman, pers comm., 2022). Their goal is to re-establish a population of this species in the area, where it disappeared from, by releasing 300 captive-bred individuals in 15 years (J.M. Pittman, pers comm., 2022).

Ex situ management can benefit species' conservation (section 1.2), and captive-bred scarlet macaws have been successfully reintroduced in Mexico (Amaya-Villarreal et al., 2015), Peru and Costa Rica (Brightsmith et al., 2005). Nevertheless, some organisations and researchers involved in the *in situ* conservation of this species in Costa Rica are opposed to releasing captive-bred animals into the wild, claiming the risks, such as the introduction of diseases and maladaptive behaviours into the environment, outweigh the potential benefits, and that resources are better spent in *in situ* conservation actions such as habitat restoration (Vaughan, 2019).

The aims of this study are to (1) provide an initial behavioural description, that can inform and be built on by future research, for free-living scarlet macaws in two locations in Costa Rica, (2) use those behavioural observations to understand activity budgets, and quantify space use, manipulation and foot use, structural support characteristics, and social behaviour and proximity, (3) collect data for comparison with captive macaws, and (4) gather evidence to inform *ex situ* management and husbandry of this taxon.

2.2. Materials and methods

2.2.1. Study's locations in Costa Rica

Data were collected in February 2022, during dry season (Vaughan et al., 2006), at two sites in Costa Rica: (1) Rescate Wildlife Rescue Center's Bosque Escondido release site, near Pilas de Canjel, Nicoya Peninsula (Figure 2.2A), and (2) Hotel y Club Punta Leona, in Puntarenas (Figures 2.2A and 2.2B),

The scarlet macaws at the Bosque Escondido site were part of a reintroduction programme started in 2016. As there were no remaining scarlet macaws in that site prior to 2016, it is most likely that the scarlet macaws observed were captive-bred, and no older than seven years old (J.M. Pittman, pers comm., 2022). In contrast, the scarlet macaws observed at Punta Leona (PL) were part of one of the two remaining viable populations of scarlet macaws in Costa Rica, and although it is possible captive-bred individuals that were released elsewhere dispersed to this area, the observations in this location were most likely on wild scarlet macaws of various ages.

This study was approved by the University of Birmingham's Science, Technology, Engineering and Mathematics (STEM) ethics committee (code: ERN_19-0974).

2.2.2. Data collection on free-living scarlet macaws in Costa Rica

Three line transects of approximately 1,500 m length were walked within the paths available at each location (i.e. paths already used by the visitors and staff of the resort at PL, and by the staff of the reintroduction programme at Nicoya). At PL, one transect crossed two beaches (light blue line, Figure 2.2B), one crossed an area of rainforest interspersed with holiday houses (orange line; Figure 2.2B), and the third one crossed an area with holiday and staff houses, a swimming pool and bar within patches of rainforest (dark blue line; Figure 2.2B). Detailed location of the transects at Nicoya could not be shared, for protection of the released animals, but all transects were within areas of secondary dry tropical forest, and one of them included the artificial feeders provided for supplementary feeding of the released macaws. The transects were

randomly walked between 06:00 and 16:00 hrs at Nicoya, and 06:00 to 18:00 hrs at PL (Central Standard Time). Data collection finished earlier in the day at Nicoya due to safety reasons, to give the observer time to return to the accommodation before dark, which was not an issue at PL. While walking the paths, if scarlet macaws were found within visual range, they were sampled until they moved out of sight, with the walk then proceeding until more individuals were found.

Focal interval sampling of individuals was conducted, with random selection of individual macaws in each interval when more than one was present. Focusing on one individual in each interval allowed for accurate observations and collection of detailed behavioural data, which would not be possible if multiple individuals were sampled at the same time. Data were collected using the ZooMonitor mobile application (Ross et al., 2016), in 10-minute sessions and 40-second intervals. The weather conditions (cloudy, partially cloudy, clear/sunny, rain) and average temperature (determined from Apple iPhone's weather mobile application; Apple Inc., 2019) were recorded at the start of each 10-min session. The sampling method was adapted from a pilot study on captive individuals (Appendix 1) and, after three hours of practice behavioural observations on free-living scarlet macaws, refined to reflect the challenges of *in situ* data collection. The 10-minute sessions were considered suitable for use on the highly mobile free-living macaws, to reduce the number of interrupted sessions due to individuals moving out of sight. Furthermore, 40-second intervals were found to be the shortest interval that could be used (and therefore maximising the amount of data collected in a session; i.e. 15 intervals in a 10-minute session) while allowing enough time to accurately select a random individual for sampling in each interval.

Individual macaws were sampled more than once, which was necessary to increase the sample size of behavioural data collected under the time restrictions of the study. Although auto-correlated data were collected as a result of repeated observations on the same individuals, it allowed for more detailed behavioural data to be collected (de Solla et al., 1999). To reduce issues of over-sampling individuals and auto-correlation, when only one macaw or pair was visible, they were sampled for up to 30 minutes (three 10-min sessions/protocols), while groups of 3-4 were sampled for up to an hour (six 10-min sessions/protocols). Groups with more than four individuals had no time limits. However, due to the high mobility of free-living macaws, it was noticed these limits were rarely necessary, as the scarlet macaws almost always moved out of sight before the 30-minute/three session limits and were often replaced by other individuals that arrived in the area. If no individuals remained visible for sampling, the session was terminated earlier, otherwise it continued with the new individuals that arrived. The transects in each location were walked at least twice a day (once in the morning and once in the afternoon), although at PL it was often possible to make multiple daily walks, and in random directions to ensure the limited locations available for observations were sampled at different times of the day.

The released scarlet macaws at Nicoya received supplementary feeding through artificial feeders hanging in the tree canopy on a pulley system. This was carried out twice a day (once at dawn, shortly after sunrise, and once in the afternoon/evening, between 15:30 and 17:00 hrs, by the local staff of the reintroduction programme. They were fed a mixture of fruit and vegetables chopped in halves or quarters, nuts, and beans. No supplementary feeding occurred at PL, but some of the (occupied) artificial

nests placed in the area, part of the *in situ* conservation management for the species discussed in section 2.1, were within the area of the observations. Although the chance of observing scarlet macaws was higher at these areas, the group size-dependent time limits and the randomised transect walks likely reduced the bias towards the individuals and/or behaviours associated with those areas.

2.2.3. Individual selection in group sampling

Focal sampling of multiple individuals within a group was done by selecting a random individual in each interval, based on their relative position to other individuals, and using a pre-defined list of random numbers (Figure 2.3A) generated using Microsoft Excel (function “RANDBETWEEN”). The relative position of the individuals was used to select an individual, by counting heads left to right (e.g. if the interval listed random number “3”, the third individual from left to right was selected for sampling in that interval). When the heads of two individuals were in the same horizontal position, then the one higher up was counted first (Figures 2.3B and 2.3C). The number in the right column was used (Figure 2.3A) unless the number was greater than the number of visible individuals to be sampled (e.g. if there were four visible individuals for selection, the right column had number “6”, and left column had number “2”, then the latter would be selected). When the numbers in both columns were greater than the number of visible individuals, then the individual furthest to the right was selected. As the total number of individuals could not be pre-defined, several lists were created with maximum numbers of 8, 12, and 16 (and random numbers of up to 4, 6, and 8, respectively, in their ½ columns; Figure 2.3A).

A

INTERVAL	<1/2	>1/2
1	3	13
2	4	15
3	7	3
4	1	4
5	8	13

B C

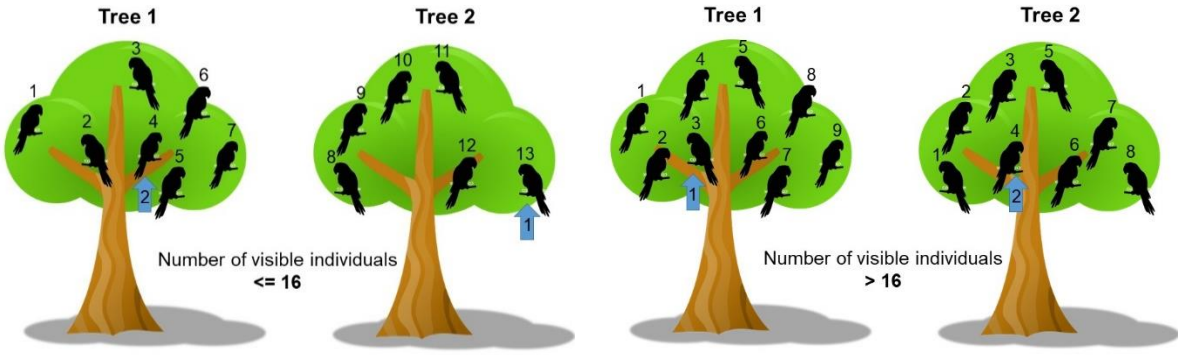


Figure 2.3. Schematic representation of the method for random selection of individuals during focal interval sampling of groups, used while sampling free-living scarlet macaws in Costa Rica.
(A) List of random numbers created for individual selection in each interval, based on a group of up to 8 (<1/2 column) or 16 individuals (>1/2 column). (B) Schematic representation of random individual selection based on relative position within the group, when the number of visible individuals was up to 16 individuals, and (C) when the number of visible individuals was greater than 16. Arrows represent the individuals that would be selected in intervals 1 and 2 in each scenario, based on the numbers on the list.

These lists were used for varied group sizes, with 16 being a maximum number that was considered feasible to count to in each interval. When there were more than 16 visible individuals, they were divided into subgroups based on location and alternated between sessions (e.g. each tree, or half tree, with visible individuals sampled in rotation on successive intervals; Figure 2.3C). For example, in scenario B there are 13 parrots visible across two trees (Figure 2.3B) and therefore the whole group, which has less than 16 parrots, is used for random individual selection. In the first interval the 13th individual (number “13” on the list; Figure 2.3A) is sampled, while in the second

interval the fourth individual (number “4” on the list; Figure 2.3A) is selected. The figure in the left column was used in this situation because the number in the right column is 15 and there are only 13 visible individuals. In scenario C, however, there are 17 visible parrots across two trees (Figure 2.3C), and therefore they are divided into two subgroups of nine parrots in tree 1, and eight parrots in tree 2. In the first interval, the subgroup on tree 1 is sampled, with the 3rd individual selected (number “3” on the list; Figure 2.3A), and in the second interval, the subgroup on tree 2 is sampled and the fourth individual is selected (number “4” on the list, Figure 2.3A and 2.3C). When sampling two individuals, the individual on the left and right were selected in uneven and even intervals, respectively. However, a list was always ready for use in case more individuals joined the single individual or pair during a session, and were used from the interval they joined (e.g. if more scarlet macaws became visible on interval 4 of observations on a pair, then a list of random numbers would be used from the next full interval).

Most observations at Nicoya were on groups of scarlet macaws, and therefore there were more parrots for random individual selection in each interval than at PL, where most observations were on pairs and single individuals). However, there were more interrupted data collection sessions, where all scarlet macaws moved out of sight during a session, at PL, confirming their high mobility. Furthermore, the complete sessions also included new arrivals and replacements of the focal animals, which means that a completed session could have included multiple individuals that have arrived and departed. No quantitative data were available for these changes in

individuals within sessions, but the observer noticed these were regular occurrences, and that consecutive observations on the same individuals were uncommon.

2.2.4. Ethogram of behaviours of grey parrots and macaws

Three protocols were used for data collection: cognition, locomotion and social behaviour, which were used on rotation for sampling. An ethogram of behaviours was created during a pilot study on captive scarlet macaws and grey parrots (Appendix 1) featuring contextual behaviours (Table 2.1), applicable to all protocols. Some behaviours in the ethogram are applicable to captive parrots only (Chapters 3-5).

Table 2.1. Ethogram of broad/contextual behaviours, and respective modifiers, for application across parrot species. NA = Not applicable as no modifiers for that behaviour.

Category	Description	Modifier	Description
Out of sight	Individual obscured, no behaviour can be identified.	NA	NA
Perching	Individual is standing in one position, completely immobile or showing head movements only. The individual may be alert, sleeping or resting, or engaged in comfort behaviours (see modifier column).	None	Individual is immobile and not engaged in any other behaviour.
		Unknown	Individual is immobile, but it is partially obscured, and it is unclear whether it is performing any of these behaviours.
		Stretching	Individual is stretching a part of the body while resting.
		Yawning	Bill open widely while resting.
		Feather fluffing	Individuals fluffs feathers and shakes its body.
		Bill movements	Bill movement while perching, not associated with feeding or manipulation.
		Wing flapping	Individual is flapping wings without changing location.

Category	Description	Modifier	Description
		Vocalising	Individual is vocalising while perching.
Self-maintenance	Individual is cleaning or tidying its own body.	Preening	Using part of the body (usually bill or head) to clean own feathers.
		Scratching	Using foot in a rapid movement to scratch part of the body.
		Foot Maintenance	Using mouth to gently manipulate own foot.
		Bathing	Feather fluffing, body shaking and head movements while inside water (e.g. in a provided bath or in a puddle).
		Rain bathing	Feather fluffing, wings flapping and/or open while in the rain.
		Bill wiping	Wiping bill on a structure.
Oral stereotypies (*ex situ* birds)	Repetitive (>2x) oral-related behaviours.	Wire chewing	Gnawing wire mesh: may include violent pulling, making a loud snap sound.
		Dribbling	Repetitively grab and drop an object or food item.
		Feather plucking	Biting and removing own feathers with bill.
Motor stereotypies (*ex situ* birds)	Repetitive (>2x) motor-related behaviours.	Perch circles	Walking on the perch to its end, climbing up enclosure to the top, and until the other side of the perch, completing a vertical circle.
		Corner flips	Turning in small circles in the top corners of the enclosure.
		Route trace	Walking and/or climbing an identical route around the enclosure.
		Head circles	Repetitively moving head around.
Feeding/Drinking	Food/water search, manipulation	More detailed behaviour collected when conducting cognition protocol.	

Category	Description	Modifier	Description
	and consumption.		
Geophagy	Soil and clay ingestion.	More detailed behaviour collected when conducting cognition protocol.	
Object manipulation	Utilising and interacting with a non-food object.	More detailed behaviour collected when conducting cognition protocol.	
Social	Social interactions with other individuals.	More detailed behaviour collected when conducting social protocol.	
Locomotion	Individual moving between locations.	More detailed behaviour collected when conducting locomotion protocol.	

In addition, an ethogram of specific feeding and object manipulation behaviours (Table 2.2), as well as object and food categories (Table 2.3), was created for the cognition protocol.

Table 2.2. Ethogram of cognition-specific behaviours, and respective modifiers, for application across parrot species. NA = Not applicable as no modifiers for that behaviour.

Category	Description	Modifier	Description
Feeding	Food/water ingestion and/or manipulation.	Mouth (body parts used)	Mouth is being used to manipulate the food/object but it is unclear whether the bill and tongue are both being used or just one of them.
		Bill (body parts used)	Bill is being used to manipulate the food/object.
		Tongue (body parts used)	Tongue is being used to manipulate the food/object.
		Foot (body parts)	Foot is being used to manipulate the food/object.
Object manipulation	Manipulating a non-food object.	Passive (level)	Searching for or holding an object or food item without manipulating it.
		Basic (level)	Basic manipulation: may include rotation with foot

Category	Description	Modifier	Description
			and/or soft biting (e.g. biting a twig or leaf, biting off chunks of fruit).
		Intermediate (level)	May include persistent handling and/or gnawing (e.g. cracking seeds, peeling food item, gnawing on a perch).
		Advanced (level)	Advanced manipulation that may include solving puzzles or extreme persistent handling and/or gnawing (e.g. cracking nuts, puzzle feeder).
		Stationary (movement)	The individual's body stays in same location while manipulating food or object.
		In Motion (movement)	Individual's body changes location while manipulating the object.
Geophagy	Ingestion of earth or soil-like substrates.	Soil (type)	The individual is ingesting soil.
		Wall (type)	The individual is ingesting earth from a wall (e.g. clay lick).

Table 2.3. Food and object categories considered during observations of food and object manipulation (cognition protocol; Table 2.2). NA = Not applicable as no modifiers for that behaviour.

Category	Description	Modifier	Description
No object	No object is being used	NA	NA
Free	Object that is not attached to another feature and can be freely moved by the bird (e.g. being grabbed, held and/or transported).	Destructible (toughness)	Easily, almost instantaneously, breakable, requiring little manipulation (e.g. twig, leaf, branch).
		Hard (toughness)	Cannot be destroyed at once but requires repetitive manipulation (e.g. wooden platform or perch).
		Malleable (toughness)	Can be manipulated repeatedly ("chewed") without destruction, even though this may occur with continuous use (e.g. rope).
		Indestructible (toughness)	Very tough and rigid, virtually indestructible, even though

Category	Description	Modifier	Description
Attached	Object that is attached to another feature, the position of which can be partially controlled by the bird (e.g. grabbed and/or held) but cannot be transported away. (e.g. hanging feeder).		destruction may still occur with continuous use (e.g. metal structure).
Fixed	Object fixed, the position of which cannot be altered by the bird.	Simple (complexity)	Requires low cognitive ability, just basic manipulation such as biting (e.g. twig, leaf).
		Medium (complexity)	Requires some cognitive ability in order to manipulate (e.g. simple puzzle feeder with one task and reward).
		High (complexity)	Requires more advanced cognitive ability in order to manipulate (e.g. complex puzzle feeder with multiple tasks).
		Social (complexity)	Requires social cooperation in order to manipulate (e.g. puzzle feeder with a task that can only be solved socially).
External (*ex situ* birds)	Object on the outside of the enclosure but still within reach of the bird.	Temporary (novelty) (*ex situ* birds)	The object is not a permanent part of the enclosure and it was temporarily added.
		Permanent (novelty) (*ex situ* birds)	The object is a permanent feature of the enclosure.
Food		Bare (cover)	Edible component is uncovered, partially covered or fully covered by an edible case. It can be immediately ingested (e.g. apple, grape, carrot, broccoli, pellet, chopped banana, chopped orange).
		Full cover (cover)	Edible component is fully concealed within a non-edible

Category	Description	Modifier	Description
			cover (e.g. seeds, nuts, whole banana, whole orange).
		Soft (toughness)	Soft or mushy consistency that requires little bill strength (e.g. apple, grape, banana, leaves)
		Intermediate (toughness)	Harder consistency that requires some bill strength (e.g. carrot, pineapple, broccoli, seeds, pellet).
		Hard (toughness)	Extremely hard food items that require high bill strength (e.g. nuts, some seeds, tougher pellets).
		Small (size)	Can be grabbed and held by the bird.
		Large (size)	Cannot be grabbed or held by the bird.

The locomotion protocol featured locomotion-specific behaviours (Table 2.4) and support categories (Table 2.5.).

Table 2.4. Ethogram of locomotion-specific behaviours, and respective modifiers, for application across parrot species. NA = Not applicable as no modifiers for that behaviour.

Category	Description	Modifier	Description
Hop	Jumping between nearby locations, without using any support. Wings may be open and may include up to one wing beat.	NA	NA
Flight	Moving between locations without using any support.	Short (*ex situ* birds)	Flight distance is half or under the maximum possible distance to fly within the enclosure.

Category	Description	Modifier	Description
	Wings open and at least two wing beats.	Long (*ex situ* birds)	Flight distance is over half the maximum possible distance to fly within the enclosure.
		Extra (*ex situ* birds)	Flight distance is over the total length of enclosure (e.g. it flies one way and back without perching).
Walk	Moving on a support by moving one foot after the other, without bill assistance.	NA	NA
Climb	Moving upwards or sideways on a support, using both feet and bill to assist.	Vertical	Individual is moving upwards on the structure.
		Horizontal	Individual is moving sideways on the structure (up to 20° angle with the ground)
		Upside down	Individual is moving while inverted.
Descend	Moving downwards on a support, using both feet and bill to assist.	NA	NA

Table 2.5. Support categories considered during observations of all behaviours, collected under Locomotion protocol (Table 2.3). NA = Not applicable as no modifiers for that behaviour.

Category	Description	Modifier	Description
No Support	No support is being used (e.g. while flying).	NA	NA
Unstable perch	A structure within the enclosure that the birds can hold on to and use to stand on, but that is not steadily attached to the enclosure (i.e. its position fluctuates as the birds move on it).	Thin (thickness)	Toes overlap when feet grasp the perch.

Category	Description	Modifier	Description
Stable perch	A structure within the enclosure that birds can hold on to and use to stand on, firmly attached to the enclosure (i.e. its position stays unchanged as the birds move on it).	Medium (thickness)	Feet closed around at least half the support, or fully but loosely.
		Thick (thickness)	Feet closed around less than half the support, or with toes extended flat.
		Simple (complexity)	Single support (nearest support can only be reached by flight, wire mesh or ground), homogeneous in thickness and orientation.
		Intermediate (complexity)	Single support but with at least two different types of orientation AND thickness areas along its surface (e.g. a perch that divides into thinner branches in a different orientation).
		Network (complexity)	Multiple supports connected with each other (or within reach of each other by the bird without flying, via wire mesh or ground), with a diversity of orientation and thickness levels.
		Horizontal (orientation)	Makes an angle between approximately 0° to 20° with ground.
		Diagonal (orientation)	Makes an angle between approximately 20° and 70° with ground.
		Vertical (Orientation)	Makes an angle between approximately 70° and 90°.
Wire Mesh	Mesh delimiting enclosure limits.	NA	NA
Platform	Flat structure that can be stood on but cannot be grasped with the feet.	NA	NA
Ground	Bottom limit of the enclosure.	Rigid	Substrate cannot be changed or manipulated by the bird (e.g. concrete)
		Flexible	Substrate can be manipulated by the bird (e.g. sand, gravel, soil).

Finally, the social protocol included social behaviours and proximity to other individuals (Table 2.6). In addition to these data, the approximate height of the location of the individual was recorded in all protocols, as well as the number of visible individuals considered for individual selection in group sampling were also recorded.

Table 2.6. Ethogram of social-specific behaviours, and respective modifiers, as well as proximity categories, for application across parrot species. NA = Not applicable as no modifiers for that behaviour.

Category	Description	Modifier	Description
Allofeeding	The individual is feeding or being fed by another individual (bills connected, food transference).	Conspecific (target)	The target of the interaction is of the same species of the focal individual.
Allopreening	The individual is preening or being preened by another individual (cleaning and tidying its feathers).	Heterospecific (target)	The target of the interaction is of a different species from the focal individual.
Nibbling	The individual gently nibbles or is nibbled by another individual, usually very briefly and associated with vocalisations.	Keeper (target)	The target of the interaction is one of the animal keepers.
Threatening	Birds aggressively interacting, including threatening posture (head movements, feathers ruffled, mouth open) and loud vocalisations but NO physical contact.	Visitor (target)	The target of the interaction is one of the visitors.
Fighting	Birds aggressively and physically interacting, including biting and feather pulling.	Active	The individual is performing the behaviour.
Chasing	An individual is chasing or being chased by another individual, as it forces or is forced to move to move to another location.		
Courtship	The individual is displaying to another individual, which may include head bobbing, ruffled feathers, vocalisations, touching	Passive	The individual is the recipient of the behaviour.
		Mutual	The behaviour is being performed

Category	Description	Modifier	Description
	bills, and backward-and-forward movements on the support.		mutually by the individuals.
Mating	The individual is on top or underneath another individual, cloacas are in contact, associated body movements.		
Other interactions	Any other social interactions not included in the other categories.	Aggressive	NA
		Affiliative	NA
Proximity scans			
Proximity Scans (Wing length)	NA	Number of conspecifics	Number of conspecifics within a wing length distance.
		Number of heterospecifics	Number of heterospecifics within a wing length distance.
Proximity Scans (< 2 m)	NA	Number of conspecifics	Number of conspecifics within 2 m.
		Proportion of group (conspecifics)	Proportion of the group within 2m (conspecifics).
		Proportion of group (heterospecifics)	Proportion of the group within 2 m (heterospecifics).

The relative location of the focal individual in each interval was recorded based on their position within the tree, man-made structure (e.g. buildings, electricity post) or other natural structure (e.g. understory vegetation, clay lick or other non-tree natural feature; Figure 2.4).

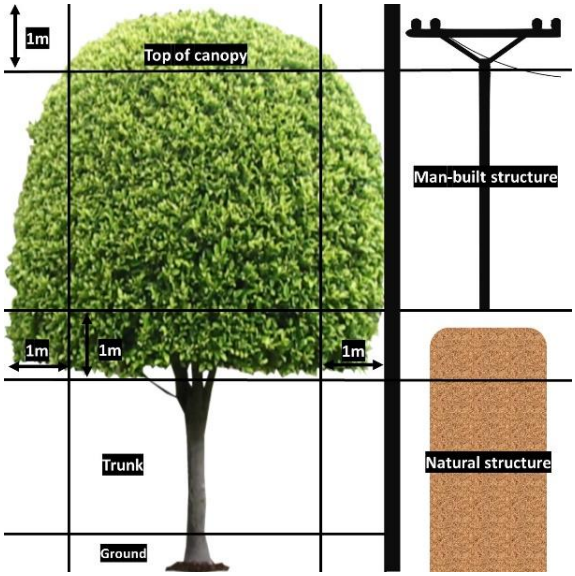


Figure 2.4. Diagram used for data collection on space use of free-living scarlet macaws in Costa Rica.
Ground level was selected if the scarlet macaws were directly on the ground (natural such as soil or human-modified such as concrete). If close to the ground but using another structure as support, then the respective category (e.g. natural structure, such as shrubs) would be selected. Man-made structure consisted of anything not naturally occurring in the environment, such as buildings and electricity posts.

2.2.5. Data analysis

Data analysis was conducted in Rstudio (R version 4.2.1; R Core Team, 2022), using the packages “tidyverse” version 1.3.2 (Wickham et al., 2019), “lubridate” version 1.8.0 (Grolemund & Wickham, 2011), “janitor” version 2.1.0 (Firke, 2021), and “gmodels” version 2.18.1.1 (Warnes et al., 2022). The percentages of visible group size, based on the total number of individuals observed and used for random individual selection in each interval, were calculated for the scarlet macaws at both locations. While the percentages of total observations (i.e. across the whole observation period) were calculated for all behaviours investigated (i.e. feeding complexity, foot use in manipulation, type of locomotion, support characteristics, type of social behaviours and proximity to other individuals), the daily percentages of each behaviour recorded were

also estimated to include variations in the broad time budgets across days of observations. To compare activity across three time periods (morning: 06:00 – 10:59 hrs, middle of the day: 11:00 – 14:59 hrs, afternoon/evening: 15:00 – 18:00 hrs), behaviours were grouped into three activity levels (high: perching, feeding, locomotion and object manipulation; medium: self-maintenance and social; low: perching). Although my study was mostly descriptive, a comparison of the time budgets between locations was conducted, using a Chi-squared test of independence. Adjusted standardised residuals were calculated as post-hoc tests to the Chi-square, accounting for differences in sample size between locations, which were interpreted with Bonferroni-corrected critical values, to reduce the risk of Type I error due to the comparison of multiple categories (Macdonald & Gardner, 2000). The alpha threshold for the p-value was reduced to 0.001 to account for the non-independent data collected from the occasional repeated sampling of the same individuals.

2.3. Results

Data on free-living scarlet macaws were collected over 17 days, seven of those from the reintroduced population at Nicoya and 10 from the wild population at PL, in a total of 11.4 and 12.1 hours of behavioural observations, respectively. The weather was mostly clear/sunny at both locations (Nicoya: 59%, PL: 74% of observations), it did not rain during that period, and full cloud cover was rare (Nicoya: 5.7%, PL: 1.0%). The mean approximate temperature during observations was 28.5ºC (26-30ºC) at Nicoya and 27.3ºC (24-30ºC) at PL. While the observations at Nicoya were more often done on groups with more than five individuals, with single individuals only recorded in 6% of observations, at PL they were mostly on pairs and single individuals (Figure 2.5A).

At Nicoya, 79.5% of the data collection sessions were completed, while the remaining were interrupted early due to the macaws moving out of sight. At PL, the percentage of completed data collection sessions was 68% (Figure 2.5B).

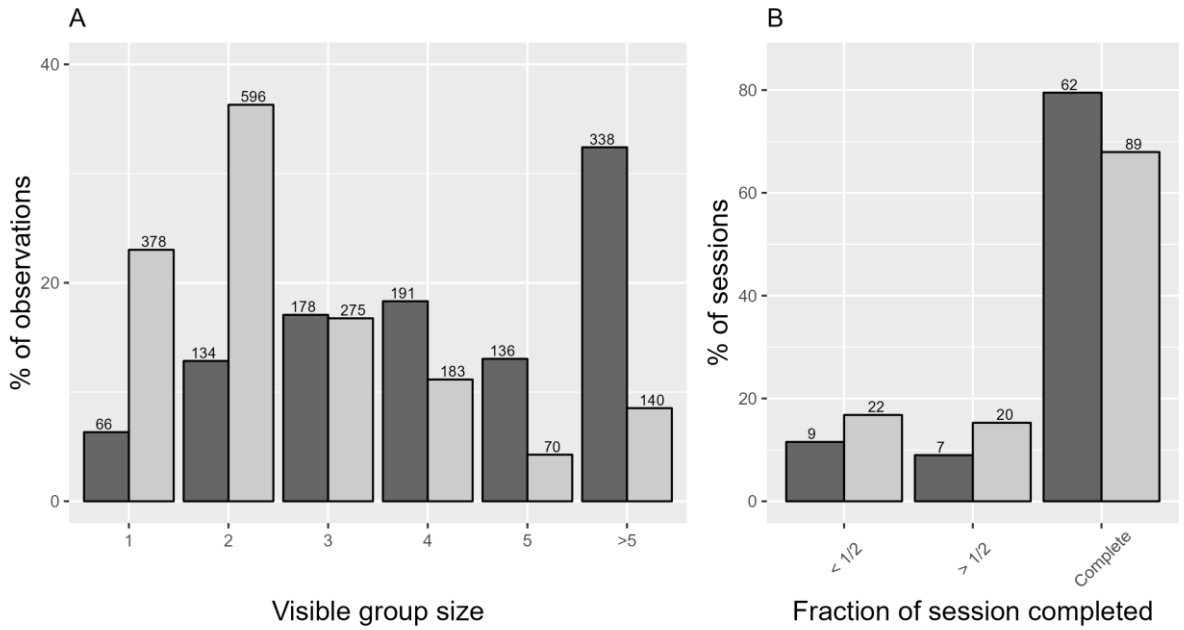


Figure 2.5. Group sizes of free-living scarlet macaws observed in Costa Rica in February 2022, and fraction of data collection sessions completed.
(A) Percentage of observations of different group sizes of scarlet macaws (visible individuals), at Nicoya (dark grey bars) and Punta Leona (light grey bars) in Costa Rica. (B) Percentage of 10-minute data collection sessions that were complete and those that ended before 10 minutes elapsed due to parrots moving out of sight. Numbers above bars correspond to number of intervals.

2.3.1. Time budgets and space use of free-living scarlet macaws in Costa Rica

The macaws' activity budgets significantly differed between locations ($X^2_{(5,\ n\ =\ 2644)}$ = 112.01, $p < 0.001$; Figure 2.6B and Table 2.7). Although perching was the most common single behaviour observed in both locations, it was recorded in under half the observations at both Nicoya and PL.

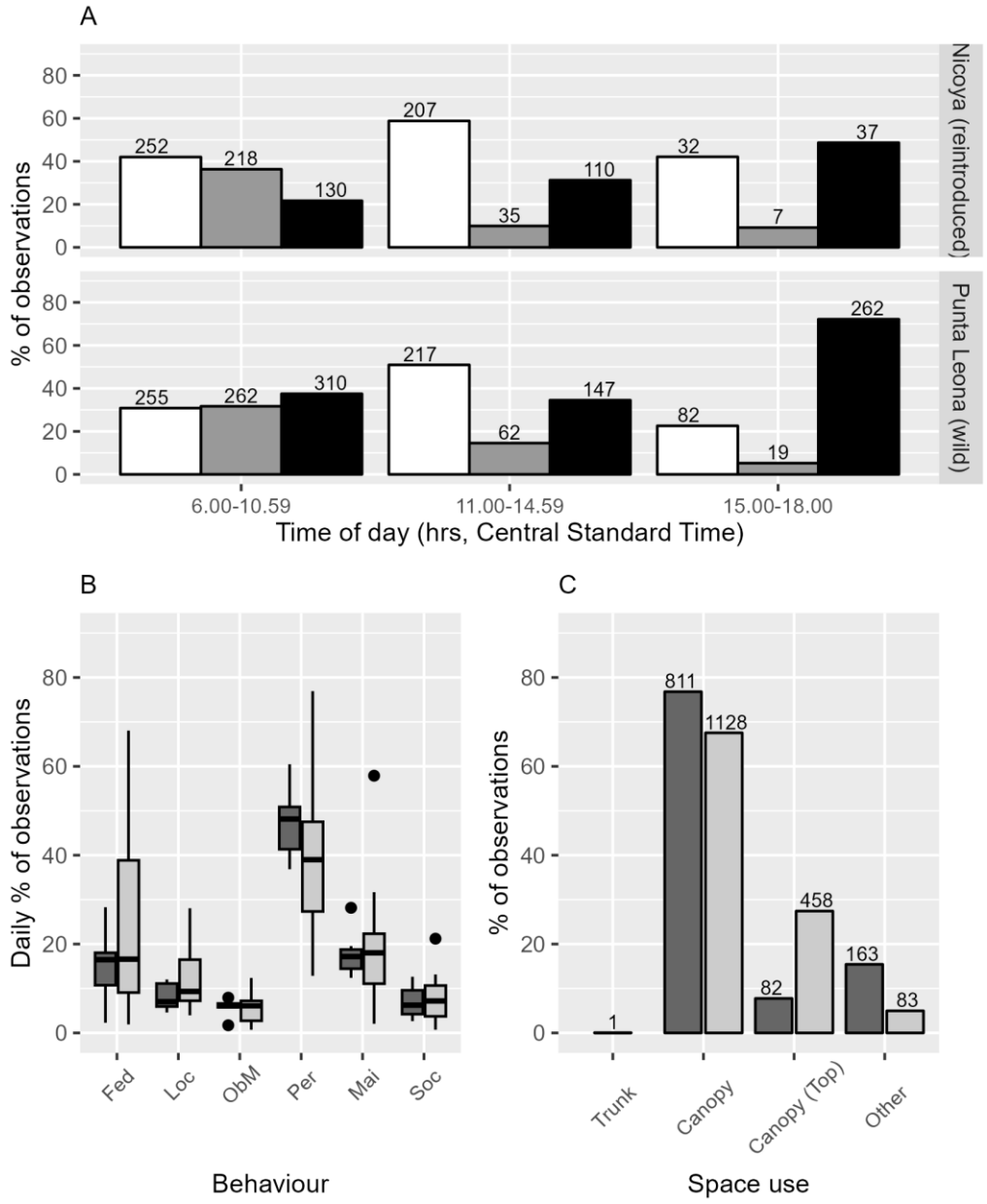


Figure 2.6. Time budgets, activity patterns, and space use in free-living scarlet macaws observed in Costa Rica in February 2022.

(A) Total percentages of low (white bars), medium (grey bars) and high activity (black bars) behaviours across three time periods. (B) Boxplots of daily time budgets recorded at Nicoya Peninsula (dark grey bars) and Punta Leona (light grey bars). The median, first and third quartiles are represented by the box, the whiskers represent the minimum and maximum values, and the black dots show the outliers. (C) Percentages of observations of space use (i.e. tree trunk, canopy, top of canopy, other non-tree structures). Numbers above bars correspond to number of intervals. Fed = Feeding; Loc = Locomotion; ObM = Object Manipulation; Per = Perching; Mai = Self-Maintenance; Soc = Social.

Table 2.7. Summary of the Chi-squared test comparing the time budgets of the reintroduced scarlet macaws from Nicoya Peninsula and the wild scarlet macaws from Punta Leona, observed in Costa Rica in February 2022.
Blue and red cells show significant positive and negative differences in adjusted standardised residuals, respectively, according to the corrected critical value.

X^2	df	p-value	Adjusted standardised cell residuals		
112.01	5	< 0.001	Corrected critical value: 2.87		
				Nicoya (reintroduced)	Punta Leona (wild)
			Feed/Drink	-8.47	8.47
			Locomotion	-4.27	4.27
			Object Manipulation	2.63	-2.63
			Perching	6.91	-6.91
			Self-Maintenance	2.19	-2.19
			Social	0.86	-0.86

Therefore, most observations consisted of active behaviours (feeding, locomotion, object manipulation, self-maintenance and socialising; Figure 2.6B). The adjusted standardised residuals (Table 2.7) showed that perching was more frequent in Nicoya compared to PL, while feeding and locomotion were more frequent at PL than Nicoya (Figure 2.6B).

While perching, the macaws rarely engaged in comfort behaviours, although there was a high percentage of unclear perching observations (i.e. Nicoya: 37%; PL: 34%). Self-maintenance consisted mostly of preening (Nicoya: 96%, PL: 93%). Low activity, i.e. perching, was more frequent in the middle of the day, while observations of medium (i.e. self-maintenance and socialising) and high (i.e. feeding, manipulation and locomotion) activities were more frequent in the morning and after 15:00 hrs, respectively (Figure 2.6A). The tree canopy was the preferred location of the scarlet macaws at both locations (Figure 2.6C). Use of the tree trunk was rare in both locations

(Figure 2.6C), and other (non-tree) structures were also rarely used and consisted mostly of the artificial feeders (Nicoya) and nest boxes (PL). The macaws in both locations were mostly observed at heights over 10 m, were never seen on the ground and were rarely close to it. Similarly, the trees and other structures they used to perch on were predominantly of heights over 10 m.

2.3.2. Cognition: feeding and manipulation of free-living scarlet macaws in Costa Rica

Over 90% of the feeding observations at Nicoya (n = 133) were on the artificial feeders rather than naturally occurring food. The food trays high in the trees obscured visibility and it was not possible to determine what the scarlet macaws were eating in 82% of the observations. At PL, this was not an issue (i.e. no access to artificial feeders) and only 5% of feeding observations were unclear. Out of the clear feeding observations that were recorded at Nicoya (n = 24), most were of intermediate manipulation complexity. Contrastingly, clear feeding observations at PL (n = 207) consisted mostly of advanced manipulation (65%). Basic food manipulation was not observed at PL, and passive manipulation was rarely observed (Figure 2.7A). The scarlet macaws at Nicoya used their feet for food manipulation in 22% of feeding observations (n = 133; Figure 2.7B). The visual obstacles reported above for feeding observations at Nicoya did not interfere with the recording of the body parts used for food manipulation, as it was still possible to see whether they were using their feet while feeding in most observations. At PL, general foot use in feeding was relatively high (42.5% of feeding observations; n = 200; Figure 2.7B), but it differed across the three plant species they were seen feeding on (Figure 2.7C).

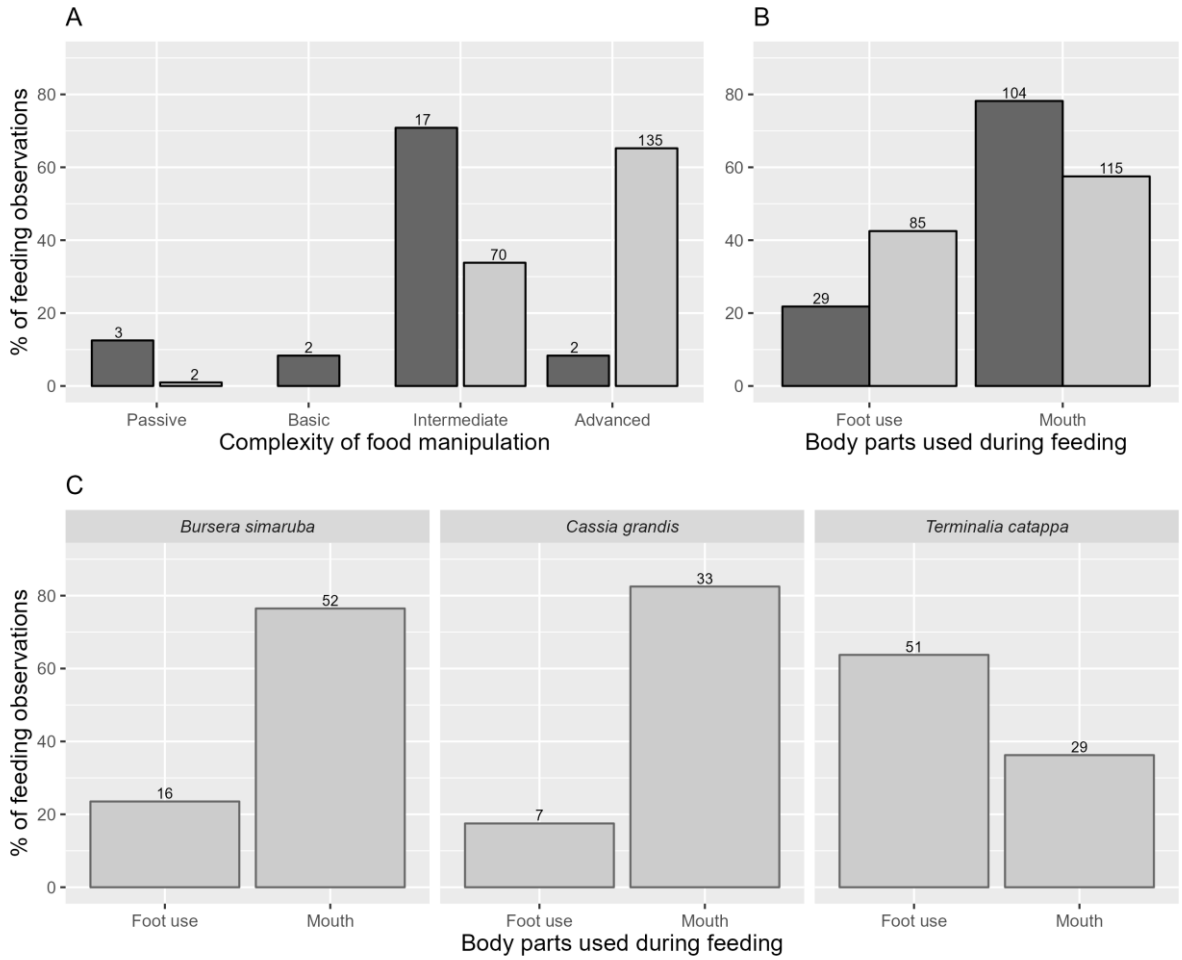


Figure 2.7. Food manipulation and foot use in free-living scarlet macaws observed in Costa Rica in February 2022.
Percentage of feeding observations on the scarlet macaws at Nicoya (dark grey bars) and PL (light grey bars) for (A) different levels of food manipulation (B) body parts used for feeding/food manipulation, (C) body parts used for feeding/food manipulation on the fruits from gumbo limbo (*Bursera simaruba*), pink shower tree (*Cassia grandis*) and Indian beach almond tree (*Terminalia catappa*) at PL. Numbers above bars correspond to number of intervals.

The gumbo-limbo (*Bursera simaruba;* 38% of feeding observations) produces a small circular fruit (~1.5 cm diameter; Figure 2.8A) on which the scarlet macaws were seen feeding. As these fruits were often located at the extremities of branches, the macaws had to navigate the nearby branches and explore several positions to reach them. Once they reached them, they either managed to consume them directly with their mouths without the aid of their feet (76% of observations) or they used their feet to

adjust the fruit's position or aid in its manipulation. Contrastingly, the fruits produced by the pink shower tree (*Cassia grandis;* 22% of feeding observations) are up to 50 cm-long (Figure 2.8C), and to feed on them, the scarlet macaws were seen hanging from nearby vertical perches or the fruit itself to extract the seeds within. They used their feet in 17.5% of the feeding observations on this species (Figure 2.7C), to pull the fruit towards their bills and/or to keep it in position while eating. Indian beach almonds (*Terminalia catappa;* Figure 2.8B) accounted for 40% of the feeding observations, and the scarlet macaws were observed pulling the fruit off the tree with their bills and, in 64% of the observations on this species, holding it in their feet while manipulating and consuming it (Figure 2.7C).



Figure 2.8. Food items in the diet of wild scarlet macaws observed at Punta Leona (Costa Rica) in February 2022.
Dropped fruits of (A) gumbo-limbo (*Bursera simaruba);* (B) beach almond (*Terminalia catappa)* after manipulation from a scarlet macaw; and (C) pink shower tree (*Cassia grandis)*, after manipulation and seed extraction from a scarlet macaw. Photos: RLF.

2.3.3. Locomotion and support use of free-living scarlet macaws in Costa Rica

Tripedal locomotion (i.e. climbing) was the predominant type of locomotion of the scarlet macaws at both locations (Figure 2.9A).

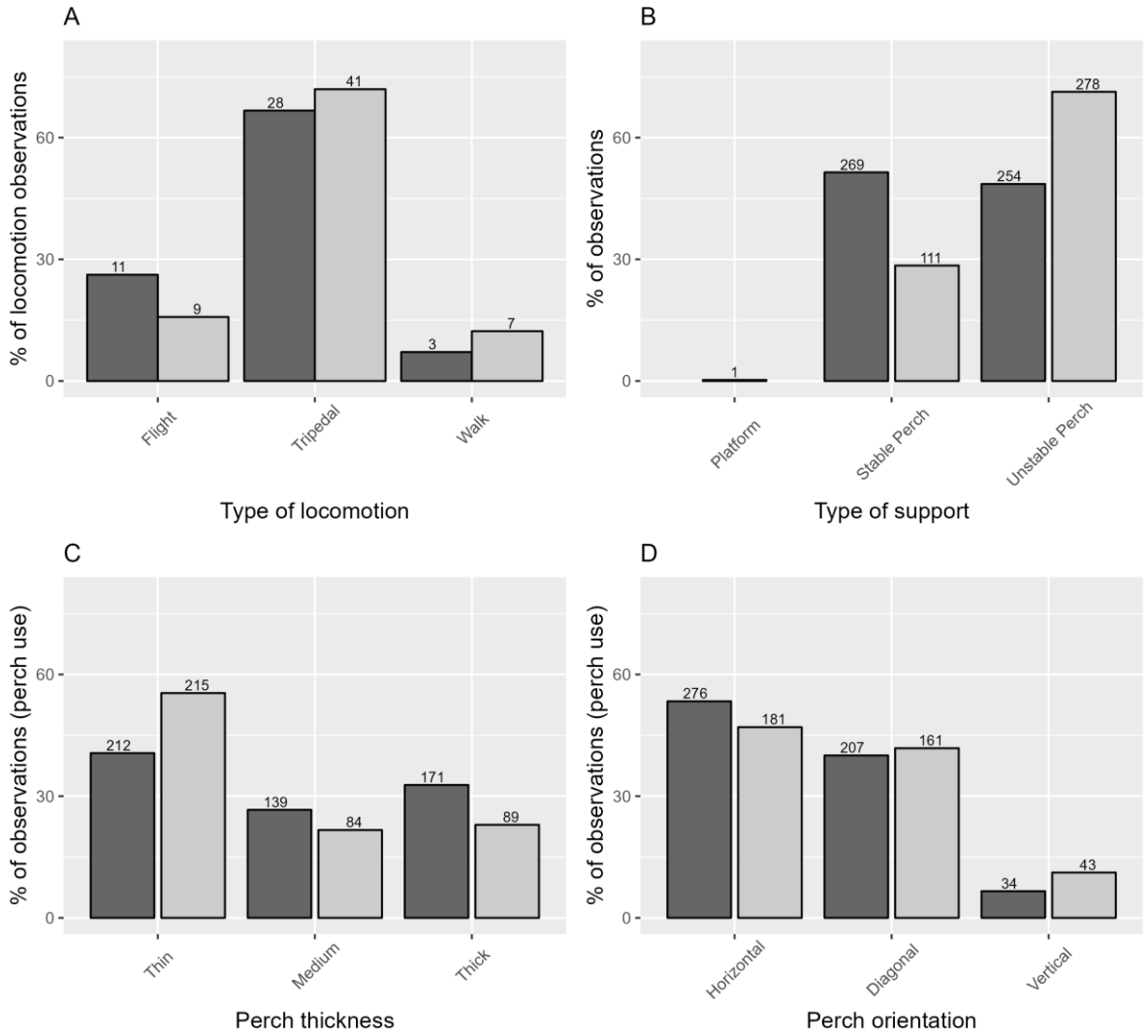


Figure 2.9. Locomotion and support use of free-living scarlet macaws observed in Costa Rica in February 2022.
Type of locomotion and the characteristics of supports used by the reintroduced scarlet macaws at Nicoya Peninsula (dark grey bars) and the wild scarlet macaws at Punta Leona (light grey bars). (A) Percentage of observations of each type of locomotion, (B) percentage of observations of each type of support used, (C) percentage of use of perches in each thickness category, and (D) percentage of use of perches in each orientation category. Numbers above bars represent number of observations.

Flying was infrequently recorded in the intervals (Figure 2.9A), and although the observer often noticed flying in both locations, with scarlet macaws covering long distances (at least as long as the degree of vision allowed), and often flying high in the sky, these observations were not recorded. Nicoya's scarlet macaws used stable and

unstable perches evenly, while scarlet macaws at PL were mostly seen on unstable perches (Figure 2.9B). The thickness of supports used was relatively homogeneous in the scarlet macaws at Nicoya, while the birds at PL used thin perches in most observations (Figure 2.9B). Support orientation was similar at both locations, with horizontal perches used in approximately half of the observations, while the use of diagonal perches was also relatively high at both locations (Figure 2.9C). The birds exhibited an apparent high confidence (i.e. with little visible hesitation) in climbing the diversity of supports in their environment and at PL, especially, they seemed to navigate the tree branches, including the more challenging thin, unstable and/or non-horizontal ones, with relative ease.

2.3.4. Social behaviour and proximity of free-living scarlet macaws in Costa Rica

The social behaviour observed at PL was almost entirely allopreening, but a higher diversity of social behaviours was recorded in Nicoya's scarlet macaws, even though allopreening was still the most common one (Figure 2.10A).

Only in 33% (Nicoya, n = 169) and 32% (PL, n = 119) of observations did the scarlet macaws have a conspecific within a wing length. With Nicoya's scarlet macaws, there were three instances (<1%) of more than one individual within wing length (Figure 2.10B), which was not observed at PL. The majority of observations showed at least one conspecific within 2 m of the focal bird, in both locations (Figure 2.10C).

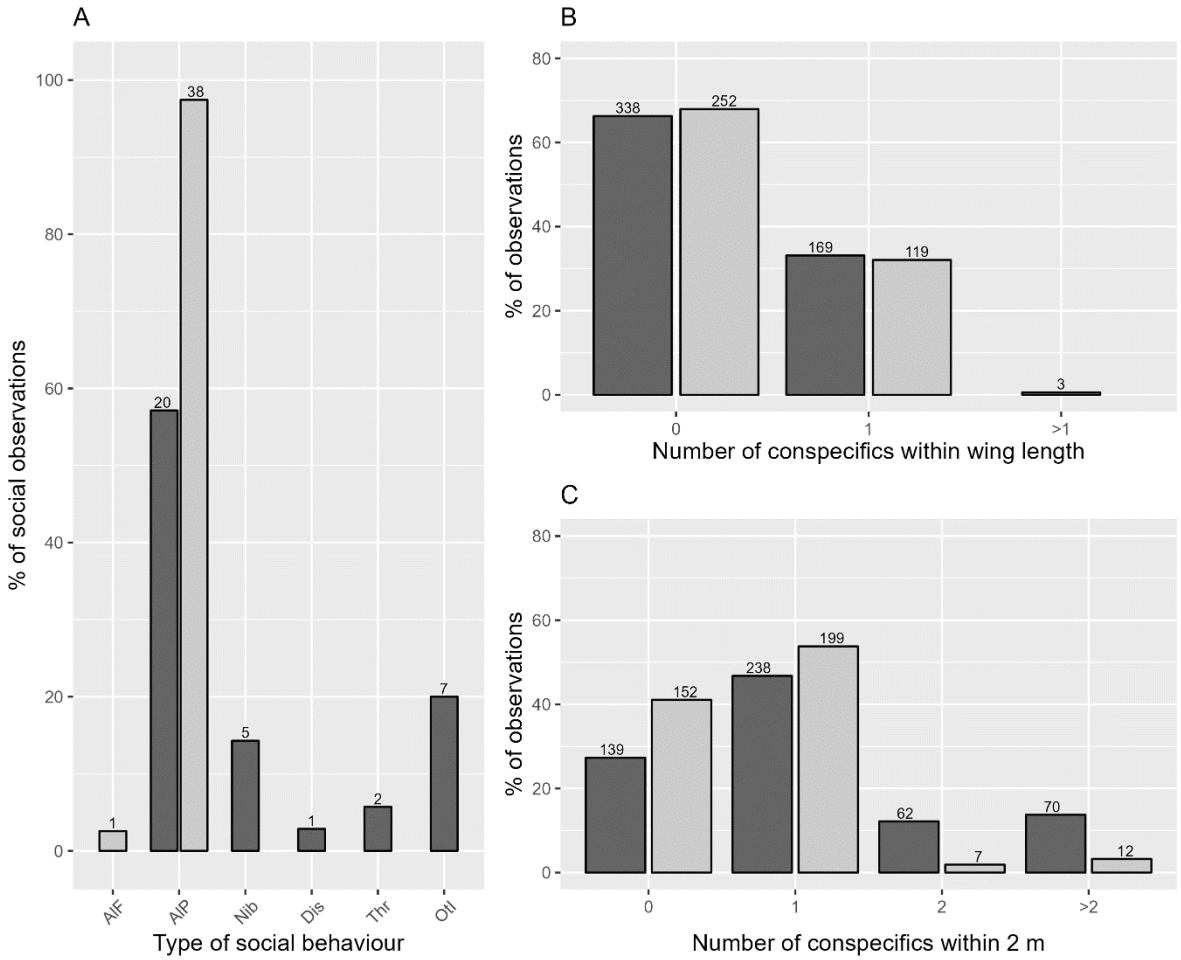


Figure 2.10. Social behaviour and proximity to conspecifics of free-living scarlet macaws observed in Costa Rica in February 2022.
Percentage of (A) each type of social interaction, (B) number of individuals within wing length of focal bird, and (C) number of individuals within 2 m of focal bird, observed on the reintroduced scarlet macaws at Nicoya Peninula (dark grey bars) and the wild scarlet macaws at Punta Leona (light grey bars). Numbers above bars represent number of observations. Types of social behaviour: AlF = Allofeeding; AlP = Allopreening; Nib = Nibbling; Dis = Displacement; Thr = Threatening; and OtI = Other Interactions.

2.4. Discussion

The results suggest the scarlet macaws at both locations were active in most observations. The scarlet macaws also exhibited a preference for heights, engagement in complex food manipulation (at PL), and use of high diversity of supports, while differences in group sizes were also detected between locations.

2.4.1. Inactivity, self-maintenance, and activity patterns of free-living scarlet macaws in Costa Rica

The scarlet macaws at both locations displayed active behaviours in most observations, but perching was the most common single behaviour observed. Perching consisted of resting or alert behaviour, both important behaviours for survival in the natural environment. While resting allows birds to reduce energy expenditure (Steiger et al., 2009) and avoid over-heating (Xie et al., 2017), alert behaviour or vigilance is beneficial for predator detection and avoidance (Beauchamp, 2010). The significantly higher proportion of perching observations at Nicoya could be a reflection of the facilitated access the scarlet macaws there had to food because of supplementary feeding, and/or due to them having been reared, and released from, captivity. Furthermore, self-maintenance, and mostly preening, was also frequently seen, which was expected, as it is an advantageous behaviour that allows birds to clean their feathers and skin, and remove parasites (Spruijt et al., 1992). It has been suggested that preening can be a comfort behaviour (Delius, 1988), and a response to stress (i.e. post-predator detection) in wild birds (Henson et al., 2012). There was no visible predator detection in the present study, and therefore its effects on preening behaviour cannot be confirmed. It is possible human disturbance influenced this behaviour, but there were no significant differences in self-maintenance between locations, despite the scarlet macaws at PL being more exposed to humans.

A bimodal diurnal pattern of activity has been reported across macaw species (*Ara* spp.) in the wild, with peaks of activity in early morning and late afternoon, and mostly resting and other low activity behaviours in the middle of the day (Gilardi and Munn,

1998; Pitter and Christiansen, 1995). Observations of low activity such as perching showed a similar pattern, with the highest proportion in the middle of the day. The increased proportion of high activity later in the day, especially at PL, also agrees with the activity patterns previously reported for free-living macaws (e.g. Gilardi and Munn, 1998; Pitter and Christiansen, 1995), although there were few differences between morning and middle of the day at both locations. As long-range movements were not recorded, it is possible the scarlet macaws' reduced flight activity in the middle of the day, but still remained active within the same area (e.g. activities within the same tree), which has been observed in grey-headed parrots (*Poicephalus fuscicollis*), on days with cooler temperatures (Symes and Perrin, 2003a). Patterns of self-maintenance and socialising (i.e. medium activity) indicate they were highest in the morning, and although these behaviours have been observed throughout the day in previous studies, they have also been observed before and in-between feeding bouts (Pitter and Christiansen, 1995; Symes and Perrin, 2003a).

The scarlet macaws were within the tree canopy in most observations, which concurs with the known arboreal habit of macaws (Bodmer et al., 2018; Brunon et al., 2014), which offers advantages such as lower risk of predation and disease (Shattuck and Williams, 2010). A preference for heights, also consistent with their arboreal habit, was clearly observed, as they most often stayed high in the trees, and at PL they were also often seen on the top of the canopy. They also fully avoided the ground and only on rare occasions were they below 10 m high. This preference for heights has been suggested in previous studies focussing on their diet, as they feed mostly from trees, in the canopy (Renton, 2006; Vaughan et al., 2006), and have also been observed

drinking water from hollows on the tree trunks (Renton, 2006), potentially reducing the need to descend to the ground to drink. Furthermore, their nesting requirements also support their preference to be high in their environment, as their natural nests have been previously found on trees that were on average 45 m high, with the nest cavities placed 26 m above ground, on average, and none found below 8.8 m (Olah et al., 2014).

2.4.2. Cognition: Feeding and manipulation of free-living macaws in Costa Rica.

The scarlet macaws at PL were seen feeding in over a quarter of observations, engaged mostly in complex manipulation and using their feet in almost half of the feeding observations. However, they were seen feeding on only three tree species, a small sample of the species that have been previously reported to be part of the diet of scarlet macaws in Costa Rica (e.g. 43; Vaughan et al., 2006). No other potential food sources for the macaws were observed in the locations used for observations, which was also confirmed by the local ecologists working with the species in the area (R. Taylor, pers comm., 2023). The small number of tree species the scarlet macaws were observed foraging on could have been due to a combination of season variations in food availability in the area (Vaughan et al., 2006) and the present study's limited number and diversity of locations to conduct behavioural observations. Nevertheless, the scarlet macaws showed a diversity of foraging behaviours within and across those three plant species. They had to adapt their locomotion, position on the branches, and/or use their bills and feet to reach and manipulate the different sized and shaped fruits and seeds. This behavioural flexibility influenced by the diversity of food sources

in the environment has been previously highlighted across macaw species. For example, Nemeth and Vaughan (2004) reported a pair of adult scarlet macaws, also in Costa Rica, removing hanging palm nuts (*Scheelea rostrata*) mid-air and taking them to nearby perches for consumption, while their offspring, two juveniles, were feeding from a nearby tree, presumably not yet able to feed from the more difficult to reach palm nuts. Blue-and-yellow macaws (*Ara ararauna*) were also seen feeding on unripe slash pinecones (*Pinus elliottii*) in an urban area in Brazil, an exotic species that they adapted to feed from in a human-dominated environment (Silva, 2018), while green-winged macaws in Venezuela had to use their feet and bills to open the hard nuts of multiple tree species (Norconk et al., 1997).

The scarlet macaws at Nicoya were mostly seen feeding from the artificial feeders, and although some of the food items provided required more complex manipulation (e.g. corn cob), the tray set-up likely facilitated direct consumption, with less need for foraging-related behaviours such as searching for food and manipulation. This facilitated access to food could explain why the proportion of feeding observations was significantly lower for the scarlet macaws at Nicoya than PL, as it has been previously suggested that parrots adapt their foraging strategies according to food availability (Renton et al., 2015). Supplementary feeding is an important factor in the success of parrot reintroduction programmes (White et al., 2012), and released parrots have been found to rely less on it as they start dispersing and consuming wild foods (Lopes et al., 2018; Sanz & Grajal, 2008). In the present study, no conclusions can be made on the dispersal rates or wild-type foraging skills of the released scarlet macaws at Nicoya, as they were not individually tracked. Furthermore, despite confirmation from local staff

that released macaws were seen feeding on wild foods (M. Gonzaléz, pers comm., 2022), this was very rarely observed in the present study, likely because observations were limited to the release site and surrounding areas, and therefore biased towards the individuals that were still reliant on the artificial feeders.

2.4.3. Locomotion and support use of free-living scarlet macaws in Costa Rica

The significantly lower proportion of locomotion detected in the Nicoya's scarlet macaws could have also been related to the easier access to food (i.e. reduced need to move within the trees searching for food) or deficient locomotion skills in comparison to their wild-hatched counterparts, as previously reported for other species (e.g. golden-lion tamarins [*Leontopithecus rosalia*]; Stoinski et al., 2003). The scarlet macaws at both locations mostly climbed while moving around the tree canopy. Parrots are proficient climbers, using several body parts (e.g. bill, feet, tail) to achieve balance and push and pull themselves across branches and other supports (Reader et al., 2022). Their climbing proficiency was also detected in the variety of supports they used, with the scarlet macaws at both locations using unstable, thin, and non-horizontal perches in relatively high proportions, which are more challenging to move and hold on to while perching. No quantification of support characteristics used by free-living parrots has been found in the literature, and therefore this may be the first. However, as scarlet macaws in the wild forage on several parts of multiple tree species (Renton, 2006; Vaughan et al., 2006), it can be assumed they have to navigate frequently the challenging heterogeneity of tree structures to reach their food. Furthermore, their climbing abilities, and the challenging supports they use, are also highlighted by how they can hold on to and climb up vertical clay licks for geophagy

(i.e. voluntary soil ingestion, Brightsmith et al., 2018), which offer few opportunities for support grasping (Reader et al., 2022)

The heterogeneity and complexity of supports they have to navigate may also explain the low frequencies of walking observed. Even when moving horizontally, parrots often use their bills (and therefore tripedal locomotion/climbing) together with their feet for balance (Reader et al., 2022), if the supports they are on are not stable under their weight. The low percentage of flights in the time budget, however, is most likely an underestimation resulting from the sampling method, as (1) only visible individuals in each interval were sampled, and flying individuals often moved out of sight, and (2) short flights within trees or between neighbouring trees were often quick events and not captured in the intervals. Furthermore, frequent flights were noticed in qualitative observations, some covering long distances high in the sky, which concurs with previous observations of free-living scarlet macaws covering long daily distances by flight (Brightsmith et al., 2021).´

2.4.4. Group size, social behaviour, and proximity of free-living scarlet macaws in Costa Rica

The reintroduced population at Nicoya had bigger observable group sizes for random individual selection than in PL, and more often showed higher numbers of individuals within 2 m of the focal bird in the proximity scans. These results were likely influenced by several factors. First, most of the observations at Nicoya were at or relatively close to the supplementary feeding site, where the released macaws gathered for feeding,

and therefore bigger groups were to be expected. Furthermore, as the macaws at Nicoya were captive-bred, and no older than seven years old, they likely showed lower dispersal than their wild-hatched counterparts at PL, and stayed around the release area with their conspecifics. Post-monitoring data from two other parrot reintroduction programmes showed the captive-bred individuals, and especially the younger ones, showed varied dispersal rates but generally stayed within the release area (Lopes et al., 2018; Sanz & Grajal, 2008). Furthermore, unlike the released parrots in both these studies, that had the opportunity to flock with wild-hatched conspecifics and likely benefitted from social learning of wild-type behaviours and skills (Lopes et al., 2018; Sanz & Grajal, 2008), the scarlet macaws at Nicoya were reintroduced into an area without a local wild population. As social learning plays a key role in the behavioural development of scarlet macaws (Myers & Vaughan, 2004), the released individuals at Nicoya may therefore take longer to develop the necessary skills before dispersing further into the wild.

Scarlet macaws at PL were more often observed in pairs, although there were also observations of single individuals and small groups. These data agree with previous studies on wild scarlet macaws, suggesting they sometimes flock in large numbers (McReynolds, 2012), but more often travel in pairs or small family units (Gilardi & Munn, 1998). Social behaviour was observed in a relatively low percentage of intervals, and within-wing length proximity had similar proportions in both locations. Although allopreening was the more common social behaviour in both populations, at Nicoya several other interactions were also observed. As mentioned before, the population at Nicoya was young, and likely engaged in social play, as previously reported in this

species (Myers & Vaughan, 2004). No breeding had yet been confirmed among the scarlet macaws at Nicoya, but the records of allopreening, which serves both hygienic and social purposes (Morales Picard et al., 2020), plus qualitative observations suggest pair bonding has occurred within that population. At PL, pair bonding was shown by allopreening and further confirmed by ongoing breeding, as chicks of various ages in both natural and artificial nest boxes were confirmed (R. Taylor, pers comm., 2022).

2.4.5. Limitations of study

As a result of time constraints, the behavioural observations were conducted in a short period of time and in a low number of locations, which did not reflect the species' wide geographic distribution across Central and South America (section 1.6). Therefore, this study does not account for potential differences in behaviour across seasons (e.g. breeding vs non-breeding season; seasonality in food availability) and populations. Within both locations, only certain areas could be accessed for data collection, which likely biased observations towards certain individuals and behaviours. Furthermore, the macaws at both locations were exposed to high levels of human disturbance, which could have affected their behaviour. The locations of this study also differed in type of habitat, which potentially confounded differences in behaviour between the wild-hatched macaws at PL and the captive-hatched macaws at Nicoya.

Therefore, further studies should assess the behaviour of free-living scarlet macaws throughout their geographic distribution and across seasons. More behavioural data

from both wild-hatched and captive-bred birds across habitats would also help in understanding how reintroduced macaws adapt to their new environment over time.

2.5. Conclusion

Despite the limitations of this study, it provides new insights into the behavioural ecology of free-living scarlet macaws, including, to the best of my knowledge, the first quantitative descriptions of foot use in manipulation and support characteristics. The overall findings suggest that the free-living scarlet macaws in our study: (1) were generally active, varying their activity levels throughout the day; (2) preferred to stay high in the tree canopy and avoided descending to the ground or close to it; (3) showed complex feeding behaviours, adapting to varied food items with different foraging strategies, including foot use; (4) navigated and perched on a high diversity of supports, and used challenging (i.e. unstable, thin and non-horizontal) structures at least as often; and (5) were more often seen alone, in pairs or small groups in the natural population at PL, and bigger groups in the reintroduced population at Nicoya.

This study was planned and conducted with the primary goal of generating evidence to inform *ex situ* management and husbandry. Data from free-living parrots can be used for behavioural comparisons with captive counterparts to understand better which behaviours naturally occur in the species and which behaviours are a result of the captive environment. Furthermore, by understanding how free-living macaws interact with their environment, we can determine what features of the natural habitat need to be replicated in *ex situ* enclosures to enable wild-type behaviours. These data were

used to compare with, and understand better, the behavioural repertoire of the captive scarlet macaws included in the present thesis (Chapters 3 and 4), supplementing the limited previous research on the behavioural ecology of the species in the wild. Both Chapters 3 and 4 consist of behavioural assessments of the same zoo-housed scarlet macaws and grey parrots, before and after alterations to their environment (modifications to their enclosures and changes to their social environment). While Chapter 3 focusses on the activity budgets and enclosure use of those parrots, Chapter 4 is focussed on their cognition, locomotion, and social behaviours. This vast amount of detailed data would result in a large chapter, if combined into one, which would be an increased challenge when presenting, interpreting, and summarising the results. A large chapter would also be more difficult to prepare for submission to a scientific journal. Therefore, the behavioural data from the captive grey parrots and scarlet macaws are presented across Chapters 3 and 4.

CHAPTER 3

THE EFFECTS OF ALTERATIONS IN THE ENCLOSURE AND SOCIAL STRUCTURE ON THE ACTIVITY BUDGETS AND ENCLOSURE USE OF ZOO-HOUSED GREY PARROTS AND SCARLET MACAWS

Paper planned for publication:

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[1]Collected and analysed all data.

ABSTRACT

Assessing the proportion of time that captive animals spend on different behaviours (i.e. activity or time budgets), and how they use the available space within their enclosure, can help to evaluate their welfare and inform *ex situ* management. The activity budgets and enclosure use of two groups of grey parrots and eight individual scarlet macaws (a group of five and a group of three birds) in two zoos were assessed, with the aim of investigating the effects of enclosure modifications and changes to the social environment on the behaviour of the parrots. Behavioural data were collected across two periods of observations (baseline and post-modification, before and after the changes in the parrots' environment, respectively), using focal interval sampling. Baseline behavioural observations revealed marked differences from their wild counterparts, including overall high inactivity, with low engagement in behaviours such as feeding and locomotion, a heterogeneous horizontal use of the enclosure, and a high proportion of time spent on the ground. Enclosure modifications were applied to target those behaviours, including an increase in, and re-organisation of, structural complexity within the enclosures, and new suspended feeders that partially hid the food from the parrots. Changes in the social structure of all parrots, with the addition and/or loss of birds, also occurred between periods of observations. Post-modification observations revealed some parrots showed significant decreases in inactivity and significant increases in feeding, locomotion and/or object manipulation, while some parrots also showed a more even use of the different horizontal sections of the enclosure. Furthermore, all parrots showed a higher use of the top section of the enclosure, suggesting they benefitted from increased opportunities to be as high within their environment as possible, which agrees with the behaviour of their wild

counterparts. Despite intra- and inter-specific variation in behavioural responses, most parrots exhibited changes in their activity budgets and enclosure use in the post-modification period of observations, which could have been a response to the physical and/or social alterations in their environment.

Keywords: *ex situ*, Psittaciformes, space use, time budgets

3.1. Introduction

Activity or time budgets (i.e. the proportion of time animals dedicate to each activity in their behavioural repertoire), are a widely used tool in fundamental and applied research on animals, in both their natural environment (e.g. Christiansen et al., 2013; Hickey & Titman, 1983) and in captivity (e.g. Horback et al., 2014; Mallapur & Chellam, 2002). Time budgets are also a proxy for how animals invest their energy (Brown et al., 2022). As resources are limited in the natural environment, trade-offs in energy investment are necessary for *in situ* animals, which is not an issue for their captive counterparts that are usually not limited by low resource availability (Ricklefs & Cadena, 2007). Determining the activity budgets of captive animals provides information on their behavioural repertoire and diversity, a welfare indicator (Mellor, 2016), and how they cope and interact with their environment and/or respond to changes in it, including enclosure moves (Finch et al., 2022), husbandry changes (James et al., 2021), enrichment (Schneider et al., 2014) and visitor effects (Podturkin, 2022). Comparing the time budgets of captive animals with those of their wild counterparts provides guidelines on which behaviours are normal for the species (i.e. part of the behavioural repertoire they evolved in their natural environment), and which

ones are missing or underrepresented in captivity. However, it has been suggested their use in welfare assessments has limitations, and should be used in integration with other indicators (Howell & Cheyne, 2019; Veasey et al., 1996). From a conservation perspective, time budgets can also help in evaluating and refining research methods and technology with applications to both *in situ* and *ex situ* research and conservation (Simeone et al., 2002).

It can be challenging to determine in detail the activity budgets of free-living animals, as some species are particularly difficult to follow and observe in their natural habitat (Christiansen et al., 2013). Parrots, being highly mobile and living in complex environments, are difficult to follow over large distances. Technology such as GPS tagging has been proven useful in determining movements and budgets of free-living parrots (Yeap et al., 2021), but the available literature with quantitative data is currently limited and shows high variability in the methodologies used (Berg et al., 2007; Pinho & Nogueira, 2003; Pitter & Christiansen, 1997). When data on the target species are missing, an alternative is to use data from closely related taxa for comparison, when possible. Closely related species are more likely to share ecological traits (Burns & Strauss, 2011), even though they can also diverge behaviourally (Mettke-Hofmann et al., 2012) and therefore this approach has limitations which must be taken into consideration.

The *Poicephalus* genus, comprising parrot species from the African region, is a sister taxon to *Psittacus* (Mayr, 2010). Like grey parrots, *Poicephalus* parrots are mostly

found in forest and savannah habitats across sub-Saharan Africa (IUCN Red List, 2023). The overlap in geographic distribution and habitat, and the close genetic relatedness between *Poicephalus* parrots and the grey parrots makes this taxon a suitable choice for *in situ–ex situ* behavioural and ecological comparisons. Macaw species within the subfamily Arinae, tribe Arini, are also closely related (Joseph et al., 2012) and a reasonable alternative for comparisons among each other (Figure 3.1). Species within this taxon share a Neotropical distribution and the use of forest habitat, although some species have wider distributions and can also be found in savannahs and grasslands (Table 1.1)

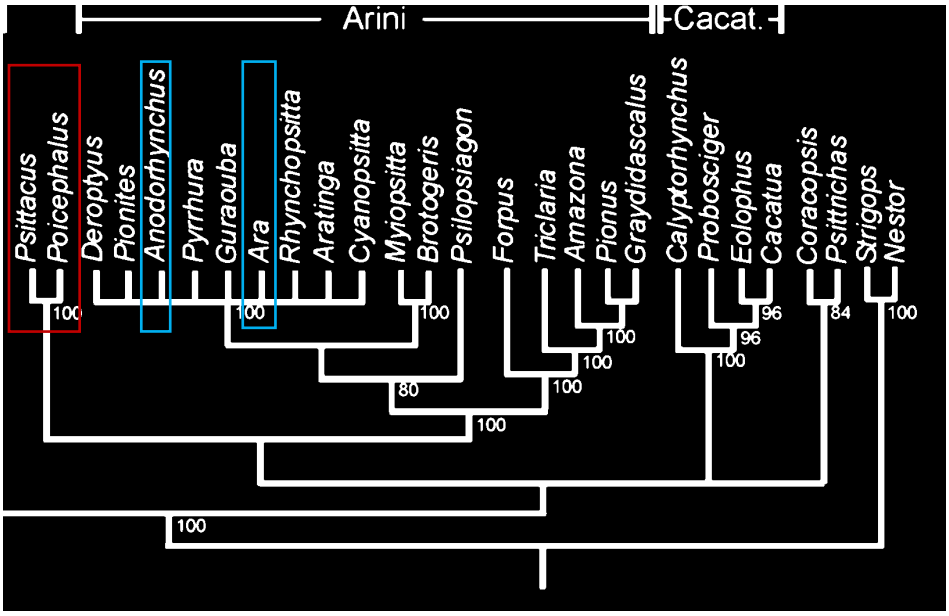


Figure 3.1. Section of the molecular phylogeny of parrots.
The red and blue shapes highlight the genera of the parrots included in the present study (grey parrots (*Psittacus*) and scarlet macaws (*Ara)*, respectively) and the corresponding related taxa that were considered for the behavioural comparisons (*Poicephalus* spp. for comparisons with the grey parrots; other *Ara* spp. and *Anodorhynchus* spp. for comparisons with the scarlet macaws). Adapted from Mayr (2010).

Another useful, and widely applied, tool in behaviour and welfare assessments is the evaluation of enclosure/space use (Brereton, 2020a). It provides information on the suitability of those enclosures to the animals and species they house (Ross et al.,

2009) and how the animals respond to physical and social modifications within them (Brereton, 2020a). In the wild, parrots must travel between sites with different features and challenges for various activities, such as foraging (Matuzak et al., 2008), roosting (Warburton and Perrin, 2005a), nesting/breeding (Warburton and Perrin, 2005b), and geophagy (Downs et al., 2019). This level of environmental complexity and diversity is virtually impossible to achieve in captivity, especially in traditional enclosures, which are typically non-naturalistic spaces with severe spatial constraints. However, improving the available space, and providing areas for varied behavioural expression, can enhance the use of the enclosure, as observed in other captive species whose wild counterparts also live in complex environments (e.g. elasmobranch [Chondrichthyes] and teleost fish [*Osteichthye*]; Lawrence et al., 2021); and lion-tailed macaques [*Macaca Silenus*]; Mallapur et al., 2005). Free-living grey parrots and scarlet macaws also exhibit a preference for height, as they mostly forage in the tree canopy (Nemeth & Vaughan, 2004; Tamungang & Ajayi, 2003), and nest high in trees (mean nest height: 22.1m and 26.6 m for grey parrots [Simon et al., 2016] and scarlet macaws [Olah et al., 2014], respectively), where they are safer from predators. It is logistically challenging to provide such heights for parrots in captivity, but increasing vertical complexity in the environment can give captive animals the choice to be as high as possible within the available space. For example, captive rhesus monkeys (*Macaca mulatta*), an arboreal species in the wild, spent most of their time higher up in the enclosure when provided with increased vertical complexity (Clarence et al., 2006).

Visitors are a prominent feature of the environment of zoo-housed animals and can positive or negatively influence their welfare (Sherwen & Hemsworth, 2019). Even

though visitor effects on zoo animals have been investigated in multiple studies, these have been mostly focussed on mammals, especially primates (Rose et al., 2019; Sherwen & Hemsworth, 2019). The available literature on these effects on avian taxa reveals high variability in responses to visitors across individuals and species (e.g. Blanchett et al., 2020; Dowes, 2012; Sherwen et al., 2015), and within parrot taxa, specifically, both negative and positive responses to visitors have been observed in citron-crested (*Cacatua sulphurea citrinocristata*) and Moluccan cockatoos (*Cacatua moluccensi*; Collins & Marples, 2015), and red-and-green macaws, military macaws (*Ara militaris*), and blue-and-yellow macaws (Frost et al., 2022).

The present study aims to (1) assess the time budgets and space use of scarlet macaws, grey parrots and other macaw species at two zoos, (2) evaluate the impact of enclosure modifications on time budgets and space use, and (3) assess potential visitor effects on the target parrots at one of the zoos where data was available from days the zoo was open and closed to visitors.

3.2. Materials and methods

3.2.1. Location, species and individual information of captive parrots included in the study

This study took place at two zoological parks: Drayton Manor Park and Zoo (Tamworth, West Midlands, United Kingdom), and Jurong Bird Park (part of Mandai Wildlife Group, Singapore), which will hereafter be referred to as zoo A and zoo B. This study was approved by the University of Birmingham's Science, Technology, Engineering and

Mathematics (STEM) ethics committee (code: ERN_19-0974) and the animal management teams of both zoos.

Included in this study were two groups of zoo-housed African grey parrots (zoo A: 7.9.0 [number of males, females and juveniles]; zoo B: 4.3.1), eight individual scarlet macaws (zoo A: 1.1.1; zoo B: 1.4.0), and a multi-species macaw group (zoo B; great green macaw: 0.0.3; green-winged macaw: 2.0.0; red-fronted macaw: 0.2.3; hyacinth macaw: 0.1.1; Table 3.1).

Table 3.1. **Summary of species, individual parrots or groups at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) on which data were collected for this study.**
For each individual parrot or group, it is stated whether they were bred in captivity or hatched in the wild (i.e. their origin) and, if the former, whether they were reared by their parents (PR) or hand-reared by humans (HR), with "Unk" if that information was not known. The year each individual parrot hatched is stated, and whether they were included (√) or not (×) in each period of observations (baseline and post-modification: before and after modifications were applied to the enclosure). For groups, the number of parrots and group composition (number of males, females, juveniles) in each period of observations is provided. "Scarlet macaw group" in data collection and analysis consisted of the three juveniles added in the post-modification period plus scarlet macaws 1, 2 and 3.

Species	Zoo	Individual	Origin (Rearing)	Sex	Birth	Baseline	Post-Modification
Scarlet macaw (*Ara macao*)	A	Male scarlet macaw	Captive (Unk)	♂	1999	√	√
	A	Female scarlet macaw	Captive (Unk)	♀	1995	√	×
	A	Juvenile scarlet macaw	Captive (PR)	♂	2020	√	√
	B	Scarlet macaw 1	Unk	♀	2001	√	√
	B	Scarlet macaw 2	Unk	♂	2001	√	√
	B	Scarlet macaw 3	Captive (Unk)	♀	1992	√	√
	B	Scarlet macaw 4	Captive (HR)	♀	2010	√	×

Species	Zoo	Individual	Origin (Rearing)	Sex	Birth	Baseline	Post-Modification
	B	Scarlet macaw 5	Captive (HR)	♀	2008	√	×
	B	Scarlet macaw group*	Captive (HR)	1♂ 2♀	2021	×	3 (0.0.3)
Grey parrot (*Psittacus erithacus*)	A	Grey parrot group A	Wild	7♂ 9♀	2012-2014	16 (7.9.0)	11 (6.5.0)
	B	Grey parrot group B	Unk = 6 Captive (PR = 1) (HR = 1)	5♂ 3♀	2005 (6) 2009 (1) 2020 (1)	7 (4.3.0)	8 (4.3.1)
Green-winged macaw (*A. chloropterus*)	B	Green-winged macaw pair	Captive (HR)	2♂	1999 2007	×	2 (2.0.0)
Great green macaw (*A. ambiguus*)	B	Great green macaw group	Captive (Unk)	1♂ 2♀	2021	×	3 (0.0.3)
Red-fronted macaw (*A. rubrogenys*)	B	Red-fronted macaw group	Captive (HR = 3) (Unk = 2)	1♂ 4♀	2010 (1) 2011 (1) 2020 (2) 2021 (1)	×	5 (0.2.3)
Hyacinth macaw (*Anodorhynchus hyacinthinus)*	B	Hyacinth macaw pair	Captive (HR = 1) (Unk = 1)	2♀	2010 2020	×	2 (0.1.1)

3.2.2. Methods for behavioural data collection on captive grey parrots and macaws

This study consisted of two periods of behavioural data collection: baseline and post-modification periods (before and after changes to the enclosure and social environment of the parrots, respectively). Similar to the data collection on the free-living scarlet macaws (section 2.2.2), three protocols were used: cognition, locomotion

and social. All featured broad behaviours, enclosure use and specific data relative to each protocol. The ZooMonitor mobile application (Ross et al., 2016) was used for data collection. The enclosure was divided into four horizontal sections of equal size (relative to the longest side of the enclosure), and three vertical sections (the top quarter section of the enclosure, the ground, including soil and concrete, and middle section as all space in between). Both the grey parrots and scarlet macaws at zoo A also had access to an extra indoor area of smaller dimensions than each of the four sections in the outdoor enclosure, but they were not recorded using it. An extra horizontal section was added for post-modification data collection on the grey parrot group at zoo B, to reflect the extra length of the new enclosure.

It was determined during the pilot study (Appendix 1) that focal interval sampling would be used for the birds that were identifiable (i.e. scarlet macaws at zoo A plus the adult scarlet macaws at zoo B, based on their wing patterns and/or marks on their bills). The grey parrot groups at both zoos and the macaw group added to the study in the post-modification phase were sampled as a group in each session, with focal sampling of a randomly selected bird in each interval. Data on all captive grey parrots and macaws were collected every 30 seconds in 30-minute sessions per protocol and individual/group. The weather conditions (cloudy, partially cloudy, clear/rain, sunny) and average temperature (determined from Apple iPhone's weather mobile application; Apple Inc., 2019) were also recorded at the start of each 30-minute session. During the pilot study, this interval was found to be the shortest-possible interval that allowed me to (1) collect detailed data, (2) find the focal bird when its location was temporarily lost between intervals, and (3) randomly select a bird in each

interval during group sampling (Appendix 1). When sampling the macaw group added in the post-modification period of observations, all macaws in the enclosure were sampled together, with random selection of a bird for sampling in each interval (the species of the macaw sampled in each interval was recorded). The three juvenile scarlet macaws at zoo B were grouped with the three adult scarlet macaws that were also sampled individually (scarlet macaws 1, 2 and 3), as the 30-second intervals for sampling did not allow for accurate individual identification in group sampling. Therefore “Scarlet macaw group” refers to all the scarlet macaws in that enclosure during the post-modification period of observations (n = 6). Sessions were rotated throughout the day, so every individual/group and protocol were sampled at different times between 9:00 hrs and 16:00 hrs (local times; zoo A: Greenwich Mean Time [GMT]; zoo B: Singapore Standard Time [SST]). This was the period of time the observer was allowed to access the zoo premises, according to the management at each zoo. Each individual or group was sampled a maximum of once per day per protocol. The ethograms used were previously described in section 2.2.4 (Tables 2.1–2.6).

3.2.2.1. Method for random selection of birds during group sampling of captive parrots

Group sampling on the captive animals was performed by selecting a random individual in each interval, based on their relative position within the enclosure and using a pre-defined list of random numbers generated using the Microsoft Excel (function “RANDBETWEEN”). This method was developed in the pilot study to allow for detailed data to be collected during group sampling, which was not possible if

multiple birds were sampled in the same interval (Appendix 1). Several lists were created, each featuring two columns of 60 random numbers (number of intervals in a session), one with numbers between one and half the number of individuals to be sampled in the enclosure and another one with numbers between one and the total number of individuals (Figure 2.3A). Enclosures were divided in half along the longest side, and random selection of individuals for sampling in each interval was carried out alternately between sections (using "<1/2" column if up to half of the group was in that section or ">1/2" if over half of the group was there; Figure 3.2).

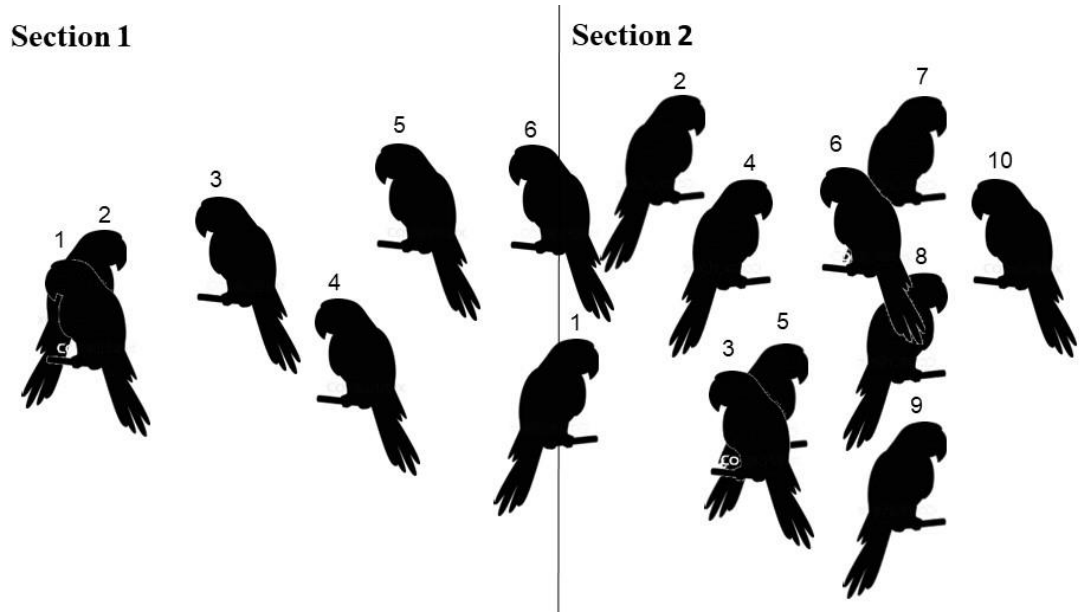


Figure 3.2. Schematic representation of how the position of each parrot in each section of the enclosure was determined for random individual selection during group sampling.
Sections 1 and 2 represent each half of the enclosure (left and right side, respectively), while the numbers above the parrots show their position in relation to other birds (considering the positions of their heads) within each section of the enclosure.

To avoid oversampling of some individuals, a section was only sampled when at least a quarter of all individuals in the group was within it. Otherwise, the alternative section

containing over three quarters of the individuals was sampled again. The relative position of the individuals within a section was used for individual selection, by counting heads left to right (e.g. random number “3” for an interval on the list, third individual from left to right on the respective section is selected for sampling in that interval). When two individuals were in the same horizontal position, then the one higher up was counted first (Figure 3.2).

When the number in the selected column was higher than the number of individuals in that section, the number in the other column was used instead. When the numbers in both columns were higher than the number of individuals in that section, then the individual furthest to the right in that section was selected. For example, if there were four individuals in the section to be sampled, and the selected column in the list of numbers, either “<1/2” or “>1/2” (section 2.2.3; Figure 2.3A), showed number “6” for that interval while the other column showed number “3”, then the third individual was sampled. However, if the other column also showed a number higher than four, then the fourth individual (which was furthest to the right in this example) was sampled.

3.2.3. Baseline period of observations of captive parrots

Baseline observations occurred between October and December 2019 (for the grey parrot group at zoo A), January and March 2020 (for all parrots at zoo B), and October and December 2020 (for the scarlet macaws at zoo A).

3.2.3.1. Scarlet macaws: housing conditions in baseline period of observations

The scarlet macaws at zoo A were housed in an enclosure comprising an outdoor (length 1440 cm × depth 540 cm × height 420 cm) and an indoor area (270 cm × 250 cm × 230 cm; Figures 3.3A and 3.3B).



Figure 3.3. Scarlet macaw enclosures at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline period of observations (before alterations to the enclosure and social environment of the parrots).
(A-B) zoo A (different views of the same enclosure, photo taken in October 2020); and (C, D) zoo B (different views of the same enclosure; January 2020). Photos: RLF.

Grey parrots and umbrella cockatoos (*Cacatua alba*) were housed in adjacent enclosures, separated by mesh but allowing close visual contact. Tree branches (mostly thick and medium, with thin branches scarcely present; thickness as defined in section 2.2.4; Table 2.5) and manila rope (24 mm diameter) were provided as supports in the outdoor area, spread over a small area of the enclosure (mostly in the left and right areas of the enclosures, Figures 3.3A and 3.3B). Other features of the enclosure included a 2 m-long log (placed in the middle of the enclosure, Figure 3.3A) and a 1.5 m-high bushy plant (Figure 3.3B). Pebbles were the substrate in most of the enclosure, except for the back left corner and the right side, which had soil instead (Figures 3.3A and 3.3B). Food was provided in metal trays, placed on a stable wooden platform raised approximately 1 m from the ground. Water was provided in an artificial pond in the middle right of the enclosure. Food was provided once a day, in the morning, between 9:00 hrs and 12:00 hrs (GMT). Enrichment was provided irregularly: weekly or bi-weekly, and consisted of hard nuts, seeds hidden in toilet roll tubes and cardboard boxes with treats such as seeds, nuts and fruit (e.g. grapes).

At zoo B, the scarlet macaws were housed in an outdoor-only enclosure (1,200 cm × 250 cm × 480 cm), with several small to large parrot species in adjacent enclosures (separated by mesh but allowing close visual contact). Stable tree branches and manilla rope of medium to high thickness (as defined in section 2.2.4; Table 2.5) were spread across several sections of the enclosure but rarely extending to the top ¼ of the enclosure. Understory vegetation was abundant, with heights up to half of that of the enclosure (Figures 3.3C and 3.3D). Substrate was soil in most of the enclosure,

except for a corridor of concrete at the back, near the entrance, which the birds had access to but was mostly used for husbandry purposes by the animal keepers. Both food and water were provided in metal trays, placed on the ground in the middle of the enclosure. Macaws were fed twice a day with pellets (Nutribird P15; NV Versele-Laga, Belgium), vegetables and fruit in the morning and seeds and nuts in the afternoon. Enrichment was provided weekly or bi-weekly and consisted of cardboard boxes filled with leaves and large nuts.

3.2.3.2. Grey parrots: housing conditions in baseline period of observations

The grey parrots' enclosure at zoo A also featured an outdoor (1,440 cm × 540 cm × 420 cm) and an indoor area (270 cm × 250 cm× 230 cm). Adjacent to their enclosure, visually accessible but separated by mesh, were the scarlet macaws and Moluccan cockatoos (*Cacatua moluccensis*). The food was provided on two metal trays attached to the back mesh in the middle of the enclosure. Water was provided in a pond on the right side of the enclosure. Suspended branches were provided on the back left corner and on the right of the enclosure. Undergrowth vegetation was abundant, particularly at the front left and middle of the enclosure, up to approximately 75% of the height of the enclosure (Figures 3.4A and 3.4B). Zoo B's grey parrot enclosure was an outdoor-only space (length 1,180 cm × depth 260 cm × height 400 cm). Tree branches and manilla rope were provided as support along the length of the enclosure but were up to approximately 50% of the height of the enclosure (Figure 3.4C). Soil was the substrate in most of the enclosure, except in the concrete corridor at the back, which the birds had access to but was mostly for keeper use.

A



B



C



Figure 3.4. Grey parrot enclosures at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline period of observations (before alterations to the enclosure and social environment of the parrots).
Enclosure at (A-B) zoo A (different views of same enclosure; photo taken in October 2019) and (C) zoo B (January 2020). Photos: RLF.

3.2.4. Behavioural assessments of captive parrots before the enclosure modifications

The behavioural data collected in the baseline period of observations were compared with available data from free-living parrots, which were found in the literature and in the study on the free-living scarlet macaws in Costa Rica (Chapter 2). These behavioural comparisons between the free-living and the captive parrots were used to determine what natural behaviours were rarely or never exhibited by the captive birds.

Modifications to the enclosures of each species at both zoos were then proposed (Figure 3.5 and Table 3.2) with the aim of enabling those natural behaviours by replicating features of each species' natural environment.

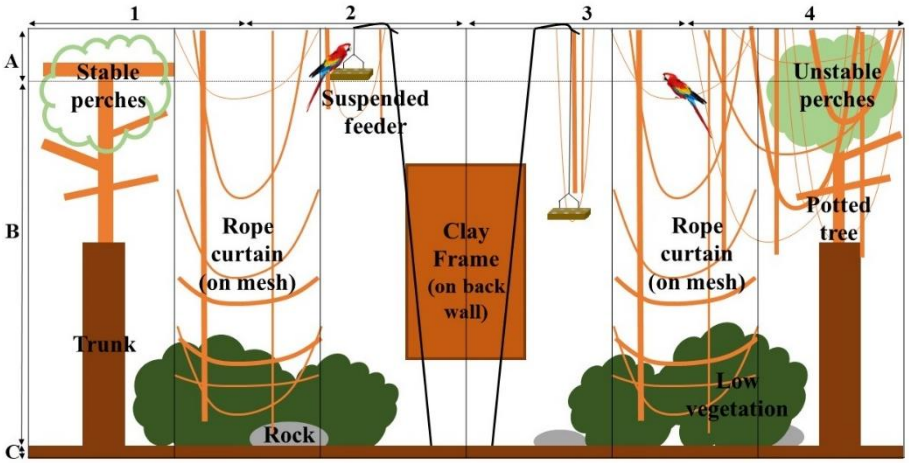


Figure 3.5. Schematic representation of modifications proposed for the scarlet macaw enclosures at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore).
The letters represent the vertical sections of the enclosure (A = Top quarter, B = Middle section, C = Ground). The numbers (1 – 4) represent the horizontal sections (from left to right) of equal size of the enclosure.

Table 3.2. Summary of modifications proposed for the enclosures of the grey parrots and scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) and whether they were implemented by each zoo.
The implementation of the proposed modifications is stated for each enclosure (grey parrots: GP; scarlet macaws: SM) at each zoo, while "x" means that proposed modification was not implemented in either of the enclosures in that zoo.

Enclosure modifications proposed	Zoo A	Zoo B
Create distinct areas within the enclosure: • Each corner: structurally complex area, with network of perches of varied stability, orientation, and thickness. • Top of the enclosure: ensure top half of the enclosure, and areas close to the mesh (top and sides) were also filled with supports. • Middle areas: provide clear space.	GP SM	GP SM

Enclosure modifications proposed	Zoo A	Zoo B
Provide suspended feeders: • Wooden box with holes on top, metal food tray slides in. • Suspended on a pully system in the middle areas of the enclosure.	GP SM	GP SM
Provide puzzle feeders.	GP SM	x
Provide whole foods or larger food chunks or pellet.	x	x
Geophagy-focused enrichment (i.e. small-scale clay wall).	SM	SM
Place obstacles (i.e. branches [B] and/or rope [R], on certain areas of the mesh).	GP^{B} SM^{B}	GP^{R}

3.2.5. Post-enclosure modification period of observations of captive parrots

After the enclosures were modified, behavioural observations were conducted between October and November 2021 at zoo A, and December 2021 and January 2022 at zoo B.

3.2.5.1. Housing conditions of captive parrots after enclosure modifications

Modifications were applied to the grey parrot and macaw enclosures at both zoos (Figure 3.6). At zoo A, the enclosures the parrots were housed in during the baseline period were modified (Figure 3.6A-D) and there were also changes to their social structure before the post-modification observations started. The female scarlet macaw died due to complications during oviposition (i.e. prolapsed oviduct), leaving only the male and juvenile, and there was a total of five deaths in the grey parrot group due to respiratory infections (11 remained). At zoo B, both grey parrots and scarlet macaws were moved to different enclosures from those they were housed in during the baseline period of observations. Their new enclosures had the same shape as their former ones, but different sizes.



Figure 3.6. Scarlet macaws and grey parrot enclosures at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) after modifications were implemented with the aim of enabling wild-type behaviours in the captive parrots.

(A-B) Scarlet macaws at zoo A (different views of the same enclosure; photo taken in October 2021), (C-D) grey parrots at zoo A (different views of the same enclosure; October 2021), (E) scarlet macaws at zoo B (December 2021), and (F) grey parrots at zoo B (December 2021). Modifications included an increase and re-organisation of structural complexity and new hanging feeders. Photos: RLF.

The grey parrots were moved to a longer enclosure but with same height and depth as their former enclosure (1,890 cm × 260 cm × 400 cm), sharing the space with another grey parrot that joined the group and three juvenile Vasa parrots (*Coracopsis vasa*; two males and one female). One of the five scarlet macaws in the study died (scarlet macaw 4) before post-modification data were collected, and a second one was removed from the group (scarlet macaw 5) due to high levels of aggression. The remaining three were moved to an enclosure of similar length to the one they were in during the baseline period, but deeper and higher (1,150 cm × 800 cm × 400 cm; Figure 3.6E). The same modifications that had been proposed for each species' former enclosures were implemented in their new ones. The scarlet macaws shared their modified enclosure with several other macaws (three juvenile scarlet macaws, two green-winged macaws, two hyacinth macaws, three great green macaws, and five red-fronted macaws). The adult macaws of each species were previously housed together in different enclosures and were all added to the modified enclosure within a period of two weeks. The juveniles were kept in mixed-species groups of similar age, in the zoo's breeding facilities, before joining the older macaws in the modified enclosure. These birds that shared the modified enclosure with the scarlet macaws were also included in the post-modification phase of the study (Table 3.1) to assess whether they engaged with the features in the modified enclosure. Scarlet macaw 3 was diagnosed with a neurological condition by the veterinary team at zoo B, reducing the possibility of behavioural responses to the enclosure modifications. Despite its condition, scarlet macaw 3 was not excluded from the study, because even though it compromised its ability to use most of the modifications applied, it was still of interest to investigate how it responded to the modified environment. However, as time was limited for data

collection at zoo B in the post-modification period, there was a reduction in sampling of scarlet macaw 3, to allow for sampling of the new macaw groups in the enclosure.

Support diversity was increased and re-distributed within each enclosure, with a network of interconnected branches and manilla rope placed in each of the four corners of the enclosure, ensuring most perches provided were unstable, diagonal or vertical and thin or medium. The top half of the enclosure within the four corners was prioritised, and areas close to the mesh were filled up with branches and/or rope, providing perching opportunities in the limits of the enclosure, including the highest points. The middle of the enclosure and areas between the support networks in the corner were left relatively clear, to increase flight opportunities, with mostly vertical supports, hanging feeders (e.g. Figure 3.7B) and enrichment placed within those areas. Branches (zoo A) and ropes (grey parrots, zoo B) were placed intermittently on areas of the mesh, interrupting routes the parrots used for repetitive climbing on the mesh (Figure 3.6).

New feeders were built, consisting of wooden boxes with holes on top, with space for the food trays to be placed within (Figure 3.7). These feeders were suspended on a pulley system that allowed changes in the vertical position of the feeder, with vertical ropes or branches around them, so they could be accessible to flying or climbing birds. The metal trays with the food were placed inside the wooden boxes, and the parrots had access to the food via the holes on top.

A B C



Figure 3.7. Wooden box feeders added to the scarlet macaw and grey parrot enclosures at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), as part of the modifications implemented with the aim of enabling wild-type behaviours in the captive parrots.
(A) Wooden box before it was placed in the scarlet macaw enclosure at zoo A (photo taken in October 2021), (B) hanging wooden box feeder surrounded by branches in the grey parrot enclosure at zoo A (October 2021), and (C) two wooden box feeders before they were placed in the macaw enclosure at zoo B (December 2021). Food metal trays were placed within the metal boxes and suspended within the enclosures. Photos: RLF.

The scarlet macaws at zoo A had one suspended feeder, while the macaws and grey parrots at zoo B had two of them in each enclosure. The grey parrots at zoo A also had two feeders, but one was the new suspended boxed system while the other was just the original system of a metal tray attached to the mesh on the main entrance to the enclosure.

The macaws in both zoos were provided with a small-scale replica of a clay lick, using commercial clay for parrots (Clay Block – Amazon River; NV Versele-Laga, Belgium). At zoo B, two designs were used. One consisted of a bamboo log, suspended in the middle of the enclosure, where the clay was placed in holes on the log, and left to dry (Figure 3.8A).

A B C



Figure 3.8. Clay lick enrichment added to the scarlet macaw enclosures at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), as part of the modifications implemented with the aim of enabling wild-type behaviours in the captive parrots.

The clay enrichment in the macaw enclosure at zoo B (December 2021 – January 2022) included (A) a bamboo log with multiple holes filled with clay and a great green macaw interacting with it, and (B) a wooden frame with clay smeared on it. (C) The clay enrichment in the scarlet macaw enclosure at zoo A (October – December 2021) consisted of a wooden frame with multiple wooden platforms attached to it where the clay was placed upon. Photos: RLF.

The second design was a wooden frame with mesh on top, leaning on and attached to a large tree trunk in the middle of the enclosure, where the clay was smeared on and left to dry (Figure 3.8B). The third design, used at zoo A, was also a wooden frame, attached to the mesh at the back, with small wooden platforms supporting small mounds of clay (Figure 3.8C). At zoo A, puzzle feeders (Caitec Inc, Halethorpe, MD, USA) were provided to the grey parrots (Figure 3.9A) and scarlet macaws (Figure 3.9B-C). They were made of plastic, which facilitated cleaning and disinfecting for use in multiple enclosures and species. They consisted of three levels of platforms on which food such as seeds and nuts could be placed in. To reach the reward, the parrots had to pull a lever to let it drop it to the level below, which when at the bottom level they could remove the reward through a lateral hole. They were left inside the enclosure for the period of post-modification observations. At zoo B these were not used (Table 3.3) due to the zoo's policy of not putting enrichment in the enclosure that is not made of natural materials.

A B C



Figure 3.9. Puzzle feeders installed in the grey parrot and scarlet macaw enclosures at zoo A (Drayton Manor Park and Zoo, UK), as part of the modifications implemented with the aim of enabling wild-type behaviours in the captive parrots.

Puzzle feeders in the enclosures of the (A) grey parrots and (B and C) scarlet macaws (different views of same puzzle feeder; October 2021). To operate the puzzle feeders, the parrots had to pull levers for the reward to drop to the levels below, and could only reach the reward through a lateral hole on the bottom level. Photos: RLF.

3.2.6. Data analysis

Data analysis was conducted using Rstudio (R version 4.2.1; R Core Team, 2022), with packages “tidyverse” version 1.3.2 (Wickham et al., 2019), “lubridate” version 1.8.0 (Grolemund & Wickham, 2011), and “janitor” version 2.1.0 (Firke, 2021) used for data processing.

3.2.6.1. Time budgets of captive grey parrots and macaws

Data from all three protocols (cognition, locomotion, social) were compiled into a larger dataset of broad behaviours (feeding/drinking, object manipulation, locomotion, perching, self-maintenance, social, and stereotypies). Intervals where the focal bird was not visible or its behaviour was unclear (i.e. “Out of Sight”) were excluded. As geophagy did not occur in the baseline period for most birds, and it remained a rare occurrence in the post-modification phase, it was grouped with object manipulation for the analysis. Each individual scarlet macaw and each of the grey parrot groups was

considered a statistical unit in the analysis. Chi-squared tests of independence (package “gmodels” version 2.18.1.1; Warnes et al., 2022) were used to determine whether there was a relationship between the time budgets (i.e. number of observations of each behaviour) of each scarlet macaw and grey parrot group and the period of observations (i.e. baseline and post-modification). This test was determined to be the most suitable for a comparison of two categorical variables involving multiple behaviours. Alternative options would have required a test for each behaviour, resulting in extensive repetitive testing (Bishop et al., 2013). The issue of autocorrelation was also considered, as the data compared between phases were from the same birds and therefore not independent (an assumption of the Chi-squared test). However, autocorrelation is more of an issue for slow-moving species that have long bouts of behaviour, in particular when they are sampled at intervals that are shorter than their average bouts of behaviour (Bishop et al., 2013). This was not found to be an issue for the fast-moving species included in this study. To reduce further the risk of autocorrelation, the intervals between data points were increased for the Chi-squared analysis, by systematically sampling every third row of the data, resulting in a dataset with a virtual 90-second sampling interval (Karniski et al., 2015). However, subsampling data can affect its biological significance, and autocorrelated data may allow for the retrieval of more complete behavioural information than independent data (de Solla et al., 1999). Therefore, for the descriptive analysis of total and daily time budgets, the whole dataset was used. For the Chi-squared analysis, the 90-second interval subsampled dataset was found to be a balanced trade-off by reducing autocorrelation without substantially deviating from the original dataset.

If over 20% of cells had expected frequencies ≤ 5, they were combined with other biologically relevant categories for the analysis. If any cells had expected frequencies ≤ 1, they were either combined, when possible, or removed from the analysis (Kim, 2017). The Chi-squared tests returned a significant result if $p<0.05$. Unlike for the data from free-living scarlet macaws, the alpha threshold was not reduced because the issue of non-independent data was addressed with subsampling. Adjusted standardised residuals were calculated as post-hoc tests of the Chi-squared tests to look for differences between each behaviour or feature of interest. The adjusted standardised residuals were used to account for differences in sample size between the periods of observations. They were interpreted with Bonferroni-corrected critical values to reduce the risk of Type I errors from the comparisons of multiple behaviours between conditions (Macdonald & Gardner, 2000). In the individuals whose morning (9:00 hrs – 11:59 hrs) and afternoon (12:00 hrs – 16:00 hrs) sampling differed between baseline and post-modification phases (e.g. more observations in the morning than afternoon in baseline but the opposite in the post-modification period) the trend of the change in each behaviour was compared between periods, to detect potential confounding effects. If detected, these confounding effects were then used to discuss the validity of those particular results.

3.2.6.2. Enclosure use of captive grey parrots and macaws

The evenness of the use of the horizontal sections of the enclosure was assessed with the “Spread of Participation Index” (SPI; Plowman, 2003). The SPI provides a scale between 0 (even use of all sections in the enclosure) and 1 (uneven use of the available space in the enclosure) the formula in equation 3.1 was used.

$$SPI = \frac{M(nb-na)+Fa-Fb}{2(N-M)} \quad \text{(equation 3.1)}$$

where *M* corresponds to the mean number of observations per zone, *N* is the total number of observations in all sections, *nb* and *na* are the number of zones with observations lower and higher than *M*, respectively, *Fb* represents the total observations in all zones with observations lower than *M*, and *Fa* the total observations in all zones with observations higher than *M* (Plowman, 2003). The enclosures were divided horizontally into sections of approximately equal size for data collection. The grey parrots and scarlet macaws at zoo A had access to indoor enclosures of smaller sizes, but they were not recorded using them, and therefore the indoor area was excluded from the analysis. The vertical use of the enclosure was assessed with Chi-squared tests of independence and adjusted standardised residuals, following the same method as described above for the time budgets, as unlike for the horizontal use of the enclosure, the main goal was to determine changes in the use of specific vertical sections of the enclosure (i.e. ground and top quarter).

3.2.6.3. Visitor effects on behaviour of captive grey parrots and macaws at zoo A

Zoo A had weekly open and closed days (i.e. closed to visitors but animal keepers and other park staff still present) during the period of observations, and therefore a comparison of the behaviour and enclosure use between those days was conducted, in order to determine potential visitor effects. Only the period of the day the zoo was open to visitors, between 10:00 hrs and 18:00 hrs, was considered in the analysis for both open and closed days. The behaviours were grouped into levels of behavioural

activity: High (feeding, object manipulation, locomotion), Medium (self-maintenance, social), Low/None (perching), and Chi-squared tests of independence were again used for comparison between open and closed days, in both baseline and post-modification periods. Changes in the use of sections of interest in the enclosure (i.e. left side of the enclosure and top quarter), when the zoo was open and closed, were analysed with randomisations (based on 10,000 permutations; Onghena & May, 1995) of differences in proportions, as they are an appropriate method to use in non-independent data, when comparing a single behaviour/feature of interest (Bishop et al., 2013). There was multiple testing of the data on each individual, and therefore the p-values were adjusted using the Benjamin-Hochberg method to control the false discovery rate (Benjamini & Hochberg, 1995). Results were considered significant if adjusted $p<0.05$.

3.3. Results

The sample size for time budgets and enclosure use in the baseline period consisted of 3,527-4,724 × 30-second intervals, sampled in 29.5-39.5 hours and 22–33 (non-consecutive) days, across individuals (Table 3.3). Data from parrots in both zoos are combined (Table 3.3) because the same methodology was applied to all parrots, and similar modifications were implemented in both zoos. Due to the reduction in sampling of scarlet macaw 3, associated with its neurological condition (section 3.2.5.1), it was observed for 15 hours across 16 days, resulting in 1,796 intervals in the post-modification phase, while the remaining individuals showed comparable sample size to baseline (3,437–4,662 intervals, 28.75–39 hours, 22–26 days; Table 3.3). The macaw group at zoo B (post-modification only) was sampled for 20.5 hours across 22 days. The random sampling of the great green macaws (17%), green-winged macaws

(12%), hyacinth macaws (11%), the red-fronted macaws (25%) and the scarlet macaw group (35%) showing similar proportions to those expected based on the size of each species group (Table 3.3).

Table 3.3. Summary of number of intervals of behavioural data collected from the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), as well as number of days and hours of observations for each individual parrot or group included in this study, in both the baseline and post-modification periods of observations.
The baseline period of observations occurred before the alterations to the enclosure and social environment of the parrots at both zoo A (grey parrots: October – December 2019, scarlet macaws: October – December 2020) and zoo B (January – March 2020). The post-modification period of observations occurred after those alterations took place (zoo A: October – December 2021, zoo B: December 2021 – January 2022). Morning (9:00–11:59 hrs); Afternoon (12:00–16:00 hrs); Total (9:00–16:00 hrs); local times (zoo A: GMT; zoo B: SGT). Zoo open/closed refers to whether zoo A was open or closed to visitors during observations.

		Baseline			Post-modification		
Individual (zoo)	Period	n	Days	Hours	n	Days	Hours
Grey parrot group (A)	Morning	2,598	17	21.75	2,361	18	19.75
	Afternoon	2,126	17	17.75	2,301	15	19.25
	Total	4,724	26	39.5	4,662	26	39
	Zoo open	1,174	12	10	1,277	9	10.75
	Zoo closed	1,650	17	13.75	2,409	19	20.25
Male scarlet macaw (A)	Morning	2,101	17	17.5	2,036	16	17
	Afternoon	1,718	15	14.5	2,272	17	19
	Total	3,819	23	32	4,308	26	36
	Zoo open	1,073	7	9	840	6	7
	Zoo closed	2,250	15	18.75	2,827	21	23.75
Female scarlet macaw (A)	Morning	1,736	16	14.5	-	-	-
	Afternoon	2,097	18	17.5	-	-	-
	Total	3,833	22	32	-	-	-
	Zoo open	1,232	8	10.25	-	-	-
	Zoo closed	2,197	15	18.5	-	-	-
Juvenile scarlet macaw (A)	Morning	2,108	17	18	2,032	17	17
	Afternoon	1,656	16	14	2,372	17	19.75
	Total	3,764	22	31.5	4,404	26	36.75
	Zoo open	1,251	9	10.5	540	3	4.5
	Zoo closed	2,002	15	16.75	3,069	23	25.5
Grey parrot group (B)	Morning	2,080	20	17.5	1,453	13	12.5
	Afternoon	2,215	21	18.5	2,085	16	17.5
	Total	4,295	33	36	3,538	22	29.5

		Baseline			Post-modification		
Scarlet macaw 1 (B)	Morning	1,720	16	14.5	1,652	13	13.75
	Afternoon	1,807	15	15	1,788	15	15
	Total	3,527	26	29.5	3,440	22	28.75
Scarlet macaw 2 (B)	Morning	1,538	14	13	1,776	14	15
	Afternoon	1,993	18	16.75	1,661	15	14
	Total	3,531	26	29.5	3,437	23	28.75
Scarlet macaw 3 (B)	Morning	1,772	15	14.75	1,068	9	9
	Afternoon	2,148	20	18	728	8	6
	Total	3,920	28	32.75	1,796	16	15
Scarlet macaw 4 (B)	Morning	1,559	13	13	-	-	-
	Afternoon	2,303	18	19.25	-	-	-
	Total	3,862	27	32.25	-	-	-
Scarlet macaw 5 (B)	Morning	1,923	20	16	-	-	-
	Afternoon	1,886	18	15.75	-	-	-
	Total	3,809	29	31.75	-	-	-
Great green macaws (B)	Morning	-	-	-	193	13	9.5
	Afternoon	-	-	-	220	14	11
	Total	-	-	-	413	22	20.5
Green-winged macaws (B)	Morning	-	-	-	147	13	9.5
	Afternoon	-	-	-	137	15	11
	Total	-	-	-	284	22	20.5
Hyacinth macaws (B)	Morning	-	-	-	122	13	9.5
	Afternoon	-	-	-	145	15	11
	Total	-	-	-	267	22	20.5
Red-fronted macaws (B)	Morning	-	-	-	288	13	9.5
	Afternoon	-	-	-	313	15	11
	Total	-	-	-	601	22	20.5
Scarlet macaw group (B)	Morning	-	-	-	384	13	9.5
	Afternoon	-	-	-	472	15	11
	Total	-	-	-	856	22	20.5

There were differences in the number of morning and afternoon observations, between the baseline and post-modification periods of observations, in the male scarlet macaw and juvenile scarlet macaw at zoo A (Table 3.3), and scarlet macaws 2 and 3 at zoo B (Table 3.3), with more observations in the morning or afternoon in the baseline period, but the opposite in the post-modification period.

3.3.1. Weather conditions during behavioural observations of captive parrots

Weather conditions were consistent between the baseline and post-modification periods of observations at each zoo. Cloudy weather conditions were predominant at zoo A in both the baseline (63.3% of observations in the grey parrots and 62.7% in the scarlet macaws), and post-modification periods (70.6%). There was rain in 18.9% and 14.7% of baseline observations of the grey parrots and scarlet macaws, respectively, and on 11.3% of post-modification observations. The mean temperature at baseline was 8.5ºC (1–14ºC) for the grey parrots and 10.7ºC (2–17ºC) for the scarlet macaws. The post-modification phase had temperatures of 10.5 ºC on average (2–19ºC) for both species. The parrots at zoo B experienced higher temperatures, with 30.3ºC (25 – 34ºC) during baseline and 29.2ºC (24 – 32ºC) during the post-modification periods of observations. Natural rain occurred in 6.5% of observations at baseline and 5.6% at the post-modification phase, although the enclosure in the latter also had an artificial rain system, which occurred in 4.5% of observations. Clear/sunny conditions were observed in 23.4% and 17.5% of intervals at baseline and post-modification, respectively, with full or partial cloud cover the most frequent weather condition observed.

3.3.2. Time budgets of captive grey parrots and macaws

During the baseline observations, perching dominated the activity budgets of both grey parrot groups (> 50%) and all the scarlet macaws (> 60%) except the juvenile scarlet macaw at zoo A (29%). Feeding and object manipulation combined consisted of 17% and 24% of observations on the grey parrot groups at zoo A and B, respectively (Figure 3.10A).

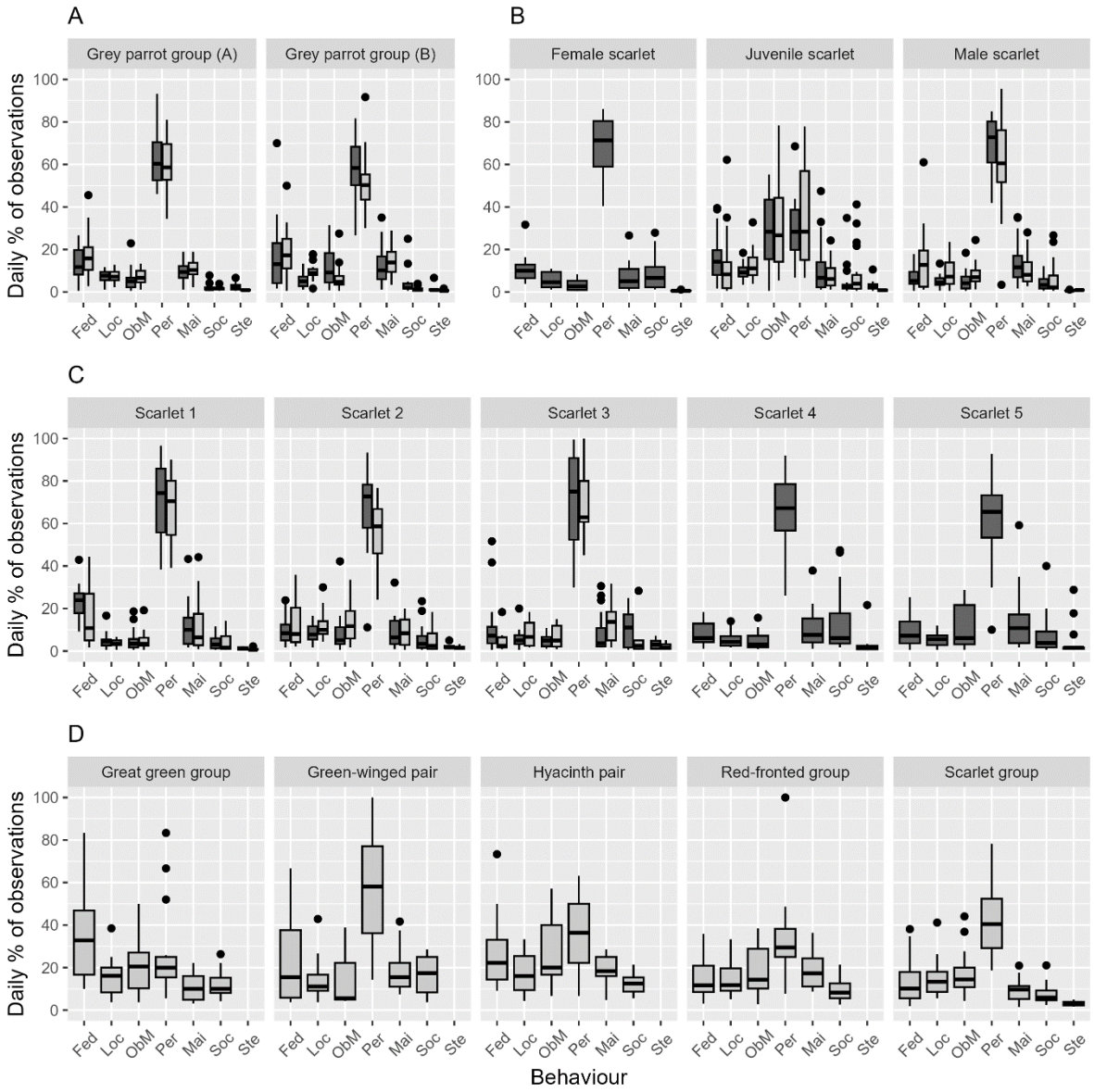


Figure 3.10. Boxplots of daily time budgets of grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline and post-modification periods of observations.

(A) Grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). The median, first and third quartiles are represented by the box, the whiskers represent the minimum and maximum values, and the black dots show the outliers. Fed = Feeding; Loc = Locomotion; ObM = Object Manipulation; Per = Perching; Mai = Self-Maintenance; Soc = Social; Ste = Stereotypies.

The combined proportions of feeding and object manipulation did not surpass 10% in the adult scarlet macaws at zoo A, but the juvenile scarlet macaw spent 45% of the time engaging in them (Figure 3.10B). In the scarlet macaws at zoo B, between 8 and 14% of the observations were either feeding or manipulating objects (Figure 3.10C). Locomotion was infrequent across all individuals, (Figures 3.10A-C), while social behaviours only exceeded 5% in the female scarlet macaw at zoo A and scarlet macaws 4 and 5 at zoo B (Figures 3.10B and 3.10C, respectively). It was noted that at zoo A, the female scarlet macaw interacted with both the male and juvenile scarlet macaws, while these rarely interacted with each other. Scarlet macaw 1's social behaviour was mostly with scarlet macaw, while scarlet macaw 4 interacted with both scarlet macaws 3 and 5. Stereotypic behaviours, which consisted mostly of wire chewing and occasionally head circles, were rarely observed (Figures 3.10A-C). Scarlet macaws 1, 2 and 3 at zoo B exhibited other abnormal behaviours (behaviours that diverge from those exhibited by the species in the natural environment; Lutz et al., 2022), such as scarlet macaw 1's frequent "hunched" posture while perching, not observed in the other macaws, and scarlet macaws 1 and 2's lack of flight behaviour observed in scarlet macaws 2 and 3, and only use of the wire mesh and ground, not exploring the other supports in the enclosure.

3.3.2.1. Post-modification changes in the time budgets of captive grey parrots and macaws

The post-modification time budgets were significantly different from those during the baseline period of observations in both grey parrot groups and all scarlet macaws

(χ^2s$_{(5\text{-}6,\ n\ =\ 1884\text{-}3130)}$ = 31.79–70.12, ps < 0.001; Tables 3.4 and 3.5) except the scarlet macaw 1 ($\chi^2_{(5,\ n\ =\ 2322)}$ = 10.22, df = 5, p = 0.100; Table 3.5).

Table 3.4. Summary of Chi-squared tests and adjusted standardised residuals comparing the time budgets of each scarlet macaw and grey parrot group at Drayton Manor Park and Zoo (zoo A), between baseline (before alterations to the enclosure and social environment of the parrots) and post-modification (after those alterations took place) periods.

Baseline observations took place in October – December 2019 (grey parrots), October – December 2020 (scarlet macaws), while post-modification observations occurred in October – December 2021. Blue and red cells show significant positive and negative differences in residuals, respectively, according to the corrected critical value. The degrees of freedom (df) and the p-values, adjusted for multiple testing (Benjamin-Hochberg method), are stated.

X^2	df	p-value	Adjusted standardised residuals		
Grey parrot group A (n = 3130): Corrected critical value: 2.91					
40.53	6	< 0.001	Behaviour	Baseline	Post-modification
			Feeding/Drinking	-1.77	1.77
			Locomotion	0.71	-0.71
			Object Manipulation	-1.48	1.48
			Perching	0.80	-0.80
			Self-Maintenance	-1.47	1.47
			Social	3.38	-3.38
			Stereotypies	4.69	-4.69
Male scarlet macaw (n = 2031): Corrected critical value: 2.87					
31.79	5	< 0.001	Behaviour	Baseline	Post-modification
			Feeding/Drinking	-3.03	3.03
			Locomotion	-3.50	3.50
			Object Manipulation	-2.17	2.17
			Perching	2.95	-2.95
			Self-Maintenance	2.21	-2.21
			Social	-0.12	0.12
			Stereotypies	-	-
Juvenile scarlet macaw (n = 2046): Corrected critical value: 2.91					
53.74	6	< 0.001	Behaviour	Baseline	Post-modification
			Feeding/Drinking	3.61	-3.61
			Locomotion	-2.34	2.34
			Object Manipulation	0.45	-0.45
			Perching	-2.80	2.80
			Self-Maintenance	2.22	-2.22
			Social	-1.89	1.89
			Stereotypies	4.93	-4.93

Table 3.5. Summary of Chi-squared tests and adjusted standardised residuals comparing the time budgets of each scarlet macaw and grey parrot group at Jurong Bird Park (zoo B), between baseline (before alterations to the enclosure and social environment of the parrots) and post-modification (after those alterations took place) periods.

Observations took place in January – March 2020 (baseline) and October – December 2021 (post-modification). Blue and red cells show significant positive and negative differences in residuals, respectively, according to the corrected critical value. The degrees of freedom (df) and the p-values adjusted for multiple testing (Benjamin-Hochberg method) are stated.

X^2	df	p-value	Adjusted standardised residuals		
Grey parrot group B (n = 2602): Corrected critical value: 2.87					
70.12	5	< 0.001	Behaviour	Baseline	Post-modification
			Feeding/Drinking	4.53	4.53
			Locomotion	-4.67	4.67
			Object Manipulation	5.26	-5.26
			Perching	3.28	-3.28
			Self-Maintenance	-1.13	1.13
			Social	1.18	-1.18
			Stereotypies	-	-
Scarlet macaw 1 (n = 2322): Corrected critical value: 2.87					
10.22	5	0.069	Behaviour	Baseline	Post-modification
			Feeding/Drinking	0.85	-0.85
			Locomotion	1.48	-1.48
			Object Manipulation	-1.33	1.33
			Perching	0.22	-0.22
			Self-Maintenance	0.19	-0.19
			Social	-2.42	2.42
			Stereotypies	-	-
Scarlet macaw 2 (n = 2321): Corrected critical value: 2.87					
46.29	5	< 0.001	Behaviour	Baseline	Post-modification
			Feeding/Drinking	-0.91	0.91
			Locomotion	-3.71	3.71
			Object Manipulation	-4.91	4.91
			Perching	5.25	-5.25
			Self-Maintenance	0.72	-0.72
			Social	-0.24	0.24
			Stereotypies	-	-
Scarlet macaw 3 (n = 1884): Corrected critical value: 2.87					
35.99	5	< 0.001	Behaviour	Baseline	Post-modification
			Feeding/Drinking	3.26	-3.26
			Locomotion	-3.25	3.25
			Object Manipulation	-1.34	1.34
			Perching	1.76	-1.76
			Self-Maintenance	-2.98	2.98
			Social	2.37	-2.37
			Stereotypies	-	-

Perching remained the most frequent behaviour in the time budgets of all birds, including the juvenile scarlet macaw that perched significantly more frequently in the post-modification period of observations (Table 3.4), but there were significant decreases in the grey parrot group B (Table 3.5), the male scarlet macaw (Table 3.4), and the scarlet macaw 2 (Table 3.5 and Figure 3.10). Comfort behaviours while perching were rare in both baseline and post-modification periods. Significant changes in self-maintenance were detected in scarlet macaw 3 (Figure 3.10C and Table 3.5). Preening was the most frequent type of self-maintenance observed in all individuals in both the baseline (82%-93% of preening observations) and post-modification (79–95%) periods of observations. Stereotypies were too infrequent to be included in the analysis in most individuals, but the grey parrot group A (Figure 3.10A) and the juvenile scarlet macaw (Figure 3.10B) showed a significant decrease (Table 3.4).

Contrastingly, feeding significantly increased in the grey parrot group B (Figure 3.10A and Table 3.5) and the male scarlet macaw (Figure 3.10B), but decreased in the juvenile scarlet macaw (Figure 3.10B and Table 3.4). While the male and juvenile scarlet macaws took time to use the new hanging feeders but eventually started using them, scarlet macaws 1 to 3 did not use them at all and kept feeding from the ground trays as in the baseline. The grey parrot group B engaged less in object manipulation in post-modification, while scarlet macaw 2 showed an increase in this behaviour (Figure 3.10C). Both the grey parrot group and the scarlet macaws at zoo A showed almost no engagement with the puzzle feeders or the other temporary enrichment that was placed in the enclosure, and most of the manipulation observed was on the branches placed as supports in the enclosure. On one occasion, the male scarlet

macaw was seen interacting with the puzzle feeder, but for no more than a few minutes, and quickly gave up without retrieving the nut that was within it. Similarly, the grey parrot group and the adult scarlet macaws at zoo B also showed low engagement with temporary enrichment added to the enclosure, and mostly manipulated bark pieces used as substrate on the ground (in both baseline and post-modification periods).

Locomotion significantly increased in the grey parrot group B (Figure 3.10A), scarlet macaws 2 and 3 (Figure 3.10C and Table 3.5) and the male scarlet macaw (Figure 3.10 and Table 3.4). All birds that used the new feeders were observed climbing up and down the surrounding supports, to access them, and the grey parrot groups, in particular, were seen flying directly to the feeders or to nearby supports to then climb to the desired spot for feeding. In contrast to observations in the baseline period, the male and juvenile scarlet macaws at zoo A interacted more with each other, while the scarlet macaw 3 at zoo B redirected his social behaviours to the hyacinth macaws after scarlet macaw 4 died.

All macaw groups but the green-winged macaws at zoo B (post-modification period of observations only) exhibited relatively high activity levels (Figure 3.10D). All groups were observed feeding on both the hanging feeders and the trays on the ground, and all but the green-winged macaws exhibited an apparent high confidence (i.e. use with little apparent hesitation) in the use of the new feeders, the supports around the enclosure and the temporary enrichment added.

Geophagy was recorded in the grey parrot group B (i.e. on the soil) and in all macaw groups (i.e. on the clay lick replicas) except the green-winged macaws. The observer did, however, notice one of the green-winged macaws descending onto the clay lick replica (Figure 3.7A) to grab a chunk of clay, which it took back to an upper perch to manipulate and consume. The male scarlet macaw at zoo A (Figure 3.7C) and scarlet macaws 1 and 2 (Figure 3.7B) at zoo B were seen approaching the clay lick replicas and touch the clay with their bills and tongues, but further interactions with the clay were not observed.

3.3.3. Enclosure use by the captive grey parrots and macaws

3.3.3.1. Horizontal use of the enclosure by the captive grey parrots and macaws

Horizontal enclosure use during the baseline period was heterogenous across all groups (SPI = 0.38–0.72; Table 3.8), with a high proportional use of a single section of the enclosure, which differed between groups. The grey parrot group at zoo B showed a preference for section 1 (i.e. the far left), as most of the baseline observations were within this area (Figure 3.11A). On the other hand, the grey parrot group at zoo A (Figure 3.11A) and all scarlet macaws spent most of their time within section 4 (i.e. the far right; Figures 3.11B-C). In the post-modification phase, section 4 was still the most frequently used by all parrots at zoo A. However, the grey parrot group and the male scarlet macaw showed decreases in the SPI (Table 3.6) and in the use of section 4, suggesting a more even use of the enclosure (Figure 3.11A–B).

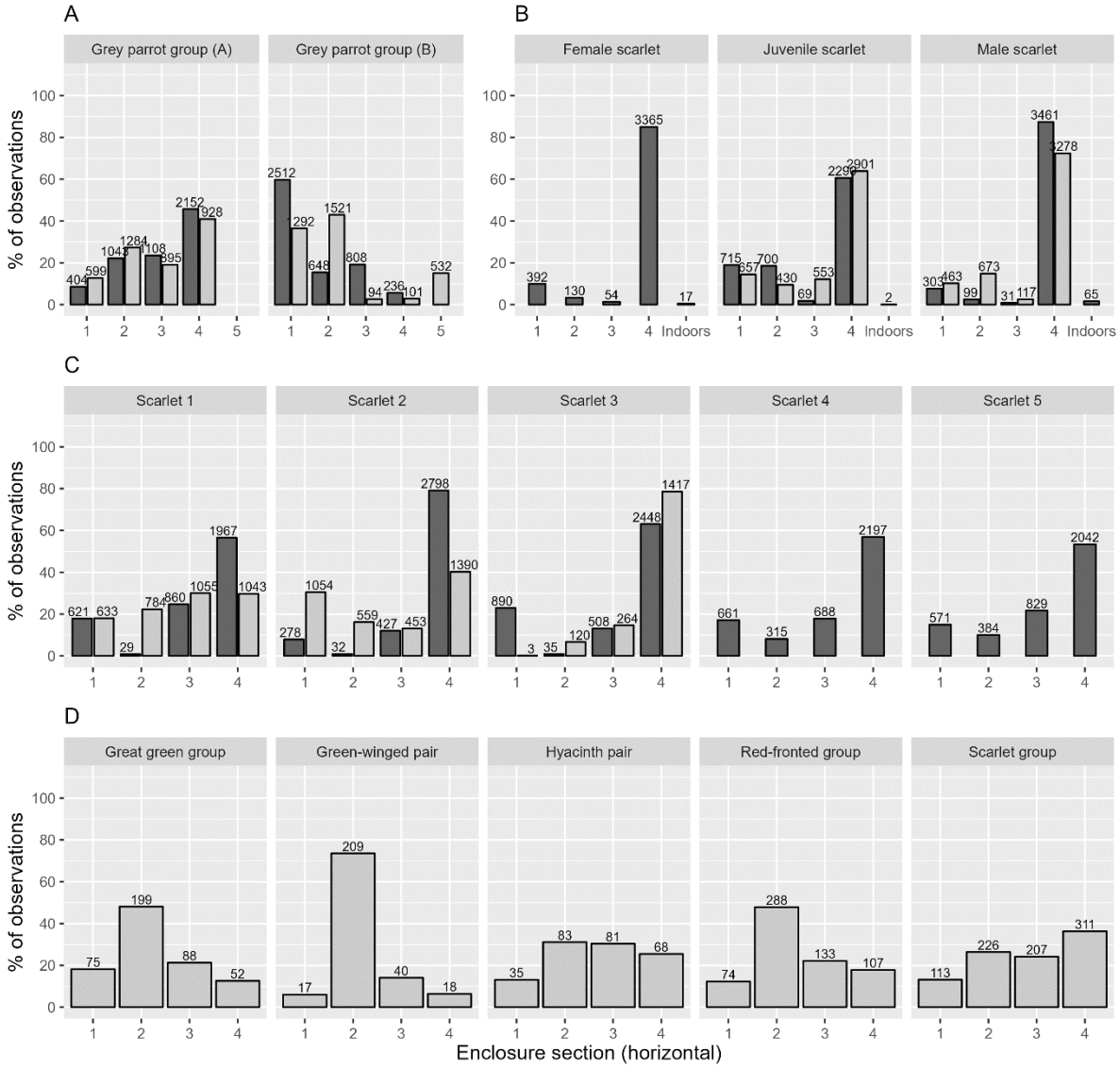


Figure 3.11. Horizontal enclosure use in grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), in the baseline and post-modification periods of observations.

Percentages of total observations of the use of each horizontal section within the enclosure in the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations.

Table 3.6. Spread of Participation Index (SPI) for enclosure use of captive grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), in both baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). (=) If difference in SPI between baseline and post-modification is 0 – 0.049; (↑) if there is an increase or (↓) decrease in SPI of 0.050 – 0.249 in the post-modification period; (↑↑↓↓) differences in SPI of 0.250 – 0.499 between periods; (↑↑↑↓↓↓) differences in SPI of 0.500 – 1.000 between periods.

Individual (zoo)	Spread of Participation Index (SPI)	
	Baseline	Post-modification
Grey parrot group (A)	0.500	0.243 (↓↓)
Grey parrot group (B)	0.464	0.493 (=)
Male scarlet macaw (A)	0.721	0.606 (↓)
Female scarlet macaw (A)	0.695	-
Juvenile scarlet macaw (A)	0.424	0.518 (↑)
Scarlet macaw 1 (B)	0.421	0.129 (↓↓)
Scarlet macaw 2 (B)	0.722	0.276 (↓↓)
Scarlet macaw 3 (B)	0.508	0.714 (↑)
Scarlet macaw 4 (B)	0.425	-
Scarlet macaw 5 (B)	0.378	-
Great green macaw group (B)	-	0.307
Hyacinth macaw pair (B)	-	0.159
Green-winged macaw pair (B)	-	0.648
Scarlet macaw group (B)	-	0.169
Red-fronted macaw group (B)	-	0.304

The juvenile scarlet macaw, on the other hand, showed a slight increase in the proportion of time spent in section 4 (Figure 3.11B) and in the SPI (Table 3.6). At zoo B, the grey parrot group showed a negligible increase in SPI (Table 3.6), and although they still spent most of their time on the left side of the (new) enclosure, they used sections 1 and 2 more evenly. More pronounced changes in the SPI were detected in scarlet macaws 1, 2 (decrease) and 3 (increase; Figure 3.11C and Table 3.6). Out of the macaw groups, only the green-winged macaws showed a high SPI (Table 3.6).

3.3.3.2. Vertical use of the enclosure by the captive grey parrots and macaws

The use of the top quarter of the enclosure, in baseline conditions, was common in all parrots at zoo A but rarely used by most parrots at zoo B (Figure 3.12).

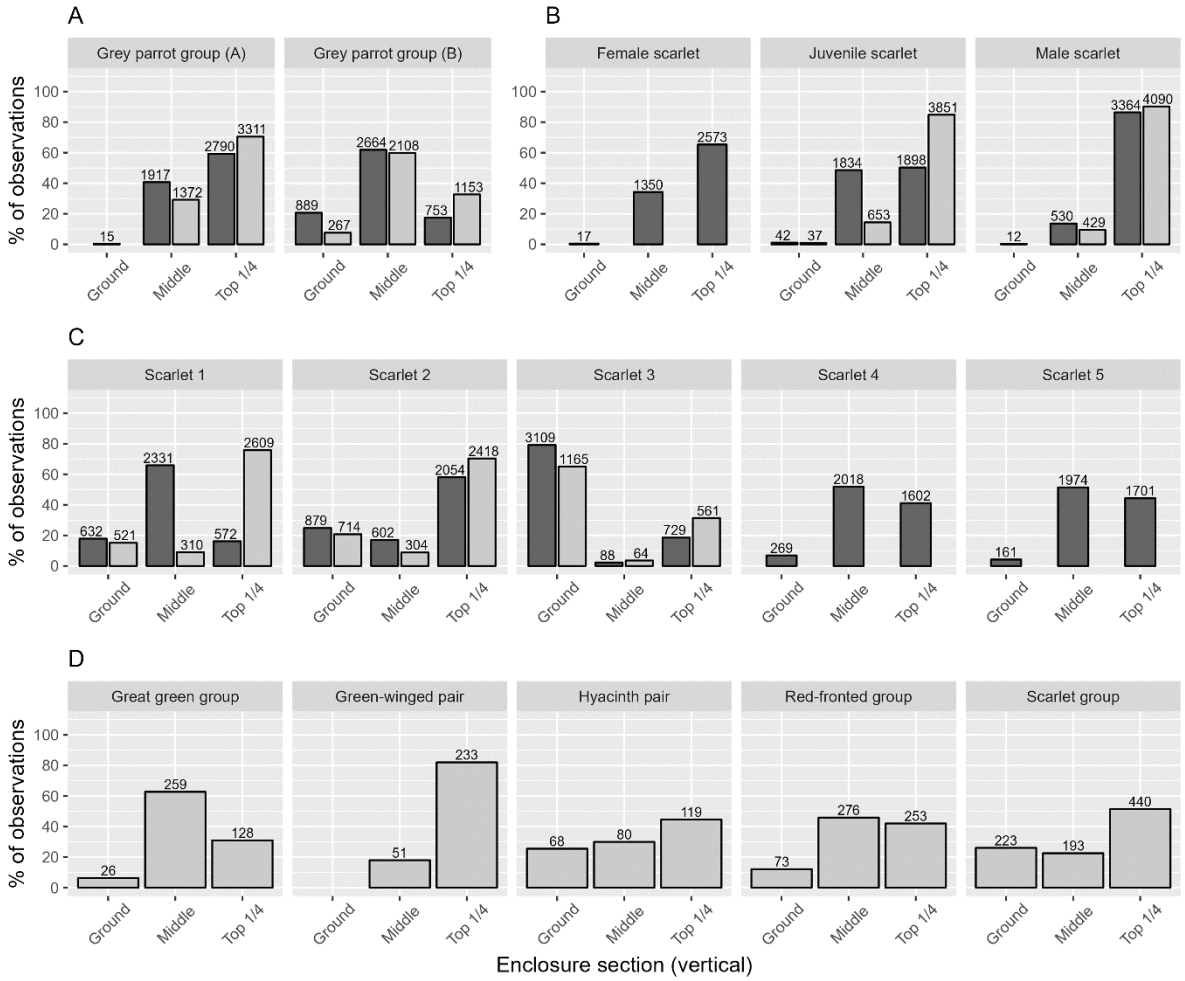


Figure 3.12. Vertical enclosure use in the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline and post-modification periods of observations.

Percentages of total observations of the use of each vertical section within the enclosure in the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations.

On the other hand, ground use was rarely observed at zoo A but it was frequent at zoo B (Figure 3.12). Following modification of enclosures, there were significant changes in the vertical use of the enclosure in all parrots at both zoos (χ^2s$_{(1\text{-}2,\ n = 1908\text{-}3132)}$ = 11.36–967.59, ps < 0.01; Table 3.7). The use of the top quarter of the enclosure, specifically, increased in all individuals (Figure 3.12). On the other hand, time spent on the ground decreased in the grey parrot group B and scarlet macaw 3 (Figure 3.12C and Table 3.7).

Table 3.7. Summary of Chi-squared tests and adjusted standardised residuals comparing the vertical use of the enclosure by the scarlet macaws and grey parrot groups at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant positive and negative differences in residuals, respectively, according to the corrected critical value. The degrees of freedom (df) and the p-value, adjusted for multiple testing (Benjamin-Hochberg method), are stated.

X^2	df	p-value	Adjusted standardised residuals		
Grey parrot group (zoo A; n = 3132): Corrected critical value: 2.50					
38.77	1	< 0.001	Enclosure section	Baseline	Post-modification
			Top ¼	-6.23	6.23
			Middle	6.23	-6.23
			Ground	-	-
Grey parrot group (zoo B; n = 2616): Corrected critical value: 2.64					
119.51	2	< 0.001	Enclosure section	Baseline	Post-modification
			Top ¼	-7.68	7.68
			Middle	-0.20	0.20
			Ground	9.37	-9.37
Male scarlet macaw (zoo A; n = 2807): Corrected critical value: 2.50					
11.36	1	0.002	Enclosure section	Baseline	Post-modification
			Top ¼	-3.37	3.37
			Middle	3.37	-3.37
			Ground	-	-
Juvenile scarlet macaw (zoo A; n = 2771): Corrected critical value: 2.64					
393.8	2	< 0.001	Enclosure section	Baseline	Post-modification
			Top ¼	-19.67	19.67
			Middle	19.79	-19.79

X^2	df	p-value	Adjusted standardised residuals		
			Ground	0.26	-0.26
Scarlet macaw 1 (zoo B; n = 2328): Corrected critical value: 2.64					
967.59	2	< 0.001	Enclosure section	Baseline	Post-modification
			Top ¼	-29.09	29.09
			Middle	28.44	-28.44
			Ground	1.85	-1.85
Scarlet macaw 2 (zoo B; n = 2322): Corrected critical value: 2.64					
47.04	2	< 0.001	Enclosure section	Baseline	Post-modification
			Top ¼	-6.14	6.14
			Middle	5.81	-5.81
			Ground	2.33	-2.33
Scarlet macaw 3 (zoo B; n = 1908) - Corrected critical value: 2.64					
40.88	2	< 0.001	Enclosure section	Baseline	Post-modification
			Top ¼	-5.60	5.60
			Middle	-2.58	2.58
			Ground	6.34	-6.34

3.3.4. Effects of visitors on behaviour and enclosure use of the grey parrots and scarlet macaws at zoo A

Significant differences in behavioural activity between the days zoo A was open and closed to visitors were detected in both periods of observation in the grey parrot group (baseline: $\chi^2_{(2,\ n\ =\ 907)} = 16.73$, $p < 0.001$; post-modification: $\chi^2_{(2,\ n\ =\ 1223)} = 14.40$, $p = 0.002$), female and juvenile scarlet macaws (χ^2s$_{(2,\ n\ =\ 1056\text{-}1177)} =$ 15.42–45.28, ps < 0.001), and in the male scarlet macaw in the post-modification period ($\chi^2_{(2,\ n\ =\ 1165)} = 7.33$, $p = 0.035$; Table 3.8). The grey parrot group showed reduced high activity when the zoo was open, in both periods of observations (Figure 3.13 and Table 3.8). In the scarlet macaws, however, the differences in behaviour when the zoo was open versus closed varied between the baseline and post-modification periods of observations (Figure 3.13A and Table 3.8).

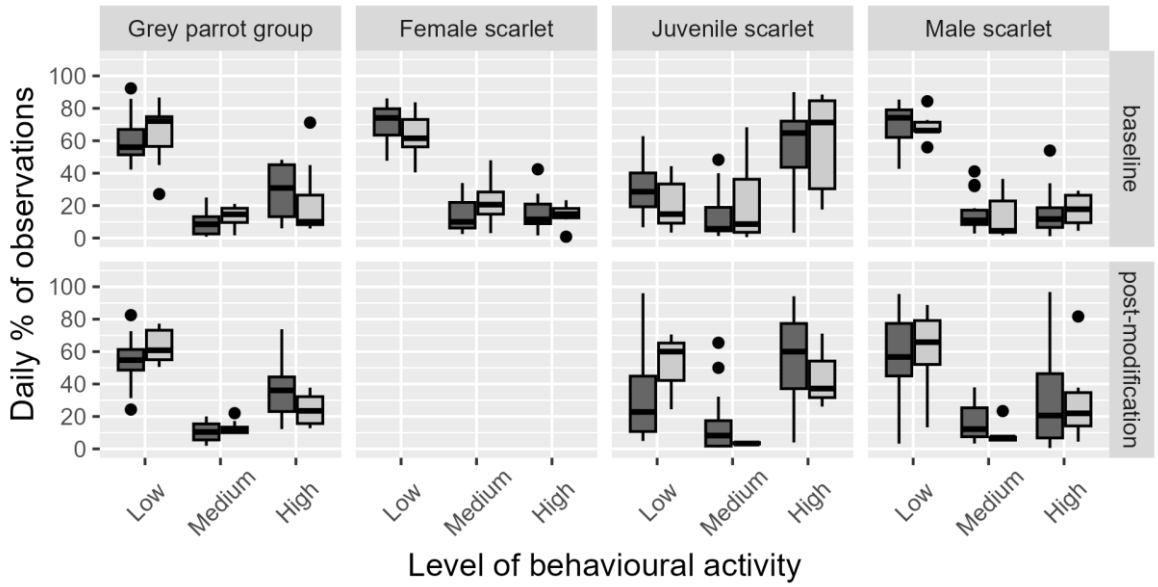


Figure 3.13. Boxplots of behavioural activity of grey parrots and scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK), when the zoo was open versus closed to visitors, in the baseline and post-modification periods of observations. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots) and October – December 2020 (scarlet macaws), while post-modification observations took place in October – December 2021. The median, first and third quartiles are represented by the box, the whiskers represent the minimum and maximum values, and the black dots show the outliers.

Table 3.8. Summary of Chi-squared tests and adjusted standardised residuals comparing activity levels of scarlet macaws and grey parrot group at zoo A (Drayton Manor Park and Zoo, UK), when the zoo was open versus closed, in the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots), October – December 2020 (scarlet macaws). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021. Blue and red cells show significant positive and negative differences in residuals, respectively, according to the corrected critical value (2.64). The degrees of freedom (df) and the p-value, adjusted for multiple testing (Benjamin-Hochberg method), are stated.

Phase	X^2	df	p-value	Adjusted standardised residuals		
Grey parrot group				Activity level	Closed	Open
Baseline (n = 907)	16.73	2	< 0.001	Low	-1.88	1.88
				Medium	-2.31	2.31
				High	3.80	-3.80
Post-modification (n = 1223)	14.40	2	0.002	Low	-2.43	2.43
				Medium	-1.64	1.64
				High	3.71	-3.71

Phase	X^2	df	p-value	Adjusted standardised residuals		
Male scarlet macaw				Activity level	Closed	Open
Baseline (n = 1061)	3.77	2	0.166	Low	1.10	-1.10
				Medium	0.53	-0.53
				High	-1.93	1.93
Post-modification (n = 1165)	7.33	2	0.035	Low	-1.06	1.06
				Medium	2.67	-2.67
				High	-1.07	1.07
Juvenile scarlet macaw				Activity level	Closed	Open
Baseline (n = 1056)	26.14	2	< 0.001	Low	3.71	-3.71
				Medium	-4.38	4.38
				High	-0.20	0.20
Post-modification (n = 1177)	45.28	2	< 0.001	Low	-6.31	6.31
				Medium	3.99	-3.99
				High	3.13	-3.13
Female scarlet macaw				Activity level	Closed	Open
Baseline (n = 1096)	15.42	2	< 0.001	Low	2.85	-2.85
				Medium	-3.90	3.90
				High	0.31	-0.31

The grey parrot group used the left side of the enclosure significantly more often when the zoo was open, but only in the post-modification period of observations. The juvenile scarlet macaw used less of the left side of the enclosure when the zoo was open, during the baseline period, but contrastingly used more of that section on open days in the post-modification period (Figure 3.14A and Table 3.9). The vertical use of the enclosure differed between days the zoo was open versus closed for all parrots except the female scarlet macaw (Table 3.9). Both the grey parrot group and the juvenile scarlet macaw used the top quarter of the enclosure more on days when the zoo was open, in both observation periods (Figure 3.14B and Table 3.9).

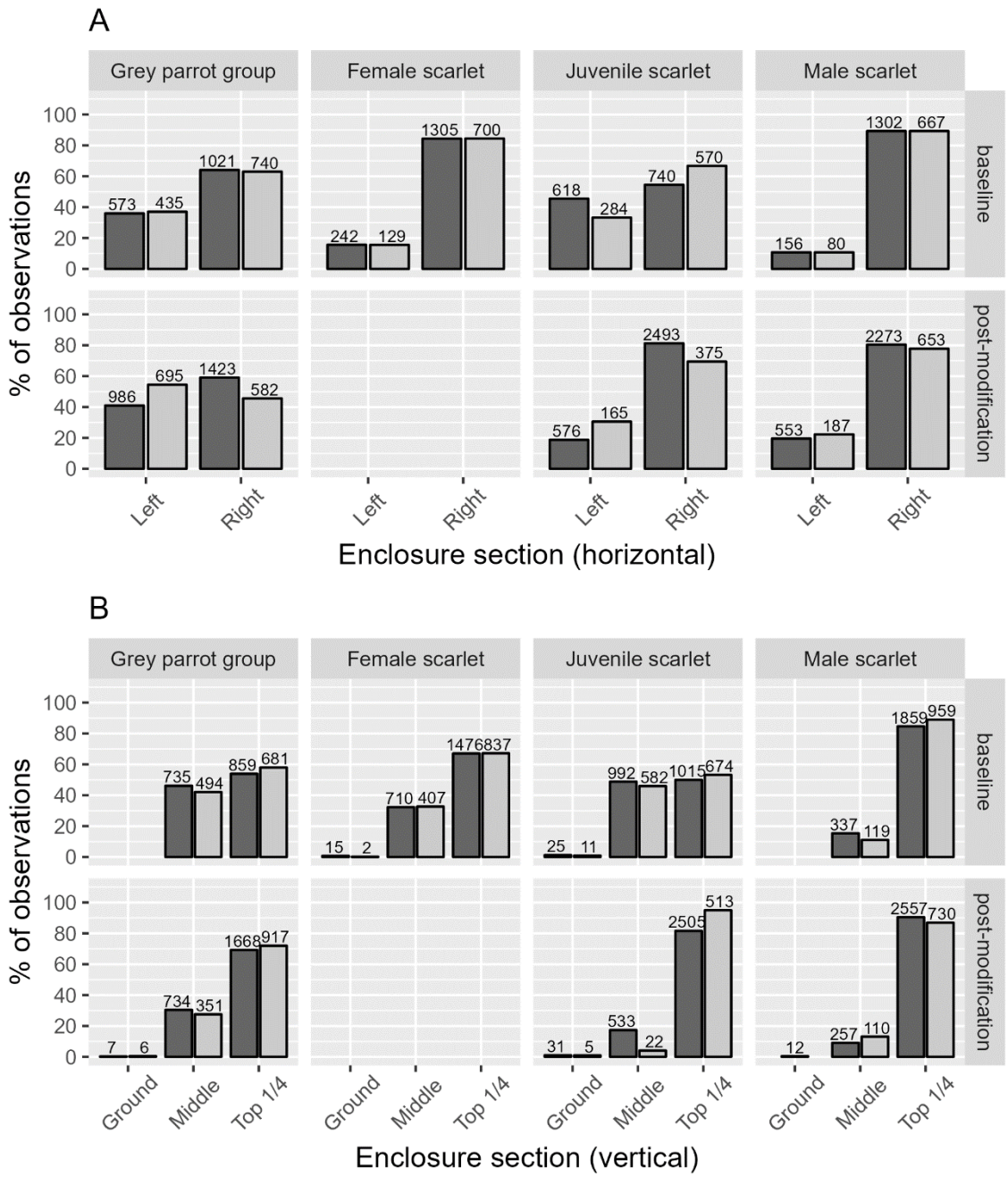


Figure 3.14. Enclosure use of grey parrots and scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK), when the zoo was open versus closed to visitors, in the baseline and post-modification periods of observations.
The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots) and October – December 2020 (scarlet macaws), while post-modification observations took place in October – December 2021. Percentages of total observations of (A) horizontal and (B) vertical enclosure use. Numbers above bars represent the number of observations.

Table 3.9. Summary of randomisations (10,000 permutations) comparing the percentage of time the scarlet macaws and grey parrot group at zoo A (Drayton Manor Park and Zoo, UK) spent in the left half side of the enclosure and in the top quarter of the enclosure, between days the zoo was open versus closed, in the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots), October – December 2020 (scarlet macaws). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021. Blue and red cells show significant ($p < 0.05$) positive and negative differences, respectively, when zoo A was open, based on the p-values adjusted with the Benjamin-Hochberg method.

Individual	Phase	Z	Standard deviation	p-value (adjusted)
Enclosure use: left side of enclosure				
Grey parrot group	Baseline	0.58	0.019	0.307
	Post-modification	7.82	0.017	< 0.001
Female scarlet	Baseline	NA	0	1
Male scarlet	Baseline	NA	0	1
	Post-modification	1.73	0.016	0.073
Juvenile scarlet	Baseline	-5.60	0.022	< 0.001
	Post-modification	6.25	0.019	< 0.001
Enclosure use: top ¼ of the enclosure				
Grey parrot group	Baseline	2.11	0.019	0.028
	Post-modification	1.87	0.016	0.049
Female scarlet	Baseline	1.79	0.017	0.062
Male scarlet	Baseline	3.35	0.013	< 0.001
	Post-modification	-2.99	0.012	0.005
Juvenile scarlet	Baseline	1.79	0.017	0.042
	Post-modification	7.76	0.017	< 0.001

3.4. Discussion

Changes in activity budgets and/or enclosure use were detected in most parrots, which could have been a result of the physical and or social changes that occurred in their environment between the baseline and post-modification periods of observations. These changes varied between zoos and across individuals. Potential visitor effects on the behaviour of the parrots at zoo A were also detected, although these were variable between species and within the scarlet macaw group.

3.4.1. Activity budgets of captive grey parrots and macaws

3.4.1.1. Inactivity and stereotypic behaviours of captive grey parrots and macaws

Inactivity is often used as a welfare indicator in captive animals, and it can be associated with both positive and negative welfare states (Fureix & Meagher, 2015). While resting and comfort behaviours can be representative of positive welfare, high levels of inactivity can also be caused by fear, illness, boredom and/or depression, all associated with poor welfare (Fureix & Meagher, 2015). Physical health issues such as obesity, hepatic lipidosis and lipomas have been linked with the diets and low activity levels of captive parrots (Perpiñán, 2015), and oxidative damage to DNA can also increase in sedentary parrots (Larcombe et al., 2010).

Previous *in situ* research showed that yellow-fronted parrots (*Poicephalus flavifrons*) were highly active and were seen resting or alert in only 18% of the observations (Hailu et al., 2019), while free-living scarlet macaws in Costa Rica were seen perching in 48% (released captive-bred; section 2.3.1), 34% (wild; section 2.3.1) and approximately 35% (released captive-bred; Cornejo et al., 2005) of observations. In contrast, in this chapter both grey parrot groups and all adult scarlet macaws were inactive or engaged in comfort behaviours in the majority of observations in the baseline period. The juvenile scarlet macaws showed lower inactivity levels, and more comparable to those of their free-living counterparts, including 11th week-old juveniles in Costa Rica (approximately 40% in perching plus maintenance behaviours; Myers & Vaughan, 2004). A reduction in inactivity was observed in some of the parrots in the post-modification period of observations, possibly due to the physical and social changes in

their environment, although inactivity still dominated their activity budgets in the post-modification period. In scarlet macaw 2, the contrasting changes in perching between the morning and afternoon budgets do not call into question the significant overall decrease observed in this individual. Instead, having the same sampling pattern in both phases could have further strengthened the difference observed. Available *in situ* data on activity budgets in other free-living macaw species showed around 45% of inactivity in hyacinth (Pinho & Nogueira, 2003) and 75% in great green macaws (Berg et al., 2007), suggesting the juvenile macaw groups of these species included in the present study (i.e. post-modification period only) exhibited relatively low activity levels.

Stereotypic behaviours (i.e. repetitive and seemingly functionless activities) are also used as a welfare indicator in captive animals (Manteca et al., 2016; Mason & Latham, 2004; Wolfensohn et al., 2018), as they are a response, and potential coping mechanism, to unstimulating and restrictive environments (Meehan et al., 2004), and rearing conditions (Schmid et al., 2006), most often associated with poor welfare (Mason & Latham, 2004). Stereotypies were rare in the present study and consisted mostly of wire chewing. The grey parrot group and the juvenile scarlet macaw were the only ones with sufficient occurrences of stereotypic behaviours to include in my data analysis, and they both showed a decrease in these behaviours in the post-modification period of observations. They were seen manipulating the new branches in the enclosure with their bills, which despite having been added primarily as supports, seemed to have reduced the parrots' attention on the wire mesh by providing them with alternatives for manipulation. Enriching the environment of captive parrots, by providing them with opportunities for foraging and locomotion, has been found to

decrease stereotypic behaviours (Meehan et al., 2004), and the provision of browse in particular has been highlighted as an effective and beneficial enrichment in these birds, giving them opportunities for natural behaviours such as engaging in object manipulation with their bills (Field & Thomas, 2000).

Using stereotypies to assess animal welfare may be unreliable, however, as they can often be a result of past experiences rather than current conditions (Mason & Latham, 2004). Furthermore, a low incidence of stereotypic behaviours does not necessarily mean the animals are not experiencing negative welfare, as they may respond to a lack of stimulation in their environment by exhibiting high levels of inactivity instead, which may be an indicator of depression-like states (Fureix et al., 2016). Also, a low incidence of negative behavioural indicators does not automatically translate into good welfare for the animal, as for that to be true, the animal must also experience rewarding behaviours (Mellor et al., 2020).

3.4.1.2. Feeding and object manipulation in captive grey parrots and macaws

The ability to search, select, manipulate and consume food (i.e. foraging) is vital for wild animals to survive in their natural environments. Many parrot species have a generalist and opportunistic diet, feeding on the various reproductive parts of plants, especially the nutritious seeds. These require cognitive and manipulation skills to prevail against the anti-predator strategies plants have evolved to protect them (Thoft & Wright, 2015). Those parrot species that require advanced manipulation skills for foraging in the wild, such as the species included in the present study, are more likely

to experience poor welfare in captivity, where the food provided is often pre-processed and unchallenging (Mellor et al., 2021).

Therefore, to meet energy demands, wild parrots spend a high proportion of their daily time budgets foraging, as evidenced by field observations of yellow-fronted parrots (44%; Hailu et al., 2019), scarlet macaws (28%; section 2.3.1) and hyacinth macaws (25%; Pinho & Nogueira, 2003). Contrastingly, the adult captive parrots in the present study showed lower proportions of feeding in their baseline activity budget, and even when combining object manipulation, which can act as a substitute for foraging behaviour in captive environments (Kim et al., 2009), the proportion was still lower than in their wild counterparts. Note, however, that field studies often include locomotion under foraging (e.g. moving while searching for food), which differs from the methodology in the present study, and could therefore inflate feeding/foraging proportions in comparison to the captive parrots. Nevertheless, the new feeders in the enclosures may have encouraged foraging behaviours as there was an increase in feeding in parrots that used the new feeders in the post-modification period of observations. These findings concur with previous research showing that increasing the complexity of food presentation, via foraging enrichment, results in an increase in feeding times in captive parrots (Lumeij & Hommers, 2008; van Zeeland et al., 2013a). Also, the differences in sampling pattern between phases that were detected in the male scarlet macaw do not conflict with the significant increase in feeding observed in this individual. Despite contrasting changes in this behavior in the morning and afternoon periods, having the same sampling pattern between periods of observations could have only strengthened this difference.

Furthermore, no changes in feeding times were observed in the parrots that did not use the new feeders and kept feeding from the ground trays as in the baseline period of observations. Due to the neurological condition of scarlet macaw 3, which evidently restricted its behaviour and movement throughout the enclosure, the ground trays could not be phased out. In addition, the adult scarlet macaws at zoo B were older animals (over 20 years old at the time of the post-modification period), and kept using the feeders they were familiar with, likely due to a combination of their age and lack of previous experience with more challenging and diverse forms of food provision. It has been shown that enrichment use by other species in captivity is affected by age (bank voles [*Clethrionomys glareolus]*; Cooper et al., 1996), enriched/non-enriched housing conditions (rats [*Rattus norvegicus]*; Bell et al., 2009) and exposure to enrichment early in life (domestic chickens [*Gallus gallus]*; Norman et al., 2018, 2019). Juvenile kākās (*Nestor meridionalis*) showed higher behavioural flexibility in problem-solving and enrichment use than their adult counterparts (Loepelt et al., 2016), while orange-winged Amazon parrots that experienced novelty early in their development (Fox & Millam, 2004) or were housed in enriched environments (Meehan & Mench, 2002), exhibited lower neophobic tendencies. That could also explain why the groups containing juvenile macaws at zoo B spent more time engaged in feeding and object manipulation than the adult scarlet macaws, and seemed to use the new feeders more promptly and with more apparent confidence. On the other hand, the juvenile scarlet macaw at zoo A exhibited a decrease in feeding during the post-modification observations, and a stronger neophobic response to the new feeder than the juveniles at the other zoo. Being under a year old during the baseline period of observations, and then a year older in the post-modification phase, he may have been more

experienced and efficient at consuming food in the later period. Therefore, a potential age-related feeding efficiency could have masked any potential positive effects of the new feeder on this individual. Furthermore, his social environment likely had a strong effect on his behaviour as well. In the wild, young scarlet macaws develop behaviours and skills post-fledging, with social learning playing a key role in this process, as they interact with parents, siblings, and, eventually, unrelated macaws (Myers & Vaughan, 2004). In contrast, the juvenile scarlet macaw at zoo A had limited opportunities for social interactions, as he had no siblings and shared the enclosure only with his parents during the baseline period of observations, and only with his father after modifications of the enclosure, which likely impacted his behavioural and social development.

Temporary enrichment was occasionally provided to the parrots, in both phases, but only the macaw groups at zoo B seemed to engage actively with it. Therefore, it is more likely the positive trend in manipulation observed in most parrots was a result of the added supports, especially the branches which were also used for manipulation, as has been previously reported in captive parrots (Field & Thomas, 2000). The grey parrot group B's decrease in manipulation could have been motivated by differences in enclosure use caused by the vasa parrots in the post-modification period, as most of the branches added to the enclosure were on the right side, which was an area apparently dominated by the vasa parrots, while the grey parrots showed a preference for the left side, which had been enriched mostly with ropes rather than browse. Furthermore, the unchanged proportion of object manipulation in the juvenile scarlet could have also been influenced by the age difference between observation periods,

as any modification-related increases in object manipulation could have been masked by an age-related decline in this behaviour.

Individual differences in personality (Fox & Millam, 2007; Medina-García et al., 2017) and rearing method (Schmid et al., 2006) could have also played a role in the varied results observed across individuals. Neophobia and exploration-related traits have been associated with problem-solving abilities in captive parrots, their willingness to participate in cognitive tasks (Medina-García et al., 2017) and to feed in the presence of novel objects (Fox & Millam, 2007). On the other hand, wild-caught captive African grey parrots have shown more phobic behaviours than captive-hatched (both hand- and parent-reared) individuals (Schmid et al., 2006), which may also explain the grey parrot group A's lack of interest in some of the enrichment provided (e.g. puzzle feeders).

3.4.1.3. Geophagy in captive grey parrots and macaws

Geophagy, the voluntary ingestion of soil, has been observed across multiple avian taxa, including parrots (Downs et al., 2019). There are several theories as to why parrots engage in this behaviour, such as to: (1) aid digestion; (2) neutralize the toxins in the diets; and (3) supplement nutritional needs (Brightsmith & Munoz-Najar, 2004; Downs et al., 2019). Several macaw species have been observed on clay licks in Peru (Brightsmith et al., 2018), Bolivia (Mee et al., 2005) and Brazil (Severo-Neto, 2012), and of the species in the present study, geophagy has been observed in scarlet, green-

winged (Brightsmith et al., 2018), hyacinth (Coelho, 2006), and red-fronted macaws (Valdés-Peña et al., 2008), and grey parrots (May, 2001).

In the present study, while some of the scarlet macaws only briefly interacted with the clay lick enrichment, all the macaw groups at zoo B (including the juvenile scarlet macaws) were seen manipulating the clay, and potentially ingesting it as well. These differences in clay lick use may have also been due to individual variation in age, previous experiences, and personality. Differences in climate between zoos may have also influenced these results, as the distribution of parrot clay licks has been linked with temperature and humidity, and strongly associated with tropical forest areas (Lee et al., 2010). Finally, differences in the mineral contents in the diets of the parrots at both zoos may have influenced variation in this behaviour across birds. A need for sodium supplementation was identified as a potential driver for this behaviour in wild macaws (Brightsmith et al., 2018) and may have also influenced this behaviour in the captive parrots. Furthermore, a calcium deficiency could also be associated with this behaviour, as calcium is an important mineral for breeding birds (i.e. for eggshell production and the development of the chicks' skeleton; Reynolds et al., 2004). In my study, none of the parrots observed in the post-modification period laid eggs, and therefore a reproduction-related need for calcium is unlikely to have driven the geophagy behaviour seen in some of the parrots. However, further research into the mineral contents of the diets of both parrots could help to clarify whether mineral deficiencies influenced this behaviour.

The grey parrot groups were not provided with geophagy-driven enrichment, but grey parrot group B was seen digging and manipulating the soil on the ground with their feet and bills, in both phases, and it is possible they were accidentally or voluntarily ingesting it too. This behaviour has been previously reported in this species in captivity, although it was assumed the digging for foraging, rather than the ingestion of soil, was the likely goal of the birds (Berger, 2016).

While macaws and other New World parrots seem to prefer clay- and sodium-rich soils, supporting the detoxification and/or nutritional supplementation hypotheses (Brightsmith et al., 2008), geophagy in grey parrots in Cameroon was on sand-rich soils instead, which suggests they may do it as an aid to digestion or also to eliminate toxins in the diet (Bentley, 1999). Either way, geophagy seems to be an important behaviour in many parrot species, in which they engage regularly in the wild. For example, a previous study recorded scarlet and green-winged macaws on a clay lick in Peru in 85% and 80% of observations, and for a median daily time of 3.50 and 5.58 hours (i.e. species representation in the clay lick rather than the time each individual parrot spent at the lick), respectively (Brightsmith et al., 2018). Therefore, encouraging it in captivity is an important step to ensure *ex situ* populations retain this activity in their behavioural repertoire, even if they are nutritionally supplemented with the necessary minerals in their normal diet.

3.4.1.4. Locomotion of captive grey parrots and macaws

Locomotion is another important behaviour in the daily activity of free-living parrots, as they must travel between and within sites to explore the resources of their environment

(e.g. Brightsmith et al., 2021). The time budgets of free-living yellow-fronted parrots showed they engaged in locomotion in 3% of observations (Hailu et al., 2019), while naturally occurring and released captive-bred scarlet macaws were seen moving in 15% (section 2.3.1) and under 6% (Cornejo et al., 2005) of observations, respectively. In the present study, the scarlet macaws showed similar to slightly lower locomotion proportions than their free-living counterparts, while the grey parrot groups A and B moved in similar and slightly higher proportions than wild yellow-fronted parrots, respectively. Note, however, that the available proportions of locomotion in the field studies are likely an underestimation, as (1) there is locomotion involved in other behavioural categories (e.g. moving while searching for food is often placed under foraging, as mentioned in section 3.4.1.2) and (2) parrots are difficult to follow and observe over large distances, and therefore these only account for observable short-range locomotion. Estimates of long-distance locomotion showed that grey-headed parrots (*Poicephalus fuscicollis suahelicus*) travelled approximately 20 km in the early morning alone (Symes & Perrin, 2003a), while scarlet macaws (Brightsmith et al., 2021) and military macaws (*Ara militaris*; Bonilla-Ruz et al., 2007) showed maximum daily flight distances of 40 and 20 km on average, respectively, which highlights the mobility of free-living parrots.

Nevertheless, data from the post-modification period highlighted a positive change in locomotion in most parrots. This is likely associated with an improvement in welfare, as locomotion has been found to be negatively associated with stress, suggesting that active parrots cope better with stressors in the environment (de Almeida et al., 2018), and that inactivity may be a response to stress, as previously discussed (section

3.4.1.1). The supports and structural complexity added as elements of enclosure modification were used by all parrots except scarlet macaw 3, and therefore likely had an impact on the results observed for those birds, as previous studies have shown that increasing the physical complexity of the environment elicits locomotion in captive parrots (Clyvia et al., 2015; van Hoek & King, 1997b). The hanging feeders also likely had an effect on the positive changes in locomotion in all birds that used them (i.e. all but adult scarlet macaws at zoo B).

A previous study that investigated the effect of several foraging enrichment items on the behaviour of captive grey parrots found no impact on locomotion from and to the feeders/enrichment, and only in the foraging process itself (van Zeeland et al., 2013a). However, unlike those, the feeders in the present study were more challenging to access and required more complex climbing and flying to access food from them. The macaw groups utilised the supports and feeders, and exhibited relatively high engagement in locomotion, which concurs with their high activity levels already discussed for other behaviours. The social environment has been found to influence the activity, including locomotion, of captive parrots (Meehan et al., 2003), and sharing an enclosure with younger and more active individuals could have influenced the changes in locomotion in scarlet macaws 2 and 3. As scarlet macaw 3, especially, did not use the new supports or feeders, and was observed socialising with heterospecifics, the social rather than physical changes in the environment are a more likely explanation for the changes in his behaviour. It is possible that the increased locomotion observed in most parrots at zoo B was associated with social tension caused by the more dynamic social environment in the post-modification period (a

negative impact on welfare would be more likely in this scenario). Although behaviours that involved locomotion but were motivated by negative social interactions (e.g. displacement, chasing or being chased by another bird) were recorded as social interactions, it is still possible that some of the locomotion recorded was subtly motivated by other birds in the enclosure. Further research should investigate the relative effects of physical and social changes in the environment on parrot behaviour and welfare.

The juvenile macaw's difference in age between periods of observations may have impacted his locomotory responses, but it is unclear why grey parrot group A and scarlet macaw 1 failed to exhibit locomotory responses to the modifications. These individuals used more complex supports in the post-modification period, and therefore their locomotory responses may have been more qualitative than quantitative.

3.4.1.5. Self-maintenance and social behaviours in captive grey parrots and macaws

Most birds engage in preening and other maintenance behaviours, which serve, among others, hygienic (e.g. feather cleaning, rearrangement and parasite removal) and social (e.g. courtship and social bonding) purposes (Spruijt et al., 1992). Preening can also serve a stress-coping function (Delius, 1988), and it has been found that wild glaucous-winged gulls (*Larus glaucescens*) engaged more in this behaviour after spotting a predator (Henson et al., 2012), while captive birds often display feather

damaging behaviour because of stress-induced excessive preening (van Zeeland et al., 2009).

The time budgets of free-living parrots showed that yellow-fronted parrots spent 22.5% of their time engaged in preening and comfort behaviours (Hailu et al., 2019), while scarlet macaws were engaged in maintenance behaviours in 15% of observations (section 2.3.1). Released captive-bred scarlet macaws spent 18.2% (section 2.3.1) and 17% (Cornejo et al., 2005) of observations in preening and other maintenance behaviours. Although some parrots in my study exhibited differences in this behaviour between both periods of observations, the overall proportion of this behaviour was still lower than reported for the free-living yellow-fronted parrots. It is unclear whether the varied changes observed across the captive parrots in my study were associated with an improvement or deterioration of welfare. On one hand, the occurrence of preening in the present study did not exceed that of the free-living parrots in any of the captive parrots, and as feather-damaging behaviour was also not detected, there is no clear evidence of excessive preening associated with stress, as is often reported in captive parrots (van Zeeland et al., 2009). On the other hand, scarlet macaw 3, being a physically and behaviourally-limited individual, could have experienced stress in the more dynamic social environment (i.e. more individuals, especially juveniles, of more species), and preened more as a coping response (Delius, 1988). Furthermore, the social function of preening behaviour (Spruijt et al., 1992) means that changes in self-maintenance behaviour could have also been linked with differences in social behaviour exhibited between observation periods. The differences in morning and afternoon observations between the baseline and post-modification periods may have

also had a confounding effect on scarlet macaw 3's significant increase in self-maintenance behaviour.

Rain bathing was seen in the parrots at zoo B but not zoo A, which could have been due to the: (1) tropical environment and higher temperatures at zoo B; (2) enclosures in zoo A being more sheltered from rain; and (3) sprinkler system at zoo B to spray the enclosure, which likely encouraged this behaviour. Murphy et al., (2011) found that spraying captive orange-winged Amazon parrots with water in a similar way to rain in their natural habitat, encouraged wild-type bathing postures and behaviours. This may have enhanced their welfare, by encouraging natural behaviours and potentially improving feather quality (Murphy et al., 2011). Further encouraging this behaviour at both zoos could therefore be beneficial for the parrots, although the low temperatures experienced at zoo A in the colder seasons must be taken into consideration as well.

Parrots are generally social animals, that can live in flocks of sizes varying from a few individuals to thousands (Gilardi & Munn, 1998), a behaviour that provides anti-predator and foraging advantages in the wild (Caraco et al., 1980). Allopreening is a particularly important social behaviour, providing mutually beneficial hygienic effects (e.g. allowing cleaning and maintenance of feathers in areas difficult to access in self-preening) and helping to develop and maintain social bonds (Morales Picard et al., 2020). Available quantitative data for wild yellow-fronted parrots showed they spent 12.2% of their time in social behaviours (Hailu et al., 2019). On the other hand, *in situ* qualitative observations of grey-headed parrots described several social activities in

the species, including allopreening, social play, and agonistic interactions (Symes & Perrin, 2014). In captivity, parrots deprived of social interactions may exhibit increased stereotypic behaviour (Meehan et al., 2003; Williams et al., 2017), decreased activity (Meehan et al., 2003), and shortened telomeres (i.e. a biomarker associated with chronic stress; Aydinonat et al., 2014), all often associated with negative welfare states. None of the parrots in the present study was housed singly or without conspecifics, but some individuals showed limited social behaviours.

The limited social behaviour observed in both grey parrot groups could have been due to low compatibility among individuals, which has been found to affect social behaviour and reproduction in captive cockatiels (*Nymphicus hollandicus*; Fox & Millam, 2014; Spoon et al., 2007). Also, grey parrot group B was composed of birds that were ex-pets that had been potentially hand-reared and thus may have impaired social behaviours due to an inadequate social environment in their early development (Schmid et al., 2006). Furthermore, the grey parrot group A's significant decrease in social behaviour in the post-modification period may be associated with the loss of five group members between periods of observations, which further reduced social opportunities, especially if these were among the few individuals in bonded pairs observed in the baseline period.

Wild scarlet macaws were seen socialising in 6.3% of observations (section 2.3.1), while their released captive-bred counterparts socialised in 9% (Cornejo et al., 2005) and 7.2% of the intervals (section 2.3.1). The proportions of social behaviour observed

in the scarlet macaws at zoo A did not greatly deviate from those of their free-living counterparts. The female's higher engagement in social behaviours was likely due to her interactions with both the male and the juvenile scarlet macaws, while these two barely interacted with each other in the baseline period. After the female's death, the male-juvenile's social dynamics changed, with an increase in interactions, which may have been due to a drop in territorial and mate guarding behaviours in the male, both having been previously reported in wild parrots (Arnett & Pepper, 1997; Renton, 2004). That change in the social environment seemed to have reduced the likely impact of the female's death on their social behaviour, as neither showed significant changes in the proportion of time spent socialising in the post-modification period, and the juvenile even showed a slight increase. However, the social behaviour of the juvenile could have been enhanced by the presence of more macaws, as wild juvenile scarlet macaws spend a relatively high proportion of their time with both related and unrelated macaws, engaging in social play and other interactions (Myers & Vaughan, 2004). The social behaviour in the male and juvenile scarlet macaws at zoo A showed contrasting changes in the morning and afternoon. However, having the same sampling pattern in both periods could have only strengthened the increase in social behaviour to a significant threshold in the juvenile scarlet macaw.

At zoo B, scarlet macaw 1 showed little engagement with the new macaws in the enclosure, so any positive trends in this behaviour were more likely due to spending more time in close proximity to scarlet macaw 2, with whom it had a social bond. Scarlet macaw 3, on the other hand, interacted with the new hyacinth macaws in the enclosure, which may have reduced but did not mitigate the effect of the death of scarlet macaw

4, with whom it had most of the interactions during the baseline period of observations. The social play, and social behaviour in general, observed in the macaw group concurs with observations of social interactions between juvenile macaws in the wild (Myers & Vaughan, 2004).

3.4.2. Enclosure use by captive grey parrots and macaws

3.4.2.1. Horizontal use of the enclosure by captive grey parrots and macaws

A more even use of the horizontal space in the enclosure was detected for several parrots in the post-modification period of observations. In the male scarlet macaw at zoo A and scarlet macaw 2 at zoo B, these results concur with their increased activity in the post-modification period, as they likely moved and explored more of the enclosure. Scarlet macaw 1 and grey parrot group A, despite showing no significant increases in activity in their time budgets, also used more of the available horizontal space, a potential response to the higher, and more scattered, complexity within.

Intra- and/or inter-specific territoriality may have also played a role in these observations, as its impact on the space use of captive birds generally in mixed-species aviaries has been previously suggested (Blanchett, 2018), and both the grey parrot group and scarlet macaws at zoo B were housed with multiple other parrot species. Increased complexity within the enclosure provided the groups with more opportunities to disperse and avoid conspecifics and/or heterospecifics. Grey parrot group B's post-modification space use was likely hindered by the presence of the vasa parrots in this period of observations, as the grey parrots avoided the right side of the

enclosure, which was apparently dominated by the other species, but used the left side of the enclosure more evenly than in the baseline period, potentially due to increased activity and/or individual dispersal.

The juvenile scarlet macaw's decrease in activity and improved social dynamics with his father (spending more time with him in his preferred section) could explain why he showed an increase in SPI, while scarlet macaw 3's decreased use of the enclosure was probably a response to a more crowded and dynamic environment caused by its enclosure mates. The low SPI observed within the macaw group concurs with the activity and exploration levels observed in these groups.

3.4.2.2. Vertical use of the enclosure by captive grey parrots and macaws

Post-modification changes in the vertical use of the enclosure were more homogeneous across parrots than horizontal space use, with significant increases in the use of the top sections by all parrots in the present study. Parrots at zoo A already used the top section the most during the baseline period, as they had some high structures in the enclosure, but increasing the vertical structural complexity further increased use of the top of the enclosure. The enclosures at zoo B during the baseline period had very limited structures in the top ¼ of the enclosure, and therefore use of that area of the enclosure was rare. In contrast, most parrots used the high structures added to the enclosure in the post-modification period of observations, which likely influenced the increased use of the top of the enclosure. Scarlet macaw 3 did not use the added high perches in the enclosure, and therefore, while those may have

motivated the improved vertical use in most individuals, the increased use of the top by this bird in the post-modification period was more likely a response to the more crowded, socially dynamic, and potentially stressful environment.

Free-living grey parrots forage mostly in the tree canopy (Tamungang & Ajayi, 2003), as there is an increased vulnerability to predators on the ground, but there are reports of ground foraging and geophagy in this species (Bentley, 1999; May, 2001). Furthermore, in captivity, ground-level enrichment can be an effective way to increase activity in these birds (Berger, 2016). In the present study, grey parrot group A's use of the ground following modifications may have been motivated by the clearing of some of the understory vegetation in the enclosure, as in the wild they seem to prefer clearings for ground foraging, probably for increased visibility and predator detection (Bentley, 1999). On the other hand, grey parrot group B's post-modification decrease in ground use was more likely due to the increased vertical complexity in the enclosure, especially the new hanging feeders, which encouraged them to feed higher up instead of on the ground trays as in the baseline period. Therefore, the post-modification pattern of vertical use in both grey parrot groups more closely resembled that of their free-living counterparts. If captive parrots are to be considered for reintroduction programmes, they need to be encouraged to spend less time on the ground, as they will otherwise be vulnerable to predation once released into the wild.

Free-living scarlet macaws in Costa Rica were not seen on the ground (section 2.3.1), concurring with long-term observations of this species in Costa Rica and Peru that

suggest they avoid the ground and only descend on riverbanks to drink water and engage in geophagy (G. Viggo, pers comm., 2022). Similar to their free-living counterparts, the scarlet macaws at zoo A were rarely on the ground, in either period of observations, and descended mostly for drinking or to pick up fallen food. In contrast, scarlet macaws 1 and 2 at zoo B spent a higher proportion of their time on the ground, without significant post-modification changes, likely because they did not use the new feeders, and still fed on the ground trays as in the baseline period. Scarlet macaw 3 still stayed on the ground the most, as expected due to its neurological condition, and the significant decrease of ground use observed in this individual is likely associated with the social environment that has also caused the increase in the top use of the enclosure, as mentioned above. The macaw groups showed relatively high diversity of vertical space use, with some ground use observed but a higher proportion of the time in the middle and of top of enclosures. All groups used the hanging feeders and added supports, and all but the green-winged macaws also used the ground trays, which may explain the results observed. Available data across wild macaw species suggest that like the scarlet macaws, they also spend most of their time in the tree canopy, although they may descend to lower vegetation or even the ground for foraging opportunities (Berg et al., 2007; Pinho & Nogueira, 2003; Pitter & Christiansen, 1995).

3.4.3. Effects of visitors on the behaviour and enclosure use of the captive grey parrots and scarlet macaws at zoo A

The responses of zoo-housed parrots to visitors differed within and across studies, with some parrots retreating in their presence, and others showing an increase in social behaviour (Collins & Marples, 2015) or even exhibiting potential behavioural signs of

trying to attract their attention (e.g. vocalisations) or missing them when the zoo was closed (e.g. increased alert-type behaviour that could have been associated with an altered auditory environment in the absence of visitors but also attempts to look out for people; Frost et al., 2022).

Differences in behaviour between days when the zoo was open versus closed to visitors, and therefore potential responses to the presence of visitors, have also varied across parrots in the present study. The grey parrot group showed lower activity when the zoo was open, in both baseline and post-modification periods, which concurs with findings on other captive species (e.g. Indian leopards [*Panthera pardus*]*;* Mallapur & Chellam, 2002; flamingos [*Phoenicopterus* spp.]; Kidd et al., 2022). As birds in the grey parrot group hatched in the wild, increased phobic behaviours, and fear of humans were expected (Schmid et al., 2006), especially because they likely experienced high physical and mental stress when captured for the pet trade (Collard, 2014). Differences in enclosure use also suggest a response to visitors, as despite their general preference for the top of the enclosure, they used it even more when the zoo was open, probably because they felt safer at height (section 3.4.2.2) and had better visibility over their surroundings. Increased vigilance in the presence of visitors has been detected in other captive bird species (Sherwen et al., 2015). The grey parrots also favoured the left side of the enclosure, which was more sheltered and concealed, but this was only observed following enclosure modification, and therefore the changes in the enclosure (i.e. increased complexity in all corners, and both sides, of the enclosure) likely gave the grey parrots increased opportunities to perch in areas in which they felt more comfortable and safer when visitors were present. A similar response to visitors has

been observed in other captive birds in a walkthrough exhibit, as they moved away from the visitor path when there were more visitors in the exhibit (Blanchett et al., 2020).

The scarlet macaws seemed to respond differently to visitors. Qualitative observations suggest the male scarlet macaw was comfortable with humans, and therefore the contrasting differences observed in his use of the top of enclosure could have been because (1) being higher up in the enclosure provided better visibility to observe visitors across the park, which concurs with anecdotal evidence some macaws look out for visitors (Frost et al., 2022), but simultaneously (2) being lower down in the enclosure allowed for closer contact with visitors in the vicinity of the enclosure, which concurs with observations of the male actively approaching the visitors. The juvenile scarlet macaw also showed mixed responses to visitor presence. On the one hand, the higher use of the more concealed right side of the enclosure on open days during the baseline period, and higher proportion of medium activity behaviours (i.e. including preening, which can be a comfort behaviour in response to stressors; Delius, 1988) could indicate a phobic response to visitors. On the other hand, the increased post-modification low activity (i.e. perching, which includes alert behaviour) and use of the left side of the enclosure (i.e. better visibility over the theme park area) on open days could have been to look out for visitors, as previously suggested by Frost et al., (2022). As the social environment can influence the phobic behaviour of captive parrots (Meehan et al., 2003), the juvenile scarlet macaw's improved relationship with the male scarlet macaw, that exhibited low fear of humans, could have had an effect on his own response to visitors. Therefore, while the grey parrot group seemed to exhibit a

consistent phobic response to visitors and may have benefitted from the enclosure modifications with increased opportunities to avoid humans, the scarlet macaws' responses were inconsistent, with evidence of varied effects across individuals.

The complexity of visitor effects on zoo animals has been highlighted before, with previous studies finding it could be overestimated in its relationship with other factors, such as weather (Goodenough et al., 2019; Rose et al., 2020). Although data were collected at the same time of year, and only subtle variation in weather and temperature was detected, they could have had a confounding effect. These apparent inconsistencies may also be explained by the "dither effect" proposed by Krebs et al., (2022), which suggests that zoo animals exhibit non-linear positive and negative responses to visitors as their densities vary. However, data on visitor densities, near the enclosures or at the zoo in general, were not available from either phase in the present study, and therefore this cannot be confirmed.

Furthermore, differences in the auditory environment between days, and not just the absence and presence of visitors, may have had an impact on the results. Previous behavioural responses of captive birds, including parrots, to various auditory stimuli suggest they can find it either stressful or enriching (Robbins & Margulis, 2016; Williams et al., 2017). Being housed at a zoo and theme park, the parrots in the present study were exposed to a rich auditory environment (e.g. rides, music). This was less pronounced on days when the zoo was closed, which were quieter, but noise could occasionally be heard (e.g. construction work within the park, sound tests) and could

have impacted their behaviour even if there were no visitors in the park or the adjacent area to their enclosures had low visitor density.

3.5. Conclusion

In the period following the modification of the enclosures, most parrots exhibited increased expression of natural behaviours (e.g. feeding and locomotion) and/or improvements in enclosure use (e.g. more even use of horizontal space and increased use of the top of the enclosure), although the behavioural responses varied across parrots. It is possible these improvements were caused by the modifications applied to the enclosures, but changes in the parrots' social environment likely played a role in these results as well. More research is required to determine the relative effects of physical and social changes to the *ex situ* environment on the behaviour and welfare of the parrots. The changes in behaviour observed in the juvenile scarlet macaw (zoo A) between periods of observations were likely affected by differences in age between periods, as he was still sexually maturing, which confounded any potential effects of the physical modifications to the enclosure. Increasing the sample size in future studies, with the inclusion of more parrots of varied ages, and enclosures across *ex situ* facilities, can help to clarify how the physical modifications affect the behaviour and welfare of captive parrots on an individual level.

Despite the improvements observed in the behavioural repertoire of some of the captive parrots, all the adult parrots showed high levels of inactivity, and some important natural behaviours, such as foraging, were still lower in frequency than

reported for their free-living counterparts. Additional adjustment and refinement of the modifications applied could be assessed in future studies, with the aim of further enabling natural behaviours in the captive parrots. Finally, there were potential visitor effects on the behaviour of the parrots at zoo A, as there were differences in behaviour and enclosure use between days when the zoo was open versus closed to visitors. These potential behavioural responses to visitors varied within and across parrots.

While this chapter focussed on the activity budgets and enclosure use of the captive grey parrots and macaws, Chapter 4 will focus on their cognition, locomotion, and social behavioural repertoires. Data generated in the present chapter will be used to contextualise the findings of Chapter 4.

CHAPTER 4

A COMPARISON OF THE COGNITION, LOCOMOTION, AND SOCIAL BEHAVIOURAL REPERTOIRES OF CAPTIVE GREY PARROTS AND MACAWS BEFORE AND AFTER PHYSICAL AND SOCIAL CHANGES IN THEIR *EX SITU* ENVIRONMENT

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[1] Collected and analysed all data.

ABSTRACT

The advanced cognitive abilities of wild parrots allow them to explore and adapt to different environments, as well as effectively forage on varied food items from multiple plant species. They are also proficient at climbing on varied and challenging supports, by using their bill as a third limb (i.e. in so-called tripedal locomotion), as well as flying, and are generally social animals that are capable of long-term social bonds. Captive parrots are often restricted from engaging in these natural behaviours, which compromises their welfare and future participation in reintroduction programmes. The enclosures of two grey parrot groups and eight scarlet macaws (a group of five and a group of three) at two zoos were modified with the aim of enabling wild-type cognition, locomotion and social behaviours in the captive parrots. The modifications included an increase and re-distribution of structural supports within the enclosure and hanging feeders that partially concealed the food from the parrots. Changes in the social environment of the parrots (i.e. addition and/or loss of birds) also occurred between the baseline (before modifications) and post-modification periods of observations. Focal interval sampling was used to assess the cognition, locomotion and social behavioural repertoires of the captive parrots in both periods of observations, while rates of flights and social interactions were recorded with *ad libitum* continuous sampling. Baseline behavioural observations showed an overall low engagement in challenging food manipulation, as well as low foot use during food and object manipulation. The captive parrots used mostly unchallenging supports (i.e. stable, horizontal and/or thick perches, or the wire mesh), and exhibited low flight rates. While all scarlet macaws engaged in affiliative behaviours with at least one conspecific, the grey parrot groups showed weak social bonding. Significant behavioural changes were

detected across parrots in the post-modification period, including an increase in climbing (some scarlet macaws) and flying (both grey parrot groups), improvements in support use, and changes in the social dynamics within parrot groups. These behavioural changes varied across parrots and were likely motivated by both physical and social changes that occurred in the parrots' environment. It is possible that the enclosure modifications had a positive effect in enabling wild-type cognition, locomotion, and social behaviours in the captive parrots, but further research is recommended.

Keywords: animal welfare, enclosure modifications, *ex situ*, Psittaciformes

4.1. Introduction

Parrots exhibit high behavioural plasticity, with the ability to switch habitats, diets and foraging strategies to meet resource requirements (Renton et al., 2015). Such flexibility is key for wild animals to adapt to novel, complex and dynamic environments, and has been linked with advanced cognitive abilities (Szabo et al., 2020), such as those already described for parrots (section 1.5.2). The varied locomotion abilities (such as climbing [Reader et al., 2022] and flying [Whitney, 1996]) and highly social behaviour (Thoft & Wright, 2015) of parrots also facilitate their adaptation to highly diverse and complex environments.

4.1.1. Cognition and manipulation skills of parrots

Both scarlet macaws and grey parrots feed from a high diversity of plant species in the wild, with 43 and 15 plant species recorded in the diets of scarlet macaws in Costa

Rica (Vaughan et al., 2006) and Belize (Renton, 2006), respectively, and 14 tree species reported for grey parrots in Cameroon (Tamungang and Ajayi, 2003). Benavidez et al., (2018) reviewed the available literature on the diets of neotropical parrots and found that scarlet macaws feed mostly on seeds (48.9% of food items consumed) and fruit (29.5%), which was also reported for other macaws (*Ara* spp.; seeds: 29.4–56.5%; fruit: 18.2–55.6%). Flowers, leaves, and bark were also present in the diets of some of the macaw species, while only seeds were reported in the diets of hyacinth macaws (Benavidez et al., 2018). On the other hand, the diets of grey parrots in Cameroon were found to consist mostly of fruit (53.3% of food sources), seeds (26.7%) and flowers (20.0%; Tamungang and Ajayi, 2003). In order to consume the nutritious contents of the fruits and seeds they primarily feed from, those parrot species need to extract them from within the (often hard) coat/cover that protects them (Thoft & Wright, 2015), as evidenced in Figure 4.1 (grey parrots) and Figure 2.7 (scarlet macaws).

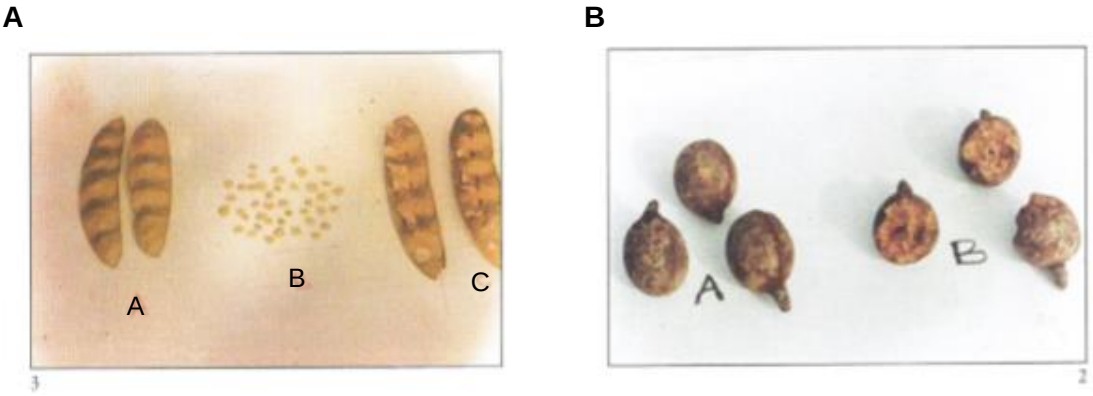


Figure 4.1. Fruits of two tree species before and after manipulation and consumption by free-living grey parrots in Cameroon.

Panel A: peacock flower (*Albizia gummifera)* (A) whole fruit, (B) seeds eaten by the grey parrots, and (C) remains after parrot manipulation. Panel B: false nutmeg (*Pycnanthus angolensis*) (A) young whole fruits, and (B) remains after grey parrots extracted seeds within. (Photos: Tamungang & Ajayi, 2003).

To do it, parrots use both their zygodactyl feet (Sustaita et al., 2013) and powerful bills and mandibles (Tokita, 2003), with larger parrots more likely to rely more on seeds than fruit pulp in their diets (Matuzak et al., 2008). Some parrots have also been observed using tools to aid in manipulation efforts, such as wild Goffin's cockatoos (*Cacatua goffiniana*; Mioduszewska et al., 2022); captive greater vasa parrots (Lambert et al., 2015) and hyacinth macaws (Borsari & Ottoni, 2005), further highlighting their cognitive and problem-solving abilities. Therefore, the high complexity of the diets of wild scarlet macaws and grey parrots is evidenced by the diversity of food items they consume across the multiple plant species they feed on, and the extensive manipulation and processing they require.

In *ex situ* settings, parrot species with larger brains (i.e. potential indicator of advanced cognitive abilities; section 1.5.2) and those that rely on substantial manipulation for feeding in their natural environment, are more likely to develop abnormal behaviours (Mellor et al., 2021). Therefore, advanced cognitive abilities of parrots, and their behavioural ecology in the wild, suggests that captive parrots benefit from increased cognitive stimulation and challenges in their *ex situ* environment.

4.1.2. Locomotion skills and adaptations of parrots

Parrots are proficient climbers and use their zygodactyl feet and bills to pull themselves upwards on vertical structures (Reader et al., 2022). The bill works therefore as a third limb during climbing (i.e. tripedal locomotion), generating propulsive forces that match or exceed those generated by the forelimbs of climbing primates (Young et al., 2022).

Parrots likely evolved this adaptation, unique among avian taxa, due to their arboreality, facilitating their locomotion across the varied branches within the trees (Reader et al., 2022). When on horizontal structures, parrots often opt for bipedal locomotion (i.e. walking; Young et al., 2022), with hopping rarely observed in this taxon (Provini & Höfling, 2020). Parrots are also generally competent flyers (Whitney, 1996), using this type of locomotion to move within and across habitats for their various daily activities (e.g. Amuno et al., 2007; McReynolds, 2012; Symes & Perrin, 2003b; Tella et al., 2015). In captivity, they have limited locomotion opportunities (Meehan & Mench, 2006), and often exhibit a reduced flight ability, which can be a result of several factors associated with the captive environment, such as space limitations (Engebretson, 2006), obesity and malnutrition (Larcombe et al., 2015), and/or a personality-dependent reduction in the fight-or-flight response (Franzone et al., 2022).

4.1.3. Social behaviour of parrots

Parrots are highly social animals, as highlighted by their ability to develop long-term pair bonds (i.e. social monogamy), which seems to be predominant across parrot taxa, even though other mating systems have also been reported (Thoft & Wright, 2015). It has been suggested that the ability to develop such bonds is linked with advanced cognitive abilities, with parrots exhibiting social alliances that are comparable in durability and stability to those of primates (Primates) and dolphins (Delphinidae; Emery et al., 2007). The sociality of parrots is also evidenced by their flocking behaviour, with flock sizes that shift throughout the day and across seasons, and can be composed of a few individuals (e.g. family units) up to much larger groups (e.g. Boyes & Perrin, 2009; Caledonia et al., 2012; Chapman et al., 1989; Symes & Perrin,

2003b). While macaw species are more often observed in small groups (Gilardi & Munn, 1998), grey parrots can be seen in large flocks (May, 2001) of up to 1,000 individuals (World Parrot Trust, 2018), although small flocks have also been previously reported in this species, which could have been a result of habitat fragmentation (Amuno et al., 2007). Captive parrots often have limited opportunities for social interactions, either because they are housed without conspecifics (Engebretson, 2006), or due to low compatibility with their enclosure mates that result in weak social bonding (e.g. Fox & Millam, 2014; Spoon et al., 2007). Those inadequate social environments have been found to result in compromised welfare (Aydinonat et al., 2014; Meehan et al., 2003) and reduce breeding success (Fox & Millam, 2014; King, 2000) of captive parrots. Therefore, it is important to consider the natural social structure of wild animals when evaluating and establishing the social environments of their captive counterparts (Whitham & Miller, 2019).

The aims of this study are to (1) assess the cognition, locomotion and social behavioural repertoires of captive grey parrots and scarlet macaws, and (2) determine the effects of physical and social changes in the *ex situ* environments on those behavioural repertoires.

4.2. Materials and methods

The location, species, individuals, and periods of observations included in this study were previously described in section 3.2.1. In addition, social data were collected on the scarlet macaws at zoo A in May and June 2021 (i.e. period between the baseline

and post-modification periods, when the female scarlet macaw died at the end of May) and included in the social section of the study. A description of housing conditions can be found in sections 3.2.3 (baseline period) and 3.2.5 (post-modification period), while a summary of the enclosure modifications was presented in section 3.2.4. The protocols for data collection were also presented in section 3.2.2, and the ethograms can be found in section 2.2.4 (Table 2.1–2.6). As flights were often quick events that were not captured in the 30-second intervals, additional *ad libitum* continuous recording of flight occurrences of individual scarlet macaws was conducted as part of the 30-minute sessions in the locomotion protocol. An occurrence was recorded each time the behaviour was observed in the focal individual between the 30-second intervals. These were categorized as: short – up to half the length of the enclosure; long – up to one length of the enclosure; extra – greater than the total length of the enclosure. However, when sampling the grey parrot and macaw groups, *ad libitum* continuous recording of flight occurrences was conducted in separate 10-minute sessions, after a session of each protocol (i.e. cognition, flights, locomotion, flights, social, flights; up to three sessions, 30 minutes in total, per day), with an occurrence recorded each time any individual within the group was seen flying. Furthermore, as some social interactions were also quick events not captured in the intervals, *ad libitum* continuous recording of affiliative and aggressive interactions in the individual scarlet macaws was also conducted as part of the 30-minute sessions in the social protocol. These data were not collected when sampling groups because it would have to be collected in separate sessions, which was not possible due to time constraints. When sampling occurrences and intervals simultaneously in individual scarlet macaws, to avoid repetition of data, an occurrence was only recorded if it was not included in either

of the two intervals it was observed between. For example, if a bout of allopreening behaviour started and finished between intervals, it was recorded as one occurrence, but if it started before a 30-second interval and lasted uninterruptedly until that interval, it was only recorded in the interval.

4.2.1. Data analysis

The software used for the statistical analysis, as well as the R packages used in data processing were the same as presented in section 3.2.6. Randomisations (based on 10,000 permutations) were used to look for differences between baseline and post-modification phases in proportions of basic manipulation, foot use, tripedal locomotion, support characteristics, allopreening, observations with no conspecifics within length, observations with no conspecifics within 2 m, hourly flight rates and hourly rates of affiliative and aggressive interactions. As previously described (section 3.2.6.3), randomisations are commonly used in zoo-based research as they are a suitable statistical test to use when comparing the same animal in two conditions (i.e. autocorrelated data) while focusing on a single variable of interest (Bishop et al., 2013). Comparing proportions of a behaviour between periods of observations allowed me to account for differences in sample size between periods of observations and determine changes in the parrots' engagement in that behaviour in relation to the other behaviours in their repertoire. For example, when comparing the parrots' use of horizontal perches between periods of observations, a significant decrease in the proportion of observations of parrots on this type of perches would mean that they opted to use horizontal perches less and instead use more the non-horizontal perches. The Chi-squared test of independence with adjusted standardised residuals (reasoning

to select this test and procedure was same as discussed in section 3.2.6.1) was conducted only for support use, as the goal was to identify any differences in use of multiple types of supports (i.e. ground, wire mesh, platform, stable perches, unstable perches). Statistical significance was determined when the adjusted $p<0.05$ (adjusted for multiple testing; section 3.2.6.3).

The body parts used during food and object manipulation were grouped into two categories for the analysis: foot (when foot was used alone or in combination with bill) and bill (when only the bill, tongue or both were used). Flight rates were estimated by dividing the number of flight occurrences of each type (short, long, with extra-long flights combined with long for the analysis as they were rarely observed) by the number of hours of observations on each day of data collection. When estimating flight rates of groups, the number of occurrences was divided by the number of individuals physically capable of flying. All individuals within grey parrot group B could fly, in both phases, but in grey parrot group A, only 12 of the 16 were capable of flying during the baseline period (as confirmed by both zoo staff and the observer), while in the post-modification period, 10 of the 11 remaining individuals were capable of flight. Within the macaw groups at zoo B, the scarlet macaw group had two individuals that were not included in the flight rate analysis (scarlet macaws 2 and 3), but all the other individuals in each species were considered. The rates of affiliative and aggressive interactions were estimated by dividing the number of occurrences by the number of hours of observations on each day of data collection.

The social data collected on the scarlet macaws at zoo A, in the summer 2021, were included to investigate weekly differences in social behaviours between the male and juvenile scarlet macaws before and after the death of the female. These data were not included with the baseline data, because even though they were collected in the pre-modification period, they were collected in a different season and with contrasting temperatures and day lengths.

4.3. Results

During the baseline period of observations, an average of 1,319 (1,197-1,616), 1,281 (1,135-1,556) and 1,276 (1,133-1,550) intervals were collected across individuals for the cognition, locomotion and social protocols, respectively (Tables 4.1 and 4.2).

Table 4.1. Summary of data collected at zoo A (Drayton Manor Park and Zoo, UK), on each protocol of data collection, per scarlet macaw and grey parrot group, in the baseline and post-modification periods of observations.
The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots), October – December 2020 (scarlet macaws). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021. The number of intervals considered for the analysis (excluding when any bird was out of sight) are represented by "n". Total numbers of hours and days of observations are also included.

		Baseline			Post-modification		
Individual	Protocol	n	Days	Hours	n	Days	Hours
Grey parrot group A	Cognition	1,616	26	13.5	1,555	26	13
	Locomotion	1,556	26	13	1,554	26	13
	Social	1,550	26	13	1,552	26	13
Male scarlet macaw	Cognition	1,287	22	11	1,501	26	13
	Locomotion	1,256	22	11	1,446	25	12.5
	Social	1,275	22	11	1,359	24	12
Female scarlet macaw	Cognition	1,268	22	11	-	-	-
	Locomotion	1,284	22	11	-	-	-
	Social	1,277	22	11	-	-	-
Juvenile scarlet macaw	Cognition	1,255	21	10.5	1,459	25	12.5
	Locomotion	1,257	21	10.5	1,482	25	12.5
	Social	1,246	21	10.5	1,458	25	12.5

Table 4.2. Summary of data collected at zoo B (Jurong Bird Park, Singapore), on each protocol of data collection, per macaw and grey parrot group, in the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in January – March 2020, while the post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in December 2021 – January 2022. The number of intervals considered for the analysis (excluding when the animal was out of sight) are represented by "n". Total numbers of hours and days of observations are also included.

		Baseline			Post-modification		
Individual	Protocol	n	Days	Hours	n	Days	Hours
Grey parrot group B	Cognition	1,430	24	12	1,200	20	10
	Locomotion	1,431	24	12	1,198	20	10
	Social	1,433	24	12	1,139	19	9.5
Scarlet macaw 1	Cognition	1,198	20	10	1,106	19	9.5
	Locomotion	1,135	19	9.5	1,197	20	10
	Social	1,133	19	9.5	1,137	19	9.5
Scarlet macaw 2	Cognition	1,197	20	10	1,097	19	9.5
	Locomotion	1,138	19	9.5	1,200	20	10
	Social	1,136	19	9.5	1,136	19	9.5
Scarlet macaw 3	Cognition	1,318	22	11	598	10	5
	Locomotion	1,260	21	10.5	599	10	5
	Social	1,280	22	11	598	10	5
Scarlet macaw 4	Cognition	1,303	22	11	-	-	-
	Locomotion	1,248	21	10.5	-	-	-
	Social	1,244	21	10.5	-	-	-
Scarlet macaw 5	Cognition	1,317	22	11	-	-	-
	Locomotion	1,245	21	10.5	-	-	-
	Social	1,182	20	10	-	-	-
Great green macaw trio	Cognition	-	-	-	148	15	7.5
	Locomotion	-	-	-	142	14	7
	Social	-	-	-	122	12	6
Green-winged macaw pair	Cognition	-	-	-	106	15	7.5
	Locomotion	-	-	-	97	14	7
	Social	-	-	-	81	12	6
Hyacinth macaw pair	Cognition	-	-	-	102	15	7.5
	Locomotion	-	-	-	87	14	7
	Social	-	-	-	77	12	6
Red-fronted macaw group	Cognition	-	-	-	203	15	7.5
	Locomotion	-	-	-	224	14	7
	Social	-	-	-	170	12	6
Scarlet macaw group	Cognition	-	-	-	305	15	7.5
	Locomotion	-	-	-	289	14	7
	Social	-	-	-	260	12	6

In the post-modification phase, the average number of intervals for each protocol was similar to those in the baseline period across individuals (Cognition: 1,320; Locomotion: 1,346; Social: 1,297; Tables 4.1 and 4.2), except for scarlet macaw 3 at zoo B (598-599), on whom sampling was reduced due to its neurological condition (already discussed in section 3.2.5.1). A total of 864, 839 and 710 intervals for the cognition, locomotion and social protocols, respectively, were collected on the macaw groups at zoo B (Table 4.2).

4.3.1. Cognition – food and object manipulation by captive grey parrots and macaws

4.3.1.1. Complexity of food and object manipulation by captive grey parrots and macaws

During the baseline period, the majority of feeding observations (> 80%) were unclear (i.e. it was possible to confirm they were feeding, but not what they were feeding on) on both grey parrot groups, and the clear observations consisted mostly of basic food manipulation (i.e. soft biting before quick ingestion), with advanced manipulation (i.e. requiring extreme persistent handling and/or gnawing, such as when cracking nuts) not observed (Figure 4.2A). On the other hand, most of the feeding observations on the scarlet macaws allowed determination of the complexity of manipulation, although the percentage of unclear observations was still substantial across individuals (i.e. 23.3-39.3% of total feeding observations). At zoo A, advanced food manipulation was not observed in any of the scarlet macaws, and food manipulation was mostly of basic complexity (Figure 4.2B).

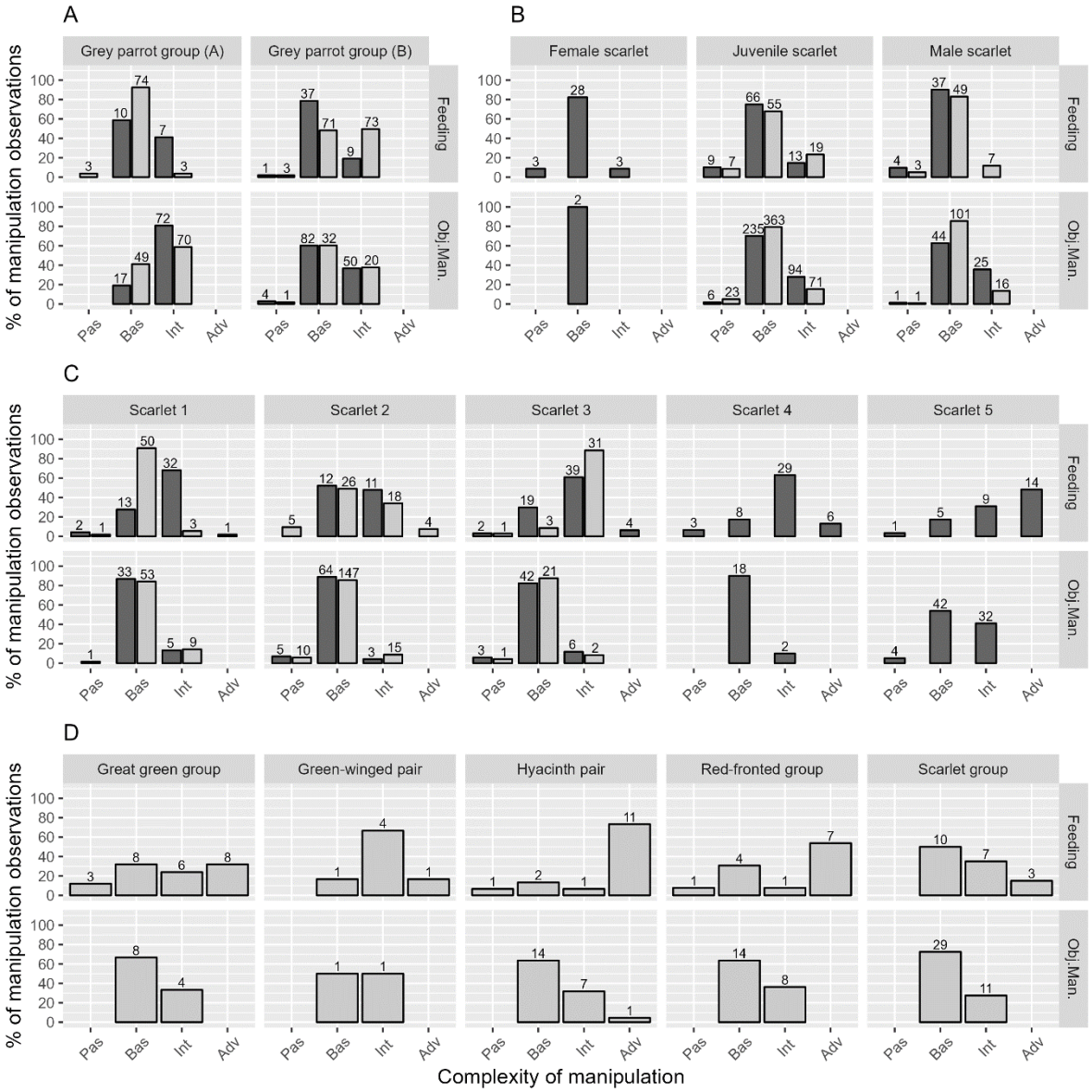


Figure 4.2. Complexity of food and object manipulation in the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), in the baseline and post-modification periods of observations.

Percentages of levels of food and object manipulation (Obj. Man.) in the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations. Pas = Passive; Bas = Basic; Int = Intermediate; Adv = Advanced (categories explained in section 2.2.4).

At zoo B, however, the clear feeding observations on the scarlet macaws showed high engagement in intermediate food manipulation (i.e. some persistent gnawing and/or handling such as when cracking seeds; 31.0-68.1%), with advanced manipulation observed in scarlet macaws 3, 4 and 5 (Figure 4.2C).

Furthermore, unclear observations of object manipulation were infrequent (<10%) across all individuals or groups in both zoos, except for the female scarlet macaw at zoo A, that was only observed manipulating objects in three intervals, one of which was unclear. During the baseline period, only the grey parrot group at zoo A engaged mostly in object manipulation of intermediate complexity (81.0%; Figure 4.2A), which consisted mostly of manipulation with the bill of thick and tough branches within the enclosure. Also, the majority of the object manipulation observations of the grey parrot group B (Figure 4.2A) and all scarlet macaws (Figure 4.2B) were of basic complexity (53.8-90.0% of clear object manipulation observations) and consisted mostly of chewing thin branches and/or the bark used as substrate on the ground.

While scarlet macaws 1, 3, 4 and 5 were most often seen feeding on food with cover during the baseline period (78.0-92.0%), clear feeding observations of the other individuals and groups most often found them eating bare food (73.0-100.0%). Regarding food toughness, except for scarlet macaw 2, that was mostly seen feeding on soft food items (50.0%) and scarlet macaws 4 and 5, who spent 51.3% and 64.0% of (clear) feeding observations manipulating hard food, all other individuals fed mostly on food items of intermediate toughness (66.7–90.0%). Manipulation of hard food

items was not observed in any individuals at zoo A, and at zoo B, only once in the scarlet macaw 1, and in 27.8% and 9.3% of clear feeding observations in scarlet macaws 2 and 3, respectively. Interaction with objects temporarily added to the enclosure (rather than permanent features of the enclosure or objects that stay in for long periods of time) was not observed in the male and female scarlet macaws at zoo A, and was not frequent in any of the other individuals (1.2-28.5%).

4.3.1.1.1. Post-modification observations of food and object manipulation by captive grey parrots and macaws

In the post-modification phase, as in the baseline period, a high proportion of the feeding observations were unclear (28.6-70.0%), not allowing to determine what food items they were manipulating. Nevertheless, the percentage of basic food manipulation during clear observations differed between the baseline and post-modification periods for some of the parrots (Figure 4.2), with randomisation tests (10,000 permutations) showing significant differences in both grey parrot groups and scarlet macaws 1 and 3 ($zs = -3.62$-6.52, $SDs = 0.08$-0.10, $ps < 0.05$; Table 4.3).

Differences in the percentage of basic object manipulation between periods of observations were also detected (Figure 4.2), with a significantly higher percentage in the post-modification period observed in all parrots at zoo A, according to randomisations tests (10,000 permutations; $zs = 3.02$-3.58, $SDs = 0.03$-0.07, $ps < 0.01$; Table 4.3).

Table 4.3. Summary of randomisation tests (10,000 permutations) comparing differences in proportions of basic (food and object) manipulation in the scarlet macaws and grey parrot groups at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) between the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant ($p < 0.05$) positive and negative differences, respectively, in the post-modification period, based on the p-values adjusted with the Benjamin-Hochberg method.

Individual (zoo)	Z	Standard deviation	p-value (adjusted)
Basic food manipulation			
Grey parrot group (A)	3.75	0.090	0.003
Grey parrot group (B)	-3.62	0.084	< 0.001
Male scarlet macaw (A)	-1.02	0.070	0.268
Juvenile scarlet macaw (A)	-1.02	0.070	0.199
Scarlet macaw 1 (B)	6.52	0.097	< 0.001
Scarlet macaw 2 (B)	-0.25	0.125	0.495
Scarlet macaw 3 (B)	-2.40	0.088	0.024
Basic object manipulation			
Grey parrot group (A)	3.40	0.065	0.001
Grey parrot group (B)	0.01	0.080	0.561
Male scarlet macaw (A)	3.58	0.063	< 0.001
Juvenile scarlet macaw (A)	3.02	0.031	0.002
Scarlet macaw 1 (B)	-0.37	0.073	0.528
Scarlet macaw 2 (B)	-0.72	0.048	0.451
Scarlet macaw 3 (B)	0.57	0.090	0.591

Advanced manipulation was not observed at zoo A in either period of observations (Figures 4.2A and 4.2B) and was rarely observed in scarlet macaws 1 and 2 at zoo B (Figure 4.2C). Even though the number of clear food (6-25) and object manipulation (2-40) observations was limited across the macaw groups at zoo B, the complexity of feeding was more even across groups, while object manipulation was mostly of basic complexity in all groups except the green-winged macaws (Figure 4.2D).

Similar to the baseline period, manipulation of bare food was predominantly observed in most individuals in the post-modification period (75.3–95.5%), although scarlet macaw 3 was only seen manipulating covered food items, and grey parrot group B and scarlet macaw 2 were observed feeding on bare (47.8% and 49.0%, respectively) and covered food in more even percentages. Feeding observations on soft food were relatively more common in scarlet macaws 1 (89.6%) and 2 (48.9%), while the others were most often seen feeding on food items of intermediate toughness (59.7-97.3%). Manipulation of hard food items was seen only in scarlet macaws 1 (one interval), 2 (8.5%) and 3 (9.3%). Engagement with objects temporarily added to the enclosure remained low across individuals (4.8-11.6%) and was not observed in both grey parrot groups and the male scarlet macaw at zoo A. Out of the clear observations that allowed identification of the food item they were manipulating, all macaw groups were observed interacting with hard food items. Only the scarlet macaw group fed mostly on bare food (47.6%), as the other groups were more frequently seen feeding on covered food items (69.0-100.0%). Finally, while the great green macaws and the green-winged macaws were not recorded interacting with temporary enrichment, the remaining groups were but in a minority of observations (5.7-23.8%).

4.3.1.2. Foot use during manipulation by captive grey parrots and macaws

Observations of foot use during food and object manipulation were infrequent in most parrots in the baseline period (Figure 4.3), with the juvenile scarlet macaw at zoo A showing the highest foot use during both food and object manipulation (Figure 4.3B). Scarlet macaw 2 did not use its feet while feeding (Figure 4.3C) and the grey parrot group B showed high foot use only during object manipulation (Figure 4.3A).

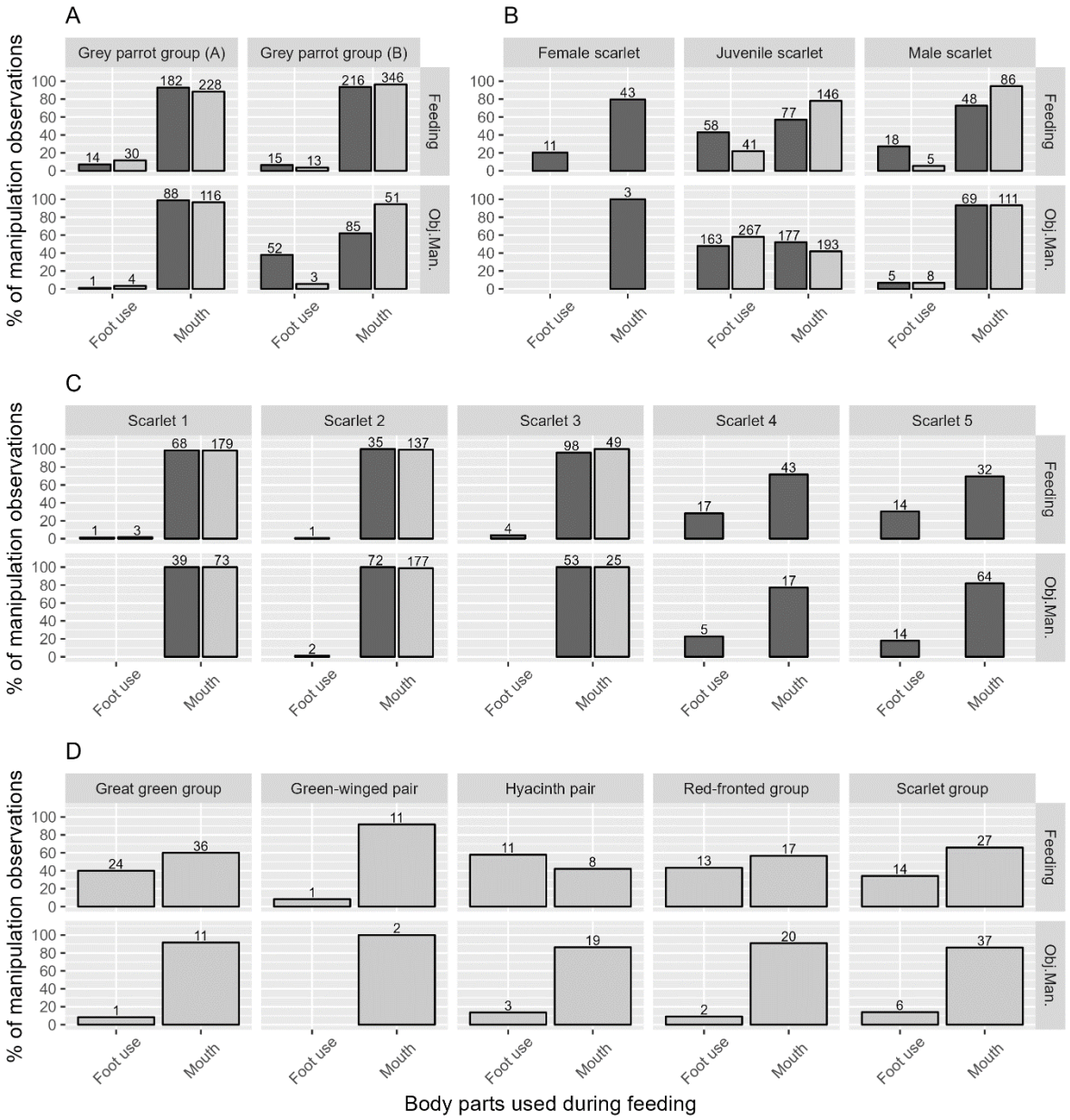


Figure 4.3. Body parts used during food and object manipulation by the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), in the baseline and post-modification periods of observations.

Percentages of use of feet and mouth (only) during food and object manipulation (Obj. Man.) in the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations.

The female scarlet macaw (Figure 4.3B), and scarlet macaws 1, 2 and 3 (Figure 4.3C) did not use their feet to manipulate objects. Despite the high proportion of unclear feeding observations previously described, it was almost always possible to determine if they were using their feet for manipulation.

4.3.1.2.1. Post-modification observations of foot use during manipulation by captive grey parrots and macaws

In the post-modification period, foot use during manipulation differed from the baseline period in some of the parrots (Figure 4.3 and Table 4.4).

Table 4.4. Summary of randomisation tests (10,000 permutations) comparing the proportions of foot use during (food and object) manipulation in the scarlet macaws and grey parrot groups at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), between baseline and post-modification periods of observations.
The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant ($p < 0.05$) positive and negative differences, respectively, in the post-modification period, based on the p-values adjusted with the Benjamin-Hochberg method.

Individual (zoo)	Z	Standard deviation	p-value (adjusted)
Foot use (feeding)			
Grey parrot group (A)	1.60	0.028	0.084
Grey parrot group (B)	-1.59	0.018	0.125
Male scarlet macaw (A)	-3.77	0.058	< 0.001
Juvenile scarlet macaw (A)	-3.97	0.053	< 0.001
Scarlet macaw 1 (B)	-	-	-
Scarlet macaw 2 (B)	-	-	-
Scarlet macaw 3 (B)	-	-	-
Foot use (object manipulation)			
Grey parrot group (A)	1.04	0.021	0.320
Grey parrot group (B)	-18.10	0.073	< 0.001
Male scarlet macaw (A)	-0.01	0.037	0.605

Individual (zoo)	Z	Standard deviation	p-value (adjusted)
Juvenile scarlet macaw (A)	2.84	0.036	0.003
Scarlet macaw 1 (B)	-	-	-
Scarlet macaw 2 (B)	-	-	-
Scarlet macaw 3 (B)	-	-	-

Randomisation tests (10,000 permutations) showed significant differences in foot use during manipulation between the baseline and post-modification periods in the grey parrot group B, male scarlet macaw and juvenile scarlet macaw (zs = -18.10-2.84, SDs = 0.04-0.07, ps < 0.01; Table 4.4). In the macaw groups, all except the green-winged macaws showed a relatively high proportion of foot use during feeding (34.1-57.9%), although that was not the case for object manipulation (0 – 14.0%; Figure 4.3D).

4.3.2. Locomotion and support use by captive grey parrots and macaws

4.3.2.1. Type of locomotion used by captive grey parrots and macaws

In the baseline period of observations, climbing (i.e. tripedal locomotion) was the most common type of locomotion in most parrots (Figures 4.4), but scarlet macaw 3 exhibited even proportions of climbing and walking (Figure 4.4C).

Flight rates were low in most parrots (Figure 4.4), and almost not observed in scarlet macaws 2 and 3 (Figure 4.4C). The juvenile scarlet macaw showed the highest rate of both short and long flights (Figure 4.5B) in the baseline period of observations.

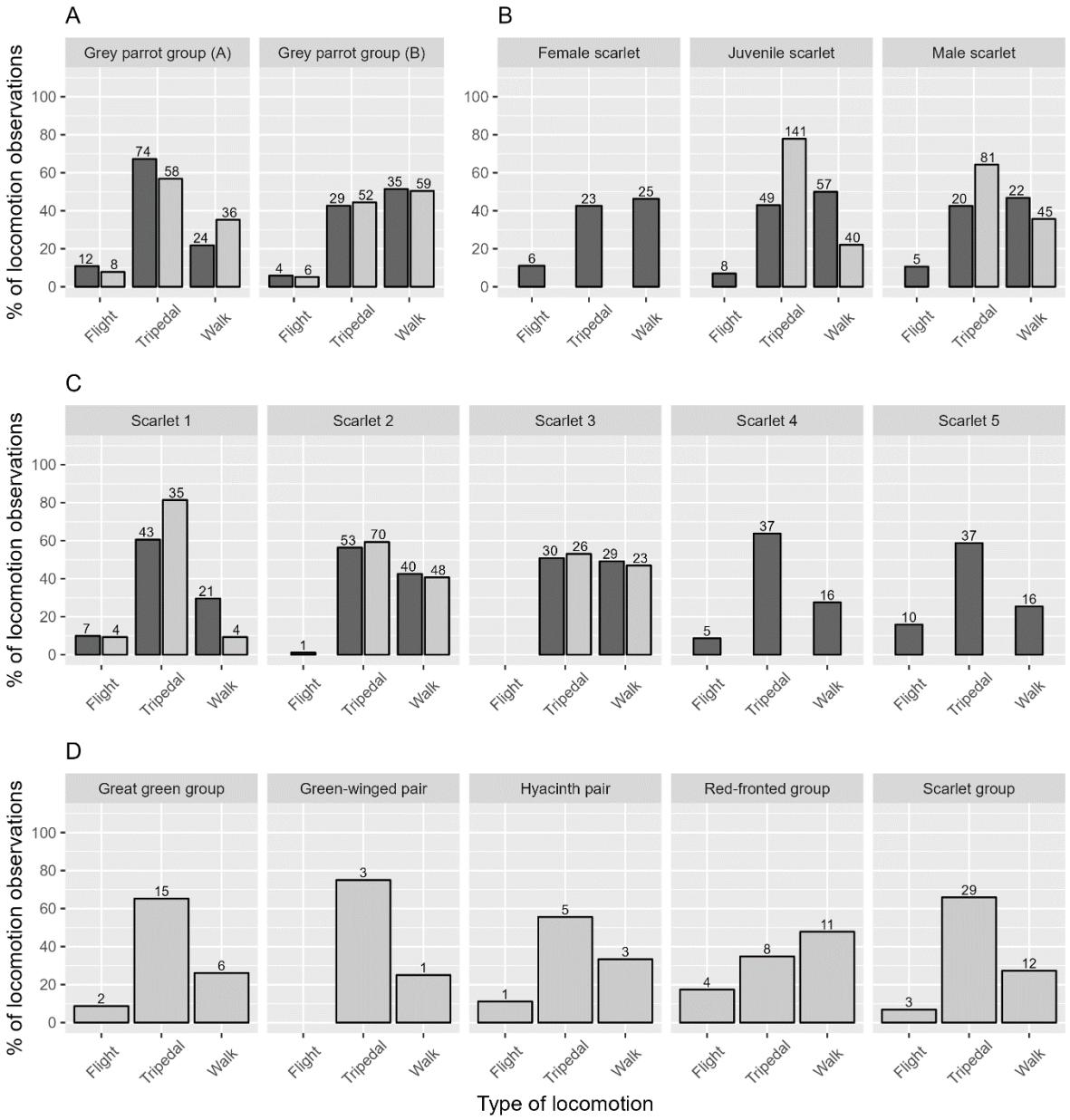


Figure 4.4. Locomotion behaviours in the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline and post-modification periods of observations.

Percentage of observations for each type of locomotion behaviour, in the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations.

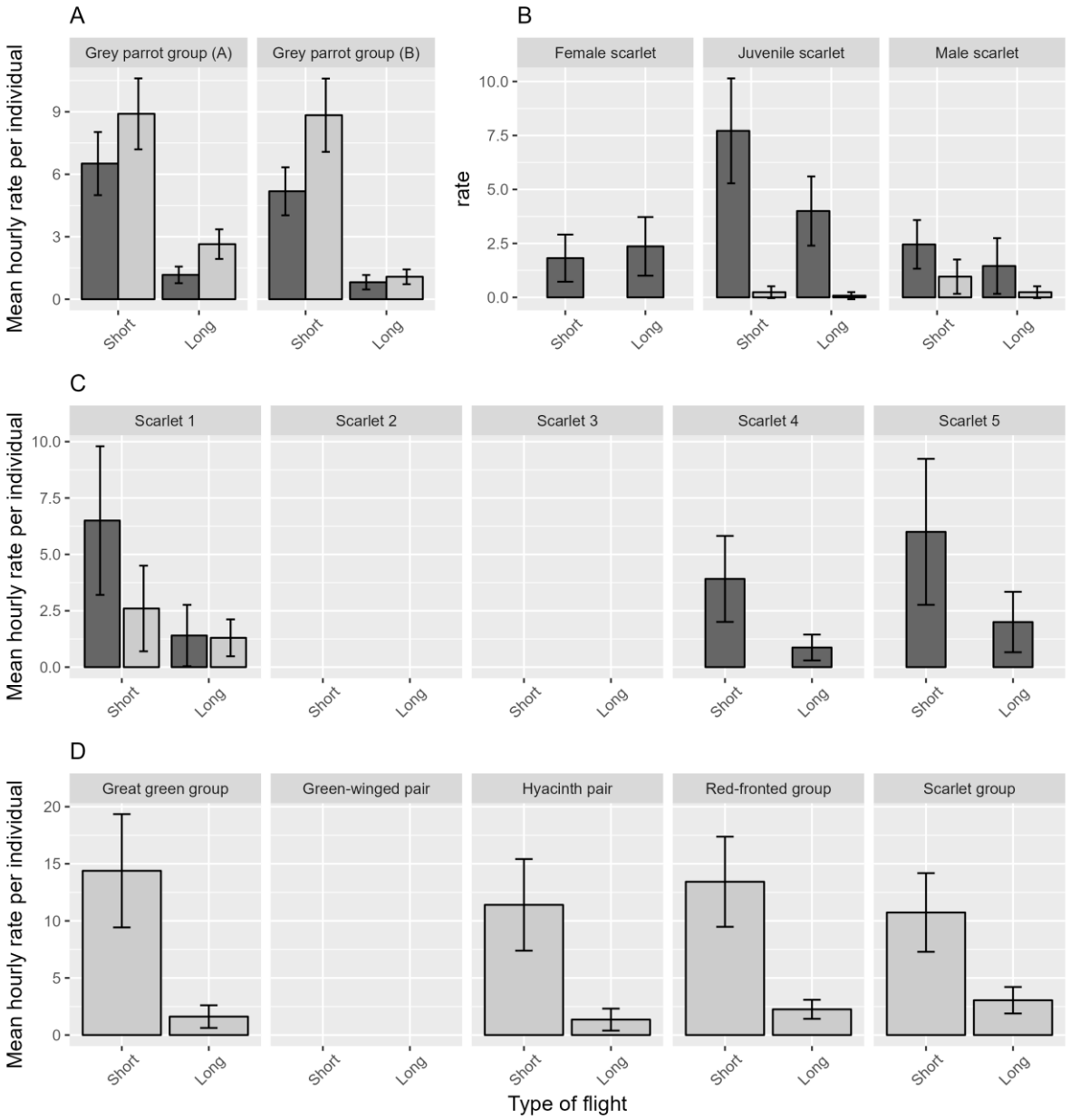


Figure 4.5. Flight rates of the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), in the baseline and post-modifications periods of observations.

Mean hourly flight rates of the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Error bars represent 95% confidence intervals.

4.3.2.1.1. Post-modification observations of type of locomotion used by captive grey parrots and macaws

Differences in both tripedal locomotion (Figure 4.4) and flight rates (Figure 4.5) were detected across parrots in the post-modification period (Table 4.5).

Table 4.5. Summary of randomisation tests (10,000 permutations) comparing proportions of tripedal locomotion and mean hourly flight rates in the scarlet macaws and grey parrots at zoo A (Drayton Manor Park and Zoo/, UK) and zoo B (Jurong Bird Park, Singapore), between baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant ($p < 0.05$) positive and negative differences, respectively, in the post-modification period, based on the p-values adjusted with the Benjamin-Hochberg method.

Individual (zoo)	Z	Standard deviation	p-value (adjusted)
Tripedal locomotion			
Grey parrot group (A)	-1.56	0.067	0.084
Grey parrot group (B)	0.235	0.077	0.500
Male scarlet macaw (A)	2.55	0.085	0.018
Juvenile scarlet macaw (A)	6.14	0.057	< 0.001
Scarlet macaw 1 (B)	2.29	0.091	0.026
Scarlet macaw 2 (B)	0.43	0.070	0.495
Scarlet macaw 3 (B)	0.23	0.096	0.608
Hourly short flight rate (up to ½ length of the enclosure)			
Grey parrot group (A)	1.74	1.373	0.052
Grey parrot group (B)	3.39	1.076	< 0.001
Male scarlet (A)	-2.22	0.674	0.030
Juvenile scarlet (A)	-4.88	1.532	< 0.001
Scarlet macaw 1 (B)	-2.04	1.909	0.034
Scarlet macaw 2 (B)	No flights observed		
Scarlet macaw 3 (B)	No flights observed		
Hourly long flight rate (> ½ length of the enclosure)			
Grey parrot group (A)	1.07	0.56	0.003
Grey parrot group (B)	0.24	0.248	0.196
Male scarlet macaw (A)	-1.80	0.622	0.037
Juvenile scarlet macaw (A)	-2.56	0.914	< 0.001
Scarlet macaw 1 (B)	-0.05	0.755	0.528
Scarlet macaw 2 (B)	Single flight observed in post-modification		
Scarlet macaw 3 (B)	No flights observed		

Randomisation tests (10,000 permutations) showed significant increases in the percentage of tripedal locomotion in the male and juvenile scarlet macaws at zoo A, and in the scarlet macaw 1 at zoo B (zs = 2.29-6.14, SDs = 0.06-0.09, $p < 0.05$; Table 4.5). Flight rates were significantly lower in the post-modification period in these macaws, but significantly higher in the grey parrot groups (zs = -4.88-3.39, SDs = 0.56-1.90, ps < 0.05; Table 4.5). Scarlet macaws 2 and 3 still almost did not fly in the post-modification phase (one long flight was seen in scarlet macaw 2, although the individual seemed unable to keep balance while in the air and landed on the ground). Except for the green-winged macaws, which were not seen flying, all macaw groups exhibited a relatively high rate of short flights (Figure 4.5D).

4.3.2.2. Type of support and perch characteristics used by captive grey parrots and macaws

During the baseline period of observations, the parrots at zoo A frequently used unstable perches (Figures 4.6A and 4.6B). Scarlet macaws 2 and 3 were almost never observed on perches and were always either on the ground or on the wire mesh while the other parrots at zoo B mostly used stable perches (Figure 4.6). Grey parrot group B (Figure 4.6A) and the scarlet macaws at zoo A (Figure 4.6B) used the wire mesh the least. Nevertheless, all parrots used the wire mesh in most climbing observations (Figure 4.7). Most parrots used thick perches in most baseline observations of perch use (Figure 4.8). Furthermore, all parrots used horizontal perches in most observations of perch use (Figure 4.9), with the male and female scarlet macaws at zoo A relying almost entirely on them (Figure 4.9B).

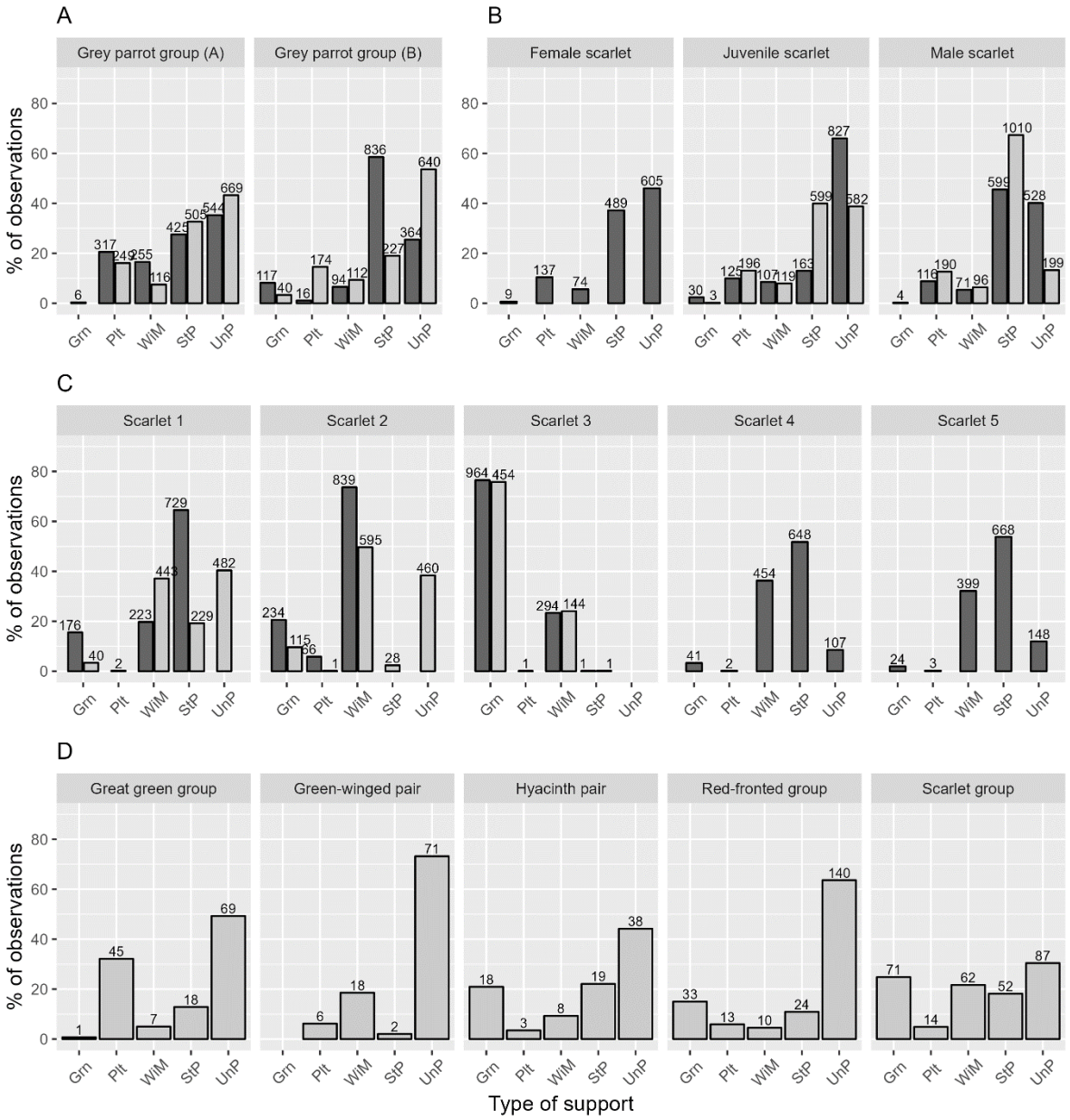


Figure 4.6. Type of support used by the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), in the baseline and post-modification periods of observations.

Percentage of total observations on each type of support in the (A) grey parrot groups, (B) scarlet macaws at zoo A. (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations. Grn = Ground, Plt = Platform, WiM = Wire Mesh, StP = Stable Perch, UnP = Unstable Perch.

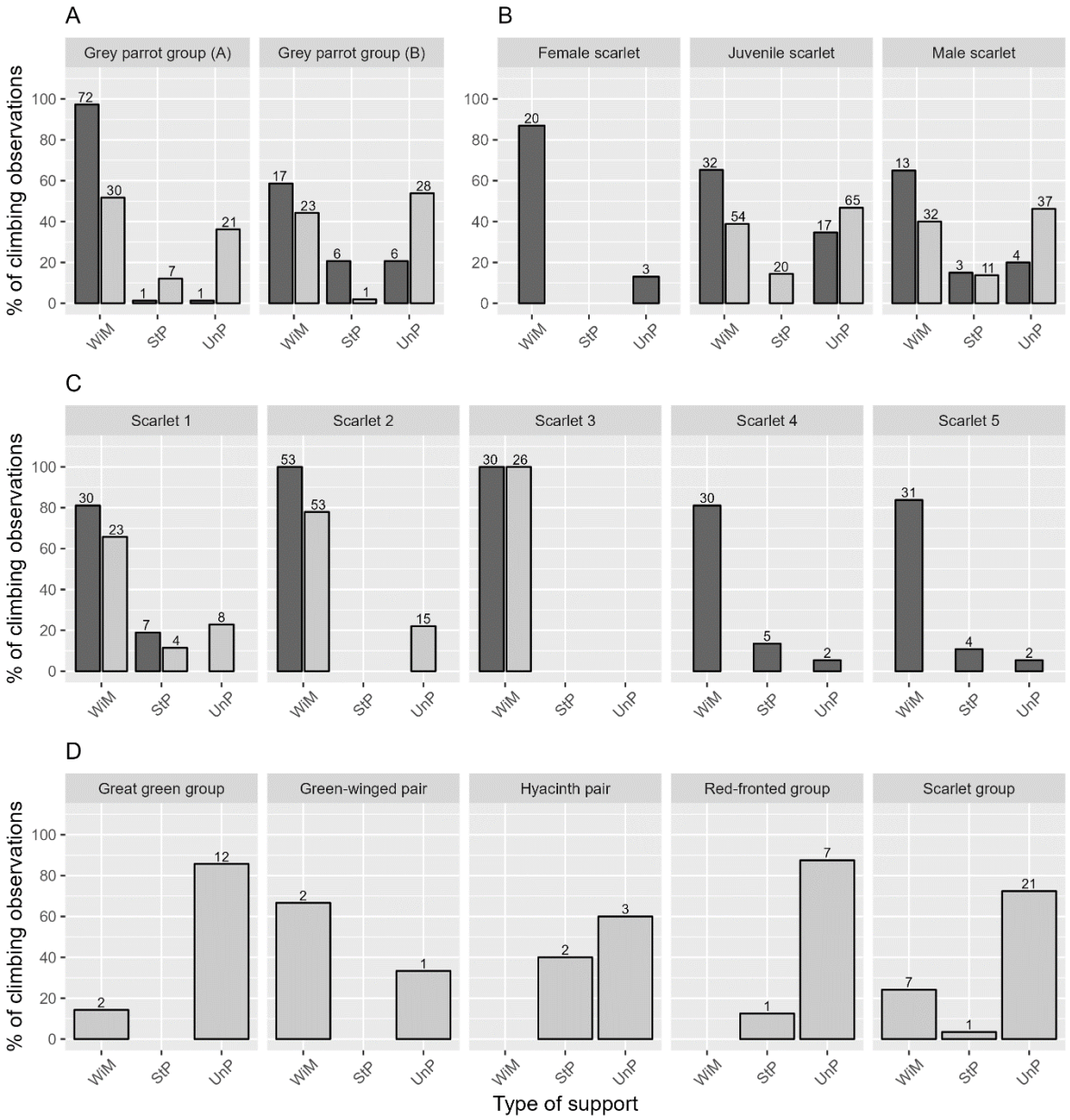


Figure 4.7. Type of support used during climbing by the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), in the baseline and post-modification periods of observations.

Percentage of climbing (i.e. tripedal locomotion) observations of (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B on different types of supports. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations. WiM = Wire Mesh, StP = Stable Perch, UnP = Unstable Perch.

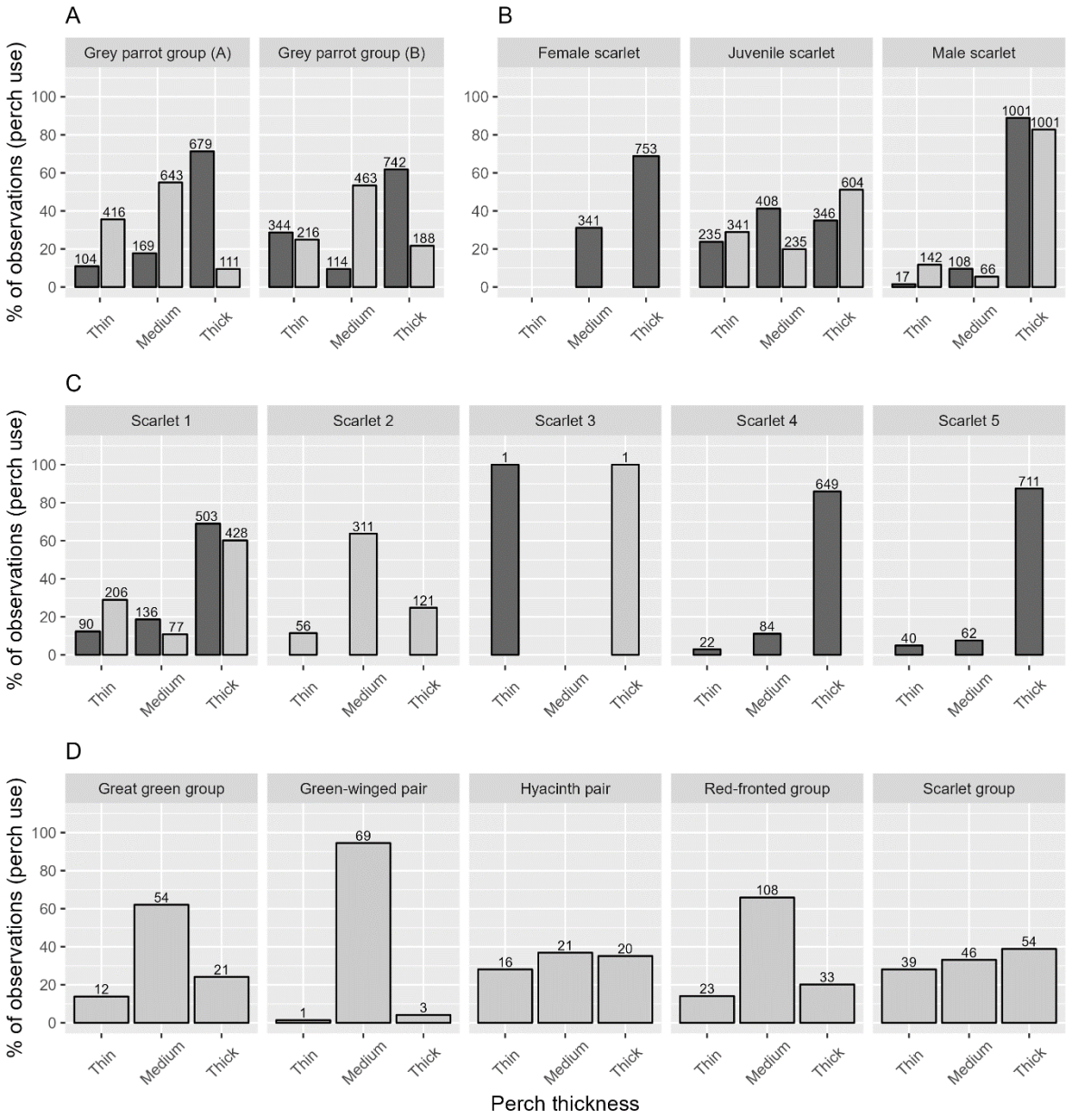


Figure 4.8. Thickness of perches used by the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapure), in the baseline and post-modifications periods of observations.

Percentage of use of perches of different thickness, by the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations.

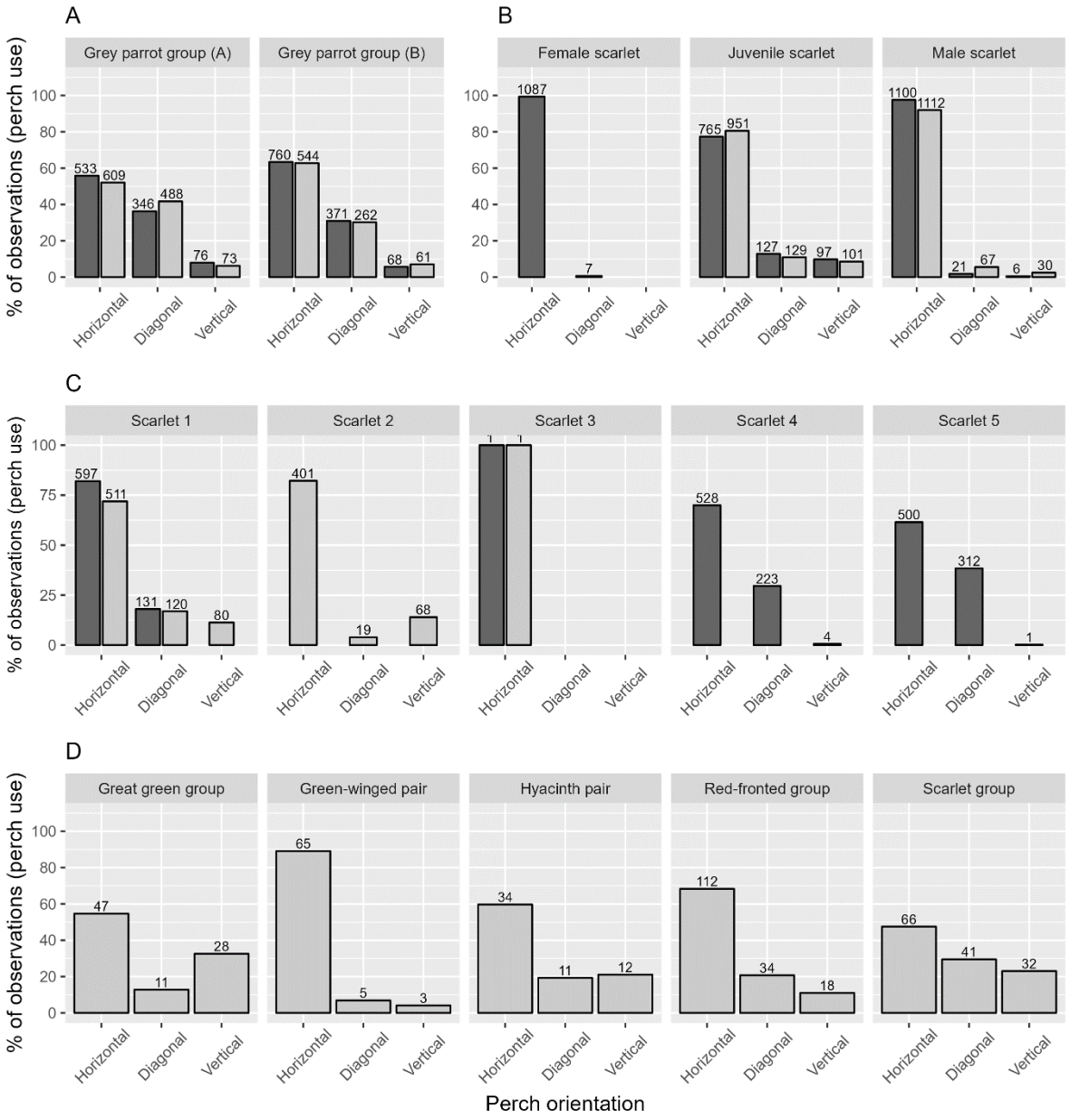


Figure 4.9. Orientation of perches used by the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline and post-modification periods of observations.

Percentage of use of perches of different orientations by (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations.

4.3.2.2.1. Post-modification observations of type of support and perch characteristics used by captive grey parrots and macaws

Significant changes in support use in the post-modification phase were detected in all parrots (χ^2s$_{(3\text{-}4,\ n\ =\ 771\text{-}1028)}$ = 16.61 – 297.85, ps < 0.001) except scarlet macaw 3 ($\chi^2_{(1,\ n\ =\ 618)}$ = 0.02, p = 0.875; Table 4.6).

Table 4.6. Summary of Chi-squared tests and adjusted standardised residuals comparing the type of support used by the grey parrots and scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) between the baseline and post-modification periods of observations.
The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant positive and negative differences in residuals, respectively, according to the corrected critical value. The degrees of freedom (df) and the p-value, adjusted for multiple testing (Benjamin-Hochberg method), are stated.

Individual (zoo)	X^2	df	p-value	Adjusted standardised cell residuals		
				Support type	Baseline	Post-modification
Grey parrot group n = 1028 (zoo A)	16.61	3	< 0.001	Corrected critical value: 2.73		
				Ground	-	-
				Platform	1.56	-1.56
				Stable perch	-1.55	1.55
				Unstable perch	-2.13	2.13
				Wire mesh	3.43	-3.43
Grey parrot group n = 871 (zoo B)	171.58	4	< 0.001	Corrected critical value: 2.81		
				Ground	3.55	-3.55
				Platform	-7.07	7.07
				Stable perch	10.74	-10.74
				Unstable perch	-8.45	8.45
				Wire mesh	-1.03	1.03
Male scarlet macaw n = 937 (zoo A)	84.13	3	< 0.001	Corrected critical value: 2.73		
				Ground	-	-
				Platform	-2.24	2.24
				Stable perch	-6.63	6.63
				Unstable perch	9.07	-9.07
				Wire mesh	0.05	-0.05
	104.86	4	< 0.001	Corrected critical value: 2.81		

Individual (zoo)	X^2	df	p-value	Adjusted standardised cell residuals		
Juvenile scarlet macaw n = 914 (zoo A)				Ground	2.67	-2.67
				Platform	-1.54	1.54
				Stable perch	-9.04	9.04
				Unstable perch	8.66	-8.66
				Wire mesh	-0.37	0.37
Scarlet macaw 1 n = 771 (zoo B)	297.85	3	< 0.001	Corrected critical value: 2.73		
				Ground	5.96	-5.96
				Platform	-	-
				Stable perch	12.71	-12.71
				Unstable perch	-13.74	13.74
				Wire mesh	-5.32	5.32
Scarlet macaw 2 n = 779 (zoo B)	213.14	4	< 0.001	Corrected critical value: 2.81		
				Ground	4.34	-4.34
				Platform	4.89	-4.89
				Stable perch	-3.25	3.25
				Unstable perch	-13.43	13.43
				Wire mesh	6.91	-6.91
Scarlet macaw 3 n = 618 (zoo B)	0.02	1	0.875	Ground	-0.16	0.16
				Platform	-	-
				Stable perch	-	-
				Unstable perch	-	-
				Wire mesh	0.16	-0.16

The use of unstable perches increased in the post-modification period in the grey parrot group B (Figure 4.6A), scarlet macaws 1 and 2 (Figure 4.6C) but decreased in the male and juvenile scarlet macaws at zoo A (Figure 4.6B and Table 4.6). The scarlet macaw 2 at zoo B (Figure 4.6C), and the male and juvenile scarlet macaws at zoo A (Figure 4.6B) showed an increased use of stable perches in the post-modification period (Table 4.6). Ground use decreased in both the grey parrot group B (Figure 4.6A) and scarlet macaw 2 (Figure 4.6C), while the use of platforms increased in the former but decreased in the latter (Table 4.6). General use of the wire mesh decreased in the grey parrot group A (Figure 4.6A) and scarlet macaw 2 but increased in the scarlet macaw

1 (Figure 4.6C and Table 4.6). On the other hand, the use of the wire mesh during climbing significantly decreased in all individuals (zs = -6.21- -2.05, SDs = 0.06-0.12, ps < 0.05; Figure 4.7) except the grey parrot group B (z = -1.23, SD = 0.12, p = 0.196) and the scarlet macaw 1 (z = -0.38, SD = 0.11, p = 0.528; Table 4.7).

Table 4.7. Summary of randomisation tests (10,000 permutations) comparing the proportions of use of different types of perches by the grey parrots and scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), between the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant ($p < 0.05$) positive and negative differences, respectively, in the post-modification period, based on the p-values adjusted with the Benjamin-Hochberg method.

Individual (zoo)	Z	Standard deviation	p-value (adjusted)
Perch thickness (thick)			
Grey parrot group (A)	-29.44	0.021	< 0.001
Grey parrot group (B)	-18.10	0.022	< 0.001
Male scarlet macaw (A)	-4.28	0.014	< 0.001
Juvenile scarlet macaw (A)	7.63	0.021	< 0.001
Scarlet macaw 1 (B)	-3.51	0.025	< 0.001
Scarlet macaw 2 (B)	-	-	-
Scarlet macaw 3 (B)	-	-	-
Perch orientation (horizontal)			
Grey parrot group (A)	-1.74	0.022	0.062
Grey parrot group (B)	-0.30	0.021	0.460
Male scarlet macaw (A)	-6.05	0.009	< 0.001
Juvenile scarlet macaw (A)	1.81	0.018	0.042
Scarlet macaw 1 (B)	-4.54	0.022	< 0.001
Scarlet macaw 2 (B)	-	-	-
Scarlet macaw 3 (B)	-	-	-
Tripedal locomotion on wire mesh			
Grey parrot group (A)	-6.21	0.073	< 0.001
Grey parrot group (B)	-1.23	0.117	0.196
Male scarlet macaw (A)	-2.05	0.124	0.045
Juvenile scarlet macaw (A)	-3.250	0.083	0.001
Scarlet macaw 1 (B)	-0.38	0.107	0.528
Scarlet macaw 2 (B)	-3.75	0.062	< 0.001
Scarlet macaw 3 (B)	-	-	-

A significant decrease in the use of thick perches was detected in all parrots (zs = -29.44- -3.51, SDs = 0.01-0.03, ps < 0.001) except the juvenile scarlet, that showed a significant increase (Figure 4.8B; z = 7.63, SD = 0.02, p < 0.001; Table 4.7). Despite this reduction in thick perch use, it was still predominant in the male scarlet macaw (Figure 4.8B), and scarlet macaw 1 (Figure 4.8C). Thin perches were used more frequently in the post-modification period by all parrots (Figure 4.8) except the grey parrot group B (Figure 4.8A). On the other hand, significant changes in the use of horizontal perches were detected in the male scarlet macaw (Figure 4.9B; z = -6.05, SD = 0.01, p < 0.001), juvenile scarlet macaw (Figure 4.9B; z = 1.81, SD = 0.02, p = 0.042) and scarlet macaw 1 (Figure 4.9C; z = -4.54, SD = 0.02, p < 0.001; Table 4.7). Most macaw groups at zoo B showed a higher use of unstable perches than other supports (Figure 4.6D), and frequently used thin (Figure 4.8D) and horizontal perches (Figure 4.9D)

4.3.3. Social behaviour and proximity in captive grey parrots and macaws

4.3.3.1. Type of social behaviour observed in captive grey parrots and macaws

Social behaviour in the baseline period consisted mostly of allopreening in the scarlet macaws at both zoos (Figures 4.10B and 4.10C). It was also the most common social behaviour in grey parrot group A, although closely followed by nibbling (Figure 4.10A). However, allopreening was not observed in grey parrot group B, and the social behaviour of the parrots within this group consisted mostly of nibbling (Figure 4.10A). Allofeeding was not observed in the male scarlet macaw (Figure 4.10B), and scarlet macaws 1, 2 and 3 (Figure 4.10C).

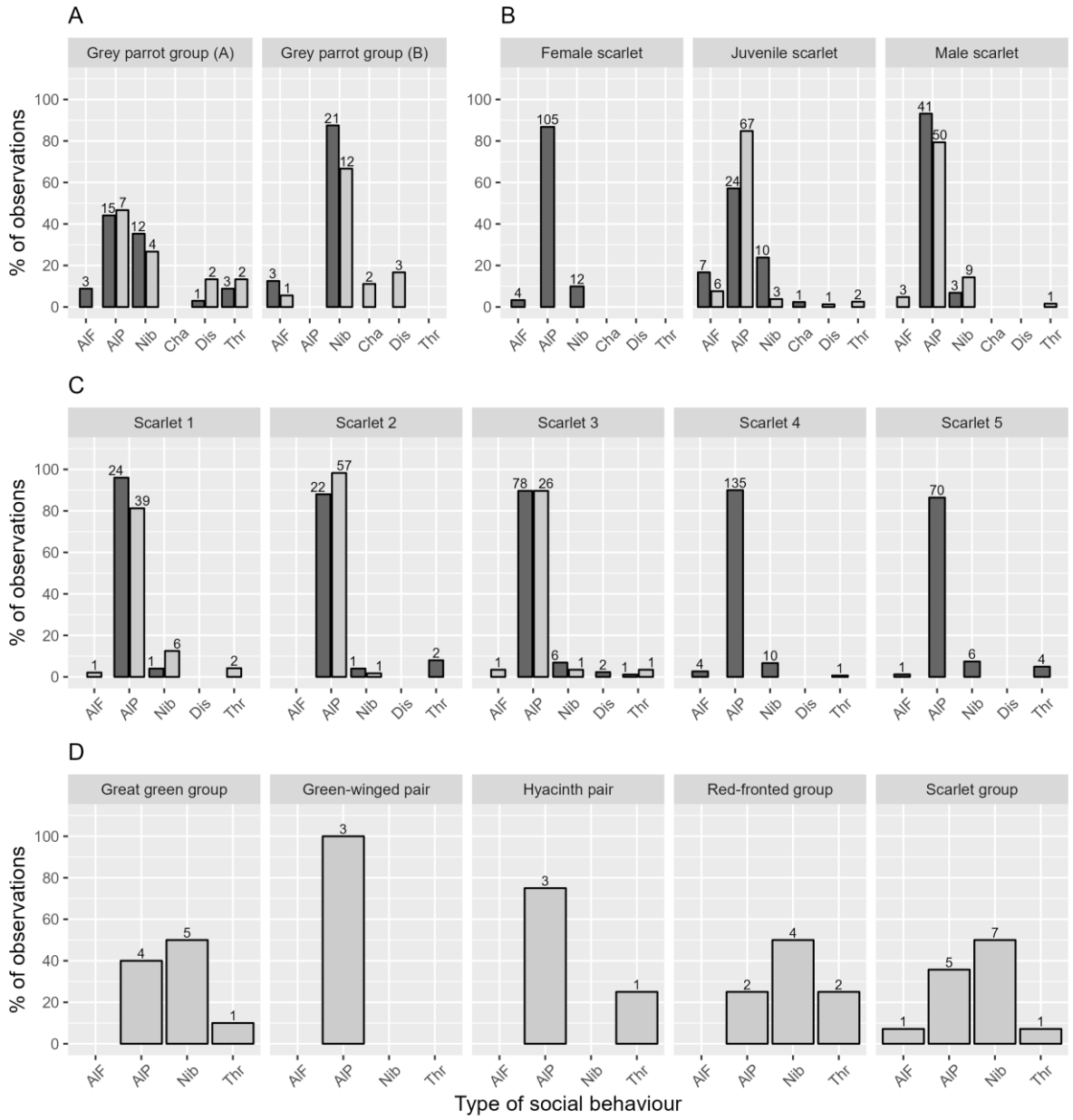


Figure 4.10. Social behaviours of the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline and post-modifications periods of observations.

Percentage of different types of social behaviours observed in the (A) grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Numbers above bars represent the number of observations. AlF = Allofeeding, AlP = Allopreening, Nib = Nibbling, Cha = Chasing, Dis = Displacement, Thr = Threatening.

Hourly rates of social occurrences were not available for the grey parrot groups (section 4.2), but scarlet macaw 4 showed a higher rate of affiliative behaviours (considering all interactions the focal was instigator or recipient of) than its conspecifics at zoo B (Figure 4.11B). Affiliative behaviours were observed between scarlet macaws 1 and 2, 3 and 4, and 4 and 5. At zoo A, the female scarlet macaw exhibited affiliative interactions with both the male and juvenile scarlet macaws, while those two rarely exhibited affiliative behaviours with each other during the baseline period of observations (Figure 4.11A).

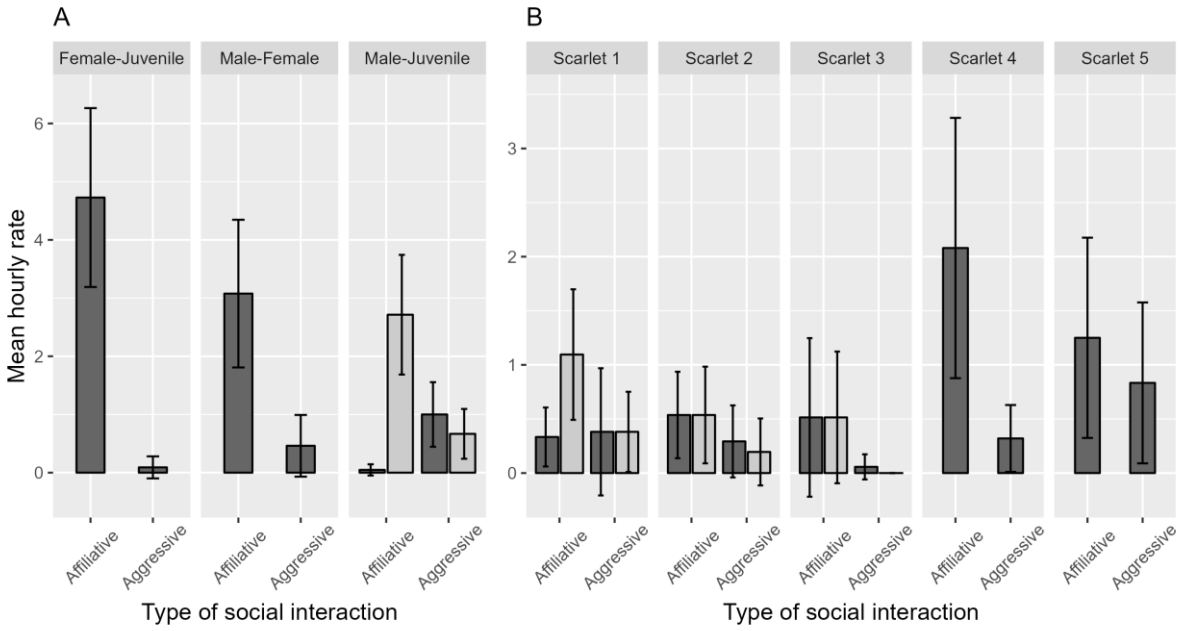


Figure 4.11. Rates of social interactions in the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) in the baseline and post-modification periods of observations.

Mean hourly rates of social occurrences in the (A) scarlet macaws at zoo A (all interactions between each dyad), and (B) scarlet macaws at zoo B (all interactions each focal individual instigated or was a recipient of). The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Error bars represent 95% confidence intervals.

Aggressive social interactions between the female scarlet macaw and both the male and juvenile scarlet macaws at zoo A were rare (Figure 4.10B and 4.11A). Aggressive interactions were more common between the male and juvenile scarlet macaws in the baseline period of observations (Figure 4.11A). Aggressive behaviours were infrequent in most parrots (Figures 4.10 and 4.11).

4.3.3.1.1. Post-modification observations of social behaviour and proximity in captive grey parrots and macaws

The post-modification observations showed significant changes in the percentage of time spent allopreening, when engaged in social behaviours, for the male scarlet macaw ($z = -1.97$, $SD = 0.07$, $p = 0.048$) and juvenile scarlet macaw at zoo A ($z = 3.37$, $SD = 0.08$, $p = 0.001$; Figure 4.10B and Table 4.8).

Furthermore, the hourly rate of affiliative behaviours (all occurrences as instigator and recipient of interaction) significantly increased in scarlet macaw 1 (Figure 4.11B; $z = 2.99$, $SD = 0.61$, $p = 0.003$) and between the male and juvenile scarlet macaws (Figure 4.11A; $z = 4.34$, $SD = 1.02$, $p < 0.001$; Table 4.8). On the other hand, significant changes in the hourly rate of aggressive behaviours were only detected between the male and juvenile scarlet macaws (Figure 4.11A; $z = -2.22$, $SD = 0.61$, $p = 0.032$; Table 4.8). As in the baseline period of observations, scarlet macaws 1 and 2 interacted mostly with each other, while scarlet macaw 3 was observed in affiliative interactions with the hyacinth macaws that were added to the enclosure in the post-modification phase.

Table 4.8. Summary of randomisation tests (10,000 permutations) comparing the proportions of allopreening behaviour and the mean hourly rates of social interactions in the grey parrots and scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), between the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant ($p < 0.05$) positive and negative differences, respectively, in the post-modification period, based on the p-values adjusted with the Benjamin-Hochberg method.

Individual (zoo)	Z	Standard deviation	p-value (adjusted)
Allopreening (proportion of social behaviours)			
Grey parrot group (A)	0.25	0.154	0.525
Grey parrot group (B)	-	-	-
Male scarlet macaw (A)	-1.97	0.070	0.048
Juvenile scarlet macaw (A)	3.37	0.082	0.001
Scarlet macaw 1 (B)	-1.72	0.086	0.105
Scarlet macaw 2 (B)	2.01	0.051	0.126
Scarlet macaw 3 (B)	0	0.065	0.725
Hourly rate of social occurrences (affiliative)			
Grey parrot group (A)	-	-	-
Grey parrot group (B)	-	-	-
Male scarlet macaw + Juvenile scarlet macaw (A)	4.34	1.024	< 0.001
Scarlet macaw 1 (B)	2.99	0.606	0.003
Scarlet macaw 2 (B)	0.29	0.544	0.495
Scarlet macaw 3 (B)	1.08	1.003	0.327
Hourly rate of social occurrences (aggressive)			
Grey parrot group (A)	-	-	-
Grey parrot group (B)	-	-	-
Male scarlet macaw + Juvenile scarlet macaw (A)	-2.22	0.607	0.032
Scarlet macaw 1 (B)	0.22	0.671	0.627
Scarlet macaw 2 (B)	-0.28	0.442	0.495
Scarlet macaw 3 (B)	-	-	-

Social behaviour was infrequently recorded across macaw groups at zoo B, and consisted of allopreening, nibbling and rare instances of aggression (Figure 4.10D).

4.3.3.2. Social proximity of captive grey parrots and macaws

Only the adult scarlet macaws at zoo A (Figure 4.12B), and scarlet macaw 4 at zoo B (Figure 4.12C) had conspecifics within a wing length in most baseline observations. All parrots had at least a conspecific within 2 m in the majority of observations (Figure 4.13), although scarlet macaw 3 did not in almost half of the observations (Figure 4.13C). The juvenile scarlet macaw (Figure 4.13B) and scarlet macaw 1 (Figure 4.13C) also showed a relatively high proportion of observations without conspecifics within that distance.

In the post-modification period, the percentage of observations with no conspecifics within wing length significantly changed for all parrots (zs = -10.82-11.87, SDs = 0.01-0.02, ps < 0.01) except the grey parrot group B (z = -1.43, SD = 0.02, p = 0.125; Table 4.9). There were significant post-modification changes for all parrots in the percentage of times with no conspecifics within 2 m (Figure 4.13; zs = -10.61-15.38, SDs = 0.01-0.02, ps < 0.001; Table 4.9). The male and juvenile scarlet macaws were more often observed near each other during the post-modification period of observations, but the percentage of time spent within a wing length of conspecifics decreased for the male scarlet macaw (Figure 4.12).

Out of the macaw groups, only the green-winged macaws spent most of their time close to conspecifics (i.e. each other; Figure 4.13D), as most macaw groups exhibited a high percentage of time away from conspecifics.

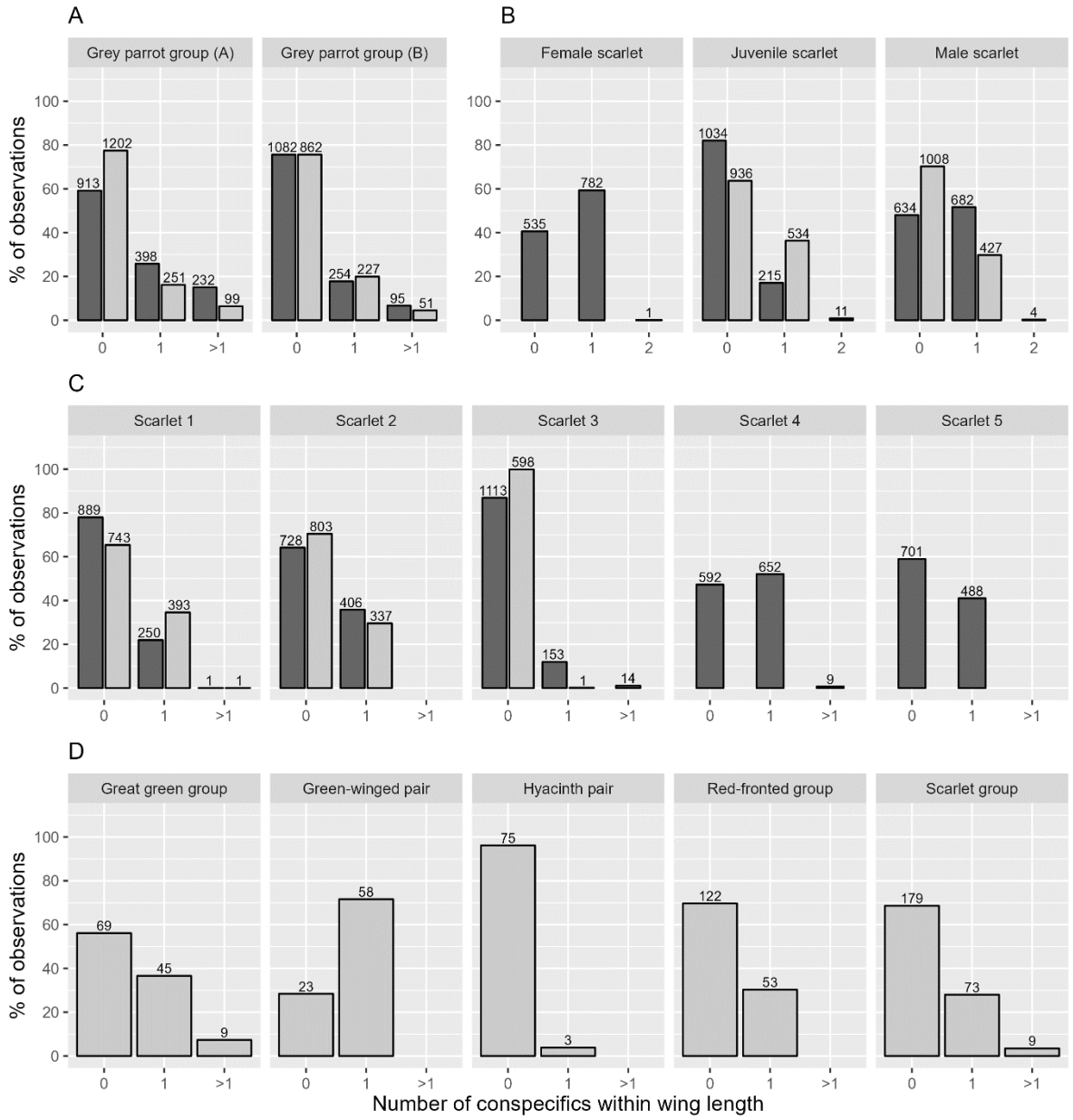


Figure 4.12. Percentage of observations where the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) were within a wing length of conspecifics, in the baseline and post-modifications periods of observations.

The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). (A) Grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. Numbers above bars correspond to number of observations.

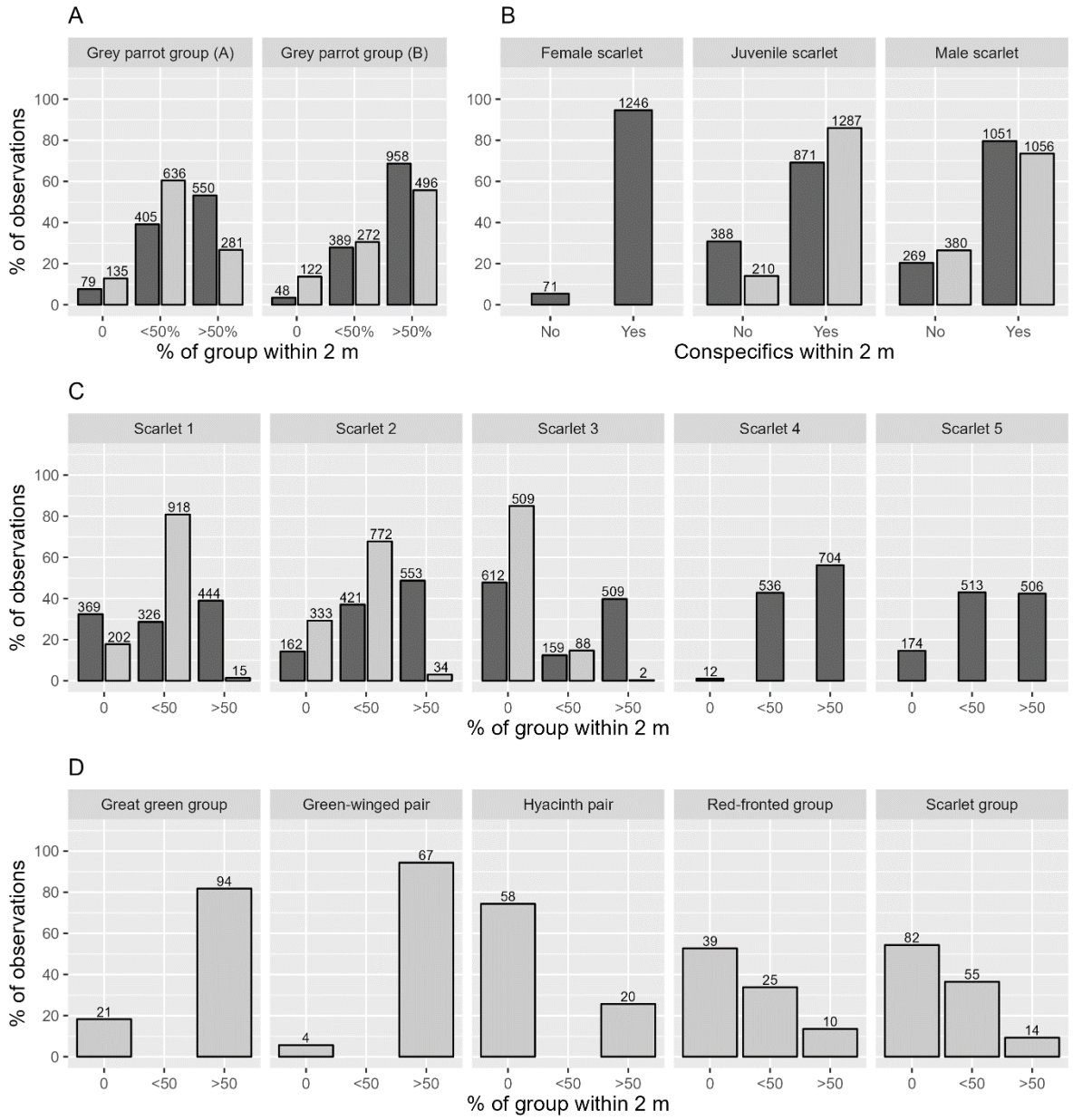


Figure 4.13. Percentage of observations where the grey parrots and macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) were within 2 m of conspecifics, in the baseline and post-modifications periods of observations.

The baseline period (before alterations to the enclosure and social environment of the parrots) is represented by the dark grey bars, while the post-modification period (after those alterations took place) is represented by the light grey bars. Baseline observations took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). (A) Grey parrot groups, (B) scarlet macaws at zoo A, (C) scarlet macaws at zoo B, and (D) macaw groups at zoo B. Numbers above bars correspond to number of observations.

Table 4.9. Summary of randomisation tests (10,000 permutations) comparing the differences in proportions of intervals with no conspecifics within wing length and within 2 m of the focal grey parrot or scarlet macaw at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore), between the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells show significant ($p < 0.05$) positive and negative differences, respectively, in the post-modification period, based on the p-values adjusted with the Benjamin-Hochberg method.

Individual (zoo)	Z	Standard deviation	p-value (adjusted)
No conspecifics within wing length			
Grey parrot group (A)	9.85	0.017	< 0.001
Grey parrot group (B)	-1.43	0.017	0.125
Male scarlet macaw (A)	11.87	0.019	< 0.001
Juvenile scarlet macaw (A)	-10.82	0.017	< 0.001
Scarlet macaw 1 (B)	-6.71	0.019	< 0.001
Scarlet macaw 2 (B)	3.17	0.020	0.002
Scarlet macaw 3 (B)	9.19	0.014	< 0.001
No conspecifics within 2m			
Grey parrot group (A)	3.69	0.009	< 0.001
Grey parrot group (B)	7.42	0.010	< 0.001
Male scarlet macaw (A)	3.76	0.016	< 0.001
Juvenile scarlet macaw (A)	-10.61	0.016	< 0.001
Scarlet macaw 1 (B)	-8.07	0.018	< 0.001
Scarlet macaw 2 (B)	8.58	0.017	< 0.001
Scarlet macaw 3 (B)	15.38	0.024	< 0.001

4.3.3.3. Weekly differences in social behaviour and proximity in the scarlet macaws at zoo A

Until the death of the female scarlet macaw (which occurred between weeks 9 and 10 of observations), the social dynamics between the male and juvenile scarlet macaws consisted mostly of aggressive interactions (Figure 4.14). Affiliative behaviours between these two parrots were observed from week 12 onwards, approximately two weeks after the death of the female but before the post-modification period of

observations, while the percentage of time the juvenile scarlet macaw spent further than 2 m away from conspecifics decreased 1-2 weeks after the death of the female (Figures 4.14A and 4.14B).

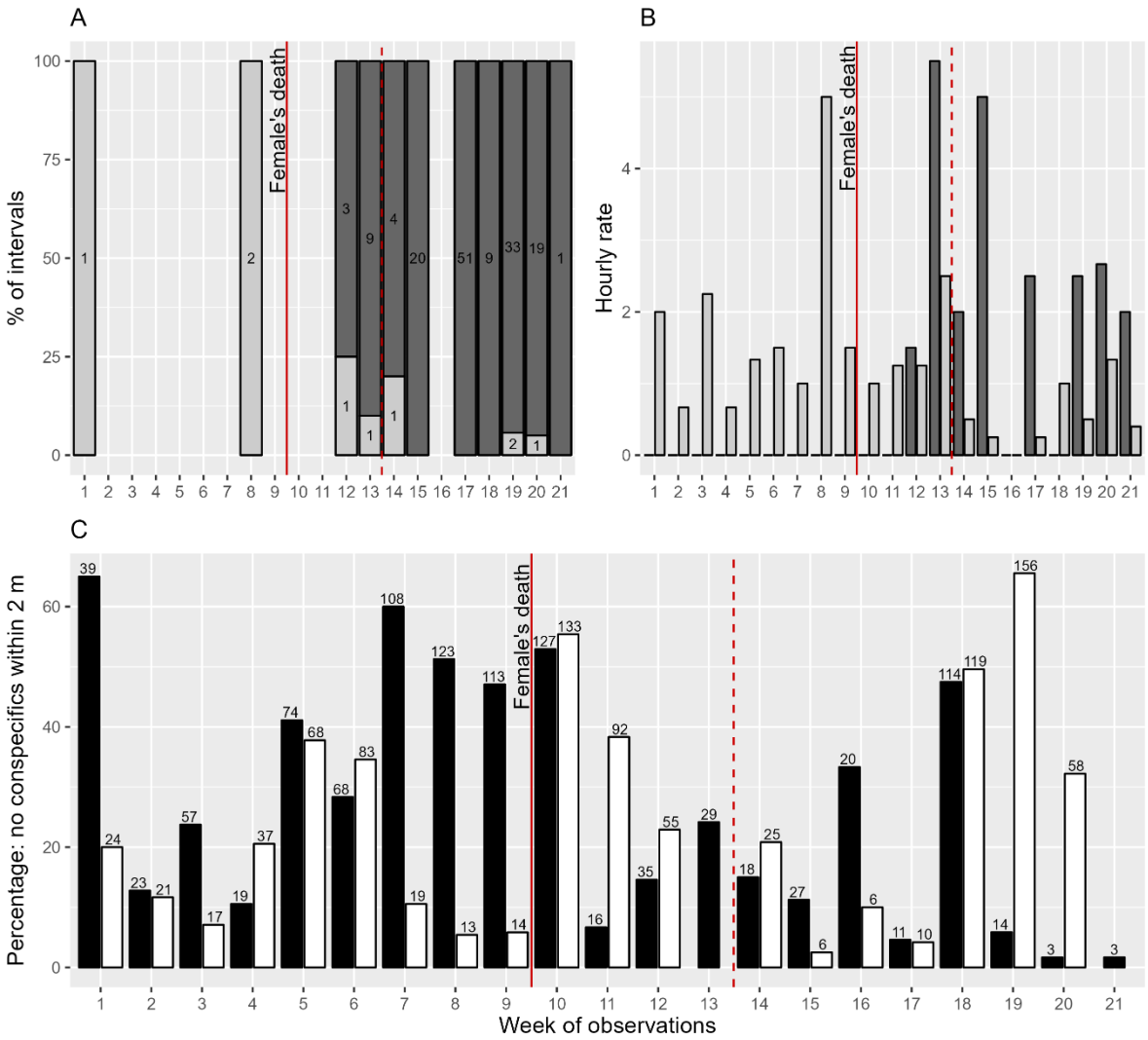


Figure 4.14. Changes in social interactions in the male and juvenile scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK) across non-consecutive weeks of observations, before and after the death of the female scarlet macaw.
(A) Percentages of affiliative (dark grey bars) and aggressive (light grey bars) behaviours in intervals with social interactions; (B) Hourly rate of affiliative and aggressive social occurrences; (C) Percentages of observations with no conspecifics within 2 m of the juvenile (black bars) and male scarlet macaws (white bars). The male and female scarlet macaws were the parents of the juvenile scarlet macaw. The solid red line represents the death of the female scarlet macaw, while the dashed red line shows when there were physical modifications applied to the enclosure. Numbers within (A) and above (C) bars represent the number of observations.

4.4. Discussion

An overall lack of physical complexity was identified in the pre-modification enclosures of the captive parrots, with limited opportunities for complex manipulation, locomotion, and support use, while some parrots exhibited low engagement in social behaviour. Observations in the post-modification period showed significant changes in the cognition, locomotion and social data, although the behavioural responses varied across individuals (Table 4.10).

Table 4.10. Summary of statistically significant differences in the behaviour of the grey parrots and scarlet macaws at zoo A (Drayton Manor Park and Zoo, UK) and zoo B (Jurong Bird Park, Singapore) between the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and social environment of the parrots, took place in October – December 2019 (grey parrots at zoo A), October – December 2020 (scarlet macaws at zoo A), and January – March 2020 (zoo B). Post-modification observations (after alterations to the enclosure and social environment of the parrots) took place in October – December 2021 (zoo A) and December 2021 – January 2022 (zoo B). Blue and red cells represent a significant increase and decrease in the frequency of a behaviour, respectively, in the post-modification period, in comparison to the baseline period of observations. Cells with "-" show that statistical tests were not conducted due to lack of observations in one or both periods of data collection. GA = Grey parrot group A; MS = Male scarlet macaw; JS = Juvenile scarlet macaw; GB = Grey parrot group B; S1 = Scarlet macaw 1; S2 = Scarlet macaw 2; S3 = Scarlet macaw 3.

Behaviour	Zoo A			Zoo B			
	GA	MS	JS	GB	S1	S2	S3
Basic feeding manipulation							
Basic object manipulation							
Foot use during feeding							
Foot use during object manipulation							
Climbing (i.e. tripedal locomotion)							
Hourly flight rates						-	-
Use of unstable perches							-
General use of wire mesh							
Use of wire mesh during climbing							
Use of thick perches						-	-
Use of horizontal perches						-	-
Allopreening							
Hourly rates of affiliative behaviour	-			-			
Hourly rates of aggressive behaviour	-			-			
% time with no conspecifics within wing length							
% time with no conspecifics within 2 m							

4.4.1. Cognition: complexity of manipulation by captive grey parrots and macaws

Complex manipulation skills were observed in the wild scarlet macaws in Costa Rica, that used various feeding strategies and engaged mostly in advanced manipulation while handling the fruits and seeds on the trees (section 2.3.2). The ability to manipulate various food items and extract the seeds within has also been reported in wild grey parrots (Tamungang and Ajayi, 2003).

In contrast, most of the food and object manipulations observed across the captive parrots in the baseline period of the present study were of basic (i.e. chopped soft fruit and vegetables) or intermediate (i.e. chopped hard fruit and vegetables, sunflower seeds) complexity. These results were expected, as the (mostly) pre-processed food provided offered few opportunities for advanced manipulation, and the negative impact of pre-processed food on the behaviour and welfare of captive parrots has been previously suggested (e.g. Mellor et al., 2021). The browse and cardboard-focused enrichment, which is occupational but low in cognitive complexity (i.e. it keeps parrots occupied and engaged, but without the need to apply their advanced cognitive abilities), most likely underlie these results. The provision of larger food items (e.g. whole food or bigger chunks, over-sized pellets) was one of the modifications proposed in this research to encourage natural feeding behaviours (Table 3.3), as it has been shown to increase food processing times (van Zeeland et al., 2013a). However, these were not implemented by the zoos due to potential risks zoo management did not wish to take by using larger chunks of food (i.e. increased competition and aggression between individuals, increased waste and proliferation of pests; Brereton, 2020b). The

provision of puzzle feeders, which was proposed to encourage complex manipulation in my research (Table 3.3), was implemented at zoo A only, but were rarely used by the parrots. Zoo B opted not to implement the puzzle feeders due to their unnaturalistic plastic materials, which could jeopardise the aesthetics of the enclosure and visitor perceptions. It has been previously suggested that visitors may associate naturalistic enrichment items with improved animal welfare (Razal & Miller, 2019), but several other studies have found that enrichment appearance has no effect on visitor perceptions (Jacobson et al., 2017; Kutska, 2009; Salas et al., 2021).

Therefore, even though significant changes in the percentage of basic food manipulation were detected in some individuals (Table 4.10), these were a result of changes between basic and intermediate levels of manipulation, as advanced manipulation remained virtually unseen. The high percentage of unclear feeding observations may have influenced these results, as both basic and intermediate levels of manipulation could have been performed while the parrot was feeding without removing its head from the food tray, obscuring the visibility, which is unlikely to be the case for advanced manipulation. On the other hand, the significant increases in basic object manipulation observed in some of the parrots (Table 4.10) were likely a response to the high diversity of branches added to the enclosure, as they manipulated them more and spent less time manipulating the thicker and more robust branches (i.e. intermediate manipulation; Table 2.3) that dominated their baseline enclosures. Browse is an effective enrichment for parrots (e.g. Field & Thomas, 2000), and although the thinner and easily breakable branches were easier to manipulate, and ultimately destroy, than the thicker branches they manipulated during the baseline

period of observations, they are both occupational but not cognitively challenging (i.e. they encourage manipulation but do not involve problem solving). Therefore, it is unlikely that changes between these two levels of object manipulation had a substantial effect on the overall behaviour and welfare of the parrots, which is further highlighted by the lack of significant changes in object manipulation observed in the time budgets of these individuals (section 3.3.2.1).

The wild scarlet macaws in Costa Rica used their feet in almost half of the feeding observations, although it varied across the three tree species they were seen feeding on (section 2.3.2), while other *in situ* studies also reported foot use during feeding in other macaw species (e.g. Pitter & Christiansen, 1995; Silva, 2018). On the other hand, grey-headed parrots in Africa used their feet in 53 to 100% of observations during feeding on various food sources (Symes & Perrin, 2003b), highlighting the importance of foot use in a sister taxon to the grey parrots.

In the present study, most parrots rarely used their feet during feeding or object manipulation. The zoos were asked to increase the size of the food items provided as part of the modifications proposed for my study (Table 3.3), which has been shown to be an effective way to encourage foot use during feeding (James et al., 2021; Rozek et al., 2010). However, the zoos opted not to provide larger food items due to the risks already described (e.g. increased food waste and pest proliferation; Brereton, 2020b). It was hoped the new suspended feeders, being a less stable structure than the previous ones, would discourage the parrots from eating directly from them, and

instead taking the food to nearby perches for further manipulation, increasing foot use, behaviour that has been documented in wild scarlet macaws (Nemeth & Vaughan, 2004). Although this was sometimes observed in the grey parrot group A, the feeders seemed to have the opposite effect on the scarlet macaws at zoo A, with a significant decrease in foot use during feeding observed. There are two potential explanations for these unexpected results. First, the new feeder discouraged these two individuals from using their feet while feeding as it was not stable compared with their previous one and they exhibited an apparent low confidence while moving on unstable supports. Secondly, the juvenile was likely still inexperienced in manipulation as young scarlet macaws develop their skills over time (Myers & Vaughan, 2004), and are sometimes less able to feed from the same food sources as their parents until they have gained more experience (Nemeth & Vaughan, 2004). This may explain why he seemed to rely more on his feet to manipulate pre-processed food than his adult counterparts, that could do it using their bills only. As he was a year older in the post-modification phase, he was likely more skilled in manipulation and was more able to handle the pre-processed food using his bill only (discussed in section 3.4.1.2).

During the post-modification period of observations, the grey parrot group B seemed to spend less time interacting with the bark chunks found on the ground of their enclosure, which may explain the significant decrease in foot use during manipulation observed in this group (Table 4.10). It is unclear why they did not interact with bark as much in the post-modification period, but it could have been due to habituation, which can result in short- and/or long-term declines in enrichment use (Tarou & Bashaw, 2007), although it is unclear how long the bark had been in the enclosure. It could have

also been because they spent less time on the ground (section 3.3.2), where the bark was. In contrast, the significant increase in foot use during object manipulation observed in the juvenile scarlet macaw (Table 4.10) was most likely a result of the added browse to the enclosure, as he was observed breaking branches into smaller pieces and then grabbing them for further manipulation. Furthermore, browse has been previously identified as important enrichment for parrots in captivity (Field & Thomas, 2000). The macaw groups at zoo B were often observed grabbing food from the feeders and moving to nearby perches to further manipulate and consume it, and therefore the new feeders may have had the desired effect on foot use in these individuals. However, it is possible this behaviour was motivated by social tension caused by competition while feeding, as there were multiple parrots in the enclosure.

4.4.2. Locomotion and support use by captive grey parrots and macaws

While free-living scarlet macaws in Costa Rica were seen climbing in most observations of locomotion (section 2.4.3), qualitative observations of free-living grey parrots in Cameroon also reported a preference for climbing rather than flying across branches within the same tree (Tamungang et al., 2016a), further confirming the importance of tripedal locomotion in both of these species. Flying is also an important form of locomotion in these animals with previous studies showing wild scarlet macaws covering long daily distances by flight (i.e. up to 40.7 km on average; Brightsmith et al., 2021) and reporting daily grey parrot flights between forests and across large areas of habitat (Amuno et al., 2007).

In contrast, flying was infrequently observed in the captive parrots in the present study, and tripedal locomotion was either rarely observed or was mostly on homogeneous and unchallenging supports. During the baseline period of observations, the captive grey parrots and scarlet macaws often climbed the entire length of the enclosure on the mesh instead of flying, which has also been previously reported in captive Amazon parrots (*Amazona ventralis*; Gustavsen et al., 2016). Even though the wire mesh enclosure sides can increase climbing opportunities for captive animals (Anderson, 2014; Kalmar et al., 2007; Ross et al., 2011), they are often stable and homogeneous structures that offer little locomotion challenges. In the present study, when the parrots climbed on the mesh, they moved in a repetitive motion, often in a straight line. In the wild, parrots rarely climb on continuous structures, such as tree trunks, generally opting to move on thinner branches that they can grasp (Reader et al., 2022), and unlike these observations on the captive parrots, the free-living scarlet macaws in Costa Rica were seen using diverse and challenging perches (i.e. thin, unstable and non-horizontal) in at least similar proportions (section 2.4.3). Furthermore, even though no quantitative data on support use were found in the literature for wild grey parrots or closely related species, it can be assumed with confidence they also use a high diversity of supports, based on the heterogeneity of vegetation they feed from (Tamungang and Ajayi, 2003) and depend on for other activities such as roosting and nesting (Tamungang et al., 2016b).

Significant changes in locomotion and/or support use (in general and during climbing) were detected in the post-modification period for most parrots, although these changes varied across individuals. Increasing the complexity of the physical environment of

captive parrots elicits locomotion-related behaviours such as climbing (Meehan et al., 2003; Meehan & Mench, 2002; van Hoek & King, 1997), and therefore the increased diversity of supports in the post-modification phase likely influenced the observed improvements in tripedal locomotion. Tripedal locomotion in free-living monk parakeets (*Myiopsitta monachus*) was primarily influenced by support orientation (Granatosky et al., 2022), and therefore, in the present study, the provision of more non-horizontal supports was likely key to increase this behaviour in some of the parrots. Grey parrot group A seemed to favour flying over climbing in the modified environment potentially explaining the slight decrease in tripedal locomotion. Furthermore, the relatively lower number of individuals physically incapable of flying in the post-modification period (9.0%) than during the baseline period (25.0%) may have also influenced those results, as fewer individuals were reliant on tripedal locomotion. Although there was an attempt to place branches on the mesh of the macaw enclosure at zoo B, these were destroyed within two days by the younger macaws in the enclosure. As zoo staff's time constraints were an impediment to regular replacement, this modification was not fully implemented as planned. As a result, scarlet macaws 1, 2, and 3 were still observed climbing the mesh from one side of the enclosure to the other.

The increased structural diversity of perches in the post-modification period, an important feature of parrot enclosures (Field & Thomas, 2000), seemed to result in improvements in general support use across individuals. A preference for thinner and terminal branches was detected among free-living monk parakeets, likely because they were able to maintain a hold on the support (Granatosky et al., 2022), which may explain why many of the parrots in the present study favoured thinner perches when

given increased perching opportunities. Scarlet macaw 1's increased general use of the mesh (Table 4.10) may have been a response to the more dynamic social environment, as it tried to avoid the active younger macaws in the enclosure (i.e. the potential effects of enclosure mates on space use has been previously suggested; e.g. Blanchett, 2018). The scarlet macaw 1 may have also used the wire mesh to spend more time close to scarlet macaw 2, while the juvenile scarlet macaw's increased use of horizontal and thick perches was potentially influenced by his improved relationship with the male scarlet macaw, as they spent more time together. Scarlet macaw 2 was observed climbing down from the top mesh directly onto the top perches, and therefore the new top perches installed likely encouraged perch use in this bird. It was also noted that the adult scarlet macaws (and, to a lesser extent, the juvenile scarlet macaw at zoo A) in the present study exhibited an apparent low confidence when initially using more challenging supports (i.e. attempting to use them but quickly retreating to more stable perches), which contrasted with observations of their free-living counterparts (section 2.4.3). This suggests reduced behavioural flexibility in these animals, a potential response to the captive environment (Mason et al., 2013), and likely influenced by their age (Loepelt et al., 2016) and long-term exposure to unstimulating environments in the past (Fox & Millam, 2004; Meehan & Mench, 2002). However, the apparent confidence in the use of challenging supports seemed to improve over time, which is also reflected in the overall improvements in support use observed in the post-modification period (Table 4.10).

Flight rates increased in both grey parrot groups (Table 4.10), likely motivated by the provision of clear spaces as previously recommended for captive parrots (e.g. Field &

Thomas, 2000) and the more challenging to reach suspended feeders, as the grey parrots at both zoos were seen flying between the supports surrounding the feeders in order to reach the food. This was not the case with the scarlet macaws, as some exhibited a decrease in flight behaviour (Table 4.10). The juvenile scarlet macaw's loss and regrowth of the tail between periods of observations may have affected flight behaviour, as the tail is important for maneuvering and stability during flight (Tobalske, 2007). Furthermore, although clear spaces were also provided to all scarlet macaws, they still had climbing routes they may have favoured over flying, which is often observed in captive parrots (Field & Thomas, 2000). More research is needed to identify how these modifications to the *ex situ* environment can be further expanded to encourage both climbing and flying in captive parrots. The frequent flight behaviour and use of high diversity of supports observed in the young macaw groups at zoo B suggest a potential age-related effect on support use, likely associated with the higher behavioural flexibility previously reported for younger parrots (e.g. kākās; Loepelt et al., 2016). They also indicate that the macaws added to the enclosure in the post-modification phase of the study used, and potentially benefitted from, the increased physical complexity in their environment.

The social environment has been previously shown to influence locomotion in captive parrots (Meehan et al., 2003) and the changes in social dynamics that occurred not only with the grey parrot group B but also grey parrot group A and scarlet macaws (i.e. loss and/or addition of other animals to the enclosure) likely affected the changes observed in locomotory behaviours. Future studies should try to isolate the potential

effects of increasing the diversity of supports on the expression of locomotory behaviours in captive parrots.

4.4.3. Social behaviour and proximity in captive grey parrots and macaws

Allopreening is an important behaviour in developing and maintaining social bonds (Morales Picard et al., 2020), and observations of free-living scarlet macaws in Costa Rica showed it was the most common social behaviour among the wild individuals (section 2.3.4). Allopreening was also the most frequent social behaviour reported for wild red-fronted macaws (Pitter & Christiansen, 1997), while grey-headed parrots "often" engaged in this behaviour as well (Symes & Perrin, 2014).

The captive scarlet macaws in the baseline period of the present study also engaged in allopreening in most social observations, and were often in close proximity to conspecifics, suggesting the presence of social bonds among individual macaws. The skewed sex ratio found in the scarlet macaw group at zoo B may have encouraged same-sex pairing, as previously observed in feral pigeons (*Columba livia;* Jankowiak et al., 2018). Furthermore, long-term same-sex pairing has been reported in captive parrots (e.g. galahs [*Cacatua roseicapilla*]; Rogers & McCulloch, 1981) and found to be beneficial for their welfare in comparison to single housing (Meehan et al., 2003). In contrast, the grey parrot groups in the present study exhibited a low expression of social behaviours (section 3.3.2) and rarely engaged in allopreening or spent time in close proximity to conspecifics. These are potential indicators of low compatibility among individuals, which may be a result of personality incompatibility due to limited

mate choice (Fox & Millam, 2014) or abnormal social behaviour due to potential hand-rearing (as applied to grey parrot group B only, as six individuals were of unknown origin and could have been hand-reared; section 3.2.1; Table 3.1) (Williams et al., 2017).

Post-modification observations showed significant improvements in the social dynamics between the male and juvenile scarlet macaws at zoo A. These improvements were most likely caused by the death of the female scarlet macaw rather than the physical modifications applied to the enclosure, as there were already changes detected in the few weeks of observations between the death of the female and the start of the post-modification period. The aggressive behaviour of the male scarlet macaw towards the juvenile during the baseline period of observations, apparently induced by the presence of the female, could have been due to mate guarding, which has been previously observed in other parrot species, such as glossy black cockatoos (*Calyptorhynchus lathami*; Arnett and Pepper, 1997) and New Caledonian parakeets (*Cyanoramphus saisset*; Theuerkauf et al., 2009). Although the juvenile scarlet macaw was a young and sexually immature male (i.e. under 5 years of age; Estrada, 2014), he may have still elicited this behaviour in the adult male. Nest territoriality could have also elicited aggression in the male scarlet macaw, as it has been observed in wild blue-and-gold macaws (*Ara ararauna*), with nesting individuals displaying agonistic behaviours towards nonbreeding conspecifics, threatening and chasing them away (Renton, 2004). While some adult parrots tolerate their fledged offspring and other immature individuals in the enclosure, even during the breeding period, some exhibit aggressive behaviour and can even kill their offspring (King,

2000). The aggressive nesting behaviour of the male scarlet macaw had been previously reported when he fatally attacked a blue-and-gold macaw that the scarlet macaw pair shared the enclosure with, when it tried to get into their nest (A. Hulbert, pers comm., 2019). Even though they were not breeding during the baseline period, they were still frequently seen near the nest with the female spending time in it. They also started the breeding cycle a few months later, in the same nest they had used the year before, until the female died due to a prolapse of the oviduct that occurred during egg laying. Furthermore, there is a possibility the male scarlet macaw was hand-reared, which is unconfirmed but supported by its lack of fear and aggressive behaviour towards humans, and that could have also influenced the aggressive behaviour towards the juvenile (van Hoek & Ten Cate, 1998). Therefore, the juvenile scarlet macaw seemed to benefit from the new social environment in the post-modification period.

The increased complexity in the enclosure may have provided the grey parrots with opportunities to increase their distance from each other, which has already been suggested in the context of enclosure use (section 3.4.2.1). Although social housing of captive parrots has been found to be paramount in ensuring their health and welfare (e.g. Aydinonat et al., 2014; Meehan et al., 2003), social animals can also experience stress from conspecific neighbours, and providing opportunities to retreat from them is therefore beneficial (Whitham & Miller, 2019). These results may have also been affected by the loss of five individuals between periods of observations.

4.5. Conclusion

Most parrots exhibited improvements in locomotory behaviours and/or support use in the post-modification period of observations. The physical modifications applied to the enclosures likely influenced these results, as the parrots were provided with increased opportunities for engagement in these behaviours (e.g. clear spaces for flying, increased diversity of supports for climbing). However, the changes in the parrots' social environment that occurred between periods of observations may have also influenced these results, and more research is needed to determine the relative effects of the physical and social alterations on the behaviour and welfare of the parrots. No improvements were observed in the occurrence of cognitive challenges or in the complexity of manipulation and foot use during manipulation. Some of the modifications proposed to encourage these behaviours could not be applied (e.g. provide whole food or increase the size of the food chunks provided), and the ones that were (e.g. puzzle feeders at zoo A) were almost never used by the parrots.

Social behaviour and proximity also differed between the baseline and post-modification periods of observation for some of the parrots, especially the scarlet macaw family group at zoo A. The male and juvenile scarlet macaws developed a social bond, with an increase in affiliative and decrease in aggressive behaviours, likely a response to the death of the female scarlet macaw. This seemed to benefit the overall social environment, and consequently welfare, of the juvenile scarlet macaw. The grey parrot groups spent less time in close proximity to conspecifics in the post-modification period, which may have been because of changes in the social structure between periods, or a response to the increased physical complexity in the enclosures. As the

grey parrots exhibited weak social bonding, increased opportunities to avoid conspecifics may have reduced stress caused by forced exposure to other parrots.

Overall, these results suggest that enhancing the physical complexity of the *ex situ* environment, with evidence-based enclosure modifications, may be an effective way to encourage specific wild-type behaviours in some captive parrots. Furthermore, the social environment of captive parrots must also be carefully assessed, to ensure that they have opportunities to engage in social behaviours and develop social bonds, but also to avoid conspecifics and retreat from them if they wish to do so. Additional alterations to the husbandry and management of captive parrots should be attempted in future studies to enable wild-type behaviours further across individual parrots in captivity. Some additional modifications that can be attempted in future research include: (1) the provision of more frequent and varied enrichment, (2) presenting food in a more challenging way that more closely replicates their foraging behaviours in the wild, and (3) training the birds to engage with the enrichment.

Like the behavioural assessments conducted for the captive grey parrots and macaws in Chapters 3 and 4, the behaviour of two zoo-housed swift parrots is assessed in Chapter 5. Their behavioural repertoire is described and compared with available literature from their wild counterparts, and their responses to small-scale changes in their enclosure and management are discussed.

CHAPTER 5

CASE STUDY: ASSESSING THE BEHAVIOUR OF TWO ZOO-HOUSED SWIFT PARROTS

Paper planned for publication:

Lemos de Figueiredo, R.[1], Shirley, M.[2], Hulbert, A., Chappell, J. (in prep). Assessing the behaviour of two juvenile zoo-housed swift parrots (*Lathamus discolor*) in a mixed-species exhibit. *Journal of Zoological and Botanical Gardens*.

[1] Collected baseline data, analysed all data.

[2] Collected post-modification data.

ABSTRACT

The swift parrot (*Lathamus discolor*) is a migratory species that breeds in Tasmania and over-winters in mainland Australia. They are critically endangered in the wild and although *in situ* conservation actions have been prioritised, *ex situ* conservation measures have also been proposed for the species. However, despite being common among private breeders, they are relatively rare in zoos, and their *ex situ* behaviour, husbandry and management have received little research attention. A case study was conducted on two juvenile swift parrots, male and female siblings, housed in a walkthrough mixed-species exhibit (i.e. closed to visitors during this study), with the aims of (1) assessing their behaviour, (2) evaluating the impact of small-scale interventions in encouraging natural feeding behaviours, and (3) generating evidence to inform the *ex situ* husbandry and management of this species. Behavioural data were collected between February and March 2021 (baseline period) and December 2021 and March 2022 (post-modification period, after implementation of interventions to encourage natural feeding behaviours), using focal interval sampling. Both swift parrots exhibited high activity levels and engaged in foraging and locomotion behaviours throughout the day, which was likely encouraged by the well vegetated enclosure that offered multiple areas for exploration. The mealybugs (Pseudococcidae) detected on the plants within the enclosure also seemed to encourage foraging, as they resemble the lerps of psyllid insects (Psyllidae) that swift parrots feed on in the wild. Nevertheless, during baseline observations, the swift parrots mostly fed on the seeds that were provided to their enclosure mates (Australian finches [Estrildidae] and a female diamond dove [*Geopelia cuneata*]), which contrasts with their nectar- and lerp-based diet in the wild. Interventions to reduce seed eating

and encourage natural feeding behaviours were conducted, included diet changes, the removal of their favoured seed feeder, and training for nectar handfeeding. Although fewer post-modifications observations were conducted, they suggest a decrease in seed consumption. A decrease in activity, likely age-related, was also detected in both individuals, in the post-modification period. This case study has applications for the *ex situ* management of swift parrots and other nectarivorous parrot species, by informing enclosure design and husbandry practices that may encourage activity and natural feeding behaviours.

Keywords: *ex situ* management, natural behaviour, nectarivorous, swift parakeet

5.1. Introduction

Swift parrots are a migratory species (already introduced in section 1.6.4) that use a variety of habitats while over-wintering in mainland Australia, including scattered trees and patches of remnant vegetation within or surrounded by human-modified environments, and extensive areas of natural forest (Saunders & Heinsohn, 2008). They rely on mature eucalyptus trees (*Eucalyptus* spp.) for foraging in winter (Kennedy & Tzaros, 2005) and during their breeding season in Tasmania, as well as for nesting (Webb et al., 2012). Even though swift parrots have retained some of the alimentary morphological features of their granivorous ancestors (i.e. muscular gizzard and long intestine), they developed a brush tongue, a wider crop, longer proventriculus and wider duodenum, which are adaptations to a nectarivorous diet (Gartrell et al., 2000). In the wild they feed mostly on nectar and lerps (i.e. sugary protective covers of psyllid

insects [Psyllidae]; Figure 5.1B) from eucalyptus trees (Kennedy & Tzaros, 2005; Saunders & Heinsohn, 2008).

A



B



Figure 5.1. Comparison of the physical similarities between the mealybugs found on the vegetation in the swift parrot enclosure at Drayton Manor Park and Zoo (UK) and the lerps of psyllid insects that swift parrots feed on in the wild.

(A) Evidence of mealybugs (Family Pseudococcidae) underneath a leaf in the swift parrot exhibit at the zoo (February 2021). Photo: RLF. (B) Lerps of the red gum psyllid insect (*Glycaspis brimblecombei*). *(*Photo: Laudonia & Garonna (2010).

They reach their sexual maturity when they are approximately one year old, although they are unlikely to breed in that year unless they hatched early in the previous season (Gartrell, 2002). Their plumage is sexually dimorphic: males have brighter red plumage in the face and throat areas, while females exhibit duller colours (BirdLife International, 2023). The swift parrot is facing a high risk of extinction (Stojanovic et al., 2018) and is one of the focus species of the Difficult Bird Research Group (DBRG), which conducts *in situ* research on the ecology and conservation of several Australian threatened species (DBRG, n.d.). Although *in situ* management has been prioritised in the conservation plan for the species (Saunders and Tzaros, 2011), *ex situ* efforts can also play a role in the conservation of the species (BirdLife International, 2018b). Although

relatively rare in zoos (Species360, 2018), they are common among private breeders (BirdLife International, 2018b). The Parrot Taxon Advisory Group (TAG) of the European Association of Zoos and Aquaria (EAZA) has been working to increase the population numbers under an European *Ex Situ* Programme (EEP) for the species (EAZA, 2022). The EAZA Parrot TAG also identified research gaps in the *ex situ* management and husbandry of this species (C. Mitchell, pers comm., 2018), which limit the development and application of evidence-based practices (Melfi, 2009).

This case study aims to (1) assess the behaviour of two zoo-housed swift parrots, (2) evaluate the impact of evidence-based small-scale husbandry changes on feeding-related behaviours, and (3) generate evidence to inform *ex situ* management and husbandry of this species.

5.2. Materials and methods

5.2.1. Location, time, and swift parrots included in this study

Data were collected at Drayton Manor Park and Zoo (Tamworth, United Kingdom), between February and March 2021 during the baseline period (before alterations to the husbandry and management of the swift parrots), and between December 2021 and March 2022 during the post-modification period (after the alterations took place). This study was approved by the University of Birmingham's Science, Technology, Engineering and Mathematics (STEM) ethics committee (code: ERN_19-0974), and by Drayton Manor's animal management team.

Two swift parrots, a male and a female hatched in April 2020, were included in this study. They were parent-reared until they were approximately one month old, and then removed from the nest and hand-reared by the animal care staff when the parents stopped feeding them. They started exploring solid food approximately a week after being removed from their parents.

5.2.2. Methods for behavioural data collection on swift parrots

Data were collected between 8:00 and 17:00 hrs (GMT) using focal interval sampling, as individuals were identifiable, despite being sexually immature in the baseline period, as the male already had a brighter red face and throat than the female. Practice observations were conducted over 12 hours across 4 days to adapt for the swift parrots the protocol used for the grey parrots and scarlet macaws (Chapters 3 and 4). Unlike with the scarlet macaws and grey parrots (Chapters 3 and 4), a single protocol was used and only two layers of data (behaviour and location within the enclosure) were collected in each interval, allowing for shorter sampling intervals of 15 seconds in 30-minute sessions. Each of the two swift parrots was sampled up to three times a day (up to six sessions a day in total) on a rotation system, with three sessions conducted between 8:00 and 12:30 hrs (GMT) and three sessions conducted between 12:30 and 17:00 hrs (e.g. day 1: male, female, male in the morning and female, male, female in the afternoon; day 2: female, male, female in the morning, and male, female, male in the afternoon). The baseline data were collected by the main researcher (RLF), while the post-modification data were collected by Marc Shirley (MS), an intern with the animal care team at the zoo. Before starting data collection, MS practised for approximately two weeks before a joint session with RLF, conducted for the purpose

of inter-observer reliability analysis. Once inter-observer reliability was confirmed to be high, MS continued with data collection for the post-modification period of the study, which started one month after the modifications were implemented. The ethogram used in this study included broad behaviours previously described (Table 2.1, 2.4, and 2.6; section 2.2.4), but new categories of feeding and foraging-related behaviours were introduced in the ethogram used in this study (Table 5.1).

Table 5.1. Ethogram of behaviours of swift parrots used for behavioural data collection at Drayton Manor Park and Zoo (UK).

Some behaviours described in section 2.2.4 were included (indicated in the "Description" column), but other species-specific behaviours were also added. The behaviours that were grouped for data analysis are indicated in the Data analysis column. NA = Not applicable.

Behaviour	Modifier	Description	Data analysis
Perching	None (Inactive)	Table 2.1	NA
	Wing flapping		Comfort behaviour
	Yawning		
	Stretching		
	Feather fluffing		
	Mouth movement		NA
Self-maintenance	Preening		NA
	Bill wiping		
	Bathing		
	Scratching		
Locomotion	Flight	Table 2.4	NA
	Hop		
	Climbing (tripedal)		
	Walk		
Geophagy	NA	Table 2.1	NA
Social	Affiliative	Includes allofeeding, allopreening, nibbling, mating (Table 2.6).	NA
	Aggressive	Includes threatening, chasing, displacement, and fighting (Table 2.6).	NA
Stereotypies	Oral	Table 2.1	Stereotypies
	Motor		
Feeding	Fruit/Vegetation	Eating directly from feeder.	Feed/Drink
	Seeds		
	Nectar		
	Insects		
	Pellets		
	Unknown		

Behaviour	Modifier	Description	Data analysis
Drinking	NA	Drinking water.	
Foraging	Plants	Searching for food: it includes leaf manipulation with their mouths and searching for scattered food on the ground. Also includes moving while simultaneously feeling the substrate with their tongues)	NA
	Ground		NA
	Other (e.g. wall)		NA
			NA
Object interaction	NA	Interacting with a non-food object: includes holding with mouth or foot, biting and chewing.	NA

The parrots' location in the enclosure was recorded based on a diagram (Figure 5.2).

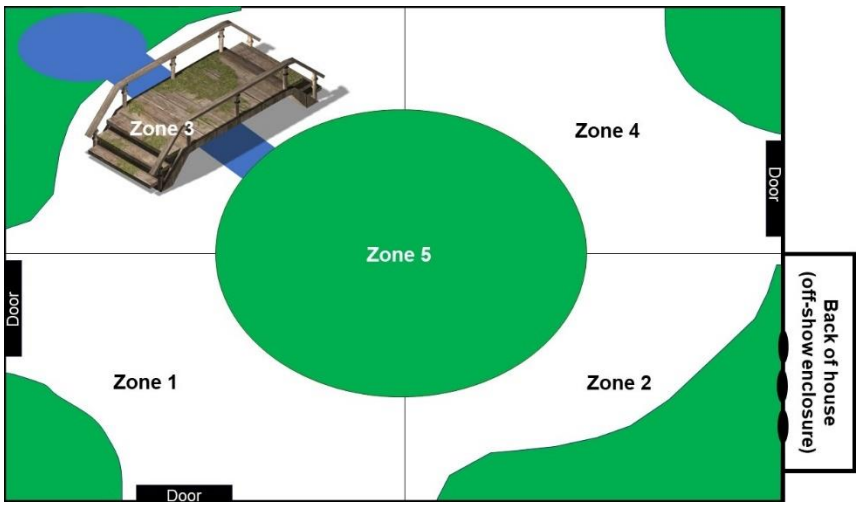


Figure 5.2. Schematic representation of the enclosure of the two swift parrots at Drayton Manor Park and Zoo (UK) that were observed between February and 2021 and March 2022 as part of this study.

The enclosure was divided in six zones for data collection on horizontal space use. Zones 1-4 are the four quadrants of the enclosure, each containing a planted area (green shapes) and the surrounding foot path (white area). Zone 5 is the circular planted area in the middle of the enclosure, while the back of house is the smaller area, inaccessible by visitors when the zoo is open, that the birds can retreat to. Zone 3 also features an artificial stream of water and a wooden bridge.

For horizontal space use, the main area of the swift parrot enclosure was divided in five zones, the four quadrants, each with a planted area and surrounding concrete path (Figures 5.2 and 5.3A-D), and a fifth zone that consisted of the soil/planted section in the middle (Figures 5.2 and 5.3E) and a smaller back-of-house area (Figure 5.3F).



Figure 5.3. Swift parrot enclosure at Drayton Manor Park and Zoo (zoo A) during baseline period of observations (before enclosure and husbandry modifications).
Baseline observations occurred between February and March 2021. (A-E) Zones 1 to 5 in walkthrough area; (F) back of house area. Photos: RLF.

The vertical space of the enclosure was divided into three sections: top quarter, ground (including concrete area, soil, and rocks and logs at the bottom of the enclosure), and middle (i.e. all space in between the other two categories).

5.2.3. Housing conditions of the swift parrots

The swift parrots were kept in a temperature-controlled (18–21ºC) indoor walkthrough enclosure, usually accessible by visitors, but closed to the public for the entire duration of the study. Artificial lighting in the enclosure consisted of two light wave units with ultraviolet (UV) bulbs, turned on between 7:00 and 19:00 hrs every day throughout the entire period of observations. Windows on the top side of the enclosure allowed for natural light in the enclosure as well. Data on the humidity levels within the enclosure were not available.

The enclosure consisted of a larger area (approximately 500 cm length × 500 cm width × 250 cm height [lowest side] or 500 cm × 500 cm × 500 cm [highest side]), and a smaller off-show, back of house area where the feeders were located (approximately 300 cm x 50 cm x 200 cm). They shared the enclosure with approximately 30 birds of six Australian species. Two of those species overlap in natural geographic distribution with the swift parrot (double-barred finch [*Taeniopygia bichenovii*] and diamond dove [*Geopelia cuneata*]), while the other four species do not (Gouldian finch [*Chloebia gouldiae*], blue-faced parrot finch [*Erythrura trichroa*], star finch [*Neochmia ruficauda*], and long-tailed finch [*Poephila acuticauda*]). The larger area consisted of five planted areas, divided into sections for data collection on enclosure use (Figures 5.2 and 5.3),

with soil, planted eucalyptus (*Eucalyptus spp.),* logs and rocks. A concrete footpath surrounded these areas. There was an artificial stream of water in one of the corners of the exhibit, which started in section 3 and flowed to section 5, under a wooden bridge on the footpath (Figure 5.3C).

A seed mixture (Gouldian & Australian Finch Maintenance Mixture, All Creatures Ltd t/a Planet Aviary, United Kingdom) was provided for the finches, in feeders placed in the back of house area, one hanging from the roof and two placed on the floor, next to a bowl with food for the swift parrots. The swift parrots were fed vegetables, fruit, pellet (NutriBird T16; NV Versele-Laga, Belgium), and nectar (Nutribird Lori; NV Versele-Laga, Belgium). The mealybugs (Family Pseudococcidae) detected in the vegetation (Figure 5.1A) around the enclosure were also a likely food source for the swift parrots.

A few husbandry changes were instigated for the post-modification period. Upon identification of excessive seed eating by the swift parrots during the baseline period of observations, and low interest in the food provided to them, the pellet was replaced with a nectar pellet for loris and lorikeets (Nectar Pellets; Vetafarm, Australia). Both swift parrots were trained to hand feed by the animal care staff, using small pots containing liquid nectar, with training occurring several days of week using positive reinforcement (with the nectar itself as the reinforcer). The suspended seed feeder at the top of the back of house area and only the two bottom feeders were retained (Figure 5.4C).

A B C



Figure 5.4. Zones in the swift parrot enclosure at Drayton Manor Park and Zoo (UK) that were altered between the baseline and post-modification periods of observations.

The baseline period of observations, which was before alterations to the swift parrot enclosure, occurred between February and March 2021, while the post-modification period of observations (after alterations to the enclosure) occurred between December 2021 and March 2022. (A) Zone 3 of the enclosure in the baseline and (B) post-modification periods. (C) Back of house area in the post-modification period, after the removal of a hanging feeder containing seeds. Photos: RLF.

The vegetation in section 3 also grew considerably between both periods of observations (Figure 5.4A-B). Despite some trimming on the top (for zoo management reasons), there was still more vegetation reaching the top section of the enclosure than during the baseline period.

5.2.4. Data analysis

Data processing was conducted using the same software and R packages described in section 3.2.6. A descriptive analysis was performed to determine the daily percentages of behaviours in each swift parrot's time budgets and the total percentages of different levels of behavioural activity, in the baseline and post-modification periods of observations. Total percentages of variations of perching,

locomotion and foraging behaviours, and of different food items consumed during feeding observations, were also calculated for each individual. The total percentage use of each horizontal and vertical sections of the enclosure by each of the swift parrots were also calculated for both periods of observations. The horizontal use of the enclosure was analysed with a modified Spread of Participation Index (SPI), with the goal of assessing the evenness of the horizontal sections of the enclosure (Plowman, 2003). The mSPI provides a scale between 0 (even use of all sections in the enclosure) and 1 (uneven use of the available space in the enclosure) and the modified formula in equation 5.1 was used.

$$\text{mSPI} = \frac{\Sigma|f0-fe|}{2(N-femin)} \qquad \text{(equation 5.1)}$$

where *f0* and *fe* are the observed and expected frequencies in each section, respectively, *N* is the total number of observations in all sections, and *femin* the expected frequency in the smallest section, that accounts for unequal sizes of different sections in the enclosure (Plowman, 2003).

Inter-observer reliability analysis was conducted by estimating the Cohen's Kappa score (R package "irr" version 0.84.1; Gamer & Lemon, 2012) as a measurement of agreement between the two observers (Cohen, 1960). A Kappa score of 0.715 was obtained, suggesting an overall substantial agreement between observers (Landis & Koch, 1977). However, there was some disagreement in specific behaviours (i.e. foraging, locomotion, object interaction), likely due to the similarity between behaviours (e.g. foraging involved locomotion while searching for food) and the speed at which the

swift parrots moved and switched between them. Therefore, these three behavioural categories (which were all high activity behaviours) were combined when comparing baseline and post-modification periods.

5.3. Results

A total of 29 hours of behavioural observations (male: n = 6,863, female: n = 6,870, excluding intervals with individuals out of sight) were conducted on each swift parrot, across 24 days, in the baseline period. In the post-modification phase, the male and female were observed for 11.5 (n = 2,748 intervals) and 12 hours (n = 2,875), across 19 and 21 days, respectively.

5.3.1. Time budgets of swift parrots

5.3.1.1. Baseline time budgets of swift parrots

Both swift parrots showed high activity in the baseline period, engaging in feeding, foraging, locomotion, and object interaction in over half of the observations (Figure 5.5A). Foraging was the most frequent behaviour in the male, while the female was more often perching (Figure 5.5A). High activity behaviours (i.e. feeding, foraging, locomotion, and object interaction) were most common across time periods for both individuals (Figure 5.4B). Foraging was the most frequent behaviour in the male, while the female was more often perching (Figure 5.5A). High activity behaviours (i.e. feeding, foraging, locomotion, and object interaction) were most common across time periods for both individuals (Figure 5.5B). Nevertheless, there were differences in activity levels across time periods in both the male and the female swift parrots. Low

activity behaviours (i.e. perching) were lower in the morning (08:00 – 10:59 hrs) in both individuals, and, in the male, they were higher in the middle of the day (11:00 – 14:59 hrs). High activity was higher in the afternoon/evening (15:00 – 17:00 hrs) in both birds.

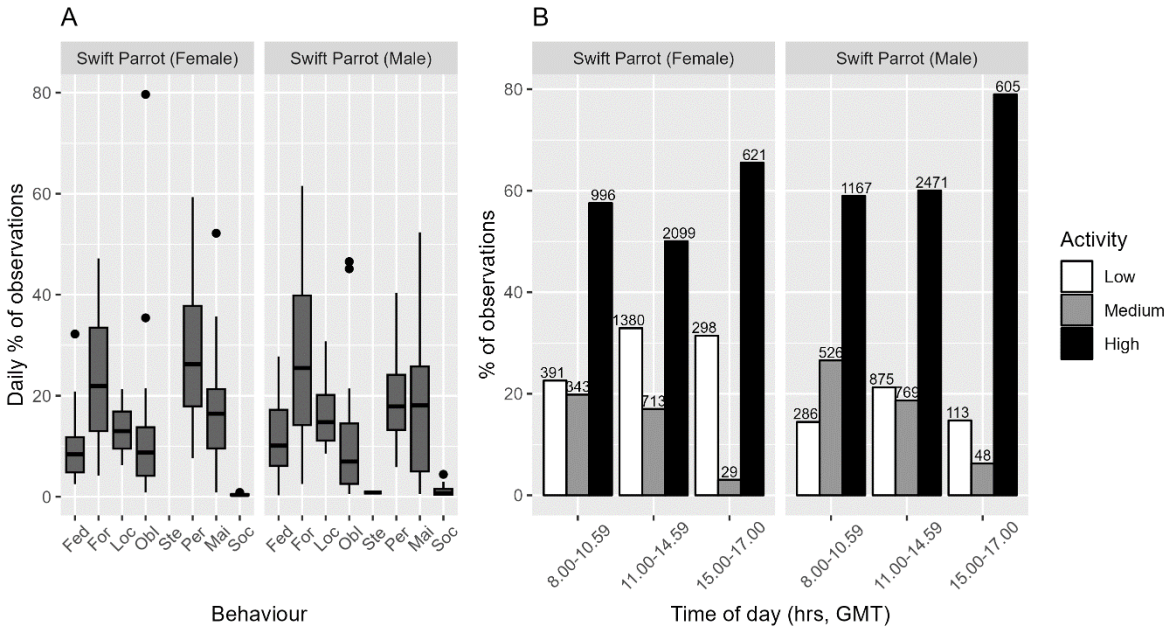


Figure 5.5. Activity budgets and patterns of the two swift parrots at Drayton Manor Park and Zoo, in the baseline period of observations (between February and March 2021, before changes to the enclosure and husbandry of the parrots).

(A) Boxplots of daily percentages of behaviours in the baseline period of observations. The median, first and third quartiles are represented by the box, the whiskers represent the minimum and maximum values, and the black dots show the outliers. (B) Percentages of low, medium, and high activity levels of swift parrots in the morning, middle of the day, and afternoon/evening during baseline period of observations.. Numbers above bars represent the number of observations. Fed = Feeding; For = Foraging; Loc = Locomotion; Obl = Object interaction; Ste = Stereotypies; Per = Perching; Mai = Maintenance; Soc = Social.

Comfort behaviours while perching were rare (Figure 5.6A), and over 90% of foraging was on plants, in both swift parrots, although they were also occasionally seen foraging on the ground, digging the soil with their feet and bills. It is unclear whether they were actively ingesting soil (i.e. geophagy) or simply manipulating it while foraging for other food items within the soil.

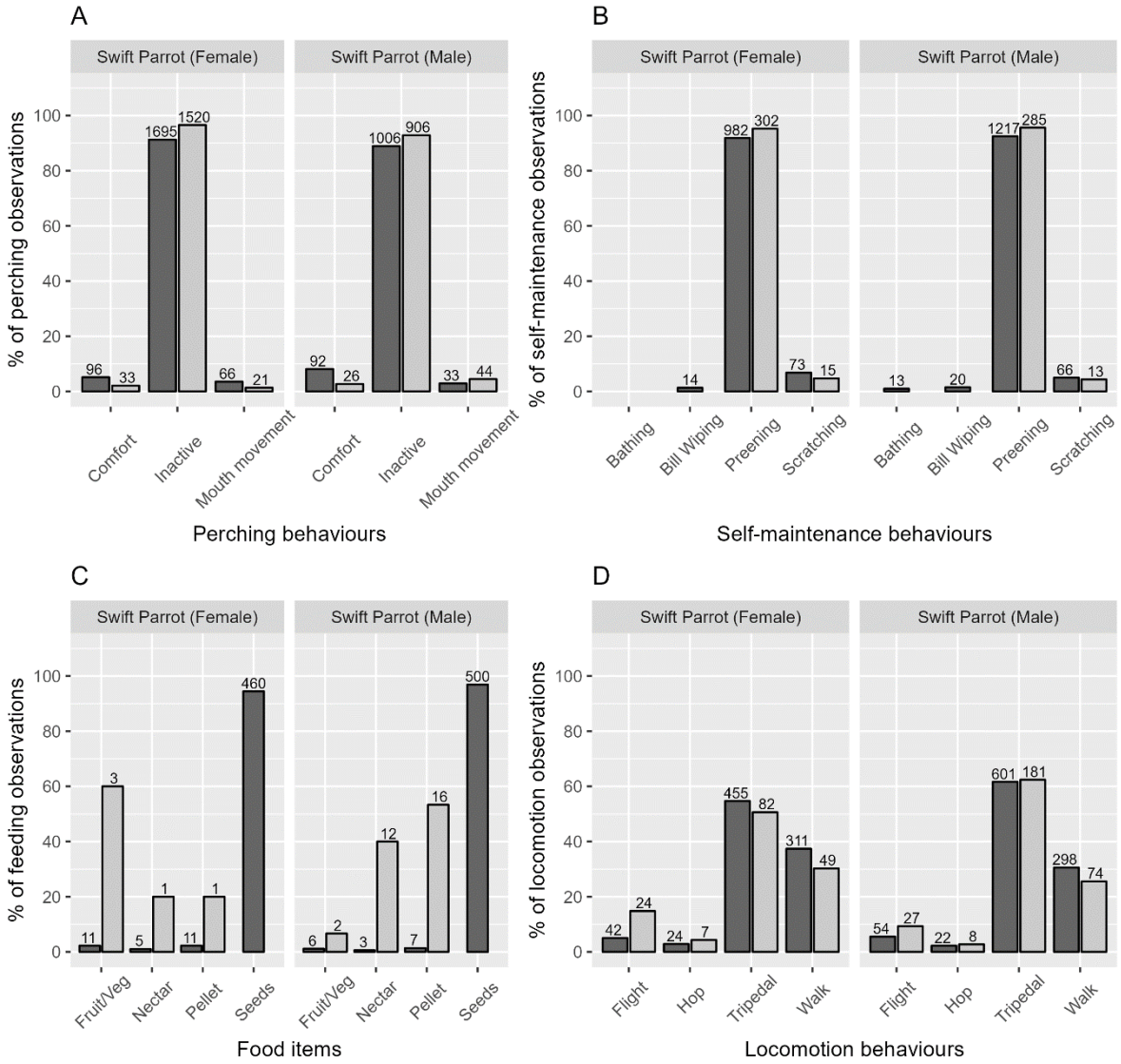


Figure 5.6. Perching, self-maintenance, and locomotion behaviours, and food consumed by the two swift parrots at Drayton Manor Park and Zoo, in the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and husbandry of the swift parrots, occurred between February and March 2021, while the post-modification period (after the alterations took place) occurred between December 2021 and March 2022. Percentages of observations of (A) perching, (B) self-maintenance, (C) feeding, and (D) locomotion behaviours, in both the baseline (dark grey bars) and post-modification (light grey bars) periods for each swift parrot. Numbers above bars represent number of observations. Fruit/Veg = Fruit and vegetables.

Feeding observations (i.e. feeding directly from feeder) were infrequent in both the male and the female, and they were mostly on seeds, with the other food items (i.e. fruit and vegetables, nectar and pellets) rarely fed on (Figure 5.6C). Both swift parrots

favoured the feeder on the top of the back of house when feeding on seeds (rather than the two bottom ones), which was used by the male and female in 100% and 99.6% of seed feeding observations, respectively. The most frequent type of locomotion observed was climbing (Figure 5.6D), while self-maintenance behaviours consisted mostly of preening (Figure 5.6B).

5.3.1.2. Post-modification time budgets of swift parrots

Perching was observed more often in both individuals during the post-modification period of observations, but feeding and self-maintenance decreased (Figure 5.7).

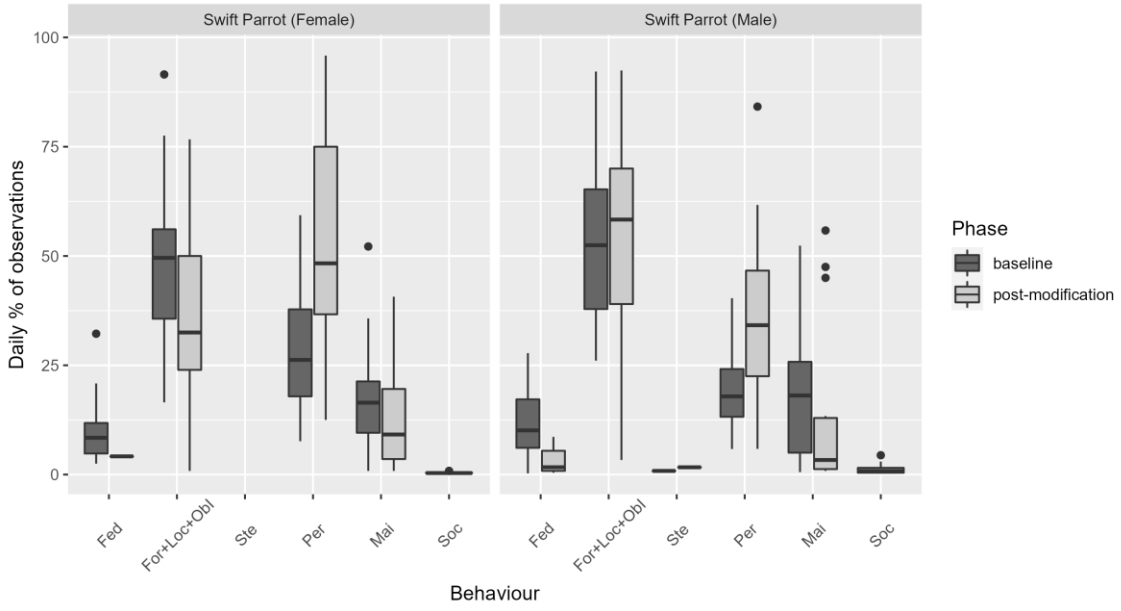


Figure 5.7. Activity budgets of two swift parrots at Drayton Manor Park and Zoo (UK) in the baseline and post-modification periods of observations.

The baseline period of observations, which was before the alterations to the enclosure and husbandry of the swift parrots, occurred between February and March 2021, while the post-modification period (after the alterations took place) occurred between December 2021 and March 2022. Boxplots of daily percentage of behaviours in the baseline and post-modification phases, for each of the two swift parrots. The median, first and third quartiles are represented by the box, the whiskers represent the minimum and maximum values, and the black dots show the outliers. Fed = Feeding; For = Foraging; Loc = Locomotion; Obl = Object Interaction; Ste = Stereotypies; Per = Perching; Mai = Maintenance; Soc = Social.

Furthermore, combined observations of foraging, locomotion, and object interaction were less frequent in the female during the post-modification period of observations. Perching was the predominant behaviour in the female's post modification's time budget, while the male still engaged in foraging, locomotion and object interaction in most observations in the post-modification period (Figure 5.7).

Both swift parrots still rarely engaged in comfort behaviours while perching, in the post-modification period of observation, and preening also remained the most common self-maintenance behaviour. Bathing and bill wiping were not recorded in this period. There were differences in the sampling pattern between periods, in the female, with more sampling in the afternoon in the baseline period. However, as the changes in time budgets detected were consistent in the morning and afternoon periods, the different sample pattern was unlikely to have impacted the overall changes in the female's time budget. Feeding observations were rare in the post-modification phase (male: n = 30; female: n = 5), but in contrast to baseline, neither individual was seen eating seeds, and were instead seen feeding on fruit and vegetables, liquid nectar and nectar pellets.

5.3.2. Enclosure use of swift parrots

Horizontal enclosure use during the baseline period of observations was heterogeneous for both the male (mSPI = 0.37) and the female (mSPI = 0.33), with section 5 alone being used in most observations of the male and female, respectively. Sections 3 and 4 were the least used by the swift parrots (Figure 5.7A).

After modifications of the enclosure, a more even (horizontal) use of the enclosure was detected in both individuals, with a decrease in the mSPI from 0.37 to 0.16 in the male and from 0.33 to 0.26 in the female. Also, in contrast to observations in the baseline period, each section was used in under 50% of observations. Section 2 was the most used by both individuals closely followed by section 5 (Figure 5.7A).

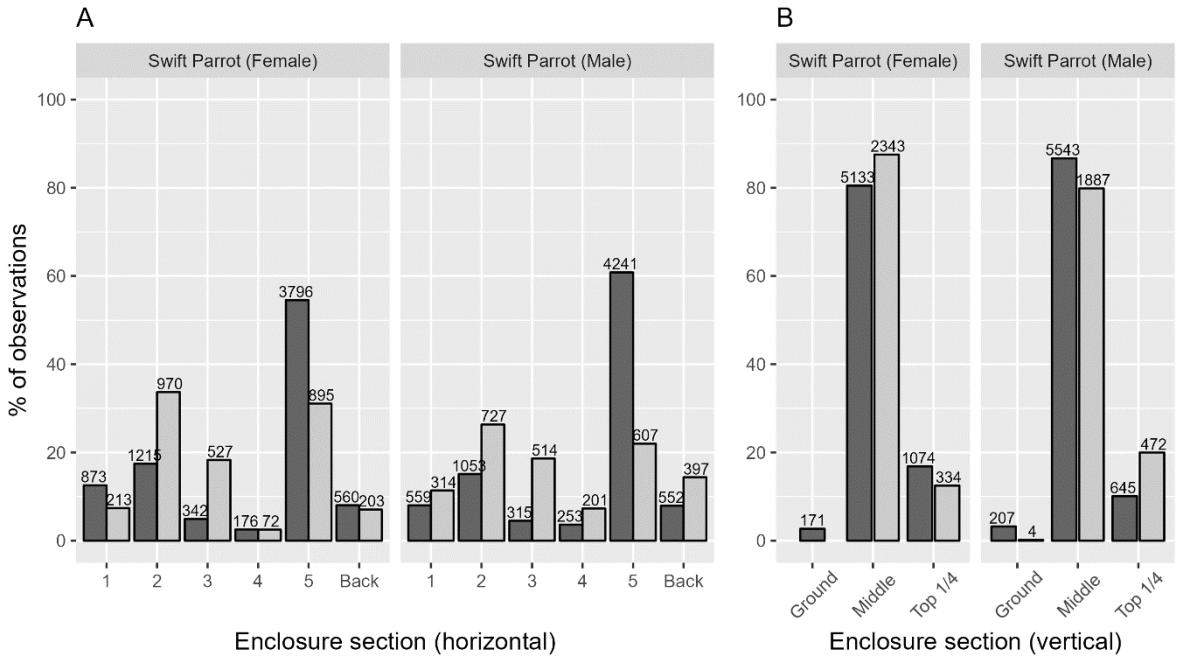


Figure 5.8. Enclosure use of the swift parrots at Drayton Manor Park and Zoo (UK) in the baseline and post-modification periods of observations.
The baseline period of observations, which was before the alterations to the enclosure and husbandry of the swift parrots, occurred between February and March 2021, while the post-modification period (after the alterations took place) occurred between December 2021 and March 2022. Percentages of observations of (A) horizontal space use. Sections 1 – 5 of enclosure as described in Figure 5.1. Back = back of house. (B) Vertical space use in the enclosure, in the baseline (dark grey bars) and post-modification (light grey bars) periods, for each swift parrot. Numbers above bars represent number of observations.

Vertically, the middle section of the enclosure was the most used by both swift parrots, in both the baseline and post-modification periods of observations (Figure 5.7B). The male used the top of the enclosure more during the post-modification period, while the

female showed the opposite response (Figure 5.8B). Ground use was low in baseline and not observed in the post-modification period (Figure 5.8B).

5.4. Discussion

It was found that both swift parrots were highly active and engaged in natural behaviours such as foraging and locomotion, although feeding observations during the baseline period of observations were mostly on seeds. Fewer observations were conducted after the enclosure modifications, and feeding was rarely observed during this period, but the results suggest a potential reduction in seed consumption. The swift parrots also seemed to favour areas of the enclosure with more vegetation. These findings will be discussed in the context of their natural behavioural ecology and *ex situ* husbandry and management.

5.4.1. Observations of swift parrots during the baseline period

High activity levels were observed in both swift parrots included in the present study, with foraging and locomotion comprising a substantial proportion of their time budgets. No time budgets of their wild counterparts were found in the literature for comparison, but wild rosellas (*Platycercus* spp*.)*, which are closely related to swift parrots (Christidis et al., 1991) but have a seed-based diet, were observed foraging in up to 64.7% of observations (Penck et al., 1995). Other nectarivorous bird species (Promeropidae, Nectariniidae, Meliphagidae) engaged in foraging on flowers in 7.6–43.8% of observations (Collins et al., 1990). Regent honeyeaters (*Xanthomyza phrygia*), for example, who like swift parrots also feed on nectar and lerps, spent approximately half

the time foraging (Oliver, 2001). On the other hand, the purple-crowned lorikeet (*Glossopsitta porphyrocephala*), another Australian parrot species, was shown to feed on nectar and pollen at a rate of one flower every 1-3 seconds, suggesting they can fulfill their daily energy requirements with 2.5 hours of flower harvesting (Hopper & Burbidge, 1979).

The captive environment can encourage inactivity (Fureix & Meagher, 2015) and reduce the time spent foraging (e.g. Quinn et al., 2006; Stoinski et al., 2003). However, the swift parrots in the present study still showed foraging levels that seemed broadly comparable to those of some parrot species and of passerines with similar diets. Inactivity levels (i.e. resting and vigilance) were also similar to those reported for wild rosellas (up to 28.6% of observations; Penck et al., 1995).

There are three potential explanations for these results. First, the free-flight exhibit where the swift parrots were housed provided several areas for exploration, and natural features such as vegetation native to the natural habitat of this species (i.e. eucalypts). Other zoo-housed species have shown increased foraging and exploratory behaviours when given access to multiple areas, such as in the case of black bears (*Ursus americanus;* Bruno et al., 2023); tigers (*Panthera tigris;* Smith et al., 2022), while Japanese macaques (*Macaca fuscataia)* housed in a vegetated enclosure exhibited increased foraging in comparison to those in a bare environment (Jaman & Huffman, 2011). Secondly, the mealybugs in the vegetation also likely encouraged natural foraging. They produce a white waxy material (Figure 5.1A) that visually

resembles that of the psyllid lerps on which swift parrots feed in the wild (Kennedy & Tzaros, 2005), and a sugar-rich honeydew (Zhou et al., 2015), which is also part of the diet of wild swift parrots (Gartrell et al., 2000). Furthermore, most of the foraging observed was on the vegetation, with the swift parrots exploring the surface of the leaves with their bills and mouth, and although it was difficult to confirm whether they were consuming the mealybugs, there were a few instances where ingestion of the mealybugs' waxy structures was directly observed. Finally, the age of both swift parrots may have also influenced the time budgets observed, as they were still sexually immature. Behavioural differences between immature and mature animals have been previously reported in other species such as crimson rosellas (*P. elegans;* Margrath & Lill, 1985) and chimango caracara (*Milvago chimango;* Biondi et al., 2010).

Self-maintenance, mostly preening, was also prominent in the time budgets of both swift parrots, which is, as already discussed for other parrot species (section 3.4.1.5), an important behaviour for hygienic purposes (Spruijt et al., 1992). Although infrequent, the male was also observed bathing, a behaviour that has been reported for free-living rainbow lorikeets (*Trichoglossus haematodus;* Cleary et al., 2016), which emphasises the importance of natural features (in this case, the artificial water pond/stream) to enable specific behaviours. On the other hand, the swift parrots rarely engaged in social behaviour. Allopreening, which is indicative of social bonding in parrots and other avian taxa (Morales Picard et al., 2020), was not observed. As swift parrots are socially monogamous (Heinsohn et al., 2019) and are often seen in flocks in their natural environment (e.g. mean flock sizes of between 4.6 [Mac Nally & Horrocks, 2000] and 5.7 [Saunders et al., 2016]), the results in the present study may suggest

an inadequate social environment, with limited opportunities for interactions with conspecifics. For example, captive fledgling budgerigars (*Melopsittacus undulatus*) interacted with parents, siblings and unrelated conspecifics, but to various degrees, dependent on their early social environment, with individuals from smaller broods less likely to interact with siblings than those from larger broods (Stamps et al., 1990). Stereotypic behaviours were rare in both individuals, even if considering the infrequent bill movements observed during perching as potential stereotypies (e.g. sham chewing; Meehan et al., 2004) although these could have also been a bill sharpening behaviour and/or comfort behaviour.

The swift parrots remained highly active throughout the day, which contrasts with the bimodal activity pattern previously reported for other parrot species in Australia, such as Carnaby's cockatoos (*Calyptorhynchus latirostris;* Stock et al., 2013) and in New Caledonia such as New Caledonian parakeets (*Cyanoramphus saisseti)*, horned parakeets (*Eunymphicus cornutus),* and rainbow lorikeets *(Trichoglossus haematodus*; Legault et al., 2012). Even though the activity patterns of both swift parrots in the present study suggest a reduction in activity in the middle of the day, and a further increase in activity in the afternoon/evening, they were both still very active in the middle of the day, which is when wild parrots are usually resting (Legault et al., 2012; Stock et al., 2013). This resting period in the middle of the day observed across wild parrots could be to avoid exposure to higher temperatures, diurnal predators and/or to digest the food consumed during the morning foraging period (Gilardi & Munn, 1998). The swift parrots in the present study were not constrained by substantial temperature variations during observations, as they were in a temperature-controlled

exhibit. When outside temperatures are higher in the summer, the exhibit sometimes over-heats at the hottest time of the day (C. Mitchell, pers comm., 2021), but this was never the case during the present study. Therefore, without temperature or predator pressures, the swift parrots were able to forage and rest more constantly throughout the day. Furthermore, the activity patterns of birds are also influenced by light-dark cycles (Kumar et al., 2010), and therefore exposure to artificial lighting may have also played a role in the behaviour and activity patterns of the swift parrots, as previously reported for other captive animals (Morgan & Tromborg, 2007). Further research could investigate if they adapt to a more wild-type bimodal activity pattern in the summer when there are temperature variations throughout the day, as well as the role of artificial lighting and the light-dark cycle in those patterns.

Most of the baseline feeding observations were on seeds provided to the other bird species in the enclosure, and they were very rarely seen eating their own food. Observations on their wild counterparts largely contrast with these findings, as they have sugar-rich diets (Brereton et al., 2004) and were found to mostly feed on nectar and lerps (51.1% and 48.9% of observations, respectively; Saunders & Heinsohn, 2008). Consumption of unidentified items on the foliage of eucalyptus trees has been previously reported in up to 35% of foraging observations of this species, as well as flower buds and fruit (up to 10%) and wattle racemes (up to 10%), with variation across years (Kennedy & Tzaros, 2005). Swift parrots may also opportunistically feed on seeds (Hindwood & Sharland, 1964). Nutrition-related issues, such as mineral and vitamin deficiencies and toxicities, have been previously listed among the health risks identified for mixed-species exhibits, due to consumption of food items aimed at other

species in the enclosure (Kaandorp, 2012), and therefore the seed-based diet of the swift parrots in the baseline period of the present study may have been nutritionally inadequate (i.e. leading to excessive fat and nutrient deficiencies; Hess et al., 2002). A previous study found that captive swift parrots on a seed diet had higher plasma uric acid concentrations than their wild counterparts, suggesting they were fed more protein than required, which may have affected their kidney function and contributed to renal disease (Gartrell et al., 2003). The seed-based diet also likely stopped the swift parrots in the present study from engaging more in natural feeding-related behaviours, as reported for their wild counterparts (e.g. compressing the anthers of flowers with their tongues to harvest pollen, and inserting their tongue into the floral cup while resting their bill on the edge of the floral receptacle to harvest nectar; Gartrell et al., 2000). The ground foraging that was infrequently observed in both swift parrots in my study, which has also been reported for their wild counterparts (Kennedy & Tzaros, 2005), may have been enabled by seeds dropped by the finches, by insects in the soil, and/or by geophagy, but it was not possible to confirm what was ingested.

During observations in baseline period, both swift parrots favoured the middle “vegetation island” in the enclosure (i.e. section 5 of the enclosure), and used sections 3 and 4 the least, which was likely a response to differences in vegetation density across areas. They may have been attracted to areas with more foliage, as it is primarily where they forage on in their natural habitat (Kennedy & Tzaros, 2005), with wild swift parrots exhibiting a preference for larger trees, which are more reliable food sources (i.e. larger diameter at breast height; Kennedy & Tzaros, 2005)., 2004; Kennedy & Tzaros, 2005). Areas with more dense vegetation provide more cover,

which could have also been sought by the swift parrots, as previously reported for zoo-housed Hottentot teals (*Spatula hottentota*) and sunbitterns (*Eurypyga helias*; Blanchett et al., 2020). On the other hand, the swift parrots were more often observed in the middle than the top section of the enclosure, which contrasts with their wild counterparts, that prefer foraging in the upper canopy (Hingston & Potts, 2005) and rarely close to the ground (Hingston et al., 2004), and nesting high in the trees (i.e. mean nest height: 14 m; Webb et al., 2012). Although some of the vegetation in the enclosure reached the top area, most of it was concentrated in the middle section, which likely encouraged the swift parrots to spend most of their time at lower levels in the enclosure.

5.4.2. Observations of swift parrots following enclosure modifications

Despite the reduction of overall activity identified in both individuals, they still exhibited high engagement in high-activity behaviours, such as foraging. These changes were, however, most likely due to them being older and having become sexually mature by the post-modification period of observations. Previous research reported higher foraging and lower inactivity in immature crimson rosellas than in their mature counterparts (Margrath & Lill, 1985), and, as previously discussed, the juvenile scarlet macaw also exhibited similar patterns of activity between periods (section 3.4.1.2).

Neither swift parrot was observed eating seeds in the post-modification period, and the few feeding observations were on fruit, liquid nectar and the nectar pellet that was new in the post-modification period. These findings agree with reports from the animal

keepers, who also perceived a reduction in observations of swift parrots consuming seeds after the modifications were applied (A. Hulbert, pers comm., 2022). It has been previously shown that zoo-housed coconut lorikeets (*Trichoglossus haematodus*) reduced their consumption of highly diluted, nutritionally deficient, nectar, while switching to other available food (i.e. fruit; Kalmar et al., 2009). It is therefore likely that the new nectar pellets that were incorporated in the swift parrot diet, which target dietary needs of nectarivorous bird species and consequently more fully meet their nutritional needs, encouraged them to eat more pellet. The training for handfeeding (using liquid nectar) also likely played a role in encouraging nectar feeding, and consequently discouraged seed eating, as captive birds have been previously trained with success to eat specific food items (e.g. Chatelain et al., 2013; Denslow et al., 1987). Finally, the removal of the seed feeder from the top of the back-of-house area, which was their primary place for seed feeding during the baseline period of observations, may have also discouraged them from eating seeds. It is possible that the removal of that feeder enabled negative affective states in the swift parrots, such as frustration. However, the animal keepers did not detect behavioural changes that could be indicative of a negative response to the feeder removal. Nevertheless, future interventions could reduce the risk of a stress response by not removing the preferred seed feeder, and instead replacing the seeds in it with appropriate food items to the target species. Furthermore, seed consumption may have been obscured by the reduced sampling in the period after the modifications, as well as the rare observations of feeding, especially in the female. Therefore, despite the potential effectiveness of the modifications implemented in this study in reducing seed consumption, future research with a larger sample size is required to draw more solid conclusions.

The more even horizontal use of the enclosure detected in the post-modification period was probably caused by the overall increased vegetation density in the enclosure. Even though section 5 of the enclosure still had the most vegetation/foliage, other sections (2 and 3 in particular) were also well vegetated in this period, which seemed to have motivated the swift parrots to use more of the enclosure. Individual differences in sex (Holmes, 1986) and/or personality (Fox & Millam, 2007; Medina-García et al., 2017) may have influenced the contrasting changes in vertical space use the male and the female showed, as well as the other differences in behaviour and activity observed between them (Greer et al., 2015; Pepper et al., 2000).

Finally, social interactions were virtually non-existent in this period, which suggests there was still no pair bonding between the swift parrots, despite them being sexually mature. Being siblings, pair bonding and breeding would be detrimental for the genetic diversity and low inbreeding goals of the *ex situ* breeding programme (Lees & Wilcken, 2009). These results highlight the need to add more individuals to the flock, in order to increase opportunities for social interactions, mate choice and pair bonding (Asa et al., 2011), while providing a more adequate, wild-type, social environment to the birds, and consequently improving welfare (Whitham & Miller, 2019). Furthermore, although agonistic interactions between the swift parrots and the other species in the enclosure were almost never observed, it is still possible that inter-specific competition for food and/or territories occurred (common issues in mixed-species exhibits; Kaandorp, 2012), potentially affecting their behaviour and enclosure use in both periods of observations. Further research into *ex situ* inter-specific interactions and their effect on behaviour and welfare of swift parrots is therefore recommended.

5.5. Conclusion

This study provides a detailed description of behaviour of two zoo-housed swift parrots and suggests that both birds exhibited high activity levels and natural behaviours. This was likely motivated by the free-flight exhibit they were housed in, which had relatively high vegetation density, and the opportunities it provided for exploration and natural foraging. A decrease in activity was detected in the post-modification period, although it remained high, which was probably a result of them being older and sexually mature in that period. Although during the baseline period of observations they mostly fed on seeds provided for other species in the mixed species exhibit, which contrasted with the nectar- and lerp-based diet of their wild counterparts, no seed eating was observed in the post-modification period. The swift parrots may have fed less on seeds as a result of adjustments to their diet, training for nectar handfeeding, and/or the removal of the seed feeder they primarily ate from prior to the enclosure modifications. However, seed eating may have been overlooked in the period after the modifications due to reduced sampling. They also used their enclosure more evenly in the post-modification period, which could have been a response to increased vegetation density in some areas of the enclosure. Nevertheless, social behaviour was rare and indicated a need to adjust their social environment, increasing opportunities for social interactions with conspecifics, mate choice and pair bonding. This study is limited by a low sample size but provides initial insights into the understudied *ex situ* behaviour of swift parrots, with applications to the *ex situ* management and welfare of this species. Although the effectiveness of the modifications in discouraging seed eating require further evaluation, this research can encourage and inform future studies into the diets and management of nectarivorous parrots in mixed-species exhibits. Finally, this study

also provides evidence to inform enclosure design and enrichment for this species, as the enclosure in this study provided the swift parrots with opportunities for engagement in some natural foraging and locomotion behaviours, although areas for improvement were also detected and highlighted.

CHAPTER 6

GENERAL DISCUSSION

6.1. Summary of thesis outcomes

This thesis aims to generate evidence to inform *ex situ* management of captive parrots, by assessing their behaviour, comparing it to their wild counterparts, modifying the *ex situ* environment (i.e. enclosures and husbandry) to recreate some of the features and challenges of the natural environment, and evaluate whether those modifications were effective in enabling wild-type behaviours.

Data collected on free-living scarlet macaws in Costa Rica (Chapter 2) were used to supplement the available literature on the behavioural ecology of the species, and to compare with the data collected on their captive counterparts (Chapters 3 and 4). Both the reintroduced and the wild scarlet macaws were generally active, stayed mostly high in the tree canopy, and used a high diversity of supports. The wild macaws were mostly seen engaging in complex food manipulation, with an overall high use of their feet. Some of the differences detected between locations (e.g. increased activity observed in the scarlet macaws at Punta Leona) could have been motivated by multiple factors, such as different rearing conditions (captive-bred versus wild), age, habitat and/or access to resources (Chapter 2).

In contrast, the captive scarlet macaws and grey parrots in both zoos exhibited low activity levels and limited use of the enclosure, with some spending a substantial amount of time on the ground (Chapter 3). Engagement in complex food and object manipulation was rare, and the parrots mostly used unchallenging supports (i.e. stable, thick, horizontal; Chapter 4). Most of the captive scarlet macaws and both grey parrot

groups seemed to exhibit improvements in wild-type behaviours in the period after the modifications were applied, although there was high intra- and inter-specific variation in behavioural responses (Chapters 3 and 4). The changes in behaviour in the post-modification period of observations included decreased inactivity, increased feeding and locomotion, a more even horizontal use of the enclosure, increased use of the top of the enclosure (Chapter 3), increases in tripedal locomotion or flight behaviour, and greater use of more challenging and complex supports (Chapter 4). These behavioural changes could have been a result of the physical modifications applied to the enclosures but were also likely influenced by other changes that occurred between the two periods of observations, such as social and developmental changes (Chapters 3 and 4). The macaw groups at zoo B also used, and seemed to have benefited from, the modifications applied to the enclosure, even though there were no baseline data for comparison (i.e. it is unlikely they would have expressed some of the behaviours observed, such as the use of varied and complex supports, in an enclosure which offered them limited opportunities to express them). Some unexpected behavioural responses were also reported (e.g. further decrease in foot use during manipulation in some individuals) which could have been motivated by the modifications, although it is not clear how, as well as age, personality, and/or long-term exposure to unenriched environments in the past (Chapters 3 and 4).

Furthermore, both swift parrots exhibited high activity levels in both periods of observations, although a decrease in activity, likely age-related, was detected in the post-modification period (Chapter 5). They also seemed to respond to the interventions to reduce the high seed consumption that was observed in the baseline period. They

were not seen feeding on seeds in the post-modification period, which suggests a decrease in this behaviour, although reduced sampling and limited feeding observations in this period could have masked seed consumption. There was a general low engagement in social behaviour, which highlights the need to improve their social environment (Chapter 5).

6.2. Further enclosure modifications

Despite the behavioural improvements observed in some of the birds, the behaviour of the captive scarlet macaws and the grey parrots in this thesis were still substantially different from those of their free-living counterparts (Chapters 3 and 4). Furthermore, the modifications applied failed to improve manipulation challenges, including foot use during manipulation (Chapter 4). It is possible that the age of some of the parrots, coupled with long-term exposure to a suboptimal *ex situ* environment in the past, will always limit, to an extent, their behavioural responses to improvements in their *ex situ* environment (e.g. Feliu et al., 2022; Nithianantharajah & Hannan, 2006). Nevertheless, further interventions can be made, to the enclosures, management, and husbandry, to attempt to enable wild-type behaviours further.

6.2.1. The importance of bird training in *ex situ* management of parrots

Animal training is a useful tool in the management of captive animals. It can be used to facilitate routine husbandry by, for example, reducing stress for the animal while it is being captured, handled and/or weighed (Bassett et al., 2003). Animals can also be trained to participate voluntarily in veterinary procedures such as radiographies (Booth

et al., 2022), blood and urine sample collection (Laule et al., 1996), and artificial insemination (Leblanc et al., 2011), reducing the need for more invasive methods such as anesthesia, capture and restraint. Furthermore, training can potentially reduce the animals' fear of humans, improving human-animal relationships and, consequently, animal welfare (Ward & Melfi, 2013). It has been suggested that training itself can be enriching for the animals (Fernandez, 2022; Westlund, 2014), although it should be used alongside other enrichment strategies, such as food-based and cognitive enrichment, and not as replacement for them (Melfi, 2013).

Training can also be used to encourage captive animals to interact with their environment. For example, bottlenose dolphins (*Tursiops truncatus*) trained with operant conditioning for object manipulation showed increased interest in interacting with the enrichment items when the trainers were not present (Neto et al., 2016). Another study on this species found that a quarantined dolphin played more with enrichment after interacting with a trainer and was more likely to play with the same toys its trainer had played with (Jaakkola et al., 2023). Similarly, zoo-housed Magellanic (*Spheniscus magellanicus*) and southern rockhopper penguins (*Eudyptes chrysocome*) presented with a feeding enrichment device only interacted with the device once they had been trained for it (Fernandez et al., 2019). Training has also been applied to captive animals for reintroduction, with the aim of enabling natural behaviours such as anti-predator responses (Lopes et al., 2017). For example, free-flight training captive-bred juvenile parrots, by gradually exposing them to wild-type areas of increased complexity (i.e. outside the enclosure), showed positive effects on

the birds' ability to flock, forage and move around the environment, with no bird losses to predation or disorientation (Woodman et al., 2021).

The potential applications of training were also seen in the swift parrots in this thesis (Chapter 5), as the apparent increase in nectar feeding, as intended, may have been motivated by the training schedule applied by the keepers. Therefore, the grey parrots and macaws could also benefit from being trained (e.g. operant conditioning) to use new feeders (N.B. adult scarlet macaws at zoo B did not use the new feeders) and to interact with any enrichment placed within the enclosure, including the puzzle feeders, which were ignored by most parrots.

6.2.2. The importance of food presentation in *ex situ* management of parrots

Although the feeders provided in the present research seemed to have enabled feeding- and locomotion-related behaviours in the parrots that used them (e.g. moving across supports surrounding the suspended feeders to reach the food, searching for food in the different holes), these behaviours could and should be further encouraged. In order to make the food less readily available and more challenging to acquire, and further motivate the parrots to search for it, the following could be tried: (1) placing more feeders in the enclosure, improving food distribution, (2) randomly filling different holes within each feeder at different feeding times, and (3) further hiding the food within each hole and mixing it with non-edible materials to encourage searching. As wild parrots have the ability to explore multiple food sources in the wild and have to travel across trees for foraging (section 4.1.1), a more unpredictable and diverse way of food

provision in captivity is more likely to replicate those challenges and stimuli, and encourage wild-type behaviours. This is supported by a previous study by van Zeeland et al., (2013a) which showed that captive grey parrots exhibited an increase in foraging-related behaviours when presented with multiple bowls containing food in different areas of the enclosure, and when provided with feeders filled with marbles and food hidden within them, although the latter seemed to have had a stronger effect. In another study on red-fronted macaws, thick-billed parrots (*Rhynchopsitta pachyrhyncha*), green-winged macaws, and chattering lorries (*Lorius garrulus*), they seemed to prefer feeding from a more complex enrichment device, where various food items were placed in holes across a wooden structure and covered with paper, than from the simple food bowls (Coulton et al., 1997). Even though in that same study, variably distributing the food across holes, rather than constantly filling them all, resulted only in a small, non-significant, increase in interaction with the device (Coulton et al., 1997), it is likely a stronger effect could be achieved by further increasing the distribution of the food and the unpredictability of its location (e.g. randomly filling multiple holes across multiple feeders).

Additionally, increasing the size of the food items (e.g. whole foods or chopped in bigger chunks) could also encourage the parrots to engage in more complex manipulation, using their feet more, and potentially spending more time active and engaged in feeding-related behaviours. In the wild, parrots rely on their zygodactyl feet to consume food items that require more extensive manipulation (e.g. holding fruit or seed in place and/or rotating it while removing the desired contents within the protective and often hard covers; see sections 2.3.2 and 4.1.1). Therefore, providing

food to captive parrots that cannot be readily ingested, and requires more extensive manipulation, is likely to encourage wild-type food manipulation, including foot use. This is supported by previous findings that blue-and-yellow macaws offered whole rather than chopped fruit showed decreased inactivity and more natural feeding-related behaviours (James et al., 2021), including foot use, and that food manipulation greatly increased in orange-winged Amazons when these were fed larger pellets (Rozek et al., 2010). The nutritional contents of the parrots' diets in captivity also should be further evaluated to ensure that the food that they are given meets both their nutritional and behavioural needs.

6.2.3. The importance of enrichment diversity and complexity in *ex situ* management of parrots

Increasing the diversity of temporary enrichment, with emphasis on cognitive challenges (e.g. puzzle feeders), could also help to stimulate the parrots to be more active and engage in a wider variety of behaviours. Parrots may also be encouraged to interact with puzzle feeders if all or most of their daily food is provided within them, instead of using puzzle feeders as an extra to the daily feeding routine. All captive scarlet macaws and grey parrot groups included in this research, except the juvenile macaws at zoo B, exhibited low or no engagement with the temporary enrichment placed in the enclosure, such as carboard boxes, egg cartons and, in zoo A only, puzzle feeders. However, perhaps continuous exposure to different devices in combination with training, as discussed in section 3.5.2, could encourage them to interact with the devices. Furthermore, to reduce habituation, which often affects enrichment use (Tarou & Bashaw, 2007), the enrichment should be varied and

unpredictable, which could be achieved by providing multiple and diverse enrichment devices on rotation, in random schedules.

Puzzle feeders have been found to be very effective in encouraging foraging behaviours in captive grey parrots (van Zeeland et al., 2013a) and in providing cognitive challenges that are vital to ensure positive welfare in captive parrots (Mellor et al., 2021), and should therefore be implemented in their enrichment schedule. Previous research has found that bottlenose dolphins, which are also cognitively advanced, benefited more from cognitive than non-cognitive foraging enrichment, as the former had a greater impact in encouraging activity and reducing abnormal behaviours (Clegg et al., 2023). Cognitive enrichment has also been found to benefit the behaviour and welfare of other taxa, including domestic pigs (*Sus scrofa domesticus;* Puppe et al., 2007), captive gorillas (*Gorilla gorilla;* Clark et al., 2019), and black rhinoceros (*Diceros bicornis;* Krebs & Watters, 2017). However, less research has focussed on cognitive enrichment than other types of enrichment. Therefore, despite its potential to enrich the lives of captive animals, an evidence-based application of cognitive enrichment is recommended, to ensure it is appropriate for the species targeted, and is having the desired effect (Clark, 2017).

6.2.4. The importance of the social environment in *ex situ* management of parrots

Improving the social environment (i.e. social conditions, including the presence of, and exposure to, conspecifics and heterospecifics) of the parrots at both zoos, especially

those that displayed low compatibility and weak social bonding with their enclosure-mates, could help to increase social interactions and, via social learning, positively affect other behaviours as well (Morales Picard et al., 2017). Free mate choice can help to improve pair compatibility and therefore increase reproductive output of captive animals (Asa et al., 2011). A case study of free mate choice in red-tailed Amazons (*Amazona brasiliensis*) reported that when five individuals were placed together in an enclosure, two of which had been together before as a pair but had not successfully bred, two pairs were formed, showing affiliative social behaviours and close proximity, while the original forced pair did not stay together (Waugh & Romero, 2000).

The more parrots are housed together, the more likely it is they will find other compatible individuals to bond with, although this can be logistically challenging due to spatial constraints (King, 2000) and may also clash with the genetic diversity goals of breeding programmes (Asa et al., 2011). Another solution may be to assess regularly the social compatibility of the parrot group or pair via behavioural monitoring, and if found to be low (e.g. low engagement in affiliative behaviours, reduced breeding success), to add new individuals or replace the existing ones by exchanging with other *ex situ* facilities. Nevertheless, parrot introductions must be done cautiously (e.g. gradual exposure to the new individual[s], opportunities to retreat from, avoid and hide from the new individuals; Whitham & Miller, 2019), to minimise risks of injury or death caused by potential aggression, and other negative impacts on the welfare of the individuals.

6.2.5. The importance of the sensory environment in *ex situ* management of parrots

The sensory environment can positively or negatively affect the welfare of captive animals, although there is potential for visual, auditory and/or olfactory enrichment to be used to mitigate sensory stressors, and/or to encourage rewarding behaviours (Wells, 2009). The use and effects of this type of enrichment on captive parrots has received little research attention (Rodríguez-López, 2016). However, a study on multiple zoo-housed parrot species, including grey parrots and scarlet macaws, showed an increase in preening when rainforest sounds and speech radio were played in their enclosure, while other sounds (e.g. different musical genres and parrot sounds) seemed to cause a reduction in calm vocalisations, such as low-volume contact calls, chucking and purring (Williams et al., 2017). Another study, focussed on zoo-housed African bird species (Lady Ross's turacos [*Musophaga rossae]*, speckled mousebirds [*Colius striatus]*, and superb starlings [*Lamprotornis superbus*]) described an increase in flight frequency and vocalisations when exposed to sound (i.e. natural forest sounds, classic or rock music), although these responses varied among species and with type of sound, and associations with welfare were not clear (Robbins & Margulis, 2016).

The captive parrots in this thesis were exposed to auditory environments that were potentially stressful (e.g. music and other theme-park related noises at zoo A, varied city sounds, including airplanes, at zoo B), and future research should investigate how their behaviour and welfare are affected by them. Also, future modifications to enhance the enclosures and husbandry should also target the sensory environment, by including modifications (e.g. background sounds) that specifically aim to mitigate,

and/or provide, varied auditory stimuli. Although natural sounds (e.g. rainforest sounds), may be an option to ameliorate stressful auditory environments, or to provide enriching stimuli, caution is required in their application. Some natural sounds, like predator sounds, conspecifics or heterospecific calls, can also be aversive (Wells, 2009) and continuous exposure to them may result in chronic stress. On the other hand, sounds that would not generally occur in the natural environment could still have an enriching outcome for the animal (Wells, 2009).

There may also be olfactory-based enrichment opportunities to explore, as a well-developed sense of smell has been reported across avian taxa (Steiger et al., 2008). A previous study showed that captive birds of prey (Andean condors [*Vultur gryphus*], bald eagles [*Haliaeetus leucocephalus*], golden eagles [*Aquila chrysaetos*], cinereous vultures [*Aegypius monachus*], and king vultures [*Sarcoramphus papa*]) engaged more with scented packages over empty, unscented ones, highlighting the potential of olfactory enrichment in these birds (Nelson Slater & Hauber, 2017). Similarly, in another study, captive scarlet macaws and toucans (*Ramphastos* spp.), but not Amazons (*Amazona spp*.), were able to detect fruit scent cues, as they interacted more with fruit-scented containers (Hernández et al., 2022). It is unclear how much wild parrots rely on olfactory cues for foraging in the wild, and how this reliance changes across species. However, there is potential to incorporate, and further research the impact of, olfactory enrichment in the husbandry of parrot species. For the parrot species that can detect and use olfactory cues, perhaps this could be used to further encourage interaction with other types of enrichment (e.g. a puzzle feeder or cardboard box which offers limited visual cues of what is inside but motivates the parrot to interact with it by containing attractive scent cues inside).

6.3. Limitations of the research in my thesis

6.3.1. Sample size

One of the main limitations in this research was the small sample size (i.e. number of individuals, species, and zoos included in the study), which is a common limitation of zoo-based research (Bishop et al., 2013). Individual animals may exhibit pronounced differences in their behavioural responses to the environment and changes within it (e.g. Stamps, 2016), which was also observed in the captive parrots in this thesis. Therefore, datasets on a small number of individuals and/or species are less likely to be representative of the whole species or wider taxonomic group. Small sample sizes are also more prone to missing and/or overestimating real effects in the data (Button et al., 2013). However, each grey parrot group, individual scarlet macaw (section 3.3) and swift parrot (section 5.3) was sampled for a substantial number of intervals, hours, and days. This allows for solid conclusions to be drawn on the behaviour of those individuals or groups in both the baseline and post-modification periods.

Multi-institutional studies are a suitable option to increase the sample size in zoo-based studies (Bishop et al., 2013). However, a multi-step methodology was used in this thesis, including (1) baseline data collection; (2) baseline data analysis and proposal of modifications, (3) application of modifications, and (4) post-modification data collection (Chapters 3-5). Each of these steps involved a considerable amount of time not only for the researcher but also the animal care and zoo management teams, which restricted the number of zoos that could be included in this research. Nevertheless, this research sets up a foundation for future research to expand on. More parrot individuals, species, and *ex situ* facilities can be added over time, which will be

facilitated by the parrot-focused EDT, once it is operational. More research will be needed before the parrot EDT is functional, but the *in situ* and *ex situ* quantitative behavioural data generated from this thesis will be used in its initial development. The EDT will simplify the time-consuming multi-step procedure mentioned above, as it will provide *ex situ* facilities with a readily available methodology to use for behavioural monitoring, as well as automated behavioural comparisons with wild conspecifics, which facilitate behavioural assessments, and suggestions for evidence-based enclosure modifications based on those comparisons (see section 1.7).

The *in situ* study on the scarlet macaws in Costa Rica was also limited by a small sample size, caused by unavoidable time constraints, as data were collected over a relatively small number of days, and from a small number of populations and locations (Chapter 2). Also, wild scarlet macaws may exhibit seasonal variations in behaviour (Vaughan et al., 2005), and the data, which were collected over a short time period, do not reflect those variations. However, the study's limitations were thoroughly acknowledged, with caution taken in the analysis and discussion of its outcomes (section 2.4). Furthermore, *in situ* research on bird species is fundamental to improve their management under human care (Rose, 2021), and as this study was conducted with that primary goal, it will potentially encourage and inform future research with similar aims.

6.3.2. Group sampling

Individual sampling of each animal within a group allows the assessment of each animal's behaviour and therefore accounts for behavioural differences across

individuals (Boyle et al., 2020; Mann, 1999). This method was prioritised in the present thesis, as one of the goals was to evaluate the behavioural responses of each individual parrot to the modifications applied. However, only the individual scarlet macaws and swift parrots could be reliably identified, and consistently followed, over time. As the grey parrots were too physically similar, and fast-moving, to identify and follow, group sampling was chosen as the best alternative for this species (Mann, 1999). Consequently, there were likely behavioural differences within each grey parrot group, as observed within the scarlet macaw groups, that could not be accounted for.

Even though marking individuals with rings (Gauthier-Clerc & Le Maho, 2001), dye (Wadkins, 1948), or wing tags (Hewitt & Austin-Smith, 1966) of different colours was considered, it was not implemented for several reasons. First, markings can have an effect on the behaviour and welfare of the animals (Calvo & Furness, 1992; Dennis et al., 2008). Secondly, marking the individual grey parrots would have required potentially stressful handling of the animals (Gauthier-Clerc & Le Maho, 2001), and especially for the wild-hatched, and human-phobic, grey parrots at zoo A. Thirdly, in order for markings to be effective in individual identification and following, they need to be conspicuous, which could have jeopardised the overall aesthetics of the zoo exhibit and, consequently, visitor experience and perceptions. For example, negative public perceptions have been previously reported for *in situ* research involving tagging of wild animals (Cooke et al., 2017), as they can jeopardise the experience of wildlife photographers and tourists (Hammerschlag et al., 2014).

There are potential mitigating actions for the issues associated with marking animals, such as engaging with the visitors to improve their perception of the markings and the research conducted (Hammerschlag et al., 2014), and marking the individuals during routine veterinary checks at the zoo, which the zoo partners in this thesis could have agreed to. However, it would still increase the challenges and complexity of the methodology, which would likely jeopardise future attempts for its wider implementation across *ex situ* facilities, as planned for the EDT. Time constraints can limit zoo staff's participation in collaborative research projects (Schulz et al., 2022), and therefore having time- and resource-efficient methodology options may facilitate successful collaborative research in the future.

As a result, for this thesis, and with its future applications in mind, it was decided that individual sampling would be used whenever possible, but a methodology for group sampling was also developed (see section 3.2.5.1).

6.3.3. Confounding variables

Zoo-based research is often limited by confounding variables, as the environment tends to be more natural, unpredictable, and difficult to control and manipulate than in laboratory-based research (Bishop et al., 2013; Ward & Hosey, 2020). Even though the more natural and unpredictable environments of animals in zoos provide opportunities for more ecologically valid research, it also increases the challenge of accurately determining the relative effects of multiple variables on the data (Bishop et al., 2013).

One of the main aims in this thesis was to determine the effects of enclosure modifications on the behaviour of captive parrots, but there were other variables that could have had an effect on the behavioural differences detected between the baseline and the post-modification periods. First, changes in the social environment, with deaths within the social groups occurring between the periods of observations (i.e. in all individuals except the grey parrot group at zoo B), as well as the addition of other individuals and species to the enclosure (zoo B only). The animal deaths could not have been predicted, or avoided, and the additions of new animals to the enclosure occurred out of necessity due to space limitations at the zoo. The zoo management could not postpone those changes until the end of the data collection, although that was the original plan, due to the delay in my returning to the zoos for the post-modification observations (caused by the COVID-19 pandemic).

Secondly, age differences between periods (1–2 years) were also a potential confounding variable. The juvenile parrots (i.e. juvenile scarlet macaw and both swift parrots at zoo A) were still maturing and in a developmental period, and age-related behavioural changes likely occurred (Margrath & Lill, 1985; Myers & Vaughan, 2004). However, age differences were unlikely to have had a significant effect on the data recorded for the adult individuals, as it was a relatively short period of time when taking into consideration that both scarlet macaws and grey parrots are long-lived species, with life expectancies that exceed 35 (Smeele et al., 2022) and 49 years (Brouwer et al., 2000), respectively. The potential confounding effects of the age differences in the

juveniles were considered when developing the methodology. However, it was decided they would still be included in the studies, to both increase sample size and assess the behavioural repertoire of younger parrots. Furthermore, shorter time differences between periods of observations were planned to reduce age effects on the results, but those plans were thwarted by the COVID-19 pandemic.

Finally, seasonal and environmental variables may have also influenced the results, but only between zoos, as they were consistent between phases of observations in each zoo (i.e. baseline and post-modification data collected at the same time of year, with similar weather, temperatures, and day length).

6.3.4. Low availability of *in situ* data in the literature

An important step in the methodology of this thesis (Chapter 3–5) was to compare the behaviour of the captive parrots with data generated from research on their wild counterparts. Therefore, the restrictions in data availability on wild parrots, especially quantitative data, limited the *in situ–ex situ* behavioural comparisons. The data collected on the free-living scarlet macaws (Chapter 2) were a helpful tool in the comparisons with their captive counterparts, but there were still gaps in knowledge of *in situ* behavioural ecology. As previously mentioned (see section 3.1), the best possible alternative was to use available data from closely related species. However, as even closely related taxa can exhibit differences in behaviour and behavioural responses (e.g. Hart, 2003; Sun et al., 2017), this approach has limitations. To strengthen the comparisons, data from multiple closely related species, and species

that shared ecological and behavioural traits with the target species, were considered. However, greater robustness in the outcomes of this research would have been achieved by using data on the same species in the wild. As previously discussed (see section 6.3.1.), future research should address these gaps in knowledge, which could be achieved with a wider integration of *in situ* and *ex situ* research, and mutually beneficial collaborations between captive- and field-based researchers and institutions (Rose, 2021).

6.4. Research applications

Despite the limitations mentioned above, this research provides new insights into the behaviour of three parrot species that are commonly found in human care and/or may benefit from short- and long-term *ex situ* conservation efforts. The modifications proposed and applied can and should be expanded and refined (section 6.2), and their effects across parrot individuals and species further investigated. The results indicate they potentially had a positive effect on the wild-type behaviours of the captive parrots. Furthermore, this research's methodology can be widely used to facilitate detailed assessments of broad and specific behaviours in captive parrots, as it was developed with its future use by *ex situ* facilities in mind (e.g. section 6.3.1). Therefore, the wider implementation of this research's findings and methodology can help to improve the management of parrots in short- and long-term captivity, with applications to animal welfare, *ex situ* conservation, *in situ* conservation, and visitor engagement and education.

Even though, as previously mentioned (e.g. section 6.3.4), closely related species may vary in their behavioural ecology and responses, some of the findings of this research are likely applicable across numerous parrot taxa. Some of the broader behaviours that were targeted and enabled are shared by most parrot species in the wild (e.g. flight, climbing on diverse supports, searching for food), and more species may therefore benefit from similar interventions in captivity. Even behaviours that are taxon-specific can also be encouraged in other species that exhibit that behaviour in the wild. For example, multiple neotropical parrot species engage in geophagy on clay licks (e.g. Brightsmith et al., 2018; Mee et al., 2005), and may therefore benefit from a replication of this behaviour in captivity. The interventions on the swift parrots in the present thesis may also be applied to other parrots that excessively consume the food of their enclosure mates in mixed-species exhibits. Therefore, the evidence-based modifications proposed have the potential to be used across parrots kept under human care, as long as their implementation is done while keeping the specific needs of the individual parrots in mind (with baseline behavioural assessments), as well as the behavioural ecology of their species in the wild.

6.4.1. Application of my research to promote parrot welfare in captivity

The behavioural alterations observed in most of the parrots suggest an overall positive impact on their welfare. The combined observations of increased activity, improved use of the modified enclosure and of its higher complexity, and/or engagement with their environment, which were observed in both grey parrot groups and most scarlet macaws, suggest they benefited from the augmented stimuli and choice (i.e. more options for what to do, where to be and where to go), which are associated with positive

welfare states (Mellor & Beausoleil, 2015). On the other hand, the decrease in inactivity observed in some individuals may have been associated with a reduction in negative affective states, such as boredom or depression (Fureix & Meagher, 2015), and was likely enabled by the increased opportunities for behavioural expression (section 1.4).

The welfare of an animal is also dependent on, and influenced by, its physical health (Mellor, 2016). Therefore, the enclosure modifications may have also positively impacted welfare by improving the parrots' health. For example, the increased activity levels observed in the activity budgets and/or flight rates of most parrots could have reduced risks of obesity and other inactivity-related diseases (see section 3.4.1.1), while the use of more varied perches, also observed in most parrots, likely reduced risk of bumblefoot (i.e. inflammatory foot condition; Kalmar et al., 2007). Furthermore, the swift parrots may have also accrued health-related benefits from the interventions that resulted in the apparent reduction in seed eating, as excessive seed consumption could have compromised their health (e.g. Gartrell et al., 2003). However, as previously stated, the behavioural responses varied across parrots, and health monitoring of individual parrots is required to evaluate how health was affected by the changes in their environment.

The changes in the social environments, however, which were not planned for this research, may have had negative effects on the welfare of some individuals. For example, the new individuals and species in the grey parrot and macaw enclosures at zoo B seemed to have discouraged the grey parrots and the adult scarlet macaws from

using some areas of the enclosure. These responses were likely indicative of unpleasant states (e.g. fear and/or anxiety), and this modified social environmental may have imposed behavioural restrictions on the exploration and use of the enclosure, consequently jeopardising welfare (Mellor & Beausoleil, 2015).

Future research should integrate other indicators of welfare with behavioural observations, to evaluate in more detail the impacts of modifications to the environment on the welfare of the parrots. For example, monitoring levels of hormones associated with stress, such as corticosterone from faecal samples, is a non-invasive method that could help to understand the parrots' physiological reactions to their environment and any changes within it (Costa et al., 2016; Young & Hallford, 2013). However, corticosterone levels may also increase in situations that are not detrimental to welfare (e.g. exercise, affiliative social interactions) and the use of this physiological indicator in welfare assessments should be done alongside behavioural observations (Wielebnowski, 2003). Assessments of health indicators, such as body (Manteca et al., 2016) and feather condition (Costa et al., 2016) can also be used to further evaluate the impacts of the modifications on physical health and consequently welfare. However, most methods to accurately assess body condition in birds require handling of the animals (Labocha & Hayes, 2012), and although it may be possible to evaluate feather condition without handling the animal, an accurate assessment likely requires close inspection, and clear visibility, of the feathers (van Zeeland et al., 2013b). Hence, these and other assessments of physical health may be better conducted with the participation of veterinary professionals. A multi-disciplinary approach is therefore recommended in future studies, although it will also involve the increased challenge of

coordinating collaborative research actions with multiple professionals across departments.

Nevertheless, the outcomes of the present research suggest that the modifications proposed, alongside careful consideration of the social environment, have the potential to help to improve the welfare of captive parrots.

6.4.2. Application of my research to promote *ex situ* conservation of parrot species

The application of the methodology and outcomes of this research can also assist parrot *ex situ* conservation, by helping to assess and enable the expression of wild-type behaviours of parrots in (1) long-term conservation breeding programmes (i.e. part of insurance populations; section 1.2); (2) breed-for-release programmes (i.e. breeding with the goal of reintroduction in the short term; Barongi et al., 2015); and (3) rescue, rehabilitation and release programmes.

For captive animals that are to be released into the wild, ensuring they are expressing the necessary behaviours to thrive in the natural environment is a vital step for a successful reintroduction (section 1.2; Barongi et al., 2015; IUCN, 2013). Hence, encouraging those behaviours in to-be-released captive-bred animals can help to improve the success of the reintroduction efforts (Tetzlaff et al., 2019). Loss of natural behaviours can occur within a few generations of captive breeding (e.g. Dixon-MacCallum et al., 2021), and therefore even animals in short-term breed-for-release

programmes are susceptible to the effects of captivity on behaviour. The husbandry and management modifications implemented as part of my research can help captive parrots to learn some of the behaviours they need for survival in the wild. For example, increasing the diversity and complexity of supports in the enclosure can help parrots to develop skills in navigating unstable supports of varied orientation and thickness (Chapter 4), which free-living parrots rely on for foraging within the tree canopy (Chapter 2).

Wild-born/hatched animals that are only in human care for a short period of time (e.g. rescued animals under rehabilitation) can also benefit from an enriched captive environment that gives them opportunities to express natural behaviours. First, it can reduce their captivity-induced stress, positively impacting their welfare and improving chances of survival when released back into the wild (Alaniz et al., 2022; Escobedo-Bonilla et al., 2022). Secondly, for wild animals that are rescued young and have not yet fully developed their foraging, locomotion, social and predator avoidance skills, it provides increased opportunities for them to learn the necessary wild-type behaviours prior to their return to the wild (e.g. Preuschoft et al., 2021), behaviours they would have naturally developed via social learning, from their parents and other conspecifics.

Lastly, enabling wild-type behaviours in animals in long-term captivity (e.g. zoos and sanctuaries) can also benefit species' conservation, even though most of those animals will not be reintroduced into the wild. Long-term captive breeding programmes, such as those in zoos and aquariums, aim to keep healthy insurance populations to

release into the wild when and if necessary (see section 1.2). Hence, even though the current animals in those *ex situ* populations are unlikely to be released, their offspring, or future generations, might be. However, animals in long-term captive breeding programmes are more susceptible to loss of natural behaviours (McPhee, 2004; O'Regan & Kitchener, 2005), and genetic adaptation to captivity (Williams & Hoffman, 2009).

Through social learning, behaviours can spread within animal groups and populations (Whitehead, 2010), evidence of which has been found in parrots (e.g. Huber et al., 2001; Morales Picard et al., 2017). For example, young scarlet macaws in the wild learn skills from their parents and other conspecifics (Myers & Vaughan, 2004), and therefore in captivity their behavioural development may depend on the (wild-type or abnormal) behavioural repertoire of their parents and other parrots. Therefore, encouraging captive animals to exhibit natural behaviours may facilitate the spread of those behaviours within the population and across generations, and the retention of the wild-type behavioural repertoire in the long term.

6.4.3. Application of my research to promote *in situ* research and conservation of parrots

By helping to enable wild-type behaviours in captive parrots, the present research may also improve the application of research on captive animals to *in situ* research and conservation. It has been previously shown that zoo-based research can contribute to advances in knowledge of species' biology (Rose et al., 2019), as well as benefit

research and conservation of their wild counterparts (Lemos de Figueiredo & Díez-León, 2022). For example, studies in *ex situ* settings allowed to gather insight into the reproductive ecology of gartersnakes (*Thamnophis rufipunctatus;* Blais et al., 2022), paw preferences in wolves (*Canis lupus;* Regaiolli et al., 2021), motor laterality in giraffes (*Giraffa camelopardalis;* Svoke, 2017), and cognitive abilities of parrots (Brucks et al., 2021; Kabadayi et al., 2017; Pepperberg, 2004). Furthermore, captive animals can also assist in the development of methodologies and/or technology for *in situ* research, by facilitating testing and refinement of such methods (e.g. Nuijten et al., 2020; Wimbles et al., 2021).

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The application of research on *ex situ* animals is contested, however, with claims that data collected on animals living in unnatural environments are of little use to their wild counterparts (e.g. Jamieson, 2015). Therefore, by replicating aspects of the natural environment in captivity, and encouraging captive animals to behave more like their wild counterparts, it may be possible to increase the robustness of data generated from *ex situ* research. For example, Edwards et al., (2022) reported that replicating the natural environmental conditions (i.e. daily temperature and humidity patterns) of golden mantellas (*Mantella aurantiaca)* in captivity elicited a daily activity pattern that was more likely similar to their wild counterparts. Those data can be used to inform field surveys on that cryptic species (Edwards et al., 2022), and further highlights how *ex situ* and *in situ* research can be of mutual benefit.

6.4.4. Application of my research to benefit zoo visitor engagement and education about parrots

Finally, the outcomes of this research may also indirectly help to improve visitor education and engagement in *ex situ* institutions that exhibit animals to the public (e.g. zoos and some sanctuaries). It has been previously shown that the zoo visitor experience can be influenced by the behaviour of the animals they are observing, with more active behaviours associated with an increase in the interest (Altman, 1998), knowledge (Pearson et al., 2013) and positive attitudes (Salas et al., 2021) of visitors. Furthermore, exhibits that provide the animals with increased opportunities for behavioural expression may also improve the visitors' appreciation for that species' natural behaviour (Price et al., 1994). Zoo visitors may not clearly associate wild-type behaviours with improved welfare (Melfi et al., 2004), but can perceive abnormal behaviours as indicative of poor welfare (Godinez et al., 2013), and prefer watching active animals (Margulis et al., 2003; Melfi et al., 2004). The visitor experience may also be jeopardised by low visibility of the animals, and therefore a conflict may arise between animal welfare (i.e. providing animals with opportunities to retreat and hide from visitors) and visitor recreation and engagement (Fernandez et al., 2009). However, encouraging active behaviours such as locomotion and foraging may counteract the effects of increased visual barriers in the enclosure (i.e. visual barriers decrease visibility, but active animals are more likely to be seen as they move within the enclosure; Lemos de Figueiredo et al., 2021).

Therefore, the increased parrot activity and behavioural expression in the present research, which were potentially enabled by the modifications applied, may have had

an indirect impact on the visitor experience at both zoos, with potential wider applications to other *ex situ* facilities.

6.5. Overall conclusion

6.5.1. The importance of natural behaviours for animal welfare and conservation

In order for captive animals to fulfil their *ex situ* conservation roles, as well as contribute to *in situ* research and conservation and, potentially, visitor education and engagement, they must remain as close as possible in morphology, physiology, and behaviour to their wild counterparts. Ensuring they have the opportunity to express wild-type behaviours, by providing them with environments that replicate the challenges of their natural habitat, as attempted in my research, is a key step in that goal. Despite some contention among animal welfare scientists about using the expression of natural/wild-type behaviours in welfare assessments of captive animals (see section 1.4.1), there seems to be an overall agreement that the natural behavioural ecology is, to an extent, useful (Browning, 2020; Howell & Cheyne, 2019; Veasey et al., 1996). However, to abandon the use of natural behaviours when evaluating welfare, as suggested by Browning (2020), can compromise the other goals of keeping wild animals in human care, especially if they are, or may be, part of a conservation breeding programme. For example, consider an extreme hypothetical scenario where captive wild animals could experience optimal welfare by exhibiting only unnatural, but rewarding behaviours. Even though optimal welfare was achieved under this scenario, the animals would not be true representatives of their wild counterparts and would have limited value for conservation, research, and education.

This scenario is unlikely to be achieved, as behaviours associated with enjoyment that are suggested by Browning (2020) as more suitable indicators of welfare, likely overlap with the expression of wild-type behaviours that are rewarding for the animals and that positively impact their welfare (section 1.4.1).

There are ethical considerations for wild-type aversive stimuli that may elicit behavioural responses associated with a negative welfare state (e.g. anti-predator training eliciting a fear and anxiety response). In reintroduction programmes, those aversive stimuli are necessary to prepare the animals to survive in the wild (Barongi et al., 2015), as the survival and welfare of the animal in the long-term are prioritised over avoiding short-term, acute, stress. In long-term breeding programmes, it may still be important to ensure those behaviours (e.g. predator recognition and evasion) are retained in the *ex situ* population (section 6.4.2). However, the ethics of deliberately exposing a captive animal to such stimuli, and the impacts on the welfare of the animal, should also be considered. Most parrots in the present thesis were in long-term breeding programmes (the wild-hatched grey parrot group A may return to the wild, but it has not been confirmed), and the modifications proposed and applied focussed on increasing challenges and stimuli associated with natural but rewarding behaviours. However, in the future, careful incorporation of such stimuli (e.g. occasional anti-predator training) in the modifications could also be considered.

Therefore, the importance of wild-type behaviours in captive animals should not be undermined. Animal welfare science is progressing and the role of certain unnatural

behaviours (i.e. behaviours that are not exhibited by the species in the natural environment) in promoting positive welfare should be explored. Furthermore, while some wild-type behaviours are associated with positive welfare, there are some whose replication in captivity raise ethical questions. However, when considering both natural and unnatural behaviours in captive animals, the welfare of the animals should be considered alongside the other conservation, research, and education roles they play, or might play, in the short and/or long term.

6.5.2. The importance of *ex situ* behavioural research for species conservation

Behavioural research is a valuable tool to assess and improve the behavioural repertoire of captive animals and, consequently, their preparedness for present or future release into the wild (sections 1.2 and 6.4.2). Therefore, research on the behaviour of both captive and free-living animals can improve the success of *ex situ* conservation efforts, which can play an integral part in the recovery of threatened species by re-establishing or boosting wild populations (section 1.2). *In situ* conservation actions, such as habitat protection and restoration, and anti-poaching measures, cannot be neglected, as *ex situ* conservation efforts without integrated *in situ* actions are unlikely to succeed. For example, reintroduction efforts are likely to fail in establishing or boosting wild populations if there is no suitable habitat to release the captive-bred animals into, or if the threats that lead to the original decline in the population were not eliminated. However, for species that are extinct in the wild, or remain in low population densities, *in situ* conservation efforts are likely not enough to ensure the recovery of those species (IUCN, 2013; Smith et al., 2023). Therefore, the integration of *ex situ* and *in situ* conservation actions is key for the preservation of the

world’s biodiversity, as highlighted in the “One Plan Approach to Conservation Planning” (IUCN CPSG, 2023).

For the many parrot species that are threatened and reliant on *ex situ* conservation (Olah et al., 2016), the integration of *in situ* and *ex situ* behavioural research is vital to improve the captive breeding and reintroduction programmes upon which their futural survival depends.

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Appendix 1. Description of pilot observations conducted for the development of the methodology for the behavioural study focusing on grey parrots and scarlet macaws.

Pilot behavioural observations were conducted at Dudley Zoo and Castle (UK; May and June 2019) and Drayton Manor Park and Zoo (UK; July and September 2019). Approximately 100 hours of pilot behavioural observations were conducted (50 hours across 24 days at each zoo), with the aims of (1) training myself in the behavioural sampling techniques needed for this research, and (2) developing and refining a protocol that was suitable for the species and birds included in this research.

The first behavioural observations were of the scarlet macaw group at Dudley Zoo. The group consisted of seven males that had been rescued from the illegal wildlife trade, and were likely wild-hatched and sexually mature, although exact age could not be determined. Initial observations consisted of making notes of the varied behaviours exhibited by the macaws, and to try to establish the feasibility of identifying and collecting data on a single bird within the group for a period of time. It was found that all scarlet macaws had identifiable features, such as marks on their bills or patterns on their wing feathers, but that some of those features were subtle and it was at times challenging to keep one individual in sight when multiple birds were moving around the enclosure. In the next step, the methodology of previous research conducted for the great ape Enclosure Design Tool (EDT) was considered as a starting point in the development of my research's methodology, due do the overlap in their aims. This methodology consisted of behavioural data collection under three protocols (cognition,

locomotion, and social) using focal interval sampling (contextual behaviours and specific behaviour for each protocol collected in 20-second intervals during 30-minute sessions). The mobile application ZooMonitor (Ross et al., 2016) was set up with that methodology, and an ethogram of behaviours that was adapted from previous studies (Meehan et al., 2004; van Zeeland et al., 2013) and my own observation was drawn up. Several practice sessions were conducted to trial different approaches, including the combination of the three protocols into one to collect all data in the same session, and the use of different intervals for sampling (from 20-second to 2-minute intervals). Combining all protocols was deemed unsuitable even for the longest intervals, as it was not possible to accurately collect all the data with the desired level of detail. A 30-second interval was determined to be the best option for data collection on scarlet macaws, as it allowed enough time to collect all of the necessary data as well as to re-locate the focal bird when it was lost within the group.

The pilot study continued at Drayton Manor, which was one of the zoos where the main study was to be conducted. The methodology that had been established during the pilot observations at Dudley Zoo was trialled on the grey parrot group (16 birds) at Drayton Manor. Despite multiple attempts and practice sessions, identification of individual grey parrots for focal sampling was not possible. Group sampling was attempted in subsequent trials, again trying interval sampling that went from 20-second to 2-minute intervals. However, it was not possible to collect the desired level of detailed data while sampling multiple birds at the same time. As a result, a method for focal sampling of multiple birds within the group was developed, by randomly selecting one bird for sampling in each interval, based on a list of random numbers and the bird's

relative location in the enclosure (e.g. number 3 on the list for an interval, 3rd bird from the left would be sampled on that interval). After more practice sessions, this methodology for focal sampling of various birds within groups was refined to include clear rules for bird selection and ensure it was randomised. The 30-second interval was again determined to be suitable for group sampling as it gave enough time for the random selection of one bird to be sampled in the following interval. The male and female scarlet macaw at Drayton Manor, which were to be included in the main study, were identifiable (male had a larger body size and brighter wing feathers than the female) and it was decided that the research's methodology would include an option for focal sampling of each bird when identification was possible, and an alternative option for focal sampling of multiple birds in the group when identification was not possible.