



MONASH University

Alloparental infant-carrying behaviour in Common Marmosets (*Callithrix jacchus*)

Noriyoshi Kawasaki

Bachelor of Science (Honours)

A thesis submitted for the degree of Doctor of Philosophy at
Monash University in 2016
School of Biological Sciences

Copyright notice

© Noriyoshi Kawasaki (2016).

I certify that I have made all reasonable efforts to secure copyright permissions for third-party content included in this thesis and have not knowingly added copyright content to my work without the owner's permission.

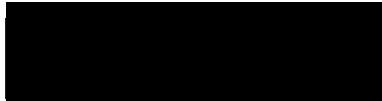
Abstract

Helping behaviour, where individuals benefit others at their own expense, is often seen in cooperative societies. In cooperative breeding systems, individuals other than the parents contributing to the care of young. However, helping others is seemingly at odds with the concept of natural selection because, by benefiting the breeders, helping behaviour reduces the relative fitness of the helper. Also, by caring for the offspring of others, the fitness of the helper might be reduced when the young become competitors for local resources later in life. For those reasons, helping behaviour should not be favoured in natural selection. Various hypotheses have been advanced to explain the evolution of helping behaviour. However, support for these hypotheses from empirical studies is still limited since there is a difficulty with isolating the effects of helping behaviour from the influence of other confounding factors, such as a habitat quality, on the fitness of breeders. One plausible method of quantifying the effects of helping behaviour on the reproductive success of breeders, while controlling for such confounding factors, is to examine the relationship between the reproductive success of breeders and the amount of help given in a controlled environment. Accordingly, my thesis investigated helping behaviour in a captive population of a cooperatively breeding primate, the common marmoset (*Callithrix jacchus*), by exploring the potential fitness effects of alloparental infant-carrying, and the mechanisms that underpin this behaviour. Common marmosets typically live in a group of extended family members, which consists of a dominant breeding pair and several male and female subordinate group members that help to carry the infants of the dominant breeding pair. In my study, I firstly examined the contribution of helpers to infant-carrying and its effect on parental infant-carrying loads and the success of parturition by the breeding females in their subsequent breeding event (Chapter 2). Second, I investigated the function of alloparental infant-carrying behaviour by examining the factors that may underpin the alloparental infant-carrying behaviour. Specifically, I examined the effects of three factors on the contribution of helpers to infant-carrying: the sex of the helpers (Chapter 3), the presence of a social observer (i.e. a dominant female from the helper's social group) (Chapter 4), and perceived predation risk (Chapter 5). I found that helpers' contribution to infant-carrying was quite minimal when the helpers were in the social groups and had no effect on the parental infant-carrying loads. Also, the contribution of helpers to infant-carrying had no effect on the parturition success of the breeding pairs in the subsequent breeding event, which the stress on the mothers from excess

contribution to infant-carrying may result in loss of pregnancy or stillbirth. However, when helpers were separated from the social groups, they carried infants as much as the mothers of the infants. This contribution of helpers to infant-carrying was not influenced by the sex of the helpers, the presence of a social observer or perceived predation risk, but it did decrease as infant age increased. The results suggest three fundamental features underpinning alloparental infant-carrying behaviour. First, its function to accommodate the carrying needs of the infant. Second, social restraints, such as the accessibility to the infants and the demand for alloparental infant-carrying, over the helpers' participation in infant-carrying in the groups. Third, its substantial fitness benefits to the helpers. Together, the chapters of my thesis highlight the persistent propensity of helpers to carry infants, which provides important implications for the evolution and maintenance of alloparental infant-carrying behaviour in common marmosets.

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.



Noriyoshi Kawasaki

28/08/2016

Acknowledgements

I would like to thank with my sincere gratitude the following people for their invaluable supports in this study.

I cannot express my gratitude enough to my principal supervisor Bob Wong for his dedication, patience, consideration and encouragements. Without a doubt, I could not complete this study if I was not under his supervision and without his selfless support and indispensable guidance throughout this protracted endeavour.

I would also like to thank my supervisor Anne Peters, especially, for her help and advice in data analysis, and for the proofreading of numerous drafts which must have been wearing. I am very grateful for her insights on the topic of cooperative breeding and helping behaviour that was the core of this study.

To my supervisor James Bourne, I am grateful for his valuable advice from his extensive knowledge and experience with marmosets. I am thankful to him for offering a great opportunity to study marmosets which allowed me to pursue my research interests in understanding helping behaviour.

I thank all the staff at Gippsland Field Station, including Nicole Ure, Nicole Harding, Nicole Dunbar, Michelle Willis, Emily Robins, Becky Lawless, Tammy Stevens, Brian Kendall, Irwin Ryan, Gregory Hunt, Graham Sillito and others for their technical support including accommodation and access to the facilities at the station. Their experience and knowledge about marmosets, as well as their support of my project made this study possible. I would like also thank them for their friendship and trust, and for accepting a complete stranger into their team. I am especially thankful for their help while I was suffering from vertebral disk herniation and immobilised in pain. Literally, I could not have continued my project without their help.

To Kasper Delhey, I am thankful for his help and advice in statistics, especially for the construction of the mix models that was a vital part of this study.

I wish to thank the members of the Wong Lab group, in particular, Krystina Mossop, Ben Wegener, Zoe Squires, Helene Lowry, Daniel Paz Decanini, John Morrongiello, Mel Klamt, Will Sowersby, Nicholas Deal, Nicholas Moran, Patrick Tomkins, Marcus Michelangeli, Michael Bertram, Rowan Jacques-Hamilton, Amy Hooper, Leonardo Guida, Emma Jensson, Lexie Slingerland, Sarah Simmonds, Skye Boyd-Gerny, Alisha McLennan, Jack Eades, Matthew Warr, Minna Saaristo, Topi Lehtonen, Andreas Svensson, Ricardo San Martin, Sheila Hamilton-Brown and several Honours and undergraduate students, for their support and company, as well as for the countless proofreadings of the early drafts of my writing, which must have been puzzling and annoying. I was privileged to be a member of this wonderful group full of talented, hard-working and thoughtful people. Because of them, my time during this project was stimulating and enjoyable rather than challenging and stressful.

To the members of the panel for this study, I thank Alan Lill and David Chapple for their valuable comments on the early plan of this study. Their insights greatly improved the integrity and focus of the study.

To fellow post-grads and friends, thank you to Clarissa Barbosa, Angélica Elizabeth Martínez Bauer, Joanne Bennett, Lotte van Boheemen, Rebecca Bray, Martin Burd, Phil Byrne, Sherrie Caarels, Florencia Camus, Paul Carnell, Valerie Caron, Ted Chun Yi Chang, Derek Dapp, Romy de Zing, Tom Dierschke, Jess Drake, Tara Draper, Adrian Dusting, Hannes Eimer, Eduardo Flores-Sandoval, Pablo Galaviz, Darren Giling, Celine Goulet, Jim Griffiths, Stephen Heap, Nataly Hidalgo-Aranzamendi, Susie Ho, David Hocking, Marianne Hoogmoed, Gillis Horner, Greg Horrocks, Christopher Johnstone, Brian Kearney, Manoj Kamalanathan, Nikki Kowalczyk, Marcelo Lagos, Richard Lee, Silk Yu Lin, Thomas Lines, Teresa Mackintosh, Gerardo Cerón Martinez, Paulina Mikulic, Lee Miles, Rebecca Miller, Alissa Monk, Ee Ling Ng, Fariba Pakdel, Amanda Pantorno, Travis Park, Giselle Perdomo, Amanda Pettersen, Mattia Pierangelini, Lynette Plenderleith, Venkatesh Nagarajan Radha, Anthony Rafferty, Emma Razeng, Mani Shrestha, Katie Smith, Tamsyne Smith-Harding, Peter Smits, Paul Sunnucks, Andrea Taylor, Matthew Thompson, Ross Thompson, Taiyo Toriba, Hernán Morales Villegas, Sailajah Vishwanathan, Avi Waksberg, Stephanie Watts-Williams, Tricia Wevill, Sean Williamson, Megan Wong, Wangsheng Zhu, including the members of the Wong Lab group and many others. All of you provided moral support through the sharing of anxieties, frustrations, encouragement and laughter, which were vital for undertaking this endeavour. The moments that I will remember most from my time during this study will be the time spent with all of you.

To the staff and academics of the School of Biological Sciences, thank you for your highly professional and dedicated support, especially, to Fiona Hibbert for her compassionate and life-saving support in dealing with all the administrative issues for every post-grad in the School.

Thanks to Tomas Zohara from Monash library and members of the Writing Group for the lessons in improving writing skills as well as for their comments on the early drafts of this thesis.

Thank you to Ian Veitch, from P. I. Plus Pty Ltd, for his expertise and friendly support in finding appropriate video recording devices for this study.

Thanks to the commercial proof-reader Greg Hill, from All Your Writing and Editing Needs, for the proofreading of the early drafts of chapters one and six of this thesis. I declare that his editorial intervention was restricted to matters of language, completeness and consistency in those chapters.

Thank you to Monash University for the scholarships, other financial support, facilities and services, as well as accepting me to undertake this study. To the Australasian Society for the Study of Animal Behaviour, thanks for the student grant. Thanks also to the International Society for Behavioural Ecology for the travel grant for the conference at Lund, Sweden in 2012. To the Department of Immigration and Citizenship of the Australian Government, thanks for allowing me to stay and study in this beautiful country. Their generous support made this wonderful experience possible.

To all the marmosets, thanks for their tolerance and contribution, which were fundamental for this study.

Finally, to my parents and family, thank you for all the support and being by my side, which enabled me to withstand and advance at every moment throughout these years.

Table of Contents

Copyright notice.....	2
Abstract	3
Declaration.....	5
Acknowledgements.....	6

Chapter One:

General introduction	10
Evolutionary explanation for helping behaviour	10
Measuring the effects of helping behaviour.....	14
Callitrichines	16
Effects of helpers in callitrichines.....	22
Aims.....	24
References	26

Chapter Two:

No evidence for effects of infant-carrying by related helpers on the fitness of breeding pairs in captive common marmosets (<i>Callithrix jacchus</i>)	41
Abstract	42
Introduction.....	43
Methods.....	46
<i>Design</i>	46
<i>Animal housing</i>	46
<i>Study subjects</i>	47
<i>Video recording</i>	47
<i>Data collection</i>	47
<i>Statistical analysis</i>	49
Results.....	50
<i>Fathers carried infants more than mothers</i>	50
<i>Maternal infant-carrying decreased with increasing paternal infant-carrying</i>	50
<i>Maternal infant-carrying time was shorter in successful subsequent parturition</i>	51
Discussion	51
Tables and Figures	55
References	60

Chapter Three:

No sex differences in infant-carrying by related helpers in captive common marmosets (<i>Callithrix jacchus</i>): An experimental study	64
Abstract	65
Introduction.....	66
Methods.....	68
<i>Design</i>	68
<i>Animal housing</i>	68
<i>Study subjects</i>	69
<i>Procedure</i>	69
<i>Statistical analyses</i>	70
Results.....	71
Discussion	72

Tables and Figures	75
References	77

Chapter Four:

No evidence that infant-carrying functions as rent payment in related helpers of captive common marmosets (<i>Callithrix jacchus</i>)	80
Abstract	81
Introduction	82
Methods	86
<i>Design</i>	86
<i>Animals housing</i>	86
<i>Study subjects</i>	87
<i>Procedure</i>	88
<i>Statistical analyses</i>	89
Results	89
Discussion	89
Tables and Figures	92
References	94

Chapter Five:

No effect of perceived predation risk on infant-carrying by related helpers in captive common marmosets (<i>Callithrix jacchus</i>)	99
Abstract	100
Introduction	101
Methods	103
<i>Design</i>	103
<i>Animal housing</i>	103
<i>Study subjects</i>	104
<i>Predatory stimulus</i>	105
<i>Procedure</i>	105
<i>Statistical analyses</i>	106
Results	107
<i>Predatory stimulus did not affect infant-carrying</i>	107
<i>Infant-carrying did not differ between helpers and mothers</i>	107
<i>Infant-carrying decreased with increasing infant age</i>	108
Discussion	108
Tables and Figures	112
References	115

Chapter Six:

General discussion	120
Alloparental infant-carrying is driven by infants' needs	121
Participation of helpers in infant-carrying is regulated by social contexts of the groups	122
Possible fitness benefits of alloparental infant-carrying behaviour	124
Potential limitations of the study	127
<i>Effects of stress from handling on the behaviour of animals</i>	128
<i>Effects of experiments performed in the colony by other researchers</i>	128
Conclusions	129
References	130

Chapter One

General introduction

Why do animals help others? Helping is commonly seen among social animals and appears to be a fundamental aspect of their societies (Wilson 1971; Stacey & Koenig 1990; Dugatkin 1997; Hammerstein 2003; Duffy & Thiel 2007; Melis & Semmann 2010). However, despite extensive research effort, we still have an incomplete understanding of what causes individuals to help others, what explains individual variation in helping effort, and how helping is maintained in populations through time. Helping behaviour can be defined as a behaviour that benefits the recipients at the expense of the actor of behaviour (West *et al.* 2007). Therefore, by its very nature, helping behaviour is expected to result in benefits to recipients. However, helping behaviours are often costly to the helper, and this is seemingly at odds with the concept of natural selection: if helping provides no benefit to the helper, it should not be favoured by selection (Darwin 1859; Hamilton 1964).

Evolutionary explanation for helping behaviour

Various hypotheses have been advanced to explain the evolution of helping behaviour, including kin selection (Hamilton 1964; Maynard Smith 1964), the green-beard effect (i.e. the gene for helping behaviour can be favoured if helping is directed towards others who share the same gene; *sensu* Hamilton 1964; Dawkins 1976), coercion (Wilson 1971; Clutton-Brock & Parker 1995), reciprocity (Trivers 1971), skill learning (Lancaster 1971; Brown 1987), social prestige (Zahavi 1974, 1995), group augmentation (Woolfenden 1975; Kokko *et al.* 2001), mutualism (West-Eberhard 1975), pay-to-stay (i.e. individuals help as 'rent' for group membership; *sensu* Gaston 1978; Kokko *et al.* 2002), parentage acquisition (Burke *et al.* 1989; Cockburn 1998) and unselected behaviour (Jamieson 1989). Some of these hypotheses have been more successful in explaining helping behaviour than others (Jennions & Macdonald 1994; Cockburn 1998).

One of the most widely invoked hypotheses to explain the evolution and persistence of helping behaviour is kin selection (Griffin & West 2002). The kin selection hypothesis posits that helpers increase the reproductive success of their close kin who are more likely to share the genes for helping behaviour than less related individuals (Hamilton 1964; Maynard Smith

1964). By doing so, helpers increase their inclusive fitness, which is the sum of the reproductive success of their own (direct fitness) and others who share the genes of interest (indirect fitness) (Hamilton 1964; Griffin & West 2002; Bourke 2011). Evidence shows that helping behaviour of many cooperatively breeding species is, indeed, directed towards close kin (Curry 1988; Komdeur 1994; Solomon & French 1997; Koenig & Dickinson 2004; Bourke 2014) and in some species, individuals preferentially help their close kin rather than unrelated individuals (Russell & Hatchwell 2001; Nam *et al.* 2010; Wright *et al.* 2010; Browning *et al.* 2012). Therefore, kinship among group members seems to be an important factor mediating social relationships in some species. However, a close genealogical kinship between interacting individuals is not, on its own, sufficient evidence to validate kin selection as a mechanism underpinning helping behaviour. Limitations to dispersal, for instance, can cause close kin to remain within a social group regardless of whether kin helpers provide more help than non-kin helpers (Creel & Waser 1994; Dunn *et al.* 1995; Magrath & Whittingham 1997; Clutton-Brock *et al.* 2001a; Nelson-Flower 2010). Therefore, even in groups composed of close kin, indirect fitness benefits might not be the major adaptive factor regulating helping behaviour, and other mechanisms could potentially be important (Griffin & West 2002). Moreover, in order to verify the indirect fitness benefits of helping behaviour, the positive effects of helping behaviour on the frequency of the helping trait/genes in the population may also need to be demonstrated (Hamilton 1964; Gardner *et al.* 2011). For example, helping behaviour may have indirect fitness benefits when helpers selectively increase the fitness of individuals that possess the helping trait over those that do not (Smukalla *et al.* 2008).

Another popular explanation for the evolution of helping behaviour is the group augmentation hypothesis, which posits that helping behaviour provides fitness benefits to the helpers through increased group size, which enhances the survival and reproductive success of group members, including the helpers (Woelfenden 1975; Kokko *et al.* 2001; Kingma *et al.* 2014). Helpers in larger groups often attain improved survival and future reproductive success when they remain within the group (Emlen & Wrege 1989; Cockburn 1998; Clutton-Brock *et al.* 2001b; Lawson Handley & Perrin 2007). Larger group size can reduce predation risk through increased vigilance, as well as dilution and confusion effects (Williams 1964; Hamilton 1971; Powell 1974; Foster & Treherne 1981; Godin 1986; Landeau & Terborgh 1986; Elgar 1989). Larger groups are also at an advantage when it comes to defending their territories against neighbouring groups (Heg *et al.* 2005; Kleiber *et al.* 2007; Garay & Varga

2011) and obtaining food resources (Stacey & Ligon 1987; Parker *et al.* 1994; Gilby 2006; Carter & Wilkinson 2013). Moreover, large number of younger members in the group can potentially increase the future reproductive success of helpers by assisting the helpers after they subsequently inherit the breeding position within the existing group (Creel & Waser 1994; Clutton-Brock *et al.* 2000) or when dispersing together to establish their own groups elsewhere (Rood 1990; Heinsohn *et al.* 2000; Ridley 2012). Therefore, helping fellow group members to survive or reproduce will maintain and increase group size and, hence, associated benefits to the helpers (Kokko *et al.* 2001; Garay 2009; Garay & Varga 2011). However, since group augmentation can be associated with almost any of the actual or potential positive effects of group size on the fitness of helpers, the hypothesis has frequently been applied to explain helping behaviour without demonstrating both of the assumptions of positive effects of helping behaviour on group size and positive effects of group size on the fitness of helpers (Wright 2007; Kingma *et al.* 2014).

One hypothesis that has relatively strong empirical support is the pay-to-stay hypothesis, which argues that helping behaviour functions as ‘rent’ paid by the helpers to be tolerated within the group (Gaston 1978; Clutton-Brock & Parker 1995; Kokko *et al.* 2002). Joining a group provides benefits for the helpers, such as access to resources in the communal territory, reduced predation risk, enhanced opportunities in intra- or extra-group mating, and the possibility of attaining the breeding position in the group (Gaston 1978; Reyer 1984; Creel & Waser 1994; Dunn *et al.* 1995; Balshine-Earn *et al.* 1998; Kokko & Johnstone 1999; Pen & Weissing 2000). Pay-to-stay has been observed in several species (*Polistes fuscatus* wasp: Reeve & Gamboa 1983; *Lamprologus brichardi* fish: Taborsky 1985; pied kingfisher, *Ceryle rudis*: Reyer 1986; naked mole-rat, *Heterocephalus glaber*: Reeve 1992; superb fairy-wren, *Malurus cyaneus*: Mulder & Langmore 1993; *Neolamprologus pulcher* fish: Balshine-Earn *et al.* 1998). For example, in a cooperatively breeding bird, the superb fairy-wren, helpers were attacked by the dominant male when being returned to the group after a temporary removal experiment (Mulder & Langmore 1993). Removed and returned helpers were attacked by the dominant males during the breeding season only, when helpers are supposed to assist the breeding pairs in caring for young and territory defence (Mulder & Langmore 1993). However, convincing evidence of the pay-to-stay hypothesis in free-living social animals remains rare (Santema & Clutton-Brock 2012; Nomano *et al.* 2015), probably since the causal relationship between punishment and helping behaviour is often difficult to detect, especially in the wild (Heinsohn & Legge 1999). Also, punishment will not be observable

when helpers avoid it by performing submissive behaviour or increasing helping to compensate for the shortfall in rent (Bergmuller & Taborsky 2005; Wong *et al.* 2007; Cant 2011). Moreover, the need for rent-paying will decrease when helpers can benefit from increasing the fitness of breeders or group size, and helpers will be more likely to provide help voluntarily (Kokko *et al.* 2002).

The skill learning hypothesis suggests that helping can increase the subsequent breeding success of individuals by allowing them to practice their parental skills by helping others (Lancaster 1971; Brown 1987). Strong evidence for this hypothesis has been shown in Seychelles warblers (*Acrocephalus sechellensis*), where individuals with experience in alloparental care possess better skills in nest building, egg incubation and nest guarding, and attain higher reproductive success at their first breeding attempt compared to individuals without alloparental experience (Komdeur 1996). However, the effects of alloparental experience on breeding success have not clearly demonstrated in other species (Emlen & Wrege 1989; Khan & Walters 1997; Tardif 1997). Demonstrating the effects of alloparental experience on breeding success is problematic since effects of the quality of the breeders and habitat on breeding success are often difficult to control. For example, breeding success is generally higher for older breeders due to increased foraging efficiency and reproductive effort (Pianka & Parker 1975; Newton *et al.* 1981; Pugesek 1981; Curio 1983; Nur 1984; Perrins & McCleery 1985; Nol & Smith 1987; Desrochers 1992b, a). Indeed, individuals with alloparental experience are typically older than individuals with less alloparental experience (Woolfenden 1975; Nelson 1988; Komdeur 1996; Khan & Walters 1997). Therefore, the higher breeding success of experienced breeders could be due to their experience or age or both, and few study systems allow for these effects to be disentangled.

Accordingly, despite the theoretical appeal, conclusive empirical support for these explanations is still limited and remains controversial (Brosnan & Bshary 2010; Connor 2010; Leimar & Hammerstein 2010). One main reason for the lack of supportive evidence is that there are difficulties with isolating the effects of helping behaviour from the influence of other confounding factors on the fitness of the recipients (Dickinson & Hatchwell 2004).

Measuring the effects of helping behaviour

Benefits enjoyed by recipients are a fundamental assumption underpinning many of the explanations for the evolution of helping behaviour. However, the expected positive effect of helping behaviour on the fitness of recipients is extremely difficult to detect and measure (Wright & Russell 2008). For example, explanations for helping behaviour in some cooperative breeding systems that older siblings stay with their parents and provide help in the care of younger siblings, are often based on kin selection: by increasing reproductive success of parents, helpers are increasing the production of close kin (siblings) that are more likely to share the gene for helping behaviour than less related individuals (Hamilton 1964; Maynard Smith 1964). Thus, if cooperative systems are, indeed, based on the increased fitness of the recipients that are assisted, helping behaviour of the older siblings must have positive effects on the fitness of the parents. Therefore, breeders with more helpers can be expected to have higher reproductive success than breeders with fewer helpers in their group. However, a simple comparison of productivity between groups with a different number of helpers will not reveal the effects of helping behaviour. Since these helpers are the offspring of the breeder from previous breeding seasons, breeders that were more productive in previous seasons will have more helpers in subsequent seasons. The higher productivity of the breeder with more helpers might, therefore, be due to the better quality of the breeders and/or their habitats rather than the effects of helpers *per se* (Brown *et al.* 1982; Cockburn 1998; Eguchi *et al.* 2002; Dickinson & Hatchwell 2004).

To resolve this problem, experimental approaches have been employed to measure helper effects on the productivity of groups while controlling the effects of breeders and habitat. Manipulations of the number of helpers in cooperatively breeding groups have demonstrated the effect of helper presence on the reproductive success of breeders (Brown *et al.* 1982; Mumme 1992). However, this approach cannot distinguish whether the positive effects of helper presence was due to helping behaviour (e.g. provisioning of young) or the beneficial effects of larger group size (e.g. through improved predator avoidance and territory defence) (Brown *et al.* 1982). Moreover, changes in group size by removal of helpers potentially has distractive effects on the social relationship and, hence, the behaviour of the remaining group members (Cockburn 1998). Alternatively, manipulations of the number of dependent offspring in cooperatively breeding groups have demonstrated that the higher ratio of helpers in the groups result in improved weight gain of the offspring (Clutton-Brock *et al.* 2001b) or

reduced maternal investment (Russell *et al.* 2008). However, the results do not clearly demonstrate the effects of helper presence or helping behaviour on the reproductive success of breeders (Wright & Russell 2008). Sophisticated statistical approaches have also been employed to disentangle helper effects from the confounding effects of breeder and habitat qualities on the productivity of groups. The results of such analyses further demonstrate the complexities involved in measuring helper effects. For instance, the presence of helpers at the nest was found to correlate with the greater reproductive success of dominant breeding pairs in superb fairy-wrens (Cockburn *et al.* 2008). However, further analysis showed that this positive correlation between helper presence and reproductive success was due to helpers being more likely to be found at the nests of older breeding females during periods of high rainfall (Cockburn *et al.* 2008). The results indicate that heightened reproductive success was due to the higher fecundity of the breeding females and the better environmental conditions during the breeding season. Therefore, the presence of helpers at the nest was not the cause of the greater reproductive success of the breeding pairs, but, rather, the consequence of the better quality of breeding females and their habitats, both of which are more likely to increase group size (Dickinson & Hatchwell 2004).

One plausible method of quantifying the effects of helping behaviour on the reproductive success of breeders – while controlling for such confounding factors – is to examine the relationship between the reproductive success of breeders and the amount of help given under controlled environmental conditions in captivity. The captive environment provides a much more simplified setting than those seen in the wild and, although this can have limitations, captive settings also allow researchers to directly control confounding factors that are not possible to tease apart in field based studies, and therefore provide relevant information that is complementary to the type of information that can be collected in the wild (Campbell *et al.* 2009). Therefore, important insights into the understanding of helping behaviour can be obtained in a captive environment with well-designed experiments and proper regard to an organism's natural history (Tinbergen 1963; Solomon & Getz 1997; Campbell *et al.* 2009). Moreover, captive studies also allow for more accurate measurements of the actual amount of help given by helpers rather than having to rely on the presence or number of helpers in the groups as a proxy. By measuring the actual amount of help given by the helpers, confounding effects associated with group size and composition (i.e. habitat quality and group augmentation effects), and the quality of breeders can be more easily disentangled from the effects of helpers on the reproductive success of the breeders. And in this respect, one group

of cooperatively breeding animals that is especially conducive to the study of helping behaviour in controlled environments is the marmosets and tamarins (Subfamily: Callitrichinae).

Callitrichines

Marmosets and tamarins are small, arboreal and diurnal primates that live in extended family groups (Digby & Barreto 1993; Nievergelt *et al.* 2000; Rylands *et al.* 2009) typically consisting of a dominant breeding pair and their siblings and offspring as subordinate group members (Ferrari & Digby 1996; Digby *et al.* 2007). Callitrichinae consists of seven genera (*Callimico* (Goeldi's monkey), *Callithrix* (Atlantic marmosets), *Cebuella* (pygmy marmoset), *Leontopithecus* (lion tamarins), *Mico* (Amazonian marmosets), and *Saguinus* (tamarins)) with a total of 60 species and subspecies (Rylands *et al.* 2000; Schneider & Sampaio 2015), found in the Central and South America, from Costa Rica to southern Brazil (Digby *et al.* 2007; Buckner *et al.* 2015). Callitrichines possess a set of traits, which is rather unusual among the primates (Rylands 1997; Digby *et al.* 2007; Diaz-Munoz 2016). Callitrichines are primarily frugivores and insectivores (Kinzey 1997; Rylands *et al.* 2009). They also feed on plant exudates (saps, gums, resins and latexes), nectar, flowers, buds, fungi, and small invertebrates and vertebrates (e.g. scorpions, snails, spiders, frogs, lizards, bird eggs and nestlings) (Stevenson & Rylands 1988; Garber 1993; Rylands & de Faria 1993; Kinzey 1997; Porter 2001a). Callitrichines occupy a wide range of ecosystems including tropical and subtropical rainforests, seasonally inundated and riverine forests, relatively drier and semi-deciduous forests, and forest patches within drier regions (Pook & Pook 1981; Rylands 1993; Rylands & de Faria 1993; Kinzey 1997; Digby *et al.* 2007). As well as mature primary forests, secondary vegetation (with its diversity in microhabitats) is important for callitrichines, because it provides a wide range of fruits and a high abundance of insects for food, and dense vegetation for shelter and travelling (Garber 1993; Rylands & de Faria 1993; Rylands 1997). Home ranges of callitrichines vary from 0.1 (*Cebuella*) to over 300 ha (*Leontopithecus*) (reviewed in Digby *et al.* 2007). Although body size (ranges from 120 g in *Cebuella* to 600 g in *Leontopithecus*, Ford & Davis 1992) and home range size positively correlate with each other, home range sizes considerably vary among and within species, and are primarily determined by habitat quality such as seasonal change, distribution and nutritional context of food sources (Stevenson & Rylands 1988; Garber 1993; Digby *et al.* 2007; Diaz-Munoz 2016). Day ranges, in contrast, vary less with habitat quality and more consistent with body

size (Stevenson & Rylands 1988; Garber 1993; Digby *et al.* 2007; Diaz-Munoz 2016). Average day ranges of callitrichine species vary from 300 m (*Cebuella*) to over 2 km (*Leontopithecus*) (Soini 1988; Ferrari & Lopes Ferrari 1989; Rylands 1993). Callitrichines are active for about nine to 12 hours each day (Stevenson & Rylands 1988; Kinzey 1997; Kierulff *et al.* 2002). Typically, a group leave their sleeping sites at sunrise and travel to feeding sites (Soini 1988; Stevenson & Rylands 1988; Kinzey 1997; Kierulff *et al.* 2002). Members of a group travel and forage in a cohesive manner (Goldizen 1987a; Garber 1988; Snowdon & Soini 1988; Porter & Garber 2009). They eat intensively for the first few hours and spend the rest of the day alternating between travelling, eating, foraging for prey, resting and socialising (Stevenson & Rylands 1988; Kinzey 1997; Kierulff *et al.* 2002; Porter 2004). They travel to the sleeping site for the night before sunset and sleep together (Ramirez *et al.* 1977; Snowdon & Soini 1988; Soini 1988; Stevenson & Rylands 1988; Kinzey 1997; Kierulff *et al.* 2002; Porter 2004). Callitrichines often sleep in dense tangles of vines and epiphytes at five to 20 m off the ground (Snowdon & Soini 1988; Soini 1988; Stevenson & Rylands 1988).

Callitrichines are vulnerable to a range of predators, including raptors, mammalian carnivores and snakes (Pook & Pook 1981; Goldizen 1987b; Kinzey 1997; reviewed in Ferrari 2009; Ferrari & Beltrao-Mendes 2011). Due to their small body size, they suffer one of the highest predation rates among primates (Cheney & Wrangham 1987) and show a high level of vigilance behaviour (Goldizen 1987b; Ferrari & Ferrari 1990). Their cooperative antipredator behaviour includes sentinelling, alarm calling and predator mobbing although the response to predation differs across species and populations (Caine 1993; Tardif 1994; Kinzey 1997; Kirchhof & Hammerschmidt 2006). Adult group members often take turns acting as sentinels by position on an open branch and scan the surroundings while other members of the group feed (Moynihan 1970; Goldizen 1987b; Caine 1993). Callitrichines use predator-specific alarm calls (Heymann 1990; Peres 1993; Kirchhof & Hammerschmidt 2006). In response to alarm calls for aerial predators, they look upwards and quickly move downwards or run from the periphery of a tree to the tree trunk (Pook & Pook 1981; Goldizen 1987b; Buchanan - Smith 1990; Heymann 1990; Peres 1993; Kirchhof & Hammerschmidt 2006; Ferrari 2009). In response to alarm calls for terrestrial predators, they look downwards and move to a higher level in the tree (Moynihan 1970; Bartecki & Heymann 1987; Kirchhof & Hammerschmidt 2006). In the presence of a potential predator, they emit loud excitation calls and sometimes

approach and mob the predator (Moynihan 1970; Pook & Pook 1981; Bartecki & Heymann 1987; Heymann 1987; Kirchhof & Hammerschmidt 2006).

Group sizes of callitrichines vary between two to 20, which tend to be larger in *Callithrix* and *Mico* compared to *Callimico*, *Saguinus* and *Leontopithecus* (reviewed in Digby *et al.* 2007; Faulkes *et al.* 2009; Diaz-Munoz 2016). *Cebuella* has the smallest group size comprising of a single breeding pair and the young (Soini 1982, 1988). Usually, groups are stable over time with occasional migrations (Ferrari & Digby 1996; Goldizen *et al.* 1996; Lazaro-Perea *et al.* 2000; Nievergelt *et al.* 2000; Baker *et al.* 2002; Faulkes *et al.* 2009). In general, the breeding pair is socially dominant over all other members of the group, and older individuals are dominant over younger individuals among non-breeding group members (Soini 1988; Baker *et al.* 1993; Dietz & Baker 1993; Digby 1995a, b; Goldizen *et al.* 1996; Kinzey 1997). Members in a group often groom each other while resting and huddling together (Pook & Pook 1981; Kleiman *et al.* 1988; Snowdon & Soini 1988; Soini 1988; Digby 1995b; Heymann 1996). Aggressive interactions between group members rarely occur and it occurs most often in feeding contexts with relatively mild expressions (Snowdon & Soini 1988; Goldizen 1989; Baker *et al.* 1993; Digby 1995b; Heymann 1996; Garber 1997). Callitrichines react to other conspecific groups by exchanging vocalisations and, occasionally, physical aggression, such as chasing and fighting (Hubrecht 1985; Garber 1988; Snowdon & Soini 1988; Peres 1989; Garber 1993; Lazaro-Perea 2001). By contrast, intergroup interactions can be peaceful involving grooming, playing and copulation (Hubrecht 1985; Digby 1999; Lazaro-Perea 2001). Intergroup interactions also provide opportunities for non-breeding group members to assess dispersal and reproductive prospects into neighbouring groups (Hubrecht 1985; Ferrari & Diego 1992; Goldizen *et al.* 1996; Schaffner & French 1997; Lazaro-Perea 2001). In general, both males and females disperse when they mature and groups become large in size (Stevenson & Rylands 1988; Soini 1993; Baker & Dietz 1996; Ferrari & Digby 1996; Goldizen *et al.* 1996; Savage *et al.* 1996a; Porter *et al.* 2001; Baker *et al.* 2002; Faulkes *et al.* 2009). However, dispersal could potentially be constrained by high predation risk, high intergroup tension and low food availability (Caine 1993; Araújo 1996 cited in Sousa *et al.* 2009; Sousa *et al.* 2009). Dispersal by group fission can also occur mostly after major changes in group composition, such as changes in breeding positions in the groups (Stevenson & Rylands 1988; Ferrari & Lopes Ferrari 1989; Savage *et al.* 1996a; Heymann 1998; Lazaro-Perea *et al.* 2000). Alternative to dispersing, adult subordinate group members may inherit the breeding position in their natal group when there is an unrelated

mate within the group (Ferrari & Diego 1992; Baker & Dietz 1996; Goldizen *et al.* 1996; Baker *et al.* 2002; Saltzman *et al.* 2004).

In callitrichine groups, breeding is generally restricted to single male and female of the dominant breeding pair (Lazaro-Perea *et al.* 2000; Arruda *et al.* 2005; Digby *et al.* 2007; Yamamoto *et al.* 2009; Yamamoto *et al.* 2014). Usually, subordinate males and females do not engage in intersexual copulation while living with their natal families (French *et al.* 1989; Baker *et al.* 1999; Ginther *et al.* 2001). Moreover, reproduction of adult subordinate group members is often behaviourally inhibited by dominant breeders (French 1997; Chaoui & Hasler-Gallusser 1999; Baker *et al.* 2002) and ovulation of adult subordinate females is physiologically suppressed (Epple & Katz 1984; Kuederling *et al.* 1995; Saltzman *et al.* 1997; Smith *et al.* 1997; French *et al.* 2003). Nevertheless, based on behavioural observations, the mating systems of callitrichines include monogamy, polyandry, polygyny, and polygynandry, and can vary, both within and between groups and populations (Goldizen 1988; Ferrari & Digby 1996; Garber 1997; Lazaro-Perea *et al.* 2000; Baker *et al.* 2002; Goldizen 2003; Saltzman 2003; Digby *et al.* 2007; Yamamoto *et al.* 2009). Although groups of callitrichines are generally described as comprising extended families (Ferrari & Lopes Ferrari 1989; Digby & Barreto 1993; Ferrari & Digby 1996; Nievergelt *et al.* 2000; Baker *et al.* 2002; Rylands *et al.* 2009), groups also often contain unrelated animals and, sometimes, more than one breeding female and multiple breeding males (Sussman & Garber 1987; Goldizen 1988; Dietz & Baker 1993; Soini 1993; Digby & Ferrari 1994; Savage *et al.* 1996a; Savage *et al.* 1997; Dettling & Pryce 1999; Nievergelt *et al.* 2000; Arruda *et al.* 2005; Faulkes *et al.* 2009). When there are multiple breeding males in a group, most species show little or no competition among the adult males over accessing breeding females, and breeding females may mate with multiple males (Sussman & Garber 1987; Goldizen 1988; Soini 1988; Ferrari & Diego 1992; Ferrari & Digby 1996; Savage *et al.* 1996a; Nievergelt *et al.* 2000; Schaffner & French 2004). When there are two breeding females within a group, the dominant breeding female typically produces more infants and have higher infant survival rates than subordinate breeding females (Dietz & Baker 1993; Digby & Ferrari 1994; Digby 1995a; Arruda *et al.* 2005; Digby & Saltzman 2009). Abuse, enforced neglect and infanticide by the dominant breeding females have been attributed to some of the loss of infants in subordinate females (Digby & Ferrari 1994; Digby 1995a; reviewed in Digby & Saltzman 2009). Furthermore, extra-group copulations involving breeding and non-breeding

individuals have also been observed during intergroup interactions (Digby 1999; Lazaro-Perea *et al.* 2000; Arruda *et al.* 2005; Sousa *et al.* 2009; Yamamoto *et al.* 2009).

Callitrichines typically can conceive within two to four weeks after parturition, which may result in successful delivery of dizygotic twins (except *Callimico*) (McNeilly *et al.* 1981; Heistermann & Hodges 1995; French *et al.* 2002; Tardif *et al.* 2003). However, the size of a litter can vary from one to four infants (Ziegler *et al.* 1990; Baker & Woods 1992; De Vleeschouwer *et al.* 2003; Tardif *et al.* 2003; Digby *et al.* 2007). The postpartum ovulation with the short gestation period allows callitrichines to breed once in approximately five to six months (Ziegler *et al.* 1987; French *et al.* 2002; Tardif *et al.* 2003; Digby *et al.* 2007). Species in captivity often breed twice per year, and *Cebuella*, *Callithrix*, *Mico* and *Callimico* in the wild also breed biannually (Stevenson & Rylands 1988; Soini 1993; Digby & Ferrari 1994; Koenig 1995; Porter 2001b). In contrast, *Leontopithecus* and *Saguinus* in the wild typically breed once per year (Snowdon & Soini 1988; Ferrari & Lopes Ferrari 1989; Savage *et al.* 1997; Digby *et al.* 2007). Total weight of a litter of twins at birth can be as much as 15 to 25% of the adult body weight (Kleiman 1977; Harvey *et al.* 1987; Ross 1991; Hartwig 1996). Infants become able to move around by themselves between five and eight weeks of age, and weaning occurs at two to three months of age (Tardif *et al.* 1986; Harvey *et al.* 1987; Snowdon & Soini 1988; Yamamoto 1993; Kinzey 1997; Dettling 2002). The juvenile period with a fully developed ability in locomotion occur between five and 12 months of age, sub-adulthood with fully developed body size occur between ten and 18 months of age, and adulthood with sexual maturity is reached at approximately 15 to 20 months of age (Ingram 1977; Cleveland & Snowdon 1984; Tardif 1984; Harvey *et al.* 1987; Kleiman *et al.* 1988; Snowdon & Soini 1988; Soini 1988; Stevenson & Rylands 1988; Yamamoto 1993; Carlson *et al.* 1997; French 1997; Saltzman *et al.* 1997; Dettling & Pryce 1999; Abbott *et al.* 2003). However, sexual maturity is often delayed by the social suppression of reproductive function (Epple & Katz 1984; Kuederling *et al.* 1995; Saltzman *et al.* 1997; Smith *et al.* 1997; Baker *et al.* 1999; Chaoui & Hasler-Gallusser 1999; Ginther *et al.* 2001; French *et al.* 2003). It often takes two or more years for young adults to obtain a breeding position (Arruda *et al.* 2005; Sousa *et al.* 2005; Tardif *et al.* 2008) and the first breeding occurs approximately three years of age or later (Goldizen & Terborgh 1989; Bales *et al.* 2001; Tardif *et al.* 2008). Individuals stay in the breeding position for three to four years on average (Baker *et al.* 2002; Arruda *et al.* 2005; Sousa *et al.* 2005; Tardif *et al.* 2008; Saltzman *et al.* 2009; Yamamoto *et al.* 2014).

In general, females can continue to reproduce throughout their average lifespan of ten (*Cebuella*) to 14 (*Leontopithecus*) years (Harvey *et al.* 1987; Ross 1991).

Callitrichines breed cooperatively and all members of the group participate in care of infants, including carrying, sharing solid foods, comforting and play (Locke-Haydon & Chalmers 1983; Cleveland & Snowdon 1984; Kleiman *et al.* 1988; Snowdon & Soini 1988; Soini 1988; Stevenson & Rylands 1988; Porter & Garber 2009). Lone breeding pairs without other members in the group rarely succeed in raising their young in the wild (Goldizen 1988; Koenig 1995; Bales *et al.* 2000). There are differences in the patterns of infant care among species. In *Callimico* and *Leontopithecus rosalia*, mothers tend to care for the infants exclusively for the first few weeks after birth (Hoage 1978; Kleiman *et al.* 1988; Schradin & Anzenberger 2001b; Tardif *et al.* 2002; Porter & Garber 2009). In contrast, adult males and other members of the group may care and carry the infants from the first day of birth in *Callithrix*, *Cebuella*, *Mico* and *Saguinus* (Stevenson 1976; Savage *et al.* 1996b; Snowdon 1996; reviewed in Tardif *et al.* 2002; Zahed *et al.* 2010). Mothers may care for infants as much as, or more than, the males in the group in *Callimico*, *Callithrix* and *Mico* (Rylands 1986; Digby 1995b; Yamamoto & Box 1997; Schradin & Anzenberger 2001b), whereas males may care for infants more than the mother in some tamarins (Moynihan 1970; Cleveland & Snowdon 1984; Goldizen 1987a; Tardif 1994; Savage *et al.* 1996b; Snowdon 1996; Zahed *et al.* 2010). The amount of infant care given by the mothers may also vary with the size and composition of the group, litter size and the body weights of the mothers (reviewed in Tardif *et al.* 1993; Yamamoto & Box 1997; Bales *et al.* 2002; Tardif *et al.* 2002; Zahed *et al.* 2010). Individuals that grew up in a group with an infant have higher success at their first breeding compared to individuals that did not, suggesting that experience with infant care can benefit the future reproductive success of alloparents (although the causal relationship has not been demonstrated) (Epple 1975; Ingram 1978; Sussman & Garber 1987; Goldizen & Terborgh 1989; Johnson *et al.* 1991; reviewed in Tardif 1997; Zahed *et al.* 2010). Older members in the groups carry infants more than younger members (Box 1977; Terborgh & Goldizen 1985; Tardif *et al.* 1986; Goldizen 1987a; Stevenson & Rylands 1988; Yamamoto & Box 1997; Fite *et al.* 2005; Zahed *et al.* 2010). There may be competition over infant-carrying among subordinate group members (Pryce 1988; Price 1991; Yamamoto & Box 1997), and older individuals may chastise younger individuals when they attempt to take infants from others (Stevenson & Rylands 1988). Breeding females may also chase adult

subordinate females away when the adult females approach other group members with the infants (Koenig & Rothe 1991; Albuquerque 1999 cited in Yamamoto *et al.* 2009).

Effects of helpers in callitrichines

Helpers have been suggested to play important roles in reducing the energetic cost of infant care and, in so doing, increase the reproductive success of breeding pairs in callitrichines (Goldizen 1987b; Price 1992a; Rothe & Darms 1993; Ximenes & Sousa 1996). For instance, an increase in the number of helpers in the group is associated with reduced parental infant-carrying loads in captive common marmosets (*Callithrix jacchus*) (Rothe *et al.* 1993a; Rothe *et al.* 1993b; Ximenes & Sousa 1996; Yamamoto & Box 1997). Also, the longer reproductive tenure of breeding males has been shown to correlate with an increased number of helpers in free-ranging groups of golden lion tamarins (*Leontopithecus rosalia*) (Bales *et al.* 2000). Moreover, in captive cotton-top tamarins (*Saguinus oedipus*), the contributions of helpers, as well as fathers, to infant-carrying have been suggested to improve weight gain of breeding females by reducing the energetic costs of maternal infant-carrying during the postpartum period (Sanchez *et al.* 1999; Achenbach & Snowdon 2002). This improved weight gain of breeding females is likely to result in greater reproductive success during subsequent breeding attempts since the number of ova produced per cycle and litter size correlate with maternal body weights (Tardif & Jaquish 1997; Sanchez *et al.* 1999; Bales *et al.* 2001; Tardif *et al.* 2004). However, further investigation is required to elucidate the beneficial effects of alloparental infant-carrying on the parental infant-carrying loads and reproductive success of the breeding pairs. This is because the apparent beneficial effects of helper presence on the reproductive success of breeding pairs could be due to the better quality of breeders or the advantages of larger group size in territory defence, foraging efficiency or predator avoidance rather than alloparental infant-carrying *per se*. In fact, examination of the effects of alloparental infant-carrying on the parental infant-carrying loads in captive groups of cotton-top tamarins showed that the load lightening effect of alloparental infant-carrying on the paternal but not on the maternal infant-carrying loads (Tardif *et al.* 1990).

Breeding females are under high energetic demand for lactation, which is equivalent to the energetic cost of somatic maintenance (Kirkwood & Underwood 1984). Also, since breeding females can conceive at their postpartum oestrus after two to four weeks of parturition, they are often pregnant while nursing two heavy infants (Ingram 1977; McNeilly *et al.* 1981;

Heistermann & Hodges 1995; French *et al.* 2002; Tardif *et al.* 2003). Combined with the high energetic demand for the breeding females, heavy demand for carrying infants is suggested to be the main factor underpinning the existence of cooperative breeding in callitrichines (Kleiman 1977; Goldizen 1987b). Rarity of successful breeding in lone breeding pairs without helpers in free-ranging callitrichines (Goldizen 1988; Koenig 1995; Bales *et al.* 2000) suggests that the contribution of helpers in infant-carrying may play an important role in reducing the energetic cost of infant-carrying and increasing the reproductive success of the breeding pairs (Goldizen 1987b; Price 1992a; Rothe & Darms 1993; Ximenes & Sousa 1996).

Infant-carrying has been known to be costly for the carriers. Carrying infants is energetically costly to the carrier (Tardif 1997; Sanchez *et al.* 1999), impedes mobility (Schradin & Anzenberger 2001a), decreases foraging (Tardif 1994; Caine 1996) and vigilance behaviour (Price 1992b; Caine 1993) and, therefore, it is likely to increase predation risk (Caine 1993). When carrying infants, adult group members have been shown to rest more, and feed and forage less in free-ranging groups of common marmosets (Digby & Barreto 1996). Similar effects of infant-carrying on the activities of carriers were also observed in saddle-back tamarins (*Saguinus fuscicollis*) (Goldizen 1987a) and captive cotton-top tamarins (Price 1992b). Specifically, Geoffroy's marmosets (*Callithrix geoffroyi*) in large outdoor cages never shown to forage for prey while carrying an infant (Caine 1996). Energetic costs of infant-carrying have been shown in the association of infant-carrying and weight loss of the carriers in captive cotton-top tamarins (Sanchez *et al.* 1999; Sanchez *et al.* 2005). Also, energetic costs of travelling have been estimated to increase minimum 10% when carrying an infant compared to without carrying an infant (Tardif 1997). Moreover, carrying infant has been shown to decrease the leaping ability of the carrier by 17%, which would impose substantial costs on the survival of small primates under high predation pressure (Schradin & Anzenberger 2001a). This potentially high costs of infant-carrying must be compensated by the direct and/or indirect benefits for the carriers. This, in turn, provides us with an excellent opportunity for using callitrichines as a study animal to investigate the mechanisms that potentially could be important in maintaining helping behaviour.

One species, the common marmoset, is an especially promising study subject for captive studies of helping behaviour for a number of reasons. First, common marmosets adapt well to captive environments, and self-sustaining breeding colonies have been established for

biomedical research. Second, due to their small size, they can be maintained in family groups, and their short reproductive interval facilitates the examination of their cooperative breeding behaviour (Hearn 1983; Mansfield 2003). Third, by using a captive population with a controlled, standardised environment across groups, effects of helping behaviour on the fitness of the breeding pairs can be measured independent of environmental confounds, such as variation in habitat quality. In addition, in captive colonies where the group size and composition are determined by various extrinsic reasons, such as the limitation in the size of housing cages or to maximise the reproductive output of a breeding colony, effects of variation in individual quality of the breeders can also be minimised.

Aims

My thesis investigates the behavioural ecology of alloparental infant-carrying behaviour in a captive population of common marmosets by exploring the potential fitness effects of alloparental infant-carrying and the mechanisms that underpin this behaviour. First, I investigated the effect of alloparental infant-carrying behaviour on the reproductive success of breeding pairs. Specifically, I examined the contribution of helpers to infant-carrying and its effect on parental infant-carrying loads and the success of parturition by the breeding females in their subsequent breeding attempt (Chapter 2). Next, I investigated the factors that may underpin alloparental infant-carrying behaviour. Specifically, I examined the effects of three factors on the helpers' contribution to infant-carrying: the sex of the helpers (Chapter 3), the presence of a social observer (i.e. a dominant female from the helper's social group) (Chapter 4), and perceived predation risk (Chapter 5). Combined with published information from field observations, information on potential factors that affect alloparental infant-carrying can imply possible benefits of this behaviour, since behaviour should vary with the net benefit (Tinbergen 1963; Campbell *et al.* 2009).

In this study, I used captive common marmosets in the national marmoset colony located at the Gippsland Field Station, Monash University, Australia. The focal animals used in this study were from family groups that consist of two to 12 individuals. Each family group was comprised of a dominant breeding pair and their offspring as subordinate group members. Details of the housing of the animals are described in the Methods section of Chapter 2. The primary function of the marmoset colony was to breed common marmosets for medical research. In general, medical experiments on the animals were not performed at the colony

per se, but were, instead, sent out to other research institutes. However, some animals within the colony underwent surgery for (unrelated) medical experiments, and were temporally kept in the colony during my study. Marmoset families with operated animals were not involved in the observational study (Chapter 2). Some families with operated animals, however, were involved in the manipulative experiments (Chapters 3, 4, 5). In those instances, operated animals were not used in experiments. As described in the Methods sections of the relevant chapters, the subordinate members (helpers) of groups with operated infants were separated from the operated infant, other infants from the same litter and the parents for two weeks after surgery. The experiments on these groups were performed after the group members were reunited for at least one week. Possible effects of the separation on the results of experiments in each relevant chapter were statistically controlled for, and the results did not vary with separation (see results).

By using captive common marmosets in a controlled environment as an experimental model, my thesis aimed to contribute to an understanding of how helping behaviour may have evolved and maintained within populations.

References

- Abbott, D. H., Barnett, D. K., Colman, R. J., Yamamoto, M. E. & Schultz-Darken, N. J. (2003) Aspects of common marmoset basic biology and life history important for biomedical research. *Comparative Medicine*, 53, 339-350.
- Achenbach, G. G. & Snowdon, C. T. (2002) Costs of caregiving: Weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *International Journal of Primatology*, 23, 179-189.
- Albuquerque, F. S. (1999) Cuidado cooperativo à prole em *Callithrix jacchus*: Dinâmica em ambiente natural. the Universidade de São Paulo. São Paulo, Brazil. PhD thesis.
- Araújo, A. (1996) Influence des facteurs écologiques, comportementaux et démographiques sur la dispersion de *Callithrix jacchus*. Université Paris-Nord (Paris XIII). Paris. PhD thesis.
- Arruda, M. F., Araújo, A., Sousa, M. B. C., Albuquerque, F. S., Albuquerque, A. & Yamamoto, M. E. (2005) Two breeding females within free-living groups may not always indicate polygyny: Alternative subordinate female strategies in common marmosets (*Callithrix jacchus*). *Folia Primatologica*, 76, 10-20.
- Baker, A. J., Bales, K. & Dietz, J. M. (2002) Mating system and group dynamics in lion tamarins. IN Kleiman, D. G. & Rylands, A. B. (Eds.) *Lion tamarins: Biology and conservation*. Washington DC., Smithsonian Institution Press.
- Baker, A. J. & Dietz, J. M. (1996) Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, 38, 47-56.
- Baker, A. J., Dietz, J. M. & Kleiman, D. G. (1993) Behavioral evidence for monopolization of paternity in multimale groups of golden lion tamarins. *Animal Behaviour*, 46, 1091-1103.
- Baker, A. J. & Woods, F. (1992) Reproduction of the emperor tamarin (*Saguinus imperator*) in captivity, with comparisons to cotton-top and golden lion tamarins. *American Journal of Primatology*, 26, 1-10.
- Baker, J. V., Abbott, D. H. & Saltzman, W. (1999) Social determinants of reproductive failure in male common marmosets housed with their natal family. *Animal Behaviour*, 58, 501-513.
- Bales, K., Dietz, J., Baker, A., Miller, K. & Tardif, S. D. (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica*, 71, 27-38.
- Bales, K., French, J. A. & Dietz, J. M. (2002) Explaining variation in maternal care in a cooperatively breeding mammal. *Animal Behaviour*, 63, 453-461.
- Bales, K., O'Herron, M., Baker, A. J. & Dietz, J. M. (2001) Sources of variability in numbers of live births in wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, 54, 211-221.
- Balshine-Earn, S., Neat, F. C., Reid, H. & Taborsky, M. (1998) Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology*, 9, 432-438.
- Bartecki, U. & Heymann, E. W. (1987) Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons*. *Folia Primatologica*, 48, 199-202.
- Bergmuller, R. & Taborsky, M. (2005) Experimental manipulation of helping in a cooperative breeder: Helpers 'pay to stay' by pre-emptive appeasement. *Animal Behaviour*, 69, 19-28.
- Bourke, A. F. G. (2011) The validity and value of inclusive fitness theory. *Proceedings of the Royal Society B-Biological Sciences*, 278, 3313-3320.

- Bourke, A. F. G. (2014) Hamilton's rule and the causes of social evolution. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 369.
- Box, H. O. (1977) Quantitative data on the carrying of young captive monkeys (*Callithrix jacchus*) by other members of their family groups. *Primates*, 18, 475-484.
- Brosnan, S. F. & Bshary, R. (2010) Cooperation and deception: From evolution to mechanisms. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2593-2598.
- Brown, J. L. (1987) *Helping and communal breeding in birds: Ecology and evolution*, Princeton, Princeton University Press.
- Brown, J. L., Brown, E. R., Brown, S. D. & Dow, D. D. (1982) Helpers: Effects of experimental removal on reproductive success. *Science*, 215, 421-422.
- Browning, L. E., Patrick, S. C., Rollins, L. A., Griffith, S. C. & Russell, A. F. (2012) Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proceedings of the Royal Society B-Biological Sciences*, 279, 3861-3869.
- Buchanan - Smith, H. (1990) Polyspecific association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis*, in Bolivia. *American Journal of Primatology*, 22, 205-214.
- Buckner, J. C., Alfaro, J. W. L., Rylands, A. B. & Alfaro, M. E. (2015) Biogeography of the marmosets and tamarins (Callitrichidae). *Molecular Phylogenetics and Evolution*, 82, 413-425.
- Burke, T., Davies, N. B., Bruford, M. W. & Hatchwell, B. J. (1989) Parental care and mating behavior of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature*, 338, 249-251.
- Caine, N. G. (1993) Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Caine, N. G. (1996) Foraging for animal prey by outdoor groups of Geoffroy's marmosets (*Callithrix geoffroyi*). *International Journal of Primatology*, 17, 933-945.
- Campbell, D. L. M., Weiner, S. A., Starks, P. T. & Hauber, M. E. (2009) Context and control: Behavioural ecology experiments in the laboratory. *Annales Zoologici Fennici*, 46, 112-123.
- Cant, M. A. (2011) The role of threats in animal cooperation. *Proceedings of the Royal Society B-Biological Sciences*, 278, 170-178.
- Carlson, A. A., Ziegler, T. E. & Snowdon, C. T. (1997) Ovarian function of pygmy marmoset daughters (*Cebuella pygmaea*) in intact and motherless families. *American Journal of Primatology*, 43, 347-355.
- Carter, G. G. & Wilkinson, G. S. (2013) Food sharing in vampire bats: Reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society B-Biological Sciences*, 280.
- Chaoui, N. J. & Hasler-Gallusser, S. (1999) Incomplete sexual suppression in *Leontopithecus chrysomelas*: A behavioural and hormonal study in a semi-natural environment. *Folia Primatologica*, 70, 47-54.
- Cheney, D. L. & Wrangham, R. W. (1987) Predation. IN Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds.) *Primates*. Chicago, IL, Chicago University Press.
- Cleveland, J. & Snowdon, C. T. (1984) Social development during the 1st 20 weeks in the cotton-top tamarin (*Saguinus o. oedipus*). *Animal Behaviour*, 32, 432-444.

- Clutton-Brock, T. H., Brotherton, P. N. M., O'Riain, M. J., Griffin, A. S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G. M. (2001a) Contributions to cooperative rearing in meerkats. *Animal Behaviour*, 61, 705-710.
- Clutton-Brock, T. H., Brotherton, P. N. M., O'Riain, M. J., Griffin, A. S., Gaynor, D., Sharpe, L., Kansky, R., Manser, M. B. & McIlrath, G. M. (2000) Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proceedings of the Royal Society B-Biological Sciences*, 267, 301-305.
- Clutton-Brock, T. H. & Parker, G. A. (1995) Punishment in animal societies. *Nature*, 373, 209-216.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S. & Cameron, E. Z. (2001b) Effects of helpers on juvenile development and survival in meerkats. *Science*, 293, 2446-2449.
- Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, 29, 141-177.
- Cockburn, A., Sims, R. A., Osmond, H. L., Green, D. J., Double, M. C. & Mulder, R. A. (2008) Can we measure the benefits of help in cooperatively breeding birds: The case of superb fairy-wrens *Malurus cyaneus*? *Journal of Animal Ecology*, 77, 430-438.
- Connor, R. C. (2010) Cooperation beyond the dyad: On simple models and a complex society. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2687-2697.
- Creel, S. R. & Waser, P. M. (1994) Inclusive fitness and reproductive strategies in dwarf mongooses. *Behavioral Ecology*, 5, 339-348.
- Curio, E. (1983) Why do young birds reproduce less well. *Ibis*, 125, 400-404.
- Curry, R. L. (1988) Influence of kinship on helping behavior in galápagos mockingbirds. *Behavioral Ecology and Sociobiology*, 22, 141-152.
- Darwin, C. (1859) *On the origin of species*, London, Murray.
- Dawkins, R. (1976) *The selfish gene*, New York, Oxford University Press.
- De Vleeschouwer, K., Leus, K. & Van Elsacker, L. (2003) Characteristics of reproductive biology and proximate factors regulating seasonal breeding in captive golden-headed lion tamarins (*Leontopithecus chrysomelas*). *American Journal of Primatology*, 60, 123-137.
- Desrochers, A. (1992a) Age-related differences in reproduction by european blackbirds - restraint or constraint. *Ecology*, 73, 1128-1131.
- Desrochers, A. (1992b) Age and foraging success in european blackbirds - variation between and within individuals. *Animal Behaviour*, 43, 885-894.
- Dettling, A. & Pryce, C. R. (1999) Hormonal monitoring of age at sexual maturation in female Goeldi's monkeys (*Callimico goeldii*) in their family groups. *American Journal of Primatology*, 48, 77-83.
- Dettling, A. C. (2002) Reproduction and development in Goeldi's monkey (*Callimico goeldii*). *Evolutionary Anthropology*, 11, 207-210.
- Diaz-Munoz, S. L. (2016) Complex cooperative breeders: Using infant care costs to explain variability in callitrichine social and reproductive behavior. *American Journal of Primatology*, 78, 372-387.
- Dickinson, J. L. & Hatchwell, B. J. (2004) Fitness consequences of helping. IN Koenig, W. D. & Dickinson, J. L. (Eds.) *Ecology and evolution of cooperative breeding in birds*. Cambridge, Cambridge University Press.
- Dietz, J. M. & Baker, A. J. (1993) Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Animal Behaviour*, 46, 1067-1078.
- Digby, L. & Saltzman, W. (2009) Balancing cooperation and competition in callitrichid primates: Examining the relative risk of infanticide across species. IN Davis, L. C.,

- Ford, S. M. & Porter, L. M. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Digby, L. J. (1995a) Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). *Behavioral Ecology and Sociobiology*, 37, 51-61.
- Digby, L. J. (1995b) Social organization in a wild population of *Callithrix jacchus*. II. Intragroup social behavior. *Primates*, 36, 361-375.
- Digby, L. J. (1999) Sexual behavior and extragroup copulations in a wild population of common marmosets (*Callithrix jacchus*). *Folia Primatologica*, 70, 136-145.
- Digby, L. J. & Barreto, C. E. (1993) Social organization in a wild population of *Callithrix jacchus*. I. Group composition and dynamics. *Folia Primatologica*, 61, 123-134.
- Digby, L. J. & Barreto, C. E. (1996) Activity and ranging patterns in common marmosets (*Callithrix jacchus*): Implications for reproductive strategies. IN Norconk, M., Rosenberger, A. & Garber, P. (Eds.) *Adaptive radiations of neotropical primates*. New York, Plenum Press.
- Digby, L. J. & Ferrari, S. F. (1994) Multiple breeding females in free-ranging groups of *Callithrix jacchus*. *International Journal of Primatology*, 15, 389-397.
- Digby, L. J., Ferrari, S. F. & Saltzman, W. (2007) Callitrichines: The role of competition in cooperatively breeding species. IN Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M. & Bearder, S. K. (Eds.) *Primates in perspective*. New York, Oxford University Press.
- Duffy, J. E. & Thiel, M. (Eds.) (2007) *Evolutionary ecology of social and sexual systems: Crustaceans as model organisms*. Oxford University Press.
- Dugatkin, L. A. (1997) *Cooperation among animals: An evolutionary perspective*, New York, Oxford University Press.
- Dunn, P. O., Cockburn, A. & Mulder, R. A. (1995) Fairy-wren helpers often care for young to which they are unrelated. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 259, 339-343.
- Eguchi, K., Yamagishi, S., Asai, S., Nagata, H. & Hino, T. (2002) Helping does not enhance reproductive success of cooperatively breeding *Rufous vanga* in Madagascar. *Journal of Animal Ecology*, 71, 123-130.
- Elgar, M. A. (1989) Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society*, 64, 13-33.
- Emlen, S. T. & Wrege, P. H. (1989) A test of alternate hypotheses for helping behavior in white-fronted bee-eaters of Kenya. *Behavioral Ecology and Sociobiology*, 25, 303-319.
- Epplé, G. (1975) Parental behavior in *Saguinus fuscicollis* ssp. (Callithricidae). *Folia Primatologica*, 24, 221-38.
- Epplé, G. & Katz, Y. (1984) Social influences on estrogen excretion and ovarian cyclicity in saddle back tamarins (*Saguinus-fuscicollis*). *American Journal of Primatology*, 6, 215-227.
- Faulkes, C. G., Arruda, M. F. & Monteiro da Cruz, M. A. O. (2009) Genetic structure within and among populations of the common marmoset, *Callithrix jacchus*: Implications for cooperative breeding. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Ferrari, S. F. (2009) Predation risk and antipredator strategies. IN Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. K. & Strier, K. B. (Eds.) *South American*

- primates: Comparative perspectives in the study of behavior, ecology, and conservation*. New York, Springer.
- Ferrari, S. F. & Beltrao-Mendes, R. (2011) Do snakes represent the principal predatory threat to callitrichids? Fatal attack of a viper (*Bothrops leucurus*) on a common marmoset (*Callithrix jacchus*) in the Atlantic Forest of the Brazilian Northeast. *Primates*, 52, 207-209.
- Ferrari, S. F. & Diego, V. H. (1992) Long-term changes in a wild marmoset group. *Folia Primatologica*, 58, 215-218.
- Ferrari, S. F. & Digby, L. J. (1996) Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, 38, 19-27.
- Ferrari, S. F. & Ferrari, M. A. L. (1990) Predator avoidance behavior in the buffy-headed marmoset, *Callithrix flaviceps*. *Primates*, 31, 323-338.
- Ferrari, S. F. & Lopes Ferrari, M. A. (1989) A re-evaluation of the social organization of the callitrichidae, with reference to the ecological differences between genera. *Folia Primatologica*, 52, 132-147.
- Fite, J. E., Patera, K. J., French, J. A., Rukstalis, M., Hopkins, E. C. & Ross, C. N. (2005) Opportunistic mothers: Female marmosets (*Callithrix kuhlii*) reduce their investment in offspring when they have to, and when they can. *Journal of Human Evolution*, 49, 122-142.
- Ford, S. M. & Davis, L. C. (1992) Systematics and body size - implications for feeding adaptations in New World monkeys. *American Journal of Physical Anthropology*, 88, 415-468.
- Foster, W. A. & Treherne, J. E. (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293, 466-467.
- French, J. A. (1997) Proximate regulation of singular breeding in callitrichid primates. IN Solomon, N. G. & French, J. A. (Eds.) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- French, J. A., Bales, K. L., Baker, A. J. & Dietz, J. M. (2003) Endocrine monitoring of wild dominant and subordinate female *Leontopithecus rosalia*. *International Journal of Primatology*, 24, 1281-1300.
- French, J. A., De Vleeschouwer, K., Bales, K. & Heistermann, M. (2002) Lion tamarin reproductive biology. IN Kleiman, D. G. & Rylands, A. B. (Eds.) *Lion tamarins: Biology and conservation*. Washington DC, Smithsonian Institution Press.
- French, J. A., Inglett, B. J. & Dethlefs, T. M. (1989) The reproductive status of nonbreeding group members in captive golden lion tamarin social groups. *American Journal of Primatology*, 18, 73-86.
- Garay, J. (2009) Cooperation in defence against a predator. *Journal of Theoretical Biology*, 257, 45-51.
- Garay, J. & Varga, Z. (2011) Survivor's dilemma: Defend the group or flee? *Theoretical Population Biology*, 80, 217-225.
- Garber, P. A. (1988) Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. *Behaviour*, 105, 18-34.
- Garber, P. A. (1993) Feeding ecology and behaviour of the genus *Saguinus*. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour, and ecology*. Oxford, Oxford University Press.
- Garber, P. A. (1997) One for all and breeding for one: Cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology*, 5, 187-199.
- Gardner, A., West, S. A. & Wild, G. (2011) The genetical theory of kin selection. *Journal of Evolutionary Biology*, 24, 1020-1043.

- Gaston, A. J. (1978) Evolution of group territorial behavior and cooperative breeding. *American Naturalist*, 112, 1091-1100.
- Gilby, I. C. (2006) Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, 71, 953-963.
- Ginther, A. J., Ziegler, T. E. & Snowdon, C. T. (2001) Reproductive biology of captive male cottontop tamarin monkeys as a function of social environment. *Animal Behaviour*, 61, 65-78.
- Godin, J. (1986) Antipredator function of shoaling in teleost fishes: A selective review. *Le Naturaliste Canadien*, 113, 241-250.
- Goldizen, A. W. (1987a) Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 20, 99-109.
- Goldizen, A. W. (1987b) Tamarins and marmosets: Communal care of offspring. IN Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds.) *Primates societies*. Chicago, The University of Chicago Press.
- Goldizen, A. W. (1988) Tamarin and marmoset mating systems - unusual flexibility. *Trends in Ecology & Evolution*, 3, 36-40.
- Goldizen, A. W. (1989) Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus-fuscicollis*). *Behavioral Ecology and Sociobiology*, 24, 79-89.
- Goldizen, A. W. (2003) Social monogamy and its variations in callitrichids: Do these relate to the costs of infant care? IN Reichard, U. H. & Boesch, C. (Eds.) *Monogamy: Mating strategies and partnerships in birds, humans and other mammals*. Cambridge, Cambridge University Press.
- Goldizen, A. W., Mendelson, J., van Vlaardingen, M. & Terborgh, J. (1996) Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: Evidence from a thirteen-year study of a marked population. *American Journal of Primatology*, 38, 57-83.
- Goldizen, A. W. & Terborgh, J. (1989) Demography and dispersal patterns of a tamarin population - possible causes of delayed breeding. *American Naturalist*, 134, 208-224.
- Griffin, A. S. & West, S. A. (2002) Kin selection: Fact and fiction. *Trends in Ecology & Evolution*, 17, 15-21.
- Hamilton, W. D. (1964) The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, 7, 1-52.
- Hamilton, W. D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.
- Hammerstein, P. (Ed.) (2003) *Genetic and cultural evolution of cooperation*. Cambridge, MIT Press.
- Hartwig, W. C. (1996) Perinatal life history traits in New World monkeys. *American Journal of Primatology*, 40, 99-130.
- Harvey, P. H., Martin, R. D. & Clutton-Brock, T. H. (1987) Life histories in comparative perspective. IN Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds.) *Primate societies*. Chicago and London, University of Chicago Press.
- Hearn, J. P. (1983) The common marmoset (*Callithrix jacchus*). IN Hearn, J. P. (Ed.) *Reproduction in New World primates: New models in medical science*. Dordrecht, Springer Netherlands.
- Heg, D., Brouwer, L., Bachar, Z. & Taborsky, M. (2005) Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, 142, 1615-1641.

- Heinsohn, R., Dunn, P., Legge, S. & Double, M. (2000) Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 267, 243-249.
- Heinsohn, R. & Legge, S. (1999) The cost of helping. *Trends in Ecology & Evolution*, 14, 53-57.
- Heistermann, M. & Hodges, J. K. (1995) Endocrine monitoring of the ovarian cycle and pregnancy in the saddle-back tamarin (*Saguinus fuscicollis*) by measurement of steroid conjugates in urine. *American Journal of Primatology*, 35, 117-127.
- Heymann, E. W. (1987) A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. *International Journal of Primatology*, 8, 193-195.
- Heymann, E. W. (1990) Reactions of wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology*, 11, 327-337.
- Heymann, E. W. (1996) Social behavior of wild moustached tamarins, *Saguinus mystax*, at the Estacion Biologica Quebrada Blanco, Peruvian Amazonia. *American Journal of Primatology*, 38, 101-113.
- Heymann, E. W. (1998) Sex differences in olfactory communication in a primate, the moustached tamarin, *Saguinus mystax* (Callitrichinae). *Behavioral Ecology and Sociobiology*, 43, 37-45.
- Hoage, R. J. (1978) Parental care in *Leontopithecus rosalia rosalia*: Sex and age differences in carrying behavior and the role of prior experience. IN Kleiman, D. G. (Ed.) *The biology and conservation of the callitrichidae: A symposium held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, August 18-20, 1975*. Smithsonian Institution Press.
- Hubrecht, R. C. (1985) Home-range size and use and territorial behavior in the common marmoset, *Callithrix jacchus-jacchus*, at the Tapacura Field Station, Recife, Brazil. *International Journal of Primatology*, 6, 533-550.
- Ingram, J. C. (1977) Interactions between parents and infants, and development of independence in common marmoset (*Callithrix jacchus*). *Animal Behaviour*, 25, 811-827.
- Ingram, J. C. (1978) Preliminary comparisons of parental care of wild-caught and captive-born common marmosets. IN Rothe, H., Wolters, H. J. & Hearn, J. P. (Eds.) *Biology and behaviour of marmosets*. Göttingen, West Germany, Eigenverlag.
- Jamieson, I. G. (1989) Behavioral heterochrony and the evolution of birds' helping at the nest: An unselected consequence of communal breeding. *American Naturalist*, 133, 394-406.
- Jennions, M. D. & Macdonald, D. W. (1994) Cooperative breeding in mammals. *Trends in Ecology & Evolution*, 9, 89-93.
- Johnson, L. D., Petto, A. J. & Sehgal, P. K. (1991) Factors in the rejection and survival of captive cotton top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 25, 91-102.
- Khan, M. Z. & Walters, J. R. (1997) Is helping a beneficial learning experience for red-cockaded woodpecker (*Picoides borealis*) helpers? *Behavioral Ecology and Sociobiology*, 41, 69-73.
- Kierulff, M. C. M., Raboy, B. E., de Oliveira, P. P., Miller, K., Passos, F. C. & Prado, F. (2002) Behavioral ecology of lion tamarins. IN Kleiman, D. G. & Rylands, A. B. (Eds.) *Lion tamarins: Biology and conservation*. Washington DC, Smithsonian Institution Press.
- Kingma, S. A., Santema, P., Taborsky, M. & Komdeur, J. (2014) Group augmentation and the evolution of cooperation. *Trends in Ecology & Evolution*, 29, 476-484.

- Kinzey, W. G. (1997) Synopsis of New World primates (16 genera). IN Kinzey, W. G. (Ed.) *New World primates: Ecology, evolution, and behavior*. New York, Aldine de Gruyter.
- Kirchhof, J. & Hammerschmidt, K. (2006) Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) - evidence from playback experiments. *Ethology*, 112, 346-354.
- Kirkwood, J. K. & Underwood, S. J. (1984) Energy requirements of captive cotton-top tamarins (*Saguinus oedipus oedipus*). *Folia Primatologica*, 42, 180-187.
- Kleiber, D., Kyle, K., Rockwell, S. M. & Dickinson, J. L. (2007) Sexual competition explains patterns of individual investment in territorial aggression in western bluebird winter groups. *Animal Behaviour*, 73, 763-770.
- Kleiman, D. G. (1977) Monogamy in mammals. *The Quarterly Review of Biology*, 52, 39-69.
- Kleiman, D. G., Hoage, R. J. & Green, K. M. (1988) The lion tamarins, genus *Leontopithecus*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Koenig, A. (1995) Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 35, 311-317.
- Koenig, A. & Rothe, H. (1991) Social relationships and individual contribution to cooperative behavior in captive common marmosets (*Callithrix jacchus*). *Primates*, 32, 183-195.
- Koenig, W. D. & Dickinson, J. L. (Eds.) (2004) *Ecology and evolution of cooperative breeding in birds*. Cambridge, Cambridge University Press.
- Kokko, H. & Johnstone, R. A. (1999) Social queuing in animal societies: A dynamic model of reproductive skew. *Proceedings of the Royal Society B-Biological Sciences*, 266, 571-578.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 187-196.
- Kokko, H., Johnstone, R. A. & Wright, J. (2002) The evolution of parental and alloparental effort in cooperatively breeding groups: When should helpers pay to stay? *Behavioral Ecology*, 13, 291-300.
- Komdeur, J. (1994) The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). *Proceedings of the Royal Society B-Biological Sciences*, 256, 47-52.
- Komdeur, J. (1996) Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: A translocation experiment. *Behavioral Ecology*, 7, 326-333.
- Kuederling, I., Evans, C. S., Abbott, D. H., Pryce, C. R. & Eppler, G. (1995) Differential excretion of urinary estrogen by breeding females and daughters in the red-bellied tamarin (*Saguinus labiatus*). *Folia Primatologica*, 64, 140-145.
- Lancaster, J. B. (1971) Play-mothering: The relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica*, 15, 163-182.
- Landeau, L. & Terborgh, J. (1986) Oddity and the confusion effect in predation. *Animal Behaviour*, 34, 1372-1380.
- Lawson Handley, L. J. & Perrin, N. (2007) Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, 16, 1559-1578.

- Lazaro-Perea, C. (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. *Animal Behaviour*, 62, 11-21.
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araújo, A., Arruda, M. F. & Snowdon, C. T. (2000) Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology*, 48, 137-146.
- Leimar, O. & Hammerstein, P. (2010) Cooperation for direct fitness benefits. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2619-2626.
- Locke-Haydon, J. & Chalmers, N. R. (1983) The development of infant-caregiver relationships in captive common marmosets (*Callithrix-jacchus*). *International Journal of Primatology*, 4, 63-81.
- Magrath, R. D. & Whittingham, L. A. (1997) Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. *Behavioral Ecology and Sociobiology*, 41, 185-192.
- Mansfield, K. (2003) Marmoset models commonly used in biomedical research. *Comparative Medicine*, 53, 383-392.
- Maynard Smith, J. (1964) Group selection and kin selection. *Nature*, 201, 1145-1147.
- McNeilly, A. S., Abbott, D. H., Lunn, S. F., Chambers, P. C. & Hearn, J. P. (1981) Plasma prolactin concentrations during the ovarian cycle and lactation and their relationship to return of fertility postpartum in the common marmoset (*Callithrix-jacchus*). *Journal of Reproduction and Fertility*, 62, 353-360.
- Melis, A. P. & Semmann, D. (2010) How is human cooperation different? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2663-2674.
- Moynihan, M. (1970) Some behavior patterns of platyrrhine monkeys II. *Saguinus geoffroyi* and some other tamarins. *Smithsonian Contributions to Zoology*. Washington.
- Mulder, R. A. & Langmore, N. E. (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, 45, 830-833.
- Mumme, R. L. (1992) Delayed dispersal and cooperative breeding in the Seychelles warbler. *Trends in Ecology & Evolution*, 7, 330-331.
- Nam, K. B., Simeoni, M., Sharp, S. P. & Hatchwell, B. J. (2010) Kinship affects investment by helpers in a cooperatively breeding bird. *Proceedings of the Royal Society B-Biological Sciences*, 277, 3299-3306.
- Nelson-Flower, M. J. (2010) Kinship and its consequences in the cooperatively breeding southern pied babbler (*Turdoides bicolor*). Department of Zoology. University of Cape Town. PhD thesis.
- Nelson, J. B. (1988) Age and breeding in seabirds. IN Ouellet, H. (Ed.) *Proceedings of the XIXth Ornithological Congress*. Ottawa, Canada, Ottawa University Press.
- Newton, I., Marquiss, M. & Moss, D. (1981) Age and breeding in sparrowhawks. *Journal of Animal Ecology*, 50, 839-853.
- Nievergelt, C. M., Digby, L. J., Ramakrishnan, U. & Woodruff, D. S. (2000) Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *International Journal of Primatology*, 21, 1-20.
- Nol, E. & Smith, J. N. M. (1987) Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology*, 56, 301-313.
- Nomano, F. Y., Browning, L. E., Savage, J. L., Rollins, L. A., Griffith, S. C. & Russell, A. F. (2015) Unrelated helpers neither signal contributions nor suffer retribution in chestnut-crowed babblers. *Behavioral Ecology*, 26, 986-995.
- Nur, N. (1984) Increased reproductive success with age in the california gull - due to increased effort or improvement of skill. *Oikos*, 43, 407-408.

- Parker, P. G., Waite, T. A., Heinrich, B. & Marzluff, J. M. (1994) Do common ravens share ephemeral food resources with kin? DNA-fingerprinting evidence. *Animal Behaviour*, 48, 1085-1093.
- Pen, I. & Weissing, F. J. (2000) Towards a unified theory of cooperative breeding: The role of ecology and life history re-examined. *Proceedings of the Royal Society B-Biological Sciences*, 267, 2411-2418.
- Peres, C. A. (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. *Behavioral Ecology and Sociobiology*, 25, 227-233.
- Peres, C. A. (1993) Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica*, 61, 61-76.
- Perrins, C. M. & McCleery, R. H. (1985) The effect of age and pair bond on the breeding success of great tits *Parus-major*. *Ibis*, 127, 306-315.
- Pianka, E. R. & Parker, W. S. (1975) Age-specific reproductive tactics. *American Naturalist*, 109, 453-464.
- Pook, A. G. & Pook, G. (1981) A field study of the socio-ecology of the Goeldi's monkey (*Callimico goeldii*) in northern Bolivia. *Folia Primatologica*, 35, 288-312.
- Porter, L. M. (2001a) Dietary differences among sympatric callitrichinae in northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *International Journal of Primatology*, 22, 961-992.
- Porter, L. M. (2001b) Social organization, reproduction and rearing strategies of *Callimico goeldii*: New clues from the wild. *Folia Primatologica*, 72, 69-79.
- Porter, L. M. (2004) Forest use and activity patterns of *Callimico goeldii* in comparison to two sympatric tamarins, *Saguinus fuscicollis* and *Saguinus labiatus*. *American Journal of Physical Anthropology*, 124, 139-153.
- Porter, L. M. & Garber, P. A. (2009) Social behavior of callimicos: Mating strategies and infant care. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*.
- Porter, L. M., Hanson, A. M. & Becerra, E. N. (2001) Group demographics and dispersal in a wild group of Goeldi's monkeys (*Callimico goeldii*). *Folia Primatologica*, 72, 108-110.
- Powell, G. V. N. (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour*, 22, 501-505.
- Price, E. C. (1991) Competition to carry infants in captive families of cotton-top tamarins (*Saguinus oedipus*). *Behaviour*, 118, 66-88.
- Price, E. C. (1992a) The benefits of helpers: Effects of group and litter size on infant care in tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 26, 179-190.
- Price, E. C. (1992b) The costs of infant carrying in captive cotton-top tamarins. *American Journal of Primatology*, 26, 23-33.
- Pryce, C. R. (1988) Individual and group effects on early caregiver-infant relationships in red-bellied tamarin monkeys. *Animal Behaviour*, 36, 1455-1464.
- Pugesek, B. H. (1981) Increased reproductive effort with age in the california gull (*Larus californicus*). *Science*, 212, 822-823.
- Ramirez, M. L., Freese, C. H. & Revilla, C. J. (1977) Feeding ecology of the pygmy marmoset, *Cebuella pygmaea*, in northeastern Peru. IN Kleiman, D. G. (Ed.) *The biology and conservation of the callitrichidae*. Washington DC, Smithsonian Institution Press.
- Reeve, H. K. (1992) Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature*, 358, 147-149.

- Reeve, H. K. & Gamboa, G. J. (1983) Colony activity integration in primitively eusocial wasps - the role of the queen (*Polistes fuscatus*, Hymenoptera, Vespidae). *Behavioral Ecology and Sociobiology*, 13, 63-74.
- Reyer, H.-U. (1984) Investment and relatedness: A cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Animal Behaviour*, 32, 1163-1178.
- Reyer, H. U. (1986) Breeder-helper-interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour*, 96, 277-303.
- Ridley, A. R. (2012) Invading together: The benefits of coalition dispersal in a cooperative bird. *Behavioral Ecology and Sociobiology*, 66, 77-83.
- Rood, J. P. (1990) Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour*, 39, 566-572.
- Ross, C. (1991) Life history patterns of New World monkeys. *International Journal of Primatology*, 12, 481-502.
- Rothe, H. & Darms, K. (1993) The social organization of marmosets: A critical evaluation of recent concepts. IN Rylands, A. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Rothe, H., Darms, K., Koenig, A., Radespiel, U. & Juenemann, B. (1993a) Long-term study of infant-carrying behavior in captive common marmosets (*Callithrix jacchus*): Effect of nonreproductive helpers on the parents' carrying performance. *International Journal of Primatology*, 14, 79-93.
- Rothe, H., Koenig, A. & Darms, K. (1993b) Infant survival and number of helpers in captive groups of common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 30, 131-137.
- Russell, A. F. & Hatchwell, B. J. (2001) Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 2169-2174.
- Russell, A. F., Langmore, N. E., Gardner, J. L. & Kilner, R. M. (2008) Maternal investment tactics in superb fairy-wrens. *Proceedings of the Royal Society B-Biological Sciences*, 275, 29-36.
- Rylands, A. B. (1986) Infant-carrying in a wild marmoset group, *Callithrix humeralifer*: Evidence for a polyandrous mating system. IN Thiago de Mello, M. (Ed.) *A Primatologia No Brasil, vol. 2. Sociedade Brasileira de Primatologia, Brasilia*.
- Rylands, A. B. (1993) The ecology of the lion tamarins, *Leontopithecus*: Some intrageneric differences and comparison with other callitrichids. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour, and ecology*. Oxford, Oxford University Press.
- Rylands, A. B. (1997) The callitrichidae: A biological overview. IN Pryce, C., Scott, L. & Schnell, C. (Eds.) *Handbook: Marmosets and tamarins in biological and biomedical research*. Salisbury, UK, DSSD Imagery.
- Rylands, A. B., Coimbra-Filho, A. F. & Mittermeier, R. A. (2009) The systematics and distributions of the marmosets (*Callithrix*, *Callibella*, *Cebuella*, and *Mico*) and Callimico (*Callimico*) (Callitrichidae, Primates). IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*.
- Rylands, A. B. & de Faria, D. S. (1993) Habitats, feeding ecology, and home range size in the genus *Callithrix*. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour, and ecology*. Oxford, Oxford University Press.
- Rylands, A. B., Schneider, H., Langguth, A., Mittermeier, R. A., Groves, C. P. & Rodriguez-Luna, E. (2000) An assessment of the biodiversity of New World primates. *Neotropical Primates*, 8, 61-93.

- Saltzman, W. (2003) Reproductive competition among female common marmosets (*Callithrix jacchus*): Proximate and ultimate causes. IN Jones, C. B. (Ed.) *Sexual selection and reproductive competition in primates: New perspectives and directions*. Norman, OK, American Society of Primatologists.
- Saltzman, W., Digby, L. J. & Abbott, D. H. (2009) Reproductive skew in female common marmosets: What can proximate mechanisms tell us about ultimate causes? *Proceedings of the Royal Society B-Biological Sciences*, 276, 389-399.
- Saltzman, W., Pick, R. R., Salper, O. J., Liedl, K. J. & Abbott, D. H. (2004) Onset of plural cooperative breeding in common marmoset families following replacement of the breeding male. *Animal Behaviour*, 68, 59-73.
- Saltzman, W., Severin, J. M., Schultz-Darken, N. J. & Abbott, D. H. (1997) Behavioral and social correlates of escape from suppression of ovulation in female common marmosets housed with the natal family. *American Journal of Primatology*, 41, 1-21.
- Sanchez, S., Pelaez, F., Gil-Burmann, C. & Kaumanns, W. (1999) Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 48, 99-111.
- Sanchez, S., Pelaez, F., Morcillo, A. & Gil-Burmann, C. (2005) Effect of the enclosure on carriers' body weight loss in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 66, 279-284.
- Santema, P. & Clutton-Brock, T. (2012) Dominant female meerkats do not use aggression to elevate work rates of helpers in response to increased brood demand. *Animal Behaviour*, 83, 827-832.
- Savage, A., Giraldo, K. H., Soto, K. H. & Snowdon, C. T. (1996a) Demography, group composition, and dispersal in wild cotton-top tamarin (*Saguinus oedipus*) groups. *American Journal of Primatology*, 38, 85-100.
- Savage, A., Shideler, S. E., Soto, L. H., Causado, J., Giraldo, L. H., Lasley, B. L. & Snowdon, C. T. (1997) Reproductive events of wild cotton-top tamarins (*Saguinus oedipus*) in Colombia. *American Journal of Primatology*, 43, 329-337.
- Savage, A., Snowdon, C. T., Giraldo, L. H. & Soto, L. H. (1996b) Parental care patterns and vigilance in wild cotton-top tamarins (*Saguinus oedipus*). IN Norconk, M., Rosenberger, A. & Garber, P. (Ed.) *Adaptive radiations of neotropical primates*. New York, Plenum Press.
- Schaffner, C. M. & French, J. A. (1997) Group size and aggression: 'Recruitment incentives' in a cooperatively breeding primate. *Animal Behaviour*, 54, 171-180.
- Schaffner, C. M. & French, J. A. (2004) Behavioral and endocrine responses in male marmosets to the establishment of multimale breeding groups: Evidence for non-monopolizing facultative polyandry. *International Journal of Primatology*, 25, 709-732.
- Schneider, H. & Sampaio, I. (2015) The systematics and evolution of New World primates - a review. *Molecular Phylogenetics and Evolution*, 82, 348-357.
- Schradin, C. & Anzenberger, G. (2001a) Costs of infant carrying in common marmosets, *Callithrix jacchus*: An experimental analysis. *Animal Behaviour*, 62, 289-295.
- Schradin, C. & Anzenberger, G. (2001b) Infant carrying in family groups of Goeldi's monkeys (*Callimico goeldii*). *American Journal of Primatology*, 53, 57-67.
- Smith, T. E., Schaffner, C. M. & French, J. A. (1997) Social and developmental influences on reproductive function in female Wied's black tufted-ear marmosets (*Callithrix kuhli*). *Hormones and Behavior*, 31, 159-168.
- Smukalla, S., Caldara, M., Pochet, N., Beauvais, A., Guadagnini, S., Yan, C., Vences, M. D., Jansen, A., Prevost, M. C., Latge, J. P., Fink, G. R., Foster, K. R. & Verstrepen, K. J.

- (2008) Flo1 is a variable green beard gene that drives biofilm-like cooperation in budding yeast. *Cell*, 135, 726-737.
- Snowdon, C. T. (1996) Infant care in cooperatively breeding species. IN Rosenblatt, J. S. & Snowdon, C. T. (Eds.) *Parental care: Evolution, mechanisms and adaptive significance*. San Diego, Academic Press.
- Snowdon, C. T. & Soini, P. (1988) The tamarins, genus *Saguinus*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Soini, P. (1982) Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea*. *Folia Primatologica*, 39, 1-21.
- Soini, P. (1988) The pygmy marmoset, genus *Cebuella*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Soini, P. (1993) The ecology of the pygmy marmoset, *Cebuella pygmaea*: Some comparisons with two sympatric tamarins. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour, and ecology*. Oxford (UK), Oxford University Press.
- Solomon, N. G. & French, J. A. (Eds.) (1997) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Solomon, N. G. & Getz, L. L. (1997) Examination of alternative hypotheses for cooperative breeding in rodents. IN Solomon, N. G. & French, J. A. (Eds.) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Sousa, M. B. C., Albuquerque, A., Albuquerque, F. D., Araújo, A., Yamamoto, M. E. & Arruda, M. D. (2005) Behavioral strategies and hormonal profiles of dominant and subordinate common marmoset (*Callithrix jacchus*) females in wild monogamous groups. *American Journal of Primatology*, 67, 37-50.
- Sousa, M. B. C., Araújo, A., Yamamoto, M. E., Albuquerque, A. C. S. R. & Arruda, M. F. (2009) Emigration as a reproductive strategy of the common marmosets (*Callithrix jacchus*). IN Davis, L. C., Ford, S. M. & Porter, L. M. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Stacey, P. B. & Koenig, W. D. (Eds.) (1990) *Cooperative breeding in birds: Long-term studies of ecology and behavior*. Cambridge, Cambridge University Press.
- Stacey, P. B. & Ligon, J. D. (1987) Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *The American Naturalist*, 130, 654-676.
- Stevenson, M. F. (1976) Birth and perinatal behavior in family groups of common marmoset (*Callithrix jacchus jacchus*), compared to other primates. *Journal of Human Evolution*, 5, 365-381.
- Stevenson, M. F. & Rylands, A. B. (1988) The marmosets, genus *Callithrix*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Sussman, R. W. & Garber, P. A. (1987) A new interpretation of the social organization and mating system of the callitrichidae. *International Journal of Primatology*, 8, 73-92.
- Taborsky, M. (1985) Breeder-helper conflict in a cichlid fish with broodcare helpers - an experimental analysis. *Behaviour*, 95, 45-75.
- Tardif, S., Power, M., Layne, D., Smucny, D. & Ziegler, T. (2004) Energy restriction initiated at different gestational ages has varying effects on maternal weight gain and pregnancy outcome in common marmoset monkeys (*Callithrix jacchus*). *British Journal of Nutrition*, 92, 841-849.

- Tardif, S. D. (1984) Social influences on sexual maturation of female *Saguinus oedipus oedipus*. *American Journal of Primatology*, 6, 199-209.
- Tardif, S. D. (1994) Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant-care patterns. *American Journal of Primatology*, 34, 133-143.
- Tardif, S. D. (1997) The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. IN Solomon, N. G. & French, J. A. (Eds.) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Tardif, S. D., Araújo, A., Arruda, M. F., French, J. A., Sousa, M. B. C. & Yamamoto, M. E. (2008) Reproduction and aging in marmosets and tamarins. IN Atsalis, S., Margulis, S. W. & Hof, P. R. (Eds.) *Primate reproductive aging: Cross-taxon perspectives*. Karger Publishers.
- Tardif, S. D., Carson, R. L. & Gangaware, B. L. (1986) Comparison of infant care in family groups of the common marmoset (*Callithrix jacchus*) and the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 11, 103-110.
- Tardif, S. D., Carson, R. L. & Gangaware, B. L. (1990) Infant-care behavior of mothers and fathers in a communal-care primate, the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 22, 73-85.
- Tardif, S. D., Harrison, M. L. & Simek, M. A. (1993) Communal infant care in marmosets and tamarins: Relation to energetics, ecology, and social organization. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour, and ecology*. Oxford, Oxford University Press.
- Tardif, S. D. & Jaquish, C. E. (1997) Number of ovulations in the marmoset monkey (*Callithrix jacchus*): Relation to body weight, age and repeatability. *American Journal of Primatology*, 42, 323-329.
- Tardif, S. D., Santos, C. V., Baker, A. J., van Elsacker, L., Ruiz-Miranda, C. R., Moura, A. C. A., Passos, F. C., Price, E. C., Rapaport, L. G. & De Vleeschouwer, K. (2002) Infant care in lion tamarins. IN Kleiman, D. G. & Rylands, A. B. (Eds.) *Lion tamarins: Biology and conservation*. Washington DC, Smithsonian Institution Press.
- Tardif, S. D., Smucny, D. A., Abbott, D. H., Mansfield, K., Schultz-Darken, N. & Yamamoto, M. E. (2003) Reproduction in captive common marmosets (*Callithrix jacchus*). *Comparative Medicine*, 53, 364-368.
- Terborgh, J. & Goldizen, A. W. (1985) On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 16, 293-299.
- Tinbergen, N. (1963) On aims and methods of Ethology. *Zeitschrift fur Tierpsychologie*, 20, 410-433.
- Trivers, R. L. (1971) Evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46, 35-57.
- West-Eberhard, M. J. (1975) The evolution of social behavior by kin selection. *The Quarterly Review of Biology*, 50, 1-33.
- West, S. A., Griffin, A. S. & Gardner, A. (2007) Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20, 415-432.
- Williams, G. C. (1964) Measurement of consociation among fishes and comments on the evolution of schooling. *Publications of the Museum, Michigan State University Biological Series*, 2, 349-384.
- Wilson, E. O. (1971) *The insect societies*, Cambridge, Belknap Press of Harvard University Press.

- Wong, M. Y. L., Buston, P. M., Munday, P. L. & Jones, G. P. (2007) The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proceedings of the Royal Society B-Biological Sciences*, 274, 1093-1099.
- Woolfenden, G. E. (1975) Florida scrub jay helpers at the nest. *The Auk*, 92, 1-15.
- Wright, J. (2007) Cooperation theory meets cooperative breeding: Exposing some ugly truths about social prestige, reciprocity and group augmentation. *Behavioural Processes*, 76, 142-148.
- Wright, J., McDonald, P. G., te Marvelde, L., Kazem, A. J. N. & Bishop, C. M. (2010) Helping effort increases with relatedness in bell miners, but 'unrelated' helpers of both sexes still provide substantial care. *Proceedings of the Royal Society B-Biological Sciences*, 277, 437-445.
- Wright, J. & Russell, A. F. (2008) How helpers help: Disentangling ecological confounds from the benefits of cooperative breeding. *Journal of Animal Ecology*, 77, 427-429.
- Ximenes, M. & Sousa, M. B. C. (1996) Family composition and the characteristics of parental care during the nursing phase of captive common marmosets (*Callithrix jacchus*). *Primates*, 37, 175-183.
- Yamamoto, M. E. (1993) From dependence to sexual maturity: The behavioural ontogeny of callitrichidae. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Yamamoto, M. E., Araujo, A., Arruda, M. d. F., Lima, A. K. M., Siqueira, J. d. O. & Hattori, W. T. (2014) Male and female breeding strategies in a cooperative primate. *Behavioural Processes*, 109, 27-33.
- Yamamoto, M. E., Arruda, M. d. F., Alencar, A. I., de Sousa, M. B. C. & Araújo, A. (2009) Mating systems and female-female competition in the common marmoset, *Callithrix jacchus*. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Yamamoto, M. E. & Box, H. O. (1997) The role of non-reproductive helpers in infant care in captive *Callithrix jacchus*. *Ethology*, 103, 760-771.
- Zahavi, A. (1974) Communal nesting by the Arabian babbler - a case of individual selection. *Ibis*, 116, 84-87.
- Zahavi, A. (1995) Altruism as a handicap - the limitations of kin selection and reciprocity. *Journal of Avian Biology*, 26, 1-3.
- Zahed, S. R., Kurian, A. V. & Snowdon, C. T. (2010) Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology*, 72, 296-306.
- Ziegler, T. E., Bridson, W. E., Snowdon, C. T. & Eman, S. (1987) Urinary gonadotropin and estrogen excretion during the postpartum estrus, conception, and pregnancy in the cotton-top tamarin (*Saguinus oedipus oedipus*). *American Journal of Primatology*, 12, 127-140.
- Ziegler, T. E., Snowdon, C. T. & Bridson, W. E. (1990) Reproductive performance and excretion of urinary estrogens and gonadotropins in the female pygmy marmoset (*Cebuella pygmaea*). *American Journal of Primatology*, 22, 191-203.

Chapter Two

No evidence for effects of infant-carrying by related helpers on the fitness of breeding pairs in captive common marmosets (*Callithrix jacchus*)



Gippsland Field Station, Victoria, Australia.

Abstract

Helping behaviour, where individuals benefit others at their own expense, is often seen in cooperative breeding systems, with individuals other than the parents contributing to the care of young (alloparental behaviour). The question why individuals engage in these apparently altruistic behaviours is a long-standing evolutionary puzzle since it cannot be easily explained by classical natural selection. One credible evolutionary explanation is kin selection, where alloparental behaviour increases the fitness of relatives, who share these traits with high probability. In this study, I investigated potential effects of alloparental infant-carrying behaviour of related helpers on the reproductive success of dominant breeding pairs in groups ($n = 9$) of common marmosets (*Callithrix jacchus*) in a captive breeding colony. Common marmosets are cooperatively breeding primates that live in extended family groups, in which all group members care and carry the infants of the dominant breeding pair. Alloparental infant-carrying is expected to reduce parental infant-carrying loads and increase the reproductive success of breeding pairs, which are expected to be facing high energetic demands when rearing two infants while conceiving the next litter of young two weeks after parturition. Here I show that time spent in infant-carrying behaviour by alloparents was not significantly correlated with parental infant-carrying times (with maternal infant-carrying time: $r = -0.32$, with paternal infant-carrying time: $r = -0.04$) or success of subsequent parturition of the breeding pairs (mean infant-carrying time (minutes \pm se): successful = 9 ± 1.5 , unsuccessful = 4 ± 1.0). However, paternal infant-carrying reduced maternal infant-carrying loads ($r = -0.58$). Moreover, breeding pairs were more likely to be successful in the subsequent breeding attempt if the mothers had carried infants less and the fathers had carried infants more (mean infant-carrying time (minutes \pm se): mothers: successful = 9 ± 1.8 , unsuccessful = 30 ± 4.2 ; fathers: successful = 40 ± 2.5 , unsuccessful = 33 ± 4.2). The results suggest that alloparents' contribution to infant-carrying may not be necessary for the successful reproduction of common marmosets in a captive environment, but that the fathers' contribution to infant-carrying may still be crucial.

Introduction

Helping behaviour, where individuals benefit others at their own expense is often seen in nature (Wilson 1971; Stacey & Koenig 1990; Dugatkin 1997; Hammerstein 2003; Duffy & Thiel 2007; West *et al.* 2007; Kiers & Denison 2008; Melis & Semmann 2010; Strassmann *et al.* 2011). In this respect, cooperatively breeding systems provide a classic example, where individuals other than the parents contribute to the care of young (Solomon & French 1997; Cockburn 1998; Koenig & Dickinson 2004). In such systems, alloparents in some species even forgo their own reproduction and provide care for the offspring of other individuals in the group (Brown 1987; Taborsky 1994). Such apparent altruism is not easily explained by classical natural selection, and the question why individuals engage in these behaviours is a long-standing evolutionary puzzle (Dugatkin 2011).

One plausible explanation for the evolution of alloparental behaviour is kin selection, where alloparents increase the reproductive success of their relatives who are more likely to share the alloparental traits, that is, a tendency to care for the offspring of relatives (Hamilton 1964; Maynard Smith 1964). However, quantifying the effects of alloparental care on the reproductive success of breeding pairs is often challenging. This is mainly due to difficulties with isolating the fitness effects of alloparental care from the influences of confounding factors, such as maternal effects and habitat quality. For instance, better mothers and/or better habitats may be more productive and, as a result, are able to accumulate more relatives, that provide alloparental care or, alternatively, greater numbers of alloparental care providers could boost productivity (Ridley 2007; Cockburn *et al.* 2008; Wright & Russell 2008). Therefore, in order to quantify the effects of alloparental care on the reproductive success of breeding pairs while controlling for such confounding factors, the relationship between the reproductive success of breeding pairs and the amount of given alloparental care need to be examined in a controlled environment. One group of cooperatively breeding animals that are especially conducive to the study of alloparental care are the marmosets and tamarins (Subfamily: Callitrichinae).

Marmosets and tamarins are small neotropical primates that live in extended family groups typically consist a dominant breeding pair and several male and female subordinate group members (Digby & Barreto 1993; Ferrari & Digby 1996; Nievergelt *et al.* 2000). They are cooperative breeders, in which all group members provide care and carry the infants of the

dominant breeding pair (Stevenson 1976; Ingram 1977). Generally, callitrichine mothers give birth to twins, which, in total, can weigh as much as 15 - 25 % of adult body weight at birth (Kleiman 1977). Mothers can conceive at their postpartum oestrus after two weeks of parturition (Ingram 1977). Therefore mothers are often pregnant while nursing two heavy infants and can produce two young every five to six months (Ingram 1977).

Carrying heavy infants is known to be energetically costly to the carer, impede mobility, decrease foraging and vigilance behaviour, and hence likely to increase predation risk (Goldizen & Terborgh 1986; Goldizen 1987a; Price 1992b; Caine 1993; Tardif 1994; Caine 1996; Tardif 1997; Sanchez *et al.* 1999; Bales *et al.* 2000; Schradin & Anzenberger 2001; Achenbach & Snowdon 2002; Caperos *et al.* 2012). Together with the high rate of reproduction, the heavy demand of infant-carrying is suggested to be the main factor underpinning the evolution and maintenance of cooperative breeding in callitrichines (Kleiman 1977; Goldizen 1987b). In particular, alloparents have been suggested to play important roles in reducing the energetic cost of infant-carrying and increasing the reproductive success of the breeding pairs (Goldizen 1987b; Price 1992a; Rothe & Darms 1993; Ximenes & Sousa 1996). However, the beneficial effects of alloparental infant-carrying on the reproductive success of the breeding pairs have not, to date, been clearly demonstrated.

Evidence that alloparental care increases the survival of young in the group is equivocal. It has been shown that, in natural groups of common marmosets (*Callithrix jacchus*), there are more surviving young in groups with more adult members (Koenig 1995; Bales *et al.* 2000). However, the positive correlation between the number of adults and the number of surviving young in the group may not necessarily be due to increased alloparental care, but could, instead, be due to other factors, such as higher fecundity of the breeding females, better quality of the territories, and/or larger size of the group. Breeding females with higher fecundity would have more young as well as more adult offspring in the group (Wright & Russell 2008). Similarly, a resource-rich territory would potentially increase reproductive success and therefore increase the group size (Russell & Lummaa 2009). Moreover, larger groups have advantages in territory defence and antipredator vigilance, and thus could also improve infant survival (Kokko *et al.* 2001; Heg *et al.* 2005; Garay & Varga 2011). In fact, increased number of alloparents was found to have no effect on infant survival in captive

groups, where the effects of environmental factors are largely controlled (Rothe *et al.* 1993b; but see Johnson *et al.* 1991; Snowdon 1996).

Alloparents have been suggested to reduce the energetic costs of parental infant-carrying and improve the physical condition of the breeding pairs. In captive groups of common marmosets, parental infant-carrying loads have been shown to decrease with the increasing number of alloparents (Rothe *et al.* 1993a; Rothe *et al.* 1993b; Ximenes & Sousa 1996; Yamamoto & Box 1997). Also, it has been shown that when there are alloparents in the group, the parents maintain and regain their weights better during the postpartum periods (Achenbach & Snowdon 2002). It has also been suggested that reproductive output of callitrichines may be influenced by energy availability for the breeding female during the pregnancy (Tardif & Jaquish 1997). Maternal body weights have been shown to be related to the number of ova ovulated per cycle and to be associated with pregnancy loss in captive common marmosets (Tardif & Jaquish 1997; Tardif *et al.* 2004). Also, maternal body weights at the conception have been shown to be related to the litter size in natural groups of golden lion tamarins (*Leontopithecus rosalia*) (Bales *et al.* 2001). Therefore it can be suggested that alloparental infant-carrying may increase reproductive output of breeding females by improving the physical condition after parturition by reducing the energetic costs of infant-carrying and facilitating the weight gain of the breeding female (Sanchez *et al.* 1999). However, the relationship between maternal infant-carrying load and the success of parturition in subsequent breeding event remains to be examined.

In this study, I investigated potential effects of infant-carrying by related alloparents on the success of subsequent parturition of dominant breeding females in groups of common marmosets in a captive breeding colony. By using animals in a captive environment, I controlled the quality of the living environment and its potential confounding effects on the reproductive success of the breeding pairs. I measured the amount of time spent in infant-carrying by carriers in different breeding statuses (i.e. mothers, fathers and alloparents). I then examined the relationship between the time spent in infant-carrying by carriers in each breeding status and the success of the parturition of the mothers at the subsequent breeding event, which followed the period of the observation of infant-carrying behaviour. I predicted that infant-carrying performed by alloparents will have a positive effect on the fitness of breeding pairs and time spent in alloparental infant-carrying should correlate positively with the success of subsequent parturition of the breeders.

Methods

Design

Time spent in infant-carrying by each group member was measured from video recordings for one hour each day during when the infants were 20 to 24 days old. The times infants were carried by mothers, fathers and alloparents were examined for the effect of alloparental infant-carrying on parental infant-carrying loads. The relationship between the success of parturition following the observation period and the times spent in infant-carrying by mothers, fathers and alloparents were examined for the potential effect of alloparental infant-carrying on the success of the subsequent parturition by the mothers.

Animal housing

Animals used in this study were from the national marmoset colony located at the Gippsland Field Station, Monash University, Australia. Common marmosets at the facility were separated into breeding groups, which consist of two to 12 individuals, comprising of a dominant breeding pair and their offspring as subordinate group members (alloparents). All individuals (except infants) have been previously microchipped for identification. Infants had a small patch (~1cm²) of their coat on the upper or lower back shaved to allow animals to be individually identified from their siblings. Each group was kept in an indoor cage (1.8m (H) x 1.2m x 0.75m), which is connected to an outdoor cage (2m (H) x 2m x 0.7m) by a pipe for daytime access. The indoor cages were placed within rooms, with six cages in each room. The outdoor cages were placed along the east and west side of the building under awnings and enclosed with meshed wire. Both the indoor and outdoor cages were placed next to other cages. Animals in cages were able to see, hear and smell other animals in nearby cages, though direct contact with animals in adjacent cages was prevented by the stainless-steel walls of the cages. The indoor cages were maintained at 25 - 30°C, with 40 - 60% humidity. Internal lighting was maintained on a 12 hours light-dark cycle. The floors of the indoor cages were covered with sawdust, while the floors of outdoor cages comprised of bare concrete. The cages were washed fortnightly. Nest boxes (15cm (H) x 30cm (W) x 12cm (D); stainless-steel) in the cages were washed separately in alternate weeks to the cages in order to maintain territorial pheromones in the cages after washing. All individuals were fed once a day in the late morning with marmoset pellets (Specialty Feeds, Glen Forrest, Western Australia), fruits, vegetables and mealworms. Recuperation supplements, including a

recuperation cake and nectar, were provided for the groups with animals that were birthing, lactating, losing weight or ill. The recuperation cake was made up of assorted fruits, vegetables, grains, eggs, marmoset pellets, PediaSure (Abbot Laboratory, B. V. Zwolle, the Netherlands) and filtered water. The nectar was a mixture of PediaSure, Splenda (Johnson & Johnson Pacific Pty. Ltd., Ultimo, New South Wales, Australia), a calcium supplement (Troy Laboratories Pty. Ltd., Glendenning, New South Wales, Australia) and filtered water. Water bottles were provided in each indoor cage. The facility complies with the NHMRC *Policy on the Care and Use of Non-Human Primates for Scientific Purposes* (Animal Welfare Committee of the NHMRC 2003).

Study subjects

Seven groups of captive common marmosets were used in this study. Two of the seven groups were used twice at different breeding events with different group compositions (i.e. different subordinates) to obtain nine observations. For each observation, the age of the parents and number of previous breeding events for each breeding pair at the time of the observation, number and sex of infant, juvenile (age < 10 months), sub-adult (age = 10 < 15 months) and adult (age > 15 months) subordinate group members, and the mean age of mothers, fathers and subordinate group members in each age class, except the infants, are shown in Table 1. Breeding males and some of the subordinates were collared by using ball chain with a metal plate in a unique shape (e.g. round, square, triangle and diamond. Approximately 1cm² in size) to be distinguished from other members of the group.

Video recording

Video recordings of groups were taken during the period when the infants in the group were 19 to 25 days old. The groups were video recorded for 12 hours each day between 6:00 to 18:00 using four surveillance cameras (94mm (D) x 78mm (H), WIT1035SDW, WIT Security Technology Co., Ltd. Taoyuan, Taiwan R.O.C.), which were attached to the four corners of the indoor cage's ceiling to record the entire cage.

Data collection

The amount of time each group member spent in infant-carrying was measured from the video recordings for one hour each day (30 minutes each in the morning and afternoon, beginning at 10:00 and 15:00 respectively) between days 20 and 24. The period of data collection was selected to coincide with a period without changes in group composition

(death of an infant, removal of an infant or a helper for other, unrelated experiments, or for colony management) across all focal groups. This allowed me to avoid possible effects of changes in group composition on the contribution of group members to infant-carrying. Moreover, this period covered the third and fourth weeks of infant age, when the infants are heavier than in the earlier weeks. Therefore, the potential costs of infant-carrying would also be greater compared to the earlier weeks. Time spent in infant-carrying was not measured between days 20 and 24 if the cage was due for washing or the group was due for weighing during those days. Instead, the time spent in infant-carrying was measured on day 19 or day 25. When carriers were not observable (e.g. in the nest box, pipe or outdoor cage), observation time was shifted to either before or after the unobservable period, allowing for a more continuous observation to be made. When observation time could not be shifted to avoid an unobservable period, the infant-carrying time during the unobservable period was not measured and the observation time was extended at the beginning or the end to compensate for the loss of observation time. Finally, observations were not made during 30 minutes after feeding, which could occur at any time during the late morning, or after capture and release of any animal in the group to minimise the influence of any disturbance on infant-carrying behaviour.

The number of infants that were carried by each group member at each time was not taken into account. In the current study, in groups with more than one infant, 66% of the time that infants were being carried involved two or more infants being carried by a group member simultaneously. Although the energetic cost of infant-carrying might be doubled by carrying two infants at once, the other potential costs of infant-carrying, especially the ones caused by the impeded mobility in carrying infants, such as decreased foraging and increased predation risk, are most likely not doubled by carrying two infants compared to carrying one. For instance, in a study on wild saddle-back tamarins (Goldizen 1987a), it has been reported that the changes in activities that increase in resting, and reduction in feeding and travelling appeared to be similar between adults carrying one versus two infants at once. By contrast, the activities changed significantly between adults carrying an infant, compared to those that were not carrying. For this reason, I decided not to consider the number of infants being carried by a carrier in the analysis. Therefore the total infant-carrying time for one observation day was dependent on the numbers of infants in the group and whether the infants were carried together or separately. For example, the total infant-carrying time for a

group for a day can tally up to three ‘hours’ when the three infants in the group were carried separately by different group members throughout the one-hour observation period.

Parturition success following the observation period was recorded for each group. The subsequent parturition was considered successful when the mother produced at least one live infant within six months (183 days) from the previous parturition. A successful parturition thus indicates that the mother conceived the young within the first month of the postpartum period, which is the most intensive period of infant-carrying (Arruda *et al.* 1986; Yamamoto *et al.* 1996; Yamamoto & Box 1997). When the mother did not produce any live young (including stillbirths and loss of foetuses) within six months postpartum, the subsequent parturition was recorded as unsuccessful.

Statistical analysis

In groups with alloparents, mean time spent carrying infants by mothers, fathers and all alloparents in the groups were compared using a Friedman rank sum test. Post-hoc tests were performed by using Wilcoxon signed rank tests. Mean time spent carrying infants during the one-hour observations by mothers and fathers were compared between groups with and without adult alloparents using Wilcoxon rank sum tests. Correlations between the time spent carrying infants by mothers, fathers and all alloparents in the groups were analysed by Spearman’s correlation coefficients. To analyse the relationships among the times spent carrying infants by mothers, fathers and alloparents, and between infant-carrying time and subsequent parturition success I constructed generalized linear mixed models (GLMMs) by using the lme4 package (Bates *et al.* 2012) in R 3.2.1 (R Core Team 2015). I assigned breeding event and individual ID as random factors to control for pseudo-replication (the variance associated with the random factors was very small in all models; data not shown). In the analysis of the relationship among the infant-carrying times of mothers, fathers and alloparents, time spent carrying infants (minutes) on each day by either mothers or fathers was used as the dependent variable using the ‘cbind’ command with binomial totals = 60 minutes. As independent variables, I included the time spent carrying infants (minutes) on each day by fathers (for the maternal infant-carrying time) and by all alloparents in the groups (for both maternal and paternal infant-carrying times). The effects of these independent variables were tested for each dependent variable in three separated GLMMs (i.e. mothers vs. fathers, mother vs. alloparents, and fathers vs. alloparents as dependent variable). In the analysis of the relationship between infant-carrying and the success of subsequent

parturition, I used the time spent carrying infants (minutes) in each day by mothers, by fathers or by individual alloparents separately as the dependent variable in each GLMM using the 'cbind' command with binomial totals = 60 minutes. As an independent variable, I included the success of subsequent parturition.

Results

Fathers carried infants more than mothers

Infants were carried most of the time during the observations. The amount of time infants were not carried during a single observation period (60 minutes) was 1 ± 0.3 (minutes \pm se). In the groups with alloparents ($n = 7$), means of time spent in infant-carrying (minutes \pm se) by fathers, mothers and all the alloparents in the groups were 39 ± 2.0 , 13 ± 1.8 and 23 ± 3.5 respectively. Mean time spent carrying infants during the one-hour observations by fathers, mothers and all alloparents in the groups differed significantly (Friedman rank sum test: Friedman chi-squared $(2) = 33.08$, $p < 0.01$). Fathers carried infants significantly more than mothers (Wilcoxon signed rank test: $V = 28$, $p < 0.05$). However, the time spent carrying infants by all alloparents in the groups did not vary with the time spent carrying infants by fathers or by mothers (Wilcoxon signed rank test: Fathers and Alloparents: $V = 24$, $p = 0.09$; Mothers and Alloparents: $V = 20$, $p = 0.38$). Also, the time spent carrying infants by mothers or by fathers did not differ between groups with and without adult alloparents (mean infant-carrying time (minutes \pm se): Mothers: with adult alloparents = 19 ± 1.5 , without adult alloparents = 11 ± 0.8 ; Fathers: with adult alloparents = 43 ± 0.9 , without adult alloparents = 38 ± 1.3 ; Wilcoxon rank sum test: Mothers: $W = 2$, $p = 0.33$; Fathers: $W = 4$, $p = 0.86$).

Maternal infant-carrying decreased with increasing paternal infant-carrying

Examination of time spent in infant-carrying between mothers and fathers revealed that maternal infant-carrying time decreased significantly with increasing paternal infant-carrying time (Spearman's $r = -0.58$; GLMM: $z = -5.31$, $p < 0.01$, Figure 1a). However, neither maternal nor paternal infant-carrying times decreased significantly with increasing alloparental infant-carrying time (Maternal and Alloparental: Spearman's $r = -0.32$, Paternal and Alloparental: Spearman's $r = -0.04$; GLMM: Maternal: $z = -1.74$, $p = 0.08$, Figure 1b; Paternal: $z = -0.94$, $p = 0.35$, Figure 1c).

Maternal infant-carrying time was shorter in successful subsequent parturition

Examination of the relationship between infant-carrying time and success in subsequent parturition showed that infant-carrying time was significantly shorter in mothers (mean infant-carrying time (minutes \pm se): successful = 9 ± 1.8 , unsuccessful = 30 ± 4.2 ; GLMM: $z = -5.69$, $p < 0.01$, Figure 2a) and significantly longer in fathers (mean infant-carrying time (minutes \pm se): successful = 40 ± 2.5 , unsuccessful = 33 ± 4.2 ; GLMM: $z = -3.08$, $p < 0.01$, Figure 2b) in groups that were successful in subsequent parturition (successful = 5, unsuccessful = 4, Table 1). Alloparental infant-carrying time was longer in groups with successful subsequent parturition although there was no significant relationship (mean infant-carrying time (minutes \pm se): successful = 9 ± 1.5 , unsuccessful = 4 ± 1.0 ; GLMM: $z = 1.51$, $p = 0.13$, Figure 2c).

Discussion

My results suggest that related alloparents do not reduce parental infant-carrying loads, at least in our captive population of common marmosets. Possibly, as a consequence, alloparental infant-carrying did not result in increased parturition success of breeding pairs. In this regard, my data contrast with the previous finding that increasing number of alloparents in the group was correlated with decreased parental infant-carrying loads in another study of captive common marmosets (Rothe *et al.* 1993a).

One plausible reason for the absence of an alloparental infant-carrying effect in my study could be a lack of adult alloparents in my sample. Adult alloparents have been suggested to play an important role in lightening parental infant-carrying loads (Rothe & Darms 1993). In particular, adult alloparents have been reported to carry infants more than younger members in both captive and wild groups (Stevenson & Rylands 1988; Yamamoto & Box 1997). Moreover, the presence of adult alloparents in the group seems to be important in the reduction of maternal infant-carrying load (Rothe *et al.* 1993a). Likewise, a decrease in parental infant-carrying loads has been observed to reach an asymptote at the third to fifth litter, when at least one of existing litter has reached adulthood (Rothe *et al.* 1993a). In the current study, the presence of adult alloparents in the group did not significantly reduce the maternal or paternal infant-carrying loads. Only two of the nine observations involved adult alloparents in the group (see Table 1). The lack of adult alloparents in my study groups may, therefore, have limited the contribution of alloparents to infant-carrying. Consequently, there

may have been insufficient alloparental contributions to infant-carrying to have reduced parental infant-carrying loads. The contribution of adult alloparents to infant-carrying and its load lightening effect on parental infant-carrying loads need to be quantified in future studies.

The inconsistency between the results of my study and Rothe *et al.* (1993a) study might also be due to the difference in the size of the cages that the animals were held in each colony. The animals in Rothe *et al.* (1993a) study were held in much larger cages (13.2 m³ to 73.5 m³) than the animals in my study (indoor cage = 1.62 m³, outdoor cage = 2.8m³). It can be suggested that the larger size of the cages in Rothe *et al.* (1993a) study may have increased the energetic cost of infant-carrying and facilitated the sharing of infant-carrying load among the group members, including the alloparents. Carrying infants can be energetically more costly in larger cages. In captive cotton-top tamarins (*Saguinus oedipus*), animals in larger cages have been shown to lose more weight compared to animals in smaller cages during the nine weeks of postpartum, when the infants need to be carried (Sanchez *et al.* 2005). Moreover, energetically demanding environment may facilitate the sharing of infant-carrying loads among the group members. In common marmosets, alloparents in free-ranging groups have been shown to contribute more to infant-carrying than alloparents in captive groups (Yamamoto *et al.* 1996). Nevertheless, I found that maternal infant-carrying loads negatively correlate with the success of subsequent breeding. It suggests that infant-carrying is costly for the mothers even in the small cages.

Another possibility is that regular visual contact with other groups in our colony may have caused a defensive response of the parents and increased parental infant-carrying loads in order to protect the infants. An apparent influence of housing condition on infant-carrying behaviour has previously been reported in a captive group of common marmosets. Specifically, males in a captive group, which had been housed in a separate room with no visual contact with other groups, decreased their contribution to infant-carrying when they were moved to the neighbourhood of another group where the visual contact between the groups occur (Rothe *et al.* 1993a). Although the animals in our colony would be fairly accustomed to being close to the neighbouring groups since they grew up under those conditions, the possible stress from the continuous and close contact between the neighbouring groups cannot be excluded. The stress might have induced the defensive reactions of the parents to protect the infants and increased parental infant-carrying loads. Similarly, the stress might have increased the territorial behaviour of the alloparents and

decreased their participation in infant-carrying. Further investigation on the effects of contact with other groups on infant-carrying behaviour may provide valuable insights into the fitness effects of alloparental infant-carrying behaviour and the welfare of common marmosets in captive colonies.

Nutritional stress and its effects on alloparental infant-carrying behaviour were not expected to be important since animals were fed sufficiently at the colony. The amount of food given and remained at each feeding was measured to adjust the amount of food adequate for each group. Also, recuperation supplements were provided to the focal groups as postpartum treatment (see methods for details). Therefore, it would be fair to state that the animals were not under nutritional stress, and hence, alloparental infant-carrying behaviour was less likely to be affected by factors, such as, hunger and the need for foraging.

In contrast to the absence of alloparental infant-carrying effects on parental infant-carrying loads, I found that fathers' contribution to infant-carrying significantly reduced maternal infant-carrying loads. The result showed that fathers play an important role in infant care and fathers' contribution in infant-carrying has a prominent influence on maternal infant-carrying load in captive common marmosets. Fathers have been known to play a major role in infant-carrying in both captive and wild populations of callitrichine species (Goldizen 1987a; Tardif *et al.* 1990; Yamamoto *et al.* 1996; Sanchez *et al.* 1999; Zahed *et al.* 2010). It has been observed that the absence of breeding males resulted in increased participation of the breeding females in infant-carrying compared to when the breeding males were present (Arruda *et al.* 1986; Yamamoto *et al.* 1987; Yamamoto 1990 cited in Ximenes & Sousa 1996). Fathers are also observed to react to signals given by stressed infants more readily than mothers or non-reproductive males (Ziegler *et al.* 2009; Saito *et al.* 2011). This high involvement of fathers in infant-carrying, and its prominent influence on maternal infant-carrying load, could indicate that paternal infant-carrying may play an important role in increasing the reproductive success of the breeding pairs.

The higher contribution of fathers to infant-carrying in successful subsequent parturitions suggests that paternal contributions to infant-carrying may be important for reproductive success - even under apparently 'benign' captive environments. This is concordant with the prediction that high reproductive rate and heavy energetic demands of infant care in callitrichines require a high degree of paternal care for successful reproduction in both natural

and captive environments (Ingram 1977; Goldizen 1987b; Sanchez *et al.* 1999). Therefore, although energetic demands for activities such as travelling and foraging are comparatively lower - and environmental constraints are almost absent - in captivity, reproduction may remain highly costly for mothers to require fathers' contribution to infant-carrying.

The apparent high cost of reproduction in benign captive environments suggests that, in demanding natural environments where the cost of reproduction would be higher for the breeding females, the contribution of both the father and alloparents may be important for the successful reproduction of common marmosets. This is consistent with the field observations in free-ranging callitrichines that lone breeding pairs without alloparents are rarely successful in raising their young and therefore the contribution of alloparents seems to be essential for the successful reproduction in natural environments (Goldizen 1988; Koenig 1995; Bales *et al.* 2000). Alloparents are often the offspring of the breeding pairs in free-ranging groups of common marmoset (Nievergelt *et al.* 2000; Faulkes *et al.* 2009). Therefore, if alloparental infant-carrying increases the reproductive success of the breeding pairs, alloparental infant-carrying would increase the inclusive fitness of the alloparents through kin selection. This potential indirect fitness effect of alloparental infant-carrying behaviour need to be investigated by examining the effects of alloparental infant-carrying on the infant-carrying loads and the reproductive success of the breeding pairs in natural environments.

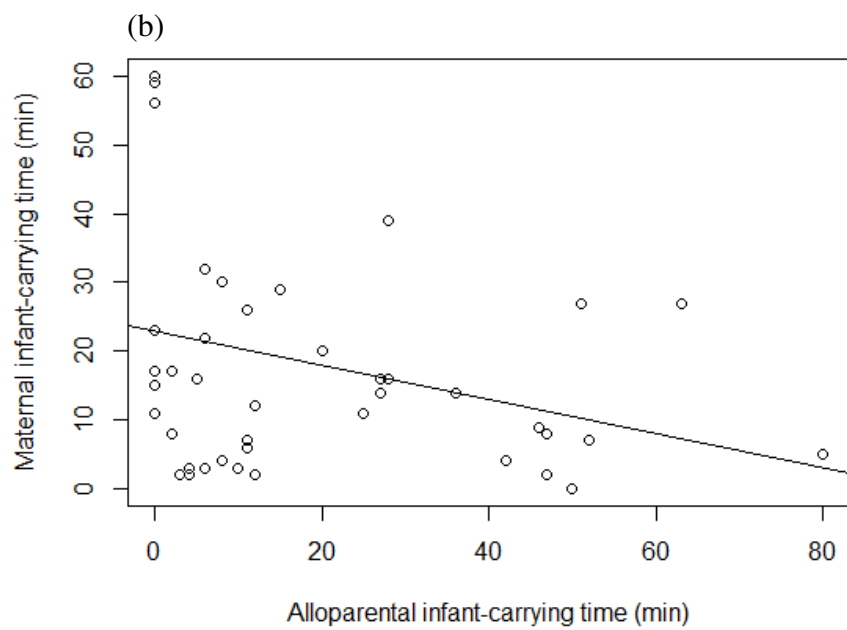
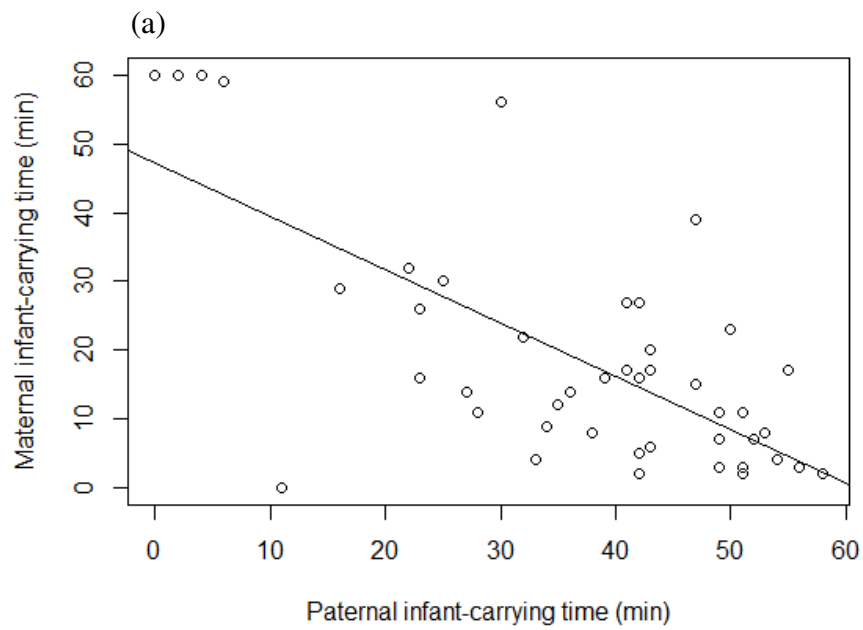
In conclusion, the results indicate that the contribution of alloparents to infant-carrying may not be substantial enough to reduce parental infant-carrying loads and may not be necessary for the successful reproduction of breeding pairs in captive environments. However, the contribution of fathers to infant-carrying appears crucial for successful reproduction since, presumably, the high reproductive rate and high energetic demands of infant care in common marmosets remains highly costly for the mothers even in benign captive environments. The apparent high cost of maternal infant-carrying in captive environments suggests that alloparental, as well as paternal infant-carrying, might be important for the successful reproduction of common marmosets in demanding natural environments, with alloparents receiving potential indirect fitness benefits through kin selection.

Tables and Figures

Table 1. Composition of each group at the time of their observation and mean ages for parents and offspring age classes. The success of parturition following each of the observations is shown as (y) successful or (n) unsuccessful.

Group	Age of Mother (years)	Age of Father (years)	Number of past breeding	Infants	Juveniles	Sub-adults	Adults	Success of subsequent parturition
205	5	7	6	1f, 2m	1f	1m	1f, 1m	y
303	8	5	0	2f				n
606	5	11	0	2m				n
801	4	3	1	1m	2m			n
802	3	2	1	1m	2f			y
803	4	4	2	1f, 1m	1m	1m		y
803	5	5	4	1f, 1m	1f	1f 1m		y
804	5	5	4	2f, 1m	1f	1m	2f, 1m	n
804	6	6	5	2m		2f, 1m		y
Mean age (months \pm se)	60 \pm 2.5	63 \pm 4.6			6 \pm 0.1	10 \pm 0.0	21 \pm 0.8	

f = female, m = male



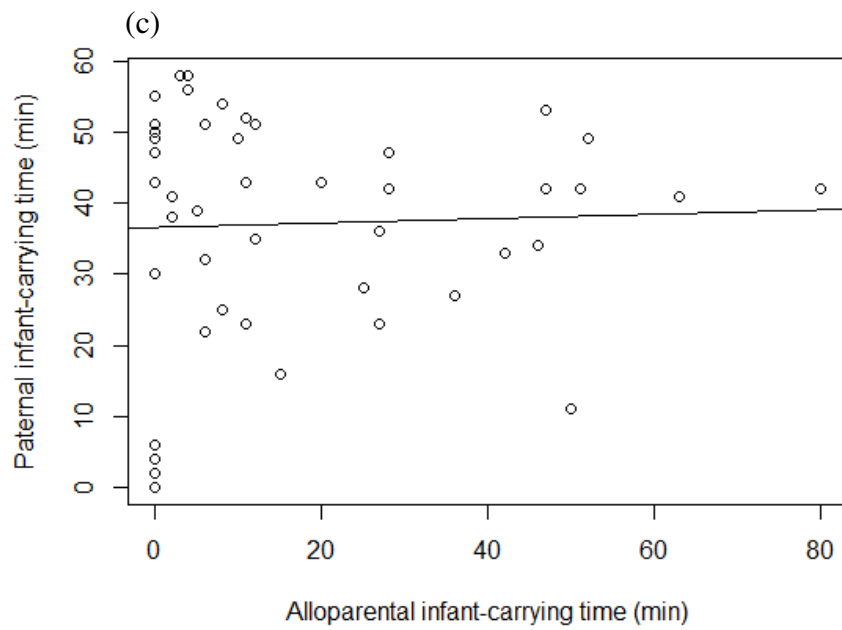
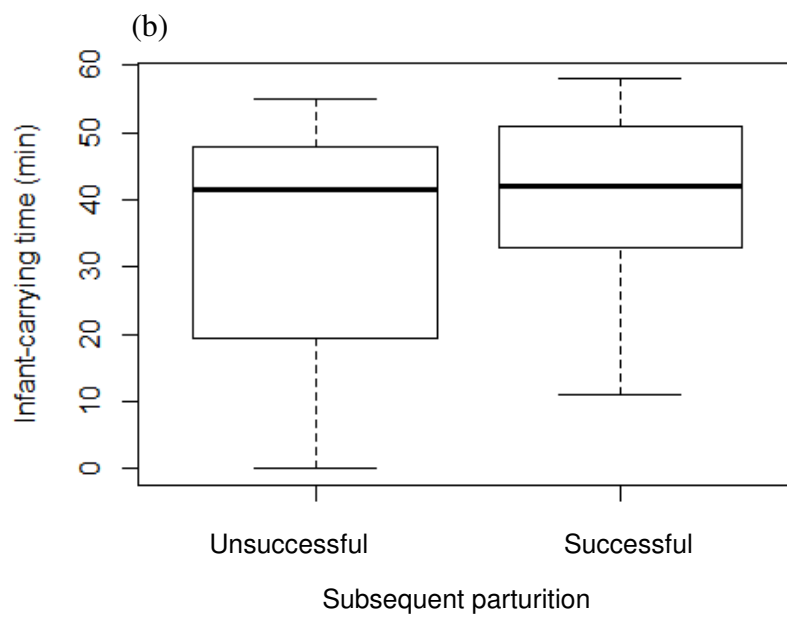
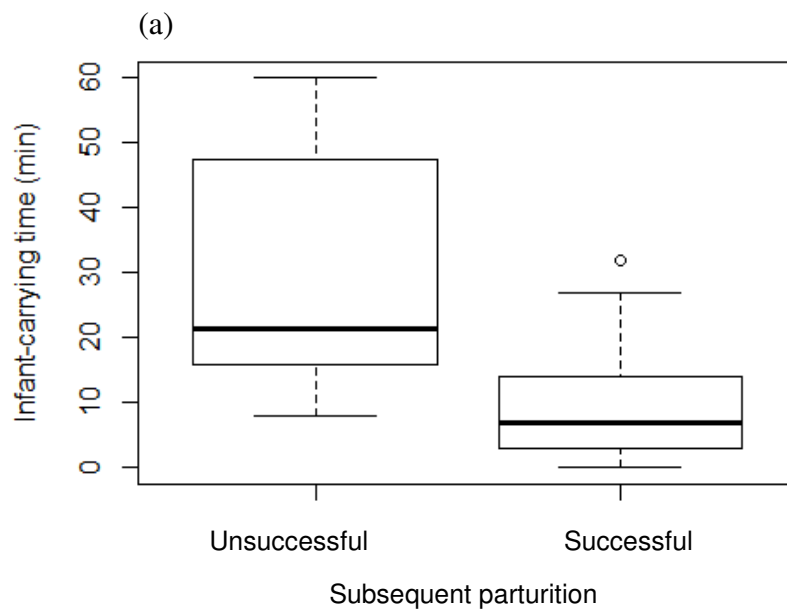


Figure 1. Scatter plots showing total infant-carrying time (minutes) spent by mothers against (a) fathers and (b) all alloparents in the group, and (c) by fathers against all alloparents in the group with regression lines. Each point represents one observation (total five days per group).



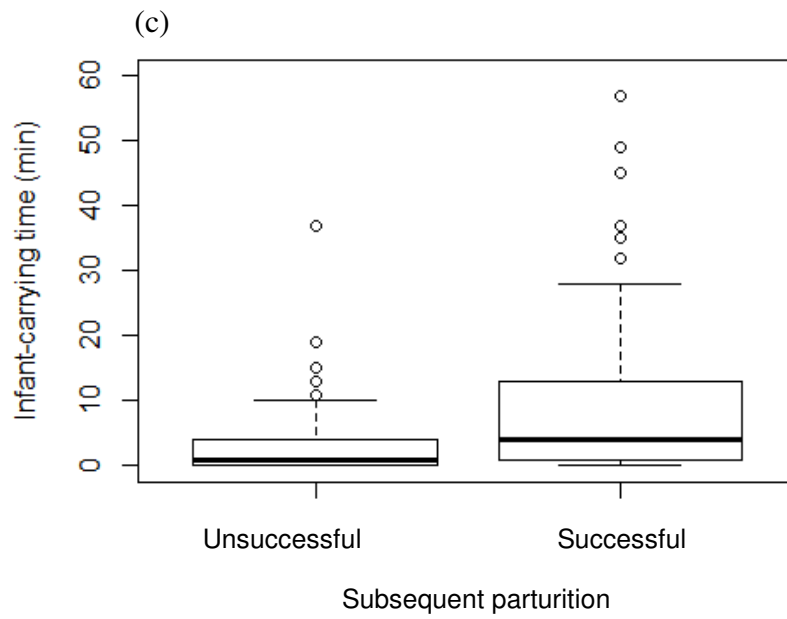


Figure 2. Box plots showing infant-carrying time (minutes) spent by (a) mothers, (b) fathers and (c) individual alloparents in the groups that were successful and unsuccessful in the subsequent parturition.

References

- Achenbach, G. G. & Snowdon, C. T. (2002) Costs of caregiving: Weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *International Journal of Primatology*, 23, 179-189.
- Animal Welfare Committee of the NHMRC (2003) Policy on the care and use of non-human primates for scientific purposes. 27th ed., The National Health and Medical Research Council.
- Arruda, M. D., Yamamoto, M. E. & Bueno, O. F. A. (1986) Interactions between parents and infants, and infants-father separation in the common marmoset (*Callithrix-jacchus*). *Primates*, 27, 215-228.
- Bales, K., Dietz, J., Baker, A., Miller, K. & Tardif, S. D. (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica*, 71, 27-38.
- Bales, K., O'Herron, M., Baker, A. J. & Dietz, J. M. (2001) Sources of variability in numbers of live births in wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, 54, 211-221.
- Bates, D., Maechler, M. & Bolker, B. (2012) lme4: linear mixed-effects models using S4 classes. R package version 0.999999-0. <http://www.CRAN.R-project.org/package=lme4>.
- Brown, J. L. (1987) *Helping and communal breeding in birds: Ecology and evolution*, Princeton, Princeton University Press.
- Caine, N. G. (1993) Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Caine, N. G. (1996) Foraging for animal prey by outdoor groups of Geoffroy's marmosets (*Callithrix geoffroyi*). *International Journal of Primatology*, 17, 933-945.
- Caperos, J. M., Morcillo, A., Pelaez, F., Fidalgo, A. & Sanchez, S. (2012) The effect of infant body mass on carrier travel speed in cotton-top tamarins (*Saguinus oedipus*). *International Journal of Primatology*, 33, 447-459.
- Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, 29, 141-177.
- Cockburn, A., Sims, R. A., Osmond, H. L., Green, D. J., Double, M. C. & Mulder, R. A. (2008) Can we measure the benefits of help in cooperatively breeding birds: The case of superb fairy-wrens *Malurus cyaneus*? *Journal of Animal Ecology*, 77, 430-438.
- Digby, L. J. & Barreto, C. E. (1993) Social organization in a wild population of *Callithrix jacchus*. I. Group composition and dynamics. *Folia Primatologica*, 61, 123-134.
- Duffy, J. E. & Thiel, M. (Eds.) (2007) *Evolutionary ecology of social and sexual systems: Crustaceans as model organisms*. Oxford University Press.
- Dugatkin, L. A. (1997) *Cooperation among animals: An evolutionary perspective*, New York, Oxford University Press.
- Dugatkin, L. A. (2011) *The altruism equation: Seven scientists search for the origins of goodness*, Princeton University Press.
- Faulkes, C. G., Arruda, M. F. & Monteiro da Cruz, M. A. O. (2009) Genetic structure within and among populations of the common marmoset, *Callithrix jacchus*: Implications for cooperative breeding. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Ferrari, S. F. & Digby, L. J. (1996) Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, 38, 19-27.

- Garay, J. & Varga, Z. (2011) Survivor's dilemma: Defend the group or flee? *Theoretical Population Biology*, 80, 217-225.
- Goldizen, A. W. (1987a) Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 20, 99-109.
- Goldizen, A. W. (1987b) Tamarins and marmosets: Communal care of offspring. IN Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds.) *Primates societies*. Chicago, The University of Chicago Press.
- Goldizen, A. W. (1988) Tamarin and marmoset mating systems - unusual flexibility. *Trends in Ecology & Evolution*, 3, 36-40.
- Goldizen, A. W. & Terborgh, J. (1986) Cooperative polyandry and helping behavior in saddle-backed tamarins (*Saguinus fuscicollis*). IN Else, J. G. & Lee, P. C. (Eds.) *Primate ecology and conservation*. New York, Cambridge University Press.
- Hamilton, W. D. (1964) The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, 7, 1-52.
- Hammerstein, P. (Ed.) (2003) *Genetic and cultural evolution of cooperation*. Cambridge, MIT Press.
- Heg, D., Brouwer, L., Bachar, Z. & Taborsky, M. (2005) Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, 142, 1615-1641.
- Ingram, J. C. (1977) Interactions between parents and infants, and development of independence in common marmoset (*Callithrix jacchus*). *Animal Behaviour*, 25, 811-827.
- Johnson, L. D., Petto, A. J. & Sehgal, P. K. (1991) Factors in the rejection and survival of captive cotton top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 25, 91-102.
- Kiers, E. T. & Denison, R. F. (2008) Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. *Annual Review of Ecology Evolution and Systematics*, 39, 215-236.
- Kleiman, D. G. (1977) Monogamy in mammals. *The Quarterly Review of Biology*, 52, 39-69.
- Koenig, A. (1995) Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 35, 311-317.
- Koenig, W. D. & Dickinson, J. L. (Eds.) (2004) *Ecology and evolution of cooperative breeding in birds*. Cambridge, Cambridge University Press.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 187-196.
- Maynard Smith, J. (1964) Group selection and kin selection. *Nature*, 201, 1145-1147.
- Melis, A. P. & Semmann, D. (2010) How is human cooperation different? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2663-2674.
- Nievergelt, C. M., Digby, L. J., Ramakrishnan, U. & Woodruff, D. S. (2000) Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *International Journal of Primatology*, 21, 1-20.
- Price, E. C. (1992a) The benefits of helpers: Effects of group and litter size on infant care in tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 26, 179-190.
- Price, E. C. (1992b) The costs of infant carrying in captive cotton-top tamarins. *American Journal of Primatology*, 26, 23-33.
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>.

- Ridley, A. R. (2007) Factors affecting offspring survival and development in a cooperative bird: Social, maternal and environmental effects. *Journal of Animal Ecology*, 76, 750-760.
- Rothe, H. & Darms, K. (1993) The social organization of marmosets: A critical evaluation of recent concepts. IN Rylands, A. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Rothe, H., Darms, K., Koenig, A., Radespiel, U. & Juenemann, B. (1993a) Long-term study of infant-carrying behavior in captive common marmosets (*Callithrix jacchus*): Effect of nonreproductive helpers on the parents' carrying performance. *International Journal of Primatology*, 14, 79-93.
- Rothe, H., Koenig, A. & Darms, K. (1993b) Infant survival and number of helpers in captive groups of common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 30, 131-137.
- Russell, A. F. & Lummaa, V. (2009) Maternal effects in cooperative breeders: From hymenopterans to humans. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364, 1143-1167.
- Saito, A., Izumi, A. & Nakamura, K. (2011) Fathers have higher motivation for parenting than mothers in common marmoset (*Callithrix jacchus*). *Behaviour*, 148, 1199-1214.
- Sanchez, S., Pelaez, F., Gil-Burmann, C. & Kaumanns, W. (1999) Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 48, 99-111.
- Sanchez, S., Pelaez, F., Morcillo, A. & Gil-Burmann, C. (2005) Effect of the enclosure on carriers' body weight loss in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 66, 279-284.
- Schradin, C. & Anzenberger, G. (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: An experimental analysis. *Animal Behaviour*, 62, 289-295.
- Snowdon, C. T. (1996) Infant care in cooperatively breeding species. IN Rosenblatt, J. S. & Snowdon, C. T. (Eds.) *Parental care: Evolution, mechanisms and adaptive significance*. San Diego, Academic Press.
- Solomon, N. G. & French, J. A. (Eds.) (1997) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Stacey, P. B. & Koenig, W. D. (Eds.) (1990) *Cooperative breeding in birds: Long-term studies of ecology and behavior*. Cambridge, Cambridge University Press.
- Stevenson, M. F. (1976) Birth and perinatal behavior in family groups of common marmoset (*Callithrix jacchus jacchus*), compared to other primates. *Journal of Human Evolution*, 5, 365-381.
- Stevenson, M. F. & Rylands, A. B. (1988) The marmosets, genus *Callithrix*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Strassmann, J. E., Gilbert, O. M. & Queller, D. C. (2011) Kin discrimination and cooperation in microbes. *Annual Review of Microbiology*, 65, 349-367.
- Taborsky, M. (1994) Sneakers, satellites, and helpers - parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, 23, 1-100.
- Tardif, S., Power, M., Layne, D., Smucny, D. & Ziegler, T. (2004) Energy restriction initiated at different gestational ages has varying effects on maternal weight gain and pregnancy outcome in common marmoset monkeys (*Callithrix jacchus*). *British Journal of Nutrition*, 92, 841-849.
- Tardif, S. D. (1994) Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant-care patterns. *American Journal of Primatology*, 34, 133-143.

- Tardif, S. D. (1997) The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. IN Solomon, N. G. & French, J. A. (Eds.) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Tardif, S. D., Carson, R. L. & Gangaware, B. L. (1990) Infant-care behavior of mothers and fathers in a communal-care primate, the cotton-top tamarin (*Saguinus-oedipus*). *American Journal of Primatology*, 22, 73-85.
- Tardif, S. D. & Jaquish, C. E. (1997) Number of ovulations in the marmoset monkey (*Callithrix jacchus*): Relation to body weight, age and repeatability. *American Journal of Primatology*, 42, 323-329.
- West, S. A., Diggle, S. P., Buckling, A., Gardner, A. & Griffins, A. S. (2007) The social lives of microbes. *Annual Review of Ecology Evolution and Systematics*, 38, 53-77.
- Wilson, E. O. (1971) *The insect societies*, Cambridge, Belknap Press of Harvard University Press.
- Wright, J. & Russell, A. F. (2008) How helpers help: Disentangling ecological confounds from the benefits of cooperative breeding. *Journal of Animal Ecology*, 77, 427-429.
- Ximenes, M. & Sousa, M. B. C. (1996) Family composition and the characteristics of parental care during the nursing phase of captive common marmosets (*Callithrix jacchus*). *Primates*, 37, 175-183.
- Yamamoto, M. E. (1990) Ontogênese das relações sociais e dinâmica do cuidado com a prole no sagui comum (*Callithrix jacchus*). Escola Paulista de Medicina. Universidade Federal do Rio Grande do Norte. São Paulo, Brazil. PhD thesis.
- Yamamoto, M. E. & Box, H. O. (1997) The role of non-reproductive helpers in infant care in captive *Callithrix jacchus*. *Ethology*, 103, 760-771.
- Yamamoto, M. E., Box, H. O., Albuquerque, F. S. & Arruda, M. D. (1996) Carrying behaviour in captive and wild marmosets (*Callithrix jacchus*): A comparison between two colonies and a field site. *Primates*, 37, 297-304.
- Yamamoto, M. E., Box, H. O., De Arruda, M. F. & Bueno, O. F. A. (1987) Compensation in abnormal conditions of infant care in the common marmoset (*Callithrix jacchus*). *International Journal of Comparative Psychology*, 1, 97-106.
- Zahed, S. R., Kurian, A. V. & Snowdon, C. T. (2010) Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology*, 72, 296-306.
- Ziegler, T. E., Prudom, S. L. & Zahed, S. R. (2009) Variations in male parenting behavior and physiology in the common marmoset. *American Journal of Human Biology*, 21, 739-744.

Chapter Three

No sex differences in infant-carrying by related helpers in captive common marmosets (*Callithrix jacchus*): An experimental study



Common Marmosets (*Callithrix jacchus*) in one of the outdoor cages, which were used as experimental cages.

Abstract

In many cooperatively breeding species, contributions to alloparental care differ between the sexes. It has been suggested that the sex that stays in the natal group should contribute more to alloparental care when group size correlates with the survival and/or reproductive success of the philopatric sex (group augmentation hypothesis). In a cooperatively breeding primate, the common marmoset (*Callithrix jacchus*), although dispersal events occur at low frequency, females are known to disperse more often than males. Therefore, males could be expected to contribute more to alloparental care than females. While in the social groups, males have been reported to contribute more to alloparental infant-carrying than females. However, the contribution of helpers to infant-carrying within the social groups is possibly under the influences of social and environmental confounding factors. Therefore, the contribution of helpers to infant-carrying observed in the presence of other group members may not demonstrate the actual capacity or motivation of the helpers to engage in infant-carrying. Accordingly, I experimentally investigated sex differences in alloparental infant-carrying behaviour in captive common marmosets by separating the helpers (13 males and 17 females) from the social groups and measuring the time spent carrying the infant. Contrary to my expectation, I found no sex differences in alloparental infant-carrying behaviour between the sexes when helpers were separated from other members of the groups (mean number of minutes spent carrying infants \pm se: male: 30 ± 0.0 ; female: 26 ± 1.1). This suggests that the underlying propensities to engage in infant-carrying are similar between male and female helpers. Therefore the benefit of carrying infants might be similar for male and female helpers when the influence of social and environmental factors are minimised. The results also suggest that the decrease in the contribution of helpers to infant-carrying with increasing infant age is not influenced by the presence of other members of the groups. The investigation into the benefits that maintain the underlying propensity of helpers to carry infants, and the effects of social and environmental factors on the contribution of helpers to infant-carrying would improve our understandings on the evolution of alloparental infant-carrying behaviour.

Introduction

Alloparental behaviour, where individuals other than the parents of the offspring contribute to its care, is relatively common in birds and mammals (Stacey & Koenig 1990; Solomon & French 1997). In many species, contributions to alloparental behaviour differ between the sexes (Cockburn 1998; Clutton-Brock *et al.* 2002). This sex difference has been attributed, in some instances, to the difference in reproductive strategies between the sexes (Greenwood 1980; Cockburn 1998; Clutton-Brock *et al.* 2002). In cooperatively breeding species, one of the sexes is frequently observed to stay in the natal group and contribute more to alloparental care, whereas the other sex tends to disperse more and achieve reproduction outside of the natal group (Koenig *et al.* 1992; Lawson Handley & Perrin 2007). It has been suggested that the sex that stays in the natal group should contribute more to cooperative breeding when group size correlates with the survival and/or reproductive success of the philopatric sex (group augmentation: Woolfenden 1975; Emlen & Wrege 1989; Cockburn 1998; Kokko *et al.* 2001; Clutton-Brock 2002, 2009). In avian societies, male helpers generally contribute more than female helpers, and males remain in their natal territory to defend resources while females disperse to suitable territory to breed (Cockburn 1998). In contrast, in mammalian societies, it is more common for female helpers to contribute more than male helpers and females remain in their natal group to raise their young while males disperse to join other groups or to establish their own group (Clutton-Brock 2009; Clutton-Brock & Lukas 2012).

However, not all mammals show female philopatry. Callitrichines, such as common marmosets (*Callithrix jacchus*), are small neotropical primates that live in a group of extended family members (Digby & Barreto 1993; Nievergelt *et al.* 2000), which usually consists of a dominant breeding pair and several male and female subordinate group members (Ferrari & Digby 1996). They are cooperative breeders whereby all group members carry and provide care for the infants of the dominant pair (Ingram 1977; Stevenson 1976). Although dispersal events occur at low frequency (0.42 to 3.44 individuals per group per year: Sousa *et al.* 2009) and, when it does occur, both sexes are known to disperse from their natal groups, females have been observed to disperse more often than males in free-ranging groups of common marmosets (66% females compared to 34% males: Sousa *et al.* 2009). Thus, on the one hand, common marmosets might show no sex bias in alloparental behaviour because the frequency of dispersal is low and, as a result, both sexes may stay in the natal group long enough to equally benefit from their contribution to the group through increased group size.

On the other hand, common marmosets could potentially show a sex bias in their alloparental behaviour more in line with avian societies, where female-biased dispersal is common. If the latter turns out to be the case, male helpers might be expected to contribute more to infant care than female helpers.

Male helpers have been reported to spend more time carrying infants than female helpers in the wild in some species of callitrichines, including common marmosets (Goldizen 1987; Ferrari 1992; Albuquerque 1999 cited in Yamamoto *et al.* 2008). However, no quantitative analysis of sex difference in alloparental infant-carrying is available in those field observations. In contrast, no sex difference in the contribution of helpers to infant-carrying has been shown in captive common marmosets although, in general, male helpers tend to be involved in infant care more than female helpers (Box 1977; Yamamoto & Box 1997; Mills *et al.* 2004). It has been speculated that the presence of other group members might affect the apparent contribution of the helpers to infant-carrying (Rothe *et al.* 1993; Yamamoto *et al.* 1996; Yamamoto & Box 1997; Yamamoto *et al.* 2008). Parents of the infants seem to regulate the helpers' participation in infant-carrying (Koenig & Rothe 1991). Also, in some callitrichines, helpers have been observed competing with each other to carry the infant (Price 1991). Moreover, in larger groups, infant-carrying loads tend to be distributed among helpers and, as a result, individual infant-carrying bouts can be decreased (Yamamoto *et al.* 2008). Therefore, the contribution to infant-carrying observed in the presence of other group members may not demonstrate the actual capacity or motivation of the helpers to engage in infant-carrying.

Accordingly, I set out to experimentally investigate sex differences in alloparental behaviour in captive common marmosets by comparing the infant-carrying behaviour of male and female helpers separated from the social group. Separation of helpers from the rest of the social group allowed me to eliminate the possibility of the helpers' infant-carrying behaviour being affected by the presence of other group members. By doing so, the difference in the intrinsic propensity of male and female helpers to carry infants can be examined. If male and female helpers differ in the benefits they gain from infant-carrying behaviour, this should, in turn, be reflected in sex differences in their propensity to carry infants. Since males stay in the natal group more than females, males may benefit more from investing in the group via the group augmentation effect than females. For that reason, I expect that male helpers would have a higher propensity to contribute to infant-carrying than female helpers.

Methods

Design

The amounts of time spent in infant-carrying by male and female helpers separated from the social groups were examined for the sex differences in alloparental behaviour in captive common marmosets. A helper and an infant from the same social group were kept in an experimental cage and video recorded. The amount of time the helper spent carrying the infant was measured for 30 minutes from the video recording. The infant-carrying times were measured from 13 male and 17 female helpers. Each pair of helper and infant was tested twice at before and after the feeding on subsequent days. The infant-carrying times of male and female helpers were compared and analysed statistically.

Animal housing

Animals used in this study were from the national marmoset colony located at the Gippsland Field Station, Monash University, Australia. Common marmosets at the facility were separated into breeding groups, which consist of two to 12 individuals and formed by a dominant breeding pair and their offspring as subordinate group members (helpers). All individuals (except infants) were microchipped for identification. Infants had a small patch (~1cm²) of their coat on the upper or lower back shaved to allow individuals to be distinguished from their siblings from the same litter. Each group was kept in an indoor cage (1.8m (H) x 1.2m x 0.75m), which is connected to an outdoor cage (2m (H) x 2m x 0.7m) by a pipe with a gate at the each end for daytime access. The indoor cages were placed within rooms, with six cages in each room. The outdoor cages were placed along the east and west side of the building under awnings and enclosed with meshed wire. Both the indoor and outdoor cages were placed next to other cages. Animals in cages were able to see, hear and smell other animals in nearby cages, although direct contact with animals in adjacent cages was prevented by the stainless-steel walls of the cages. Between the indoor and outdoor cages, olfactory and auditory contact may occur through the pipe that connects them. The possibility of visual contact between the indoor and outdoor cages cannot be completely excluded, due to windows on the walls between indoor and outdoor cages. However, visual contact between indoor and outdoor cages is considered unlikely since the cages were not facing directly towards each other. All individuals were fed once a day in the late morning with marmoset pellets (Specialty Feeds, Glen Forrest, Western Australia) and a wide variety of fruits,

vegetables and mealworms. Water bottles were provided in each indoor cage. The floors of the indoor cages were covered with sawdust, while the floors of outdoor cages comprised of bare concrete. All of the indoor cages were maintained at 25 - 30°C, with 40 - 60% humidity. Internal lighting was maintained on a 12 hours light-dark cycle. The facility complies with the NHMRC *Policy on the Care and Use of Non-Human Primates for Scientific Purposes* (Animal Welfare Committee of the NHMRC 2003).

Study subjects

Eleven male (mean age = 16 months, range = 10 - 28) and 17 female (mean age = 18 months, range = 11 - 39) helpers from 12 groups were tested with 23 infants (10 males, 13 females, range = 8 - 46 days old), that were younger full siblings of the helpers. Two male helpers were tested twice at different ages (11 and 16, and 11 and 15 months, respectively) with a new litter of infants in the group. Hence, I used 30 helper-infant pairs (13 male and 17 female helpers), which were tested in two treatments (i.e. $n = 26$ male helper trials and 34 female helper trials). Some of the helpers that belonged to the same social group at the same breeding event were tested by using the same infant when there was no other infant available in the group (e.g. singleton or other infants were in poor health). Helper ages were not different between male and female helpers (Wilcoxon rank sum test: $W = 554$, $p = 0.09$). However, the mean age of the infants paired with male helpers was younger than that of female helpers (days \pm se: 24 ± 1.9 and 33 ± 1.3 respectively. Wilcoxon rank sum test: $W = 685$, $p < 0.01$) (Figure 1). For reasons unrelated to the current study, one male and five female helpers (age = 11 – 21 months) were separated from the infants (2 males and 2 females, age = 27 - 43 days) for two weeks prior to the start of the experiment. During the separation, helpers were kept apart from the infants and parents in two cages that were facing each other to allow visual, vocal and olfactory contact. Trials for these helpers were performed more than one week after they were reunited with their social group. Separation was included in the statistical models, and infant-carrying time did not vary with separation (see results).

Procedure

Experiments were performed in the group's outdoor cage to ensure that test subjects were familiar with their surrounding environment. An acacia branch (approximately 40 cm in length, 6 cm in diameter) with holes (approximately 20 in number, 2 cm in depth) filled with reconstituted acacia gum (Bronson & Jacobs, Villawood, New South Wales, Australia) was

vertically suspended from the ceiling of the cage as a supplemental food source that the helper can access during the trial. A helper was caught by hand and separated from the group and immediately released into the outdoor cage. After a five-minute habituation period, the infant from the group, which was caught by hand and weighed, was introduced into the experimental cage by directly passing it to the helper. If the helper did not come close enough to take the infant directly, the infant was left on an object (meshed cage wall, wooden branch or metal shelf) near the helper to be picked up (all infants were picked up within 1 minute). The pair was left in the cage for 40 minutes to be video recorded by four surveillance cameras (94mm (D) x 78mm (H), WIT1035SDW, WIT Security Technology Co., Ltd. Taoyuan, Taiwan R.O.C.) that were attached to the four corners of the cage's ceiling to record the entire cage. At the completion of the trial, the pair was allowed to join the rest of the group by opening the gate at the entrance to the pipe that connects the outdoor and indoor cages. Each pair of helper and infant was tested twice on subsequent days, once before and once after the daily, late-morning feeding of the group. Thirteen pairs (6 male and 7 female helpers) were first tested before feeding, and 17 pairs (7 male and 10 female helpers) were first tested after feeding. The time spent in infant-carrying and foraging on the acacia branch was measured from the video footage for 30 minutes from the time the helper first took the infant. Infant-carrying behaviour was defined as when the four limbs of the infant were touching nowhere else but on the helper. The foraging behaviour on the acacia branch was defined as when the helper was gnawing on the acacia branch. The video footages were not processed blind, relative to the treatments of trial (i.e. before or after feeding, and the sex of helper). During the trials, helpers spent similar amounts of time accessing the acacia gum regardless of whether the trial took place before or after feeding (Wilcoxon signed rank test: $V = 105.5$, $p = 0.74$).

Statistical analyses

I analysed the proportion of time helpers spent carrying the infant. I could not directly compare male and female infant-carrying times in one statistical model because all male helpers carried infants for the entire duration of the trials (Figure 1), resulting in significant heterogeneity of variance; significant higher variance in females than males (The variances in infant-carrying times between male and female helpers were compared in a one-sided Two-sample Kolmogorov-Smirnov test; see results). Mean infant-carrying times of male and female helpers were, therefore, tested separately against the hypothetical mean of 30 minutes in one-sided Wilcoxon rank sum tests with continuity correction. In these tests, infant-

carrying times from the trials before and after feeding were pooled since there was no significant effect of feeding on infant-carrying time (Table 1). Since there was no variation in infant-carrying times of male helpers, only the infant-carrying times of female helpers were analysed for the effects of possible influential factors on time spent carrying an infant. To analyse female infant-carrying behaviour, I constructed a generalized linear mixed model, using the lme4 package (Bates *et al.* 2012) in R 3.2.1 (R Core Team 2015) including individual ID, infant ID and group ID as random factors to control for pseudoreplication (the variance associated with the random factors was very small, not shown). Time spent carrying (minutes) was included in the model as the dependent variable using the ‘cbind’ command with binomial totals = 30 minutes. As independent variables, I included: infant age (days - centred and scaled to the mean and SD), time of day (whether the observation was carried out before or after the feeding of the group) and separation (whether the helper and infant were separated prior to the study).

Results

In my experiment, all male helpers carried infants for the entire duration of the trials (Figure 1a). By contrast, female helpers varied their total infant-carrying time from 11 to 30 (mean 26) minutes (Figure 1b) though all female helpers also carried infants. Variance in female infant-carrying time was significantly greater than that of male helpers (Two-sample Kolmogorov-Smirnov test: $D_{m,f} = 0.41$, $p < 0.01$). However, the mean infant-carrying time did not differ for male and female helpers since the mean infant-carrying times were both not less than 30 minutes (minutes \pm se: male: 30 ± 0.0 ; female: 26 ± 1.1 ; Wilcoxon rank sum test: male: $W = 13$, $p = 1$; female: $W = 10$, $p = 0.23$). The time spent in infant-carrying by female helpers was not affected by feeding (time of day) or whether the infant and helper had been separated prior to the study. However, the infant-carrying time was affected by infant age (Table 1), with helpers (i.e. females) spending significantly less time carrying older infants. In the trials with female helpers, the infants four weeks old or younger ($n = 9$) were carried for the entire duration of the trial (30 minutes) except one infant (27 minutes). In contrast, the carrying time for the infants older than four weeks ($n = 25$) ranged between 11 and 30 minutes (Figure 1b).

Discussion

I found no evidence for sex differences in alloparental infant-carrying behaviour when helpers were separated from other members of the groups in captive common marmosets. The result suggests that the underlying propensity to engage in infant-carrying is similar with regard to the sex of helpers, even though the behaviour could vary between the sexes according to social and environmental circumstances, such as the number of helpers in the group, food availability or predation risk (Caine 1993; Zahed *et al.* 2010).

The underlying propensity to carry infants could be similar for male and female helpers if the benefits of alloparental infant-carrying are alike for both sexes. Larger group size often improves the survival and future reproductive success of the helpers who remain in the group (Emlen & Wrege 1989; Cockburn 1998; Clutton-Brock *et al.* 2001; Lawson Handley & Perrin 2007). In common marmosets, although females emigrate more often than males, dispersal events occur in low frequency (Sousa *et al.* 2009). Therefore the majority of male and female helpers still remain in the group for the substantial period. Hence, both sexes of helpers may equally benefit from infant-carrying through increased group size. Also, experience in infant care has been shown to increase the future reproductive success of both male and female helpers (Pryce 1993; Mota & Sousa 2000; Mota *et al.* 2006; but see Tardif *et al.* 1984). Moreover, possible indirect benefits of infant-carrying through increased survival and reproductive success of relatives is not sex specific. In the current experiment, helpers were older full siblings of the infants. This is also the case in wild populations, where helpers are typically the older siblings of the infants within the group (Nievergelt *et al.* 2000; Faulkes *et al.* 2003). Since the relatedness of helpers to their infant siblings is the same for both sexes (Faulkes *et al.* 2009), the benefits of infant-carrying for the helpers through kin selection should be same for male and female helpers (Hamilton 1964). Likewise, the costs of infant-carrying would also be similar for male and female helpers. Carrying infant has been shown to decrease the leaping distance equally for male and female helpers (Schradin & Anzenberger 2001). It suggests that the energetic costs of infant-carrying, and the probability of increased predation risk and decreased foraging efficiency caused by impeded mobility would be similar to both male and female helpers in sexually monomorphic common marmosets (Araújo *et al.* 2000). Accordingly, male and female helpers would contribute similarly to infant-carrying when the influence from social and environmental circumstances are minimised, as it was observed in this study.

Although the underlying propensity to carry infants might be similar for male and female helpers, various social and environmental factors may affect the actual contribution of helpers to infant-carrying. In social groups, breeding pairs seem to regulate the participation of helpers in infant-carrying by maintaining close interaction with a few “qualified helpers”, which are often one or two of the oldest adult male helpers in the groups (Koenig & Rothe 1991; Rothe & Darms 1993). In contrast, breeding females have been observed to prevent adult female helpers from carrying their infants (Albuquerque 1999 cited in Yamamoto *et al.* 2009) by chasing the adult females away when they approached other helpers with infants (Koenig & Rothe 1991). In common marmosets, sub-adult helpers have been shown to carry infants less and for shorter bouts than adult helpers, though they showed equal interest in infants as adult helpers (Yamamoto & Box 1997). This may suggest the possibility of competition in infant-carrying among helpers, in which older helpers may have an advantage over younger helpers (Yamamoto & Box 1997). Moreover, the preference of infants for the carriers may also influence infant-carrying behaviour (Zahed *et al.* 2010). When there are choices, infants may choose to be carried by preferred carriers, which may be more experienced and/or familiar to the infants, than by other carriers (Saito *et al.* 2011). Furthermore, helpers are involved more in infant-carrying and infants tend to be carried for a longer period in natural environments than in captive environments (Yamamoto *et al.* 1996). Accordingly, the extent of helpers’ involvement in infant-carrying seems to be determined by the accessibility to the infants, and the demand for alloparental infant-carrying in the social groups.

Female helpers carried older infant less than younger infant although the average time spent in infant-carrying did not differ between male and female helpers. This suggests that the presence of other available carriers does not influence the reduction in infant-carrying with increasing infant age. Decrease in infant-carrying with increasing infant age has been observed in groups of captive and wild marmosets. Infants start to leave the carriers and explore the surrounding environment by themselves around three to four weeks of age (Ingram 1977; Stevenson & Rylands 1988; Yamamoto 1993; Yamamoto *et al.* 2008). I also observed that, although there were no other carriers to share the infant-carrying load, the time spent in infant-carrying only decreased when the infants were older than four weeks. Infants four weeks old or younger were carried full time (30 minutes). In contrast, the carrying time for the infants older than four weeks largely varied between 11 to 30 minutes. Further

investigation on this aspect, especially on the causes of the variation in the decrease in infant-carrying, may provide insights into the proximate causes of infant-carrying behaviour.

In the current experiment, infant-carrying times of male and female helpers could not be directly compared in a single statistical test because of the lack of variation in infant-carrying time of male helpers. Ideally, it would have been desirable to pair more male helpers with older infants. Unfortunately, this was not possible due to the limited number of available animals at the time the experiment was being carried out. Future studies, in this regard, could redress this issue with a larger and more comprehensive sample involving males and females being paired with a greater range of different aged infants.

In conclusion, the contribution to infant-carrying did not differ between male and female helpers when helpers were separated from other members of the groups. It suggests that the underlying propensity to engage in infant-carrying may be similar between male and female helpers. Therefore the extent of helpers' involvement in infant-carrying seems to be determined by the accessibility to the infants, and the demand for alloparental infant-carrying in the social groups. The results also suggest that the decrease in the contribution of helpers to infant-carrying with increasing infant age is not influenced by the presence of other members of the groups. The investigation into the effects of social and environmental factors on the contribution of helpers to infant-carrying, and the causes of the decrease in alloparental infant-carrying with increasing infant age will improve our understanding of the proximate causes of infant-carrying behaviour. Understanding the causes of variation in the contribution of individuals to alloparental behaviour will illuminate the benefits, which the behaviour is expected to vary with it.

Tables and Figures

Table 1. Result of a generalized linear mixed model showing the effects of the variables on time spent carrying infant by female helpers. The model included individual ID, infant ID and group ID as random factors, and the time spent in infant-carrying (minutes) by each helper (34 female trials) as the dependent variable using the ‘cbind’ command with binomial totals = 30 minutes. Infant age was centred and scaled to the mean and SD.

	Estimate	SE	z	p
(Intercept)	-0.18	0.07	-2.42	0.02
Infant age (days)	-0.11	0.05	-2.16	0.03
Time of day ¹	0.08	0.09	0.91	0.37
Separation	-0.05	0.11	-0.47	0.64

¹relative to “after feeding”

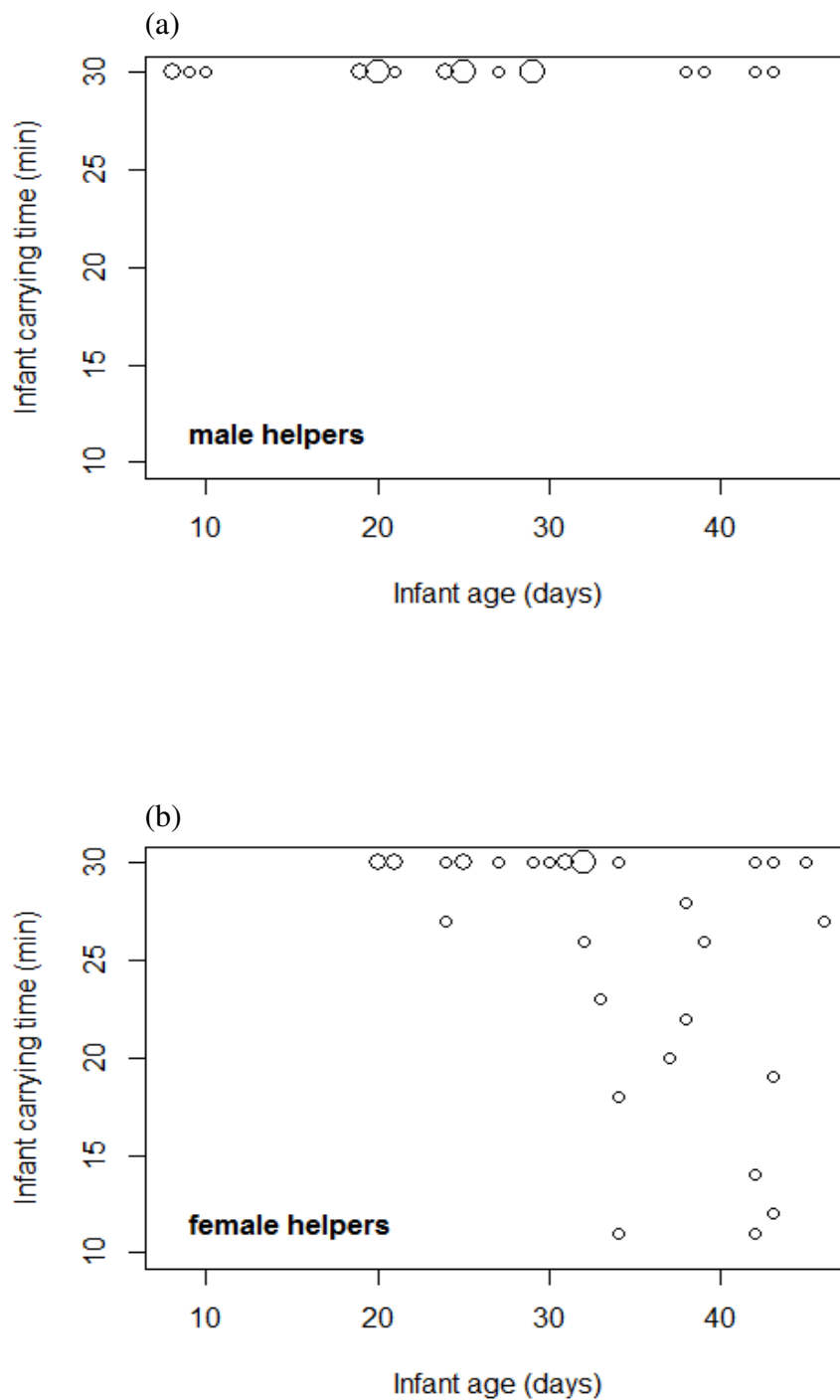


Figure 1. Total infant-carrying time (minutes) spent by (a) male and (b) female helpers with infants of various ages. The outcomes of each trial were plotted rather than the average of two trials (i.e., before and after feeding) of an individual helper. The size of each data point corresponds to the number of overlapping data points.

References

- Albuquerque, F. S. (1999) Cuidado cooperativo à prole em *Callithrix jacchus*: Dinâmica em ambiente natural. the Universidade de São Paulo. São Paulo, Brazil. PhD thesis.
- Animal Welfare Committee of the NHMRC (2003) Policy on the care and use of non-human primates for scientific purposes. 27th ed., The National Health and Medical Research Council.
- Araújo, A., Arruda, M. F., Alencar, A. I., Albuquerque, F., Nascimento, M. C. & Yamamoto, M. E. (2000) Body weight of wild and captive common marmosets (*Callithrix jacchus*). *International Journal of Primatology*, 21, 317-324.
- Bates, D., Maechler, M. & Bolker, B. (2012) lme4: linear mixed-effects models using S4 classes. R package version 0.999999-0. <http://www.CRAN.R-project.org/package=lme4>.
- Box, H. O. (1977) Quantitative data on the carrying of young captive monkeys (*Callithrix jacchus*) by other members of their family groups. *Primates*, 18, 475-484.
- Caine, N. G. (1993) Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Clutton-Brock, T. (2002) Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science*, 296, 69-72.
- Clutton-Brock, T. (2009) Structure and function in mammalian societies. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364, 3229-3242.
- Clutton-Brock, T. H. & Lukas, D. (2012) The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, 21, 472-492.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S. & Cameron, E. Z. (2001) Effects of helpers on juvenile development and survival in meerkats. *Science*, 293, 2446-2449.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z. & McIlrath, G. M. (2002) Evolution and development of sex differences in cooperative behavior in meerkats. *Science*, 297, 253-256.
- Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, 29, 141-177.
- Digby, L. J. & Barreto, C. E. (1993) Social organization in a wild population of *Callithrix jacchus*. I. Group composition and dynamics. *Folia Primatologica*, 61, 123-134.
- Emlen, S. T. & Wrege, P. H. (1989) A test of alternate hypotheses for helping behavior in white-fronted bee-eaters of Kenya. *Behavioral Ecology and Sociobiology*, 25, 303-319.
- Faulkes, C. G., Arruda, M. F. & Monteiro da Cruz, M. A. O. (2003) Matrilineal genetic structure within and among populations of the cooperatively breeding common marmoset, *Callithrix jacchus*. *Molecular Ecology*, 12, 1101-1108.
- Faulkes, C. G., Arruda, M. F. & Monteiro da Cruz, M. A. O. (2009) Genetic structure within and among populations of the common marmoset, *Callithrix jacchus*: Implications for cooperative breeding. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Ferrari, S. F. (1992) The care of infants in a wild marmoset (*Callithrix flaviceps*) group. *American Journal of Primatology*, 26, 109-118.
- Ferrari, S. F. & Digby, L. J. (1996) Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, 38, 19-27.

- Goldizen, A. W. (1987) Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 20, 99-109.
- Greenwood, P. J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28, 1140-1162.
- Hamilton, W. D. (1964) The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, 7, 1-52.
- Ingram, J. C. (1977) Interactions between parents and infants, and development of independence in common marmoset (*Callithrix jacchus*). *Animal Behaviour*, 25, 811-827.
- Koenig, A. & Rothe, H. (1991) Social relationships and individual contribution to cooperative behavior in captive common marmosets (*Callithrix jacchus*). *Primates*, 32, 183-195.
- Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. & Stanback, M. T. (1992) The evolution of delayed dispersal in cooperative breeders. *The Quarterly Review of Biology*, 67, 111-150.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 187-196.
- Lawson Handley, L. J. & Perrin, N. (2007) Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, 16, 1559-1578.
- Mills, D. A., Windle, C. P., Baker, H. F. & Ridley, R. M. (2004) Analysis of infant carrying in large, well-established family groups of captive marmosets (*Callithrix jacchus*). *Primates*, 45, 259-265.
- Mota, M. T. & Sousa, M. B. (2000) Prolactin levels of fathers and helpers related to alloparental care in common marmosets, *Callithrix jacchus*. *Folia Primatologica*, 71, 22-26.
- Mota, M. T. D., Franci, C. R. & de Sousa, M. B. C. (2006) Hormonal changes related to paternal and alloparental care in common marmosets (*Callithrix jacchus*). *Hormones and Behavior*, 49, 293-302.
- Nievergelt, C. M., Digby, L. J., Ramakrishnan, U. & Woodruff, D. S. (2000) Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *International Journal of Primatology*, 21, 1-20.
- Price, E. C. (1991) Competition to carry infants in captive families of cotton-top tamarins (*Saguinus oedipus*). *Behaviour*, 118, 66-88.
- Pryce, C. R. (1993) The regulation of maternal behavior in marmosets and tamarins. *Behavioural Processes*, 30, 201-224.
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>.
- Rothe, H. & Darms, K. (1993) The social organization of marmosets: A critical evaluation of recent concepts. IN Rylands, A. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Rothe, H., Darms, K., Koenig, A., Radespiel, U. & Juenemann, B. (1993) Long-term study of infant-carrying behavior in captive common marmosets (*Callithrix jacchus*): Effect of nonreproductive helpers on the parents' carrying performance. *International Journal of Primatology*, 14, 79-93.
- Saito, A., Izumi, A. & Nakamura, K. (2011) Development of infant common marmosets' (*Callithrix jacchus*) preference for their parents over adults from another group. *Primates*, 52, 43-50.

- Schradin, C. & Anzenberger, G. (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: An experimental analysis. *Animal Behaviour*, 62, 289-295.
- Solomon, N. G. & French, J. A. (Eds.) (1997) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Sousa, M. B. C., Araújo, A., Yamamoto, M. E., Albuquerque, A. C. S. R. & Arruda, M. F. (2009) Emigration as a reproductive strategy of the common marmosets (*Callithrix jacchus*). IN Davis, L. C., Ford, S. M. & Porter, L. M. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Stacey, P. B. & Koenig, W. D. (Eds.) (1990) *Cooperative breeding in birds: Long-term studies of ecology and behavior*. Cambridge, Cambridge University Press.
- Stevenson, M. F. (1976) Birth and perinatal behavior in family groups of common marmoset (*Callithrix jacchus jacchus*), compared to other primates. *Journal of Human Evolution*, 5, 365-381.
- Stevenson, M. F. & Rylands, A. B. (1988) The marmosets, genus *Callithrix*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Tardif, S. D., Richter, C. B. & Carson, R. L. (1984) Effects of sibling-rearing experience on future reproductive success in two species of callitrichidae. *American Journal of Primatology*, 6, 377-380.
- Woelfenden, G. E. (1975) Florida scrub jay helpers at the nest. *The Auk*, 92, 1-15.
- Yamamoto, M. E. (1993) From dependence to sexual maturity: The behavioural ontogeny of callitrichidae. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Yamamoto, M. E., Albuquerque, F. S., Lopes, N. A. & Ferreira, E. S. (2008) Differential infant carrying in captive and wild common marmosets (*Callithrix jacchus*). *Acta Ethologica*, 11, 95-99.
- Yamamoto, M. E. & Box, H. O. (1997) The role of non-reproductive helpers in infant care in captive *Callithrix jacchus*. *Ethology*, 103, 760-771.
- Yamamoto, M. E., Box, H. O., Albuquerque, F. S. & Arruda, M. D. (1996) Carrying behaviour in captive and wild marmosets (*Callithrix jacchus*): A comparison between two colonies and a field site. *Primates*, 37, 297-304.
- Zahed, S. R., Kurian, A. V. & Snowdon, C. T. (2010) Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology*, 72, 296-306.

Chapter Four

No evidence that infant-carrying functions as rent payment in related helpers of captive common marmosets (*Callithrix jacchus*)



Marmosets in outdoor cages and the pipes connected to their indoor cages.

Abstract

Alloparental behaviour, which involves individuals caring for young that are not their own, is seemingly at odds with natural selection because, by caring for the young of others, alloparental behaviour potentially reduces the relative fitness of the alloparent. One plausible evolutionary explanation for alloparental behaviour is the so called ‘pay-to-stay’ hypothesis, which posits that helping behaviour functions as ‘rent’ paid by helpers to stay within the social group. Mathematical models of the pay-to-stay hypothesis predict that although rent payment is less likely to occur when subordinate and dominant group members are highly related, rent payment can be expected within highly related groups if (1) helping is very costly for the subordinates (with low voluntary helping effort), (2) the species has a long lifespan relative to their reproductive frequency, (3) dispersal is constrained, and (4) the presence of subordinates in the group is costly for the dominants. Here, I experimentally tested the hypothesis that related helpers provide rent payment in a cooperatively breeding primate, the common marmoset (*Callithrix jacchus*). In this species, infant-carrying is costly, and helpers provide assistance to the dominant breeding pair by contributing to the carrying of infants. The adaptive value of this alloparental behaviour is unknown, but it does not appear to provide large fitness benefits to breeders. To test whether alloparental infant-carrying functions as rent payment, I measured the time spent in infant-carrying behaviour by helpers (12 males and 12 females) in captive groups for 30 minutes under the following scenarios: (1) without the presence of a social observer, (2) in the presence of a dominant female from the helpers’ social group (i.e. the mother of the infant and the helper), and (3) in the presence of an unrelated adult female. I found that the time spent carrying the infant was not affected by either the presence of a social observer or the type of social observer (mean infant-carrying time \pm se: absence of social observer: 28 ± 0.9 minutes; mother: 22 ± 2.1 minutes; other-group female: 23 ± 2.0 minutes). My results, therefore, provide no evidence that alloparental infant-carrying behaviour functions as rent payment for related helpers. Considered in light of the current literature, my results suggest that possible benefits of alloparental infant-carrying behaviour in common marmosets are most likely to be derived from kin selection, group augmentation and/or learning of parental skills.

Introduction

Alloparental behaviour, which involves the caring of young by an individual who is not the parent, is seemingly inconsistent with classic natural selection that favours the promotion of individual survival and reproductive success (Wilson 1975). There are a number of evolutionary explanations for this apparently altruistic behaviour, including kin selection, group augmentation and pseudoreciprocity (Hamilton 1964; Maynard Smith 1964; Connor 1986; Kokko *et al.* 2001), which suggest that alloparental behaviour is an investment in the young that delivers indirect or direct fitness benefit to the alloparents later (Wright 1997). Another suggested explanation for alloparental behaviour is that it functions as a signal to convey the cooperative propensity of the alloparent, which increases its social status or opportunities for additional matings and coalition formation (Zahavi 1995; Wright 1997).

One plausible mechanism for alloparental behaviour as a signal is the so called ‘pay-to-stay’ hypothesis. In this respect, it is predicted that individuals provide help as ‘rent’ to be tolerated within the group (Gaston 1978; Kokko *et al.* 2002). This rent payment has been observed across a range of taxa (Reeve & Gamboa 1983; Reyer 1986; Reeve 1992; Mulder & Langmore 1993; Balshine-Earn *et al.* 1998). For example, in a cooperatively breeding bird, the pied kingfisher (*Ceryle rudis*), helpers in a group, who are not closely related to the dominant breeding pair, provision the dominants and their young (Reyer 1980). When the helpers do not bring an adequate amount of food, they are attacked by the dominants and their relatives (Reyer 1986). Mathematical models of the pay-to-stay hypothesis predict that rent payment is more likely to occur when the relatedness between dominant and subordinate group members is low (Kokko *et al.* 2002). However, rent payment can also be expected between related subordinates and dominants if (1) helping is very costly for the subordinates (with low voluntary helping effort), (2) the species has a long lifespan relative to their reproductive frequency, (3) dispersal is constrained, and (4) the presence of subordinates in the group is costly for the dominants (Kokko *et al.* 2002; e.g. Reeve & Gamboa 1983). One group of animals that combines many of the prerequisites for the rent payment between related group members are callitrichine primates, such as common marmosets (*Callithrix jacchus*, Subfamily: Callitrichinae).

Common marmosets live in extended family groups, which generally consisting a dominant breeding pair and several male and female subordinate group members (Digby & Barreto

1993; Ferrari & Digby 1996; Nievergelt *et al.* 2000). Those subordinates are often the relatives of the dominant pair though non-relative subordinates have been observed in free-ranging groups (Nievergelt *et al.* 2000; Faulkes *et al.* 2009). Common marmosets are cooperative breeders, in which all group members carry and provide care for the infants of the dominant pair (Stevenson 1976; Ingram 1977). Infant-carrying behaviour is energetically costly to the carrier (Tardif 1997; Sanchez *et al.* 1999), impedes mobility (Schradin & Anzenberger 2001), decreases foraging (Tardif 1994; Caine 1996) and vigilance behaviour (Price 1992; Caine 1993), and is likely to increase predation risk (Caine 1993). This potentially high costs of infant-carrying must be compensated by the direct and/or indirect benefits for the carriers.

Since subordinate group members (helpers) are related to the breeding pair, infant-carrying behaviour performed by helpers has been suggested to benefit helpers through the improved reproductive success of the breeding pairs by reducing the energetic costs of maternal infant-carrying (Sanchez *et al.* 1999). However, the effects of alloparental infant-carrying on the reproductive success of the breeding pairs have not been clearly demonstrated and there seems to be a lack of strong evidence for the positive effect of alloparental infant-carrying on the reproductive success of the breeding pairs. On the one hand, the number of adult males has been shown to positively correlate with the number of surviving infants in groups of free-ranging callitrichines (Garber *et al.* 1984; Sussman & Garber 1987; Baker *et al.* 1993; Koenig 1995; Bales *et al.* 2000). Also, the number of helpers has been shown to positively correlate with the number of live birth in the groups of free-ranging golden lion tamarins (*Leontopithecus rosalia*) (Bales *et al.* 2001). On the other hand, the positive correlations between helper number and the reproductive success of breeders could also be due to other factors. For instance, breeding pairs with higher fecundity would also have more older offspring around to help with rearing subsequent young (Wright & Russell 2008). A resource rich territory would also increase the reproductive success of the breeders and survival of the infants in the group (Russell & Lummaa 2009). Further, larger groups with more helpers have advantages in territory defence against neighbouring groups (Heg *et al.* 2005; Garay & Varga 2011). Similarly, larger groups with more helpers would detect predators more efficiently and thus could also improve infant survival (Kokko *et al.* 2001; Garay & Varga 2011). Effects of the presence of helpers in the groups have also been investigated in captive populations, where the influence of the environmental confounding factors can be largely controlled. The results, however, have been equivocal. For instance, maternal infant-carrying load has been

shown to decrease with increased number of helpers in the groups (common marmosets: Ingram 1977; Rothe *et al.* 1993a), but not with increased alloparental infant-carrying load (common marmosets: Chapter 2; cotton-top tamarins, *Saguinus oedipus*: Tardif *et al.* 1990). The lack of clear evidence for the positive effect of alloparental infant-carrying on the reproductive success of the breeding pairs suggests that alloparental infant-carrying behaviour may not benefit the helpers through the mechanisms such as kin selection, group augmentation and pseudoreciprocity, which benefit the helpers via the benefits to the breeding pairs (Wright 1997). Therefore, it can be speculated that alloparental infant-carrying might benefit the helpers directly through mechanisms such as pay-to-stay (i.e. ‘rent’ payment for staying in the group).

Callitrichines exhibit several characteristics that suggest that alloparental infant-carrying behaviour could function as rent payment. First, infant-carrying is costly. In free-ranging groups of common marmosets, adult group members have been shown to rest more, and feed and forage less, when carrying infants (Digby & Barreto 1996). Similar changes in activities were also observed in saddle-back tamarins (*Saguinus fuscicollis*) (Goldizen 1987) and captive cotton-top tamarins (Price 1992). Captive Geoffroy’s marmosets (*Callithrix geoffroyi*) in large outdoor cages have also been observed not to forage for prey while carrying an infant (Caine 1996). Moreover, in captive colonies of cotton-top tamarins, infant-carrying behaviour has been shown to be associated with weight loss of the carriers, which indicates the energetic costs of infant-carrying behaviour (Sanchez *et al.* 1999; Sanchez *et al.* 2005). Second, common marmosets have a long lifespan relative to their reproductive frequency. They are sexually mature in approximately 15 months, and able to reproduce twice a year with typically two infants in a litter throughout their average lifespan of five to seven years in captive environments (Tardif *et al.* 2003; Tardif *et al.* 2008). The average lifespan of common marmosets in natural environments is unknown. However, animals in the wild have been observed to stay as dominant breeders for an average of 32.5 months (Yamamoto *et al.* 2014), and some females have been reported to remain as dominant breeders for eight years (Saltzman *et al.* 2009). The high reproductive rate of common marmosets suggests that the relative importance of future reproductive success would be high compared to current reproductive success. Therefore, subordinates may be more willing to stay in the group and wait for future breeding opportunities when current reproductive prospects are low (Kokko *et al.* 2002). Third, dispersal in free-ranging groups occurs at a low frequency (0.42 to 3.44 individuals per group per year: Sousa *et al.* 2009) and is potentially

constrained by high predation risk, high intergroup tension and low food availability (Caine 1993; Araújo 1996 cited in Sousa *et al.* 2009; Sousa *et al.* 2009). In addition, dispersal typically involves single adult individual, and occurs both voluntarily and involuntarily (Stevenson & Rylands 1988; Sousa *et al.* 2009). Fourth, even the presence of related subordinates would presumably be costly to the dominant breeding female since the presence of other adult (subdominant) females increases reproductive competition. Indeed, if this were the case, the dominant female should prevent other adult females from carrying her infants to avoid infanticide (Digby & Saltzman 2009). Hence, common marmosets show three of the four characteristics that suggest that alloparental infant-carrying behaviour could possibly function as rent payment, even when the subordinate helpers are closely related (e.g. are older offspring) to the dominant breeding pair (as in Kokko *et al.* 2002).

Rent payment can be investigated by examining the existence of punishment by dominant individuals directed towards subordinates for unpaid rent (Kokko *et al.* 2002). However, aggressive behaviour between the dominant and the non-breeding subordinate members in the group is rarely observed in common marmosets (Digby 1995; Sousa *et al.* 2005; Saltzman *et al.* 2008). Determining the causal relationship between punishment and helping behaviour is often difficult, especially from field observations in uncontrolled environments (Heinsohn & Legge 1999). Moreover, subordinates would avoid punishment by compensating for any shortcoming in rent through heightened helping and submissive behaviour (pre-emptive appeasement: Balshine-Earn *et al.* 1998; Bergmuller & Taborsky 2005). Punishment will not be observed when helpers perform this pre-emptive appeasement, therefore making it difficult to conclude whether helping behaviour is functioning as rent or not (Wong *et al.* 2007; Cant 2011). Instead, a potentially more promising way to investigate rent payment is to compare the helping behaviour of subordinates in the presence and absence of dominant individuals. When helping behaviour functions as rent payment, helpers are expected to help more in the presence of a dominant individual to publicise their effort and to help less when the dominant individual is absent to minimise the costs of helping behaviour (Wright 1997; McDonald *et al.* 2008).

Accordingly, the aim of this study was to test the pay-to-stay hypothesis in alloparental infant-carrying behaviour of related helpers in captive common marmosets. I measured the time spent in infant-carrying behaviour by helpers under three scenarios: (1) in the absence of a social observer, (2) in the presence of a dominant female from the helpers' social group (i.e.

the mother of the infant and the helper) or (3) in the presence of an unrelated adult female. I expect that, if alloparental infant-carrying behaviour functions as rent payment, helpers carry an infant more in the presence of their own dominant female to publicise their efforts, and carry less in the absence of the dominant female to minimise the costs of alloparental infant-carrying behaviour.

Methods

Design

The amount of time helpers spent carrying an infant in the presence and absence of social observer were examined to investigate the effect of the presence of a social observer on the contribution of helpers to infant-carrying. A helper and an infant from the same social group were held in an experimental cage. The helper and infant were video recorded while exposed to a social observer in an adjacent cage. In total, the helper and infant were tested three times with two different types of the social observer (i.e. the mother of the infant and an adult female from another group) and in the absence of a social observer. The time helper spent carrying the infant was measured from the video footage for 30 minutes. The infant-carrying times were statistically analysed and compared among the different treatments.

Animal housing

Animals used in this study were from the national marmoset colony located at the Gippsland Field Station, Monash University, Australia. Common marmosets at the facility were separated into family groups, which consist of two to 12 individuals comprising a dominant breeding pair and their offspring as subordinate group members (helpers). All individuals (except infants) were microchipped for identification. Infants had a small patch (~1cm²) of their coat on the upper or lower back shaved to allow animals to be individually identified from their siblings. Each group was kept in an indoor cage (1.8m (H) x 1.2m x 0.75m), which is connected to an outdoor cage (2m (H) x 2m x 0.7m) by a pipe with a gate at the each end for daytime access. All individuals were fed once a day in the late morning with marmoset pellets (Specialty Feeds, Glen Forrest, Western Australia), fruits, vegetables and mealworms. Water bottles were provided in each indoor cage. The floors of the indoor cages were covered with sawdust, while the floors of outdoor cages comprised of bare concrete. All of the indoor cages were maintained at 25 - 30°C, with 40 - 60% humidity. Internal lighting was maintained on a 12 hours light-dark cycle. The facility complies with the NHMRC *Policy on*

the Care and Use of Non-Human Primates for Scientific Purposes (Animal Welfare Committee of the NHMRC 2003).

Study subjects

Ten male and 11 female helpers from 9 groups were tested with 19 infants. Two male helpers and one female helper were each tested twice at different breeding events (at 11 and 16 months of age, and 12 and 17 months, respectively, for the male helpers; and at 35 and 40 months for the female helper) with a new litter of infants in the group, hence, a total of 24 pairs of a helper and an infant were tested in this experiment. Each pair of helper and infant was tested first in the absence of a social observer to obtain a baseline of infant-carrying behaviour. Fifteen helpers (5 males and 10 females) were then tested with the mother of the infant (i.e. the mother of the helper) as the social observer followed by the other-group female, while the remaining 9 helpers (7 males and 2 females) were tested in the reverse order. Hence, in total, each helper was tested three times with the same infant, on three sequential days. The mean age (months \pm se) of male and female helpers used in this study were 17 ± 1.0 and 23 ± 1.3 respectively. The infants used in this study comprised 7 males and 12 females. The mean age (days \pm se) of male and female infants were 38 ± 2.1 and 37 ± 1.7 respectively. The mean age of the infants that were paired with male helpers was younger than that of female helpers (days \pm se: 34 ± 1.9 and 40 ± 1.9 respectively. Wilcoxon rank sum tests: $W = 846.5$, $p < 0.05$). Nine mothers and eight other-group females were used as social observers. The mean age (years \pm se) of mothers and other-group females were 5 ± 0.2 and 7 ± 0.4 respectively. Three of these females were used as a mother for trials with the helpers from their own groups and as an other-group female for trials with the helpers from other (not their own) social groups. For reasons unrelated to the current study, one male and three female helpers (age = 11 - 21 months) had been separated from the infants (1 male and 2 females, age = 28 - 50 days) prior to the start of the experiment. During the two-week separation, all subordinate members of the social group including the focal helpers were kept apart from the infants and the parents in two cages that were facing each other to allow visual, vocal and olfactory contact. Trials for these helpers were performed more than one week after the social group was reunited. Separation was included in the statistical models, and the time spent on carrying infant was found to be unaffected by separation (see results).

Procedure

Experiments were performed in the group's outdoor cage to ensure that test subjects were familiar with their surrounding environment. A social observer was caught by hand and introduced into a cage (117cm (H) x 88cm x 68cm) placed 1m aside to the experimental cage. The social observer cage was covered with large towels to visually separate the social observer and the focal animal (helper) before the commencement of the trial. A helper was caught by hand, separated from the social group, and immediately released into the experimental cage. After a five-minute habituation period, an infant from the social group, which was caught by hand, was introduced into the experimental cage by directly passing it to the helper. If the helper did not come close enough to take the infant directly, the infant was left on an object (meshed cage wall, wooden branch or metal shelf) near the helper to be picked up (all infants were picked up within 1 minute). The social observer was introduced to the animals in the experimental cage by removing the cover on the side of the social observer cage that facing the experimental cage and moving the social observer cage immediately next to the experimental cage. The helper and infant were then left in the cage for 40 minutes to be video recorded by using four surveillance cameras (94mm (D) x 78mm (H), WIT1035SDW, WIT Security Technology Co., Ltd. Taoyuan, Taiwan R.O.C.) attached to the four corners of the experimental cage's ceiling to record the entire cage. During each trial, the helper, infant and social observer, were allowed visual, vocal, olfactory and physical contact (either directly, in the case of the helper and the infant, or through the meshed walls of the cages, in the case of the social observer). At the completion of the trial, the helper and the infant were allowed to join the rest of the social group by opening the gate at the entrance to the pipe that connects the outdoor and indoor cages. The cage containing the social observer was moved away from the side of the experimental cage, and the cover was reinstated. The social observer was then either used in subsequent trials or returned to its social group.

Total duration of the time that a helper spent carrying infant was measured from the video footage for 30 minutes from the moment the social observer was introduced to the helper. For the trials without the social observer, infant-carrying time was measured for 30 minutes from the time the helper first took the infant. Infant-carrying behaviour was defined as when the four limbs of the infant were touching the helper (and nowhere else). Unfortunately, the video footage could not be processed blind, relative to treatment (i.e. presence and the type of social observer), because the social observer could also be seen in the video footage.

All behavioural observations were carried out by N.K. The experiment was performed between October 2010 and August 2011 and was approved by the Monash Animal Ethics Committee (AEC number: BSCI/2010/13).

Statistical analyses

The time that helpers spent carrying the infant were analysed in a generalized linear mixed model, using the lme4 package (Bates *et al.* 2012) in R 3.0.1 (R Core Team 2013). Helper ID, infant ID and the group ID of the helper were included in the model as random factors to control for pseudoreplication (the variance associated with the random factors was very small in all models, not shown). Time spent carrying infant (minutes) was used as the dependent variable. Time spent carrying the infant was analysed by using the ‘cbind’ command with binomial totals of 30 minutes. As independent variables, I included: infant age (days - centred and scaled to the mean and SD), social observer (mother, other-group female, or none) and separation (whether the infant and helper had been separated prior to the study).

Results

I found no difference in infant-carrying time among treatments. The time spent on carrying infant was not affected by the presence of a social observer or type of social observer (mean \pm se: absence of social observer: 28 ± 0.9 minutes; mother: 22 ± 2.1 minutes; other-group female: 23 ± 2.0 minutes) or whether the infant and helper had been separated prior to the study. However, infant-carrying time was affected by infant age (Table 1), with helpers spending significantly less time carrying older infants (Figure 1). Except in three cases, infants that were four weeks old or younger ($n = 23$ observations) were carried for the entire 30 minutes observation period (shortest infant-carrying time was 21 minutes). In contrast, carrying time for the infants older than four weeks ($n = 49$ observations) ranged between 0 and 30 minutes (Figure 1).

Discussion

My findings do not support the hypothesis that infant-carrying behaviour by related helpers functions as rent payment in captive common marmosets: helpers were not any more likely to carry an infant when the dominant breeding female was observing them, as might be predicted by the pay-to-stay hypothesis (McDonald *et al.* 2008). The pay-to-stay model predicts that any factors that increase voluntary helping will decrease the need for rent

payment (Kokko *et al.* 2002). Helpers in this study were older siblings of the infants and, therefore, voluntary helping could be facilitated by the indirect fitness benefits of alloparental infant-carrying behaviour. Indirect fitness benefit by kin selection has been proposed to be one of the major adaptive values of alloparental infant-carrying behaviour for kin helpers in callitrichine primates (Bales *et al.* 2000). However, no positive effect of alloparental care in the reproductive success of breeders or the survival of infants has so far been demonstrated (Rothe *et al.* 1993b; Koenig 1995; Bales *et al.* 2000). Moreover, helpers' contribution to infant-carrying appears not to be sufficient to alleviate parental infant-carrying loads in captive common marmosets (see Chapter 2).

Voluntary helping could also be facilitated by the direct fitness benefits of alloparental infant-carrying behaviour through group augmentation and skill learning effects. If alloparental infant-carrying can increase the reproductive success of breeders, it would increase the size of groups, in which larger group size would benefit the helpers by its advantages in antipredator and territorial defences (Hamilton 1971; Bales *et al.* 2000; Lazaro-Perea 2001; Garay 2009). Moreover, younger group members may become helpers for the former helpers when the former helpers become breeders (Lazaro-Perea *et al.* 2000; Sousa *et al.* 2009). Therefore, increasing the number of younger group members would also be beneficial for the helpers in their future reproductive success. Likewise, in captive common marmosets and other callitrichine species, experience in alloparental infant care appears to increase the reproductive success of the helpers when they become breeders, presumably, by improving their parental skills (Epple 1978; Tardif *et al.* 1984; Pryce 1988; Baker & Woods 1992; Pryce 1993; Caine 1996; Tardif 1997). These potential benefits of alloparental behaviour may favour voluntary helping for helpers, therefore, decrease the needs for rent payment. Further investigations into the effects of alloparental infant-carrying on the reproductive success of the breeders and the skill learning effects of helper experience would be valuable for understanding what maintains alloparental infant-carrying behaviour in common marmosets.

Alloparents' propensity to carry infants was more strongly influenced by the age of the infant than by the presence of a social observer. My study demonstrates that the decrease in the infant-carrying time with increasing infant age occurred regardless of the presence of social observer and other available carriers. This decrease in infant-carrying time has been observed in other populations of captive and wild marmosets (Ingram 1977; Stevenson & Rylands 1988; Yamamoto 1993; Yamamoto *et al.* 2008). Infants start to leave the carriers and explore

the surrounding environment by themselves at around three to four weeks of age (Ingram 1977; Yamamoto 1993). In the current study, infants that were four weeks old or younger were generally carried for the entire duration of the trial (30 minutes), with the exception of three infants (shortest infant-carrying time was 21 minutes). In contrast, the carrying time for infants older than four weeks ranged between 0 and 30 minutes. It suggests that the propensity of helpers to carry infants is influenced by factors related to the increasing age of the infants. For instance, the propensity of helpers to carry infants would decrease as infants become more independent and heavier with age. Further investigation into the causes of such decreases in alloparents' propensity to carry infants may provide insight into the proximate causes of infant-carrying behaviour.

I cannot rule out the possibility that the presence of a social observer does affect alloparental infant-carrying behaviour, but that the statistical power of the current study was not sufficient enough to detect such an effect. However, the fact that my analyses detected the effect of infant age on the helpers' contribution to infant-carrying suggests that the magnitude of any effect of the presence of social observer, if it does exist, is likely to be relatively small and not a major contribution to alloparental infant-carrying behaviour.

In conclusion, my results showed that, in captive common marmoset groups, infant-carrying behaviour is unlikely to function as rent payment by sub-adult and adult alloparents that are relatives of the dominant breeding pair. Instead, it suggests that the benefits of alloparental infant-carrying behaviour could be due to other factors, such as kin selection, group augmentation and/or skill learning effects favouring voluntary helping for the helpers. The observed decrease in alloparental infant-carrying with increased infant age may also suggest that the benefits of alloparental infant-carrying behaviour are derived from increased survival of the infants through, such as, kin selection and group augmentation. The effects of alloparental infant-carrying behaviour on the reproductive success of breeders and on the future reproductive success of the helpers may warrant further investigations. Furthermore, investigations into the decrease in alloparental infant-carrying with increased infant age may provide valuable insights into the proximate causes of helping behaviour.

Tables and Figures

Table 1. Result of a generalized linear mixed model showing the effects of the variables on infant-carrying time spent by helpers. There were no differences in infant-carrying time among treatments (i.e. when the mother of the infant, other-group female or no social observer was present; $n = 24$ observations per treatment). However, helpers spent less time carrying older infants.

	Estimate	SE	z	p
(Intercept)	-0.31	0.10	-2.98	< 0.01
Infant age	-0.26	0.06	-4.12	< 0.01
Mother ¹	-0.03	0.10	-0.27	0.79
Other-group female ¹	0.02	0.10	0.21	0.84
Separation	0.24	0.20	1.17	0.24

¹relative to the absence of social observer

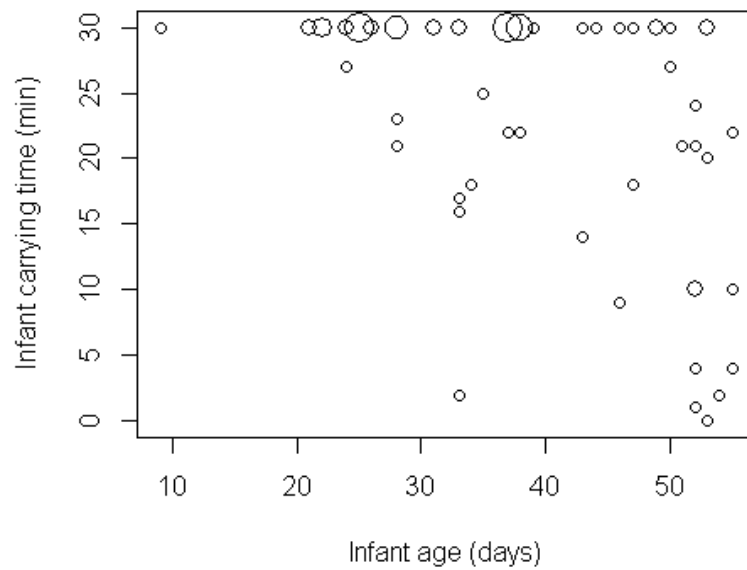


Figure 1. Infant-carrying time (minutes) decreased with increasing infant age. Each trial was plotted separately for each helper (i.e. presence of mother, other-group female or absence of social observer). The size of each data point corresponds to the number of overlapping data points.

References

- Animal Welfare Committee of the NHMRC (2003) Policy on the care and use of non-human primates for scientific purposes. 27th ed., The National Health and Medical Research Council.
- Araújo, A. (1996) Influence des facteurs écologiques, comportementaux et démographiques sur la dispersion de *Callithrix jacchus*. Université Paris-Nord (Paris XIII). Paris. PhD thesis.
- Baker, A. J., Dietz, J. M. & Kleiman, D. G. (1993) Behavioral evidence for monopolization of paternity in multimale groups of golden lion tamarins. *Animal Behaviour*, 46, 1091-1103.
- Baker, A. J. & Woods, F. (1992) Reproduction of the emperor tamarin (*Saguinus imperator*) in captivity, with comparisons to cotton-top and golden lion tamarins. *American Journal of Primatology*, 26, 1-10.
- Bales, K., Dietz, J., Baker, A., Miller, K. & Tardif, S. D. (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica*, 71, 27-38.
- Bales, K., O'Herron, M., Baker, A. J. & Dietz, J. M. (2001) Sources of variability in numbers of live births in wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, 54, 211-221.
- Balshine-Earn, S., Neat, F. C., Reid, H. & Taborsky, M. (1998) Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology*, 9, 432-438.
- Bates, D., Maechler, M. & Bolker, B. (2012) lme4: linear mixed-effects models using S4 classes. R package version 0.999999-0. <http://www.CRAN.R-project.org/package=lme4>.
- Bergmuller, R. & Taborsky, M. (2005) Experimental manipulation of helping in a cooperative breeder: Helpers 'pay to stay' by pre-emptive appeasement. *Animal Behaviour*, 69, 19-28.
- Caine, N. G. (1993) Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Caine, N. G. (1996) Foraging for animal prey by outdoor groups of Geoffroy's marmosets (*Callithrix geoffroyi*). *International Journal of Primatology*, 17, 933-945.
- Cant, M. A. (2011) The role of threats in animal cooperation. *Proceedings of the Royal Society B-Biological Sciences*, 278, 170-178.
- Connor, R. C. (1986) Pseudo-reciprocity: Investing in mutualism. *Animal Behaviour*, 34, 1562-1566.
- Digby, L. & Saltzman, W. (2009) Balancing cooperation and competition in callitrichid primates: Examining the relative risk of infanticide across species. IN Davis, L. C., Ford, S. M. & Porter, L. M. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Digby, L. J. (1995) Social organization in a wild population of *Callithrix jacchus*. II. Intragroup social behavior. *Primates*, 36, 361-375.
- Digby, L. J. & Barreto, C. E. (1993) Social organization in a wild population of *Callithrix jacchus*. I. Group composition and dynamics. *Folia Primatologica*, 61, 123-134.
- Digby, L. J. & Barreto, C. E. (1996) Activity and ranging patterns in common marmosets (*Callithrix jacchus*): Implications for reproductive strategies. IN Norconk, M., Rosenberger, A. & Garber, P. (Eds.) *Adaptive radiations of neotropical primates*. New York, Plenum Press.

- Epple, G. (1978) Reproductive and social behavior of marmosets with special reference to captive breeding. *Primates in Medicine*, Vol. 10, 50-62.
- Faulkes, C. G., Arruda, M. F. & Monteiro da Cruz, M. A. O. (2009) Genetic structure within and among populations of the common marmoset, *Callithrix jacchus*: Implications for cooperative breeding. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Ferrari, S. F. & Digby, L. J. (1996) Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, 38, 19-27.
- Garay, J. (2009) Cooperation in defence against a predator. *Journal of Theoretical Biology*, 257, 45-51.
- Garay, J. & Varga, Z. (2011) Survivor's dilemma: Defend the group or flee? *Theoretical Population Biology*, 80, 217-225.
- Garber, P. A., Moya, L. & Malaga, C. (1984) A preliminary field study of the moustached tamarin monkey (*Saguinus mystax*) in northeastern Peru - questions concerned with the evolution of a communal breeding system. *Folia Primatologica*, 42, 17-32.
- Gaston, A. J. (1978) Evolution of group territorial behavior and cooperative breeding. *American Naturalist*, 112, 1091-1100.
- Goldizen, A. W. (1987) Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 20, 99-109.
- Hamilton, W. D. (1964) The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, 7, 1-52.
- Hamilton, W. D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.
- Heg, D., Brouwer, L., Bachar, Z. & Taborsky, M. (2005) Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, 142, 1615-1641.
- Heinsohn, R. & Legge, S. (1999) The cost of helping. *Trends in Ecology & Evolution*, 14, 53-57.
- Ingram, J. C. (1977) Interactions between parents and infants, and development of independence in common marmoset (*Callithrix jacchus*). *Animal Behaviour*, 25, 811-827.
- Koenig, A. (1995) Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 35, 311-317.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 187-196.
- Kokko, H., Johnstone, R. A. & Wright, J. (2002) The evolution of parental and alloparental effort in cooperatively breeding groups: When should helpers pay to stay? *Behavioral Ecology*, 13, 291-300.
- Lazaro-Perea, C. (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. *Animal Behaviour*, 62, 11-21.
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araújo, A., Arruda, M. F. & Snowdon, C. T. (2000) Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology*, 48, 137-146.
- Maynard Smith, J. (1964) Group selection and kin selection. *Nature*, 201, 1145-1147.

- McDonald, P. G., Kazem, A. J. N., Clarke, M. F. & Wright, J. (2008) Helping as a signal: Does removal of potential audiences alter helper behavior in the bell miner? *Behavioral Ecology*, 19, 1047-1055.
- Mulder, R. A. & Langmore, N. E. (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, 45, 830-833.
- Nievergelt, C. M., Digby, L. J., Ramakrishnan, U. & Woodruff, D. S. (2000) Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *International Journal of Primatology*, 21, 1-20.
- Price, E. C. (1992) The costs of infant carrying in captive cotton-top tamarins. *American Journal of Primatology*, 26, 23-33.
- Pryce, C. R. (1988) Individual and group effects on early caregiver-infant relationships in red-bellied tamarin monkeys. *Animal Behaviour*, 36, 1455-1464.
- Pryce, C. R. (1993) The regulation of maternal behavior in marmosets and tamarins. *Behavioural Processes*, 30, 201-224.
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>.
- Reeve, H. K. (1992) Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature*, 358, 147-149.
- Reeve, H. K. & Gamboa, G. J. (1983) Colony activity integration in primitively eusocial wasps - the role of the queen (*Polistes fuscatus*, Hymenoptera, Vespidae). *Behavioral Ecology and Sociobiology*, 13, 63-74.
- Reyer, H. U. (1980) Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis rudis* L.). *Behavioral Ecology and Sociobiology*, 6, 219-227.
- Reyer, H. U. (1986) Breeder-helper-interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour*, 96, 277-303.
- Rothe, H., Darms, K., Koenig, A., Radespiel, U. & Juenemann, B. (1993a) Long-term study of infant-carrying behavior in captive common marmosets (*Callithrix jacchus*): Effect of nonreproductive helpers on the parents' carrying performance. *International Journal of Primatology*, 14, 79-93.
- Rothe, H., Koenig, A. & Darms, K. (1993b) Infant survival and number of helpers in captive groups of common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 30, 131-137.
- Russell, A. F. & Lummaa, V. (2009) Maternal effects in cooperative breeders: From hymenopterans to humans. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364, 1143-1167.
- Saltzman, W., Digby, L. J. & Abbott, D. H. (2009) Reproductive skew in female common marmosets: What can proximate mechanisms tell us about ultimate causes? *Proceedings of the Royal Society B-Biological Sciences*, 276, 389-399.
- Saltzman, W., Liedl, K. J., Salper, O. J., Pick, R. R. & Abbott, D. H. (2008) Post-conception reproductive competition in cooperatively breeding common marmosets. *Hormones and Behavior*, 53, 274-286.
- Sanchez, S., Pelaez, F., Gil-Burmann, C. & Kaumanns, W. (1999) Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 48, 99-111.
- Sanchez, S., Pelaez, F., Morcillo, A. & Gil-Burmann, C. (2005) Effect of the enclosure on carriers' body weight loss in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 66, 279-284.
- Schradin, C. & Anzenberger, G. (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: An experimental analysis. *Animal Behaviour*, 62, 289-295.

- Sousa, M. B. C., Albuquerque, A., Albuquerque, F. D., Araújo, A., Yamamoto, M. E. & Arruda, M. D. (2005) Behavioral strategies and hormonal profiles of dominant and subordinate common marmoset (*Callithrix jacchus*) females in wild monogamous groups. *American Journal of Primatology*, 67, 37-50.
- Sousa, M. B. C., Araújo, A., Yamamoto, M. E., Albuquerque, A. C. S. R. & Arruda, M. F. (2009) Emigration as a reproductive strategy of the common marmosets (*Callithrix jacchus*). IN Davis, L. C., Ford, S. M. & Porter, L. M. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Stevenson, M. F. (1976) Birth and perinatal behavior in family groups of common marmoset (*Callithrix jacchus jacchus*), compared to other primates. *Journal of Human Evolution*, 5, 365-381.
- Stevenson, M. F. & Rylands, A. B. (1988) The marmosets, genus *Callithrix*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Sussman, R. W. & Garber, P. A. (1987) A new interpretation of the social organization and mating system of the callitrichidae. *International Journal of Primatology*, 8, 73-92.
- Tardif, S. D. (1994) Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant-care patterns. *American Journal of Primatology*, 34, 133-143.
- Tardif, S. D. (1997) The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. IN Solomon, N. G. & French, J. A. (Eds.) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Tardif, S. D., Araújo, A., Arruda, M. F., French, J. A., Sousa, M. B. C. & Yamamoto, M. E. (2008) Reproduction and aging in marmosets and tamarins. IN Atsalis, S., Margulis, S. W. & Hof, P. R. (Eds.) *Primate reproductive aging: Cross-taxon perspectives*. Karger Publishers.
- Tardif, S. D., Carson, R. L. & Gangaware, B. L. (1990) Infant-care behavior of mothers and fathers in a communal-care primate, the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 22, 73-85.
- Tardif, S. D., Richter, C. B. & Carson, R. L. (1984) Effects of sibling-rearing experience on future reproductive success in two species of callitrichidae. *American Journal of Primatology*, 6, 377-380.
- Tardif, S. D., Smucny, D. A., Abbott, D. H., Mansfield, K., Schultz-Darken, N. & Yamamoto, M. E. (2003) Reproduction in captive common marmosets (*Callithrix jacchus*). *Comparative Medicine*, 53, 364-368.
- Wilson, E. O. (1975) *Sociobiology: The new synthesis*, Cambridge, Harvard University Press.
- Wong, M. Y. L., Buston, P. M., Munday, P. L. & Jones, G. P. (2007) The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proceedings of the Royal Society B-Biological Sciences*, 274, 1093-1099.
- Wright, J. (1997) Helping-at-the-nest in Arabian babblers: Signalling social status or sensible investment in chicks? *Animal Behaviour*, 54, 1439-1448.
- Wright, J. & Russell, A. F. (2008) How helpers help: Disentangling ecological confounds from the benefits of cooperative breeding. *Journal of Animal Ecology*, 77, 427-429.
- Yamamoto, M. E. (1993) From dependence to sexual maturity: The behavioural ontogeny of callitrichidae. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Yamamoto, M. E., Albuquerque, F. S., Lopes, N. A. & Ferreira, E. S. (2008) Differential infant carrying in captive and wild common marmosets (*Callithrix jacchus*). *Acta Ethologica*, 11, 95-99.

- Yamamoto, M. E., Araujo, A., Arruda, M. d. F., Lima, A. K. M., Siqueira, J. d. O. & Hattori, W. T. (2014) Male and female breeding strategies in a cooperative primate. *Behavioural Processes*, 109, 27-33.
- Zahavi, A. (1995) Altruism as a handicap - the limitations of kin selection and reciprocity. *Journal of Avian Biology*, 26, 1-3.

Chapter Five

No effect of perceived predation risk on infant-carrying by related helpers in captive common marmosets (*Callithrix jacchus*)



An example of using the snake model as a predatory stimulus (Photo: Emma Jensson. Jensson 2010).

Abstract

One of the major benefits of living in a group is reduced predation risk mediated through increased vigilance, dilution and confusion effects. In this respect, defending fellow group members from predators can be beneficial for individuals since it maintains group size and its antipredator effects. Indeed, cooperative antipredator defence occurs in many group-living animals. However, defending group members from predators may increase the predation risk for the defending individuals, suggesting potential trade-offs in cooperative antipredator defence. I investigated potential trade-offs between defending fellow group members and an individual's efforts towards defending its own survival in a cooperatively breeding primate, the common marmoset (*Callithrix jacchus*). I did so by experimentally investigating the effects of perceived predation risk on the infant-carrying behaviour of related helpers ($n = 31$) in a captive colony. To examine the relative propensity of helpers to defend infants, I also compared the infant-carrying behaviour of helpers (full siblings of the infants) with that of the mothers ($n = 12$) of the infants under perceived predation risk. I found no effect of perceived predation risk on the infant-carrying behaviour of helpers (mean infant-carrying times (minutes \pm se) in the trials with and without predatory stimulus were 26 ± 1.3 and 28 ± 0.9 respectively). Also, the infant-carrying behaviour under perceived predation risk did not differ between helpers and mothers (mean infant-carrying times (minutes \pm se) spent by helpers and mothers were 25 ± 2.3 and 27 ± 1.3 respectively). The results suggest that infant-carrying receives priority over predation avoidance regardless of perceived risk or kinship (genealogical relationship) with the infants. This propensity for helpers to carry infants also suggests that infant-carrying behaviour is likely to provide fitness benefits to the helpers.

Introduction

Living in a group imposes costs on the group members, such as increased competition over local resources and increased exposure to parasites and disease (Alexander 1974). One of the major benefits that compensate the costs of group living is reduced predation risk mediated through increased vigilance, dilution and confusion effects (Williams 1964; Hamilton 1971; Powell 1974; Foster & Treherne 1981; Godin 1986; Landeau & Terborgh 1986; Elgar 1989). Predation has been suggested as one of the most important selection pressures that promoted the evolution of cooperative behaviour within groups (Alexander 1974; Wilson 1975). Since the loss of a group member increases future predation risk for the surviving group members, members can benefit from protecting each other from predators to help maintain group size and its antipredator benefits (Garay & Varga 2011). Similarly, individuals under predation risk survive and reproduce better in larger groups (Wilson 1975). Therefore, providing help to facilitate the reproduction of group members would increase group size and, in doing so, increases the antipredator effects of the group (Kokko *et al.* 2001; Kingma *et al.* 2014).

Group-living animals often protect fellow group members from predators through, for example, alarm calling, antipredator mobbing and cooperative defences (Shank 1977; Smith 1992; Arnold 2000; Maklakov 2002; Reynolds *et al.* 2002; Hollen & Radford 2009). Evidence suggests that individuals engaged in protective behaviours can do so in ways that reduce their own risk of being predated (Dugatkin & Godin 1992; Caro 2005). It has been shown, for example, that alarm calls are often emitted by individuals when they are at a safe distance from the predator or when they are close to their own shelters (Blumstein *et al.* 1997; Clutton-Brock *et al.* 1999; Randall *et al.* 2000; Wright *et al.* 2001; Collier *et al.* 2010). Predator mobbing also tends to be performed by larger and more agile individuals (Robinson 1985; Clode *et al.* 2000; Forsman & Monkkonen 2001; Torrez *et al.* 2012). Also, having multiple group members partaking in mobbing behaviour can potentially reduce the predation risk of individual mobbers through the dilution and confusion effects (Verbeek 1985; Brown & Hoogland 1986; Poiani 1991). However, in some species, protecting fellow group members does pose a serious risk to the actor of the behaviour. In a cooperatively breeding bird, the pied babbler (*Turdoides bicolor*), sentinels are at a greater risk of predation than foraging group members, with evidence that sentinels are targeted by predators more often and, hence, are also more likely to be captured and killed (Ridley *et al.* 2013). Another group

of animals in which protecting fellow group members might impose a substantial cost on the protecting individuals are marmosets and tamarins (Subfamily: Callitrichinae).

Marmosets and tamarins are small neotropical primates that live in extended family groups (Digby & Barreto 1993; Nievergelt *et al.* 2000; Faulkes *et al.* 2009), which generally consist of a dominant breeding pair and several male and female subordinate group members (Ferrari & Digby 1996). They are cooperative breeders whereby all group members provide care and carry the infants of the dominant breeding pair (Stevenson 1976; Ingram 1977). Due to their small body size, callitrichines are vulnerable to a range of predators, including raptors, mammalian carnivores and snakes (reviewed in Ferrari 2009). Given their vulnerability, it has been suggested that high predation pressure may have promoted social organisation and cooperation in these primates (Caine 1993).

In addition to the potential anti-predation-risk benefits of living in groups, it is important to realise that infant-carrying behaviour can potentially also increase immediate predation risk for carriers. Typically, callitrichine mothers give birth to twins, which can weigh in total as much as 15 - 25 % of adult body weight at birth (Kleiman 1977). Carrying these heavy infants has been shown to impede the mobility and the vigilance of carriers (Price 1992; Caine 1993; Schradin & Anzenberger 2001; Caperos *et al.* 2012). Therefore, carrying an infant likely imposes high costs on carriers in terms of increased predation risk (Caine 1993; Tardif 1994; Bales *et al.* 2000). Hence, carriers are expected to face a trade-off between carrying infants versus their own immediate survival. Accordingly, carriers might be, on the one hand, expected to decrease their contribution to infant-carrying under elevated predation risk in order to increase their own immediate survival. On the other hand, if individual predation risk is not substantially increased by infant-carrying, carriers might increase infant-carrying during elevated predation risk to favour infant survival and future group augmentation (Kingma *et al.* 2014).

I investigated a potential trade-off between infant-carrying and antipredator behaviour in subordinate group members (helpers) in a captive colony of common marmosets. I did so by experimentally increasing the perceived predation risk of helpers through the presentation of a model snake and examining its effects on the contribution of helpers to infant-carrying. Using the captive colony enabled me to effectively manipulate perceived predation risk in a controlled environment. To examine the relative propensity of helpers to defend infants, I

also compared the effect of perceived predation risk on infant-carrying behaviour between helpers (full siblings of the infants) and the mothers of the infants, since mothers achieve greater immediate direct fitness benefits by looking after their own young (Hamilton 1964). In this regard, I predict that mothers, on average, will carry infants more than helpers.

Methods

Design

Effects of perceived predation risk on alloparental infant-carrying behaviour were investigated by examining the time spent carrying an infant by a helper in trials with and without the predatory stimulus. A helper and an infant from the same social group were held in an experimental cage. The amount of time the helper spent carrying the infant during and after the presentation of the predatory stimulus was measured. Each pair of helper and infant was also tested first in the absence of predatory stimulus to obtain a baseline of their behaviour. The amount of time the mother of the infant spent carrying the infant was also measured in a trial with the predatory stimulus for comparison. First, I compared the time spent carrying infant by helpers in trials with and without the predatory stimulus. Second, I compared the time spent carrying infant by helpers and mothers in trials with the predatory stimulus.

Animal housing

Animals used in this study were from the national marmoset colony located at the Gippsland Field Station, Monash University, Australia. Common marmosets at the facility were separated into breeding groups, which consist of two to 12 individuals comprising a dominant breeding pair and their offspring as subordinate group members. All individuals (except infants) were microchipped for identification. Infants had a small patch (~1cm²) of their coat on the upper or lower back shaved to allow animals to be individually identified from their siblings. Each group was kept in an indoor cage (1.8m (H) x 1.2m x 0.75m), which is connected to an outdoor cage (2m (H) x 2m x 0.7m) by a pipe with a gate at the each end for daytime access. All individuals were fed once a day in the late morning with marmoset pellets (Specialty Feeds, Glen Forrest, Western Australia), fruits, vegetables and mealworms. Water bottles were provided in each indoor cage. The floors of the indoor cages were covered with sawdust, while the floors of outdoor cages comprised of bare concrete. All of the indoor cages were maintained at 25 - 30°C, with 40 - 60% humidity. Internal lighting was

maintained on a 12 hours light-dark cycle. The facility complies with the NHMRC *Policy on the Care and Use of Non-Human Primates for Scientific Purposes* (Animal Welfare Committee of the NHMRC 2003).

Study subjects

Animals from ten different groups, consists of 11 male and 17 female subordinate group members (helpers) and 10 mothers were tested as focal animals. Two mothers, one female helper and two male helpers were each tested twice at different breeding events. In total, I conducted 74 trials comprising 31 trials without the predatory stimulus (13 male and 18 female helpers) and 43 trials with the predatory stimulus (13 male and 18 female helpers, and 12 mothers - i.e. mothers were only tested in the trials with the predatory stimulus). The mean age (months \pm se) of male and female helpers and mothers were 16 ± 1.2 , 20 ± 1.3 and 60 ± 2.9 respectively. The infants used in this study comprised 9 males and 15 females (mean age \pm se: 35 ± 1.5 days and 31 ± 1.7 days respectively). Each helper was paired with the same infant for both trials with and without the predatory stimulus. Some focal animals that belonged to the same social group at the same breeding event were tested by using the same infant when there was no other infant available (e.g. singleton or other infants were in poor health). The infants carried by female helpers were older than the infants carried by male helpers in both the comparisons of trials with and without predatory stimulus (mean age \pm se: infants paired with male helpers = 26 ± 1.8 days; infants paired with female helpers = 36 ± 1.4 days. Wilcoxon rank sum test: $W = 746$, $p < 0.01$), and helpers and mothers (mean age \pm se: infants paired with male helpers = 24 ± 3.6 days; infants paired with female helpers = 40 ± 2.7 days. Wilcoxon rank sum test: $W = 42$, $p = 0.01$).

For reasons unrelated to the current study, one male and five female helpers (age = 11–21 months) had been separated from the infants (2 males and 2 females, age = 28 - 48 days). During the two-week separation, helpers were kept apart from the infants and parents in two cages that were facing each other to allow visual, vocal and olfactory contact. Trials for these helpers were performed more than one week after they were reunited with their social group. Separation (i.e. whether the infant and helper had been separated prior to the study) was included in the statistical tests, and I detected no effect of separation on infant-carrying (see results).

Predatory stimulus

A rubber snake model was used as a predatory stimulus in this study (cf. Barros *et al.* 2002; Hankerson & Caine 2004; Clara *et al.* 2008; Emile & Barros 2009; Cagni *et al.* 2011) since snakes have been reported to prey on both infants and adults callitrichines (reviewed in Ferrari 2009; Ferrari & Beltrao-Mendes 2011). The model was 2m in length, coloured in black on the dorsal side and in red on the ventral side. The effectiveness of the snake model as a predatory stimulus was confirmed in a previous study that used the same snake model as a stimulus on the animals from the colony used in the current study (Jensson 2010). In that study, subordinate group members were exposed to the snake model and a playback of alarm calls for one minute compared to only the playback of alarm calls. The animals exposed to the snake model spent more time being vigilant and fewer animals produced alarm calls during the exposure to the snake model. In addition, I have also observed typical anti-snake reactions by focal animals, including alarm behaviour (pilo-tail and sway) and gazing toward the snake model (Epple 1968; Stevenson & Poole 1976; Stevenson & Rylands 1988).

Procedure

Experiments were performed in the group's outdoor cage to ensure that test subjects were familiar with their surrounding environment. A helper was caught by hand, separated from the group, and immediately released into the experimental cage. After a five-minute habituation period, the infant from the group, which was caught by hand, was introduced into the experimental cage by directly passing it to the helper. If the helper did not come close enough to take the infant directly, the infant was left on an object (meshed cage wall, wooden branch or metal shelf) near the helper to be picked up (all infants were picked up within 1 minute). After one minute of habituation period, the 2m long rubber snake model, as a predatory stimulus, was introduced to the helper and infant. The snake model was hidden under a cover and placed out of the sight from the focal animals in the experimental cage. A thin cord was attached to the snake model and the snake was pulled toward the experimental cage, was pulled up and down along the front side of the cage for one minute then pulled away to the out of the sight from the focal animals. The helper and infant were then left in the cage for 40 minutes (it is known from other studies that model snakes can elicit antipredator behaviour in marmosets for over 12 hours: Hankerson & Caine 2004). At the completion of the trial, the helper and infant were allowed to join the rest of the group by opening the gate at the entrance to the pipe that connects the outdoor and indoor cages. The same procedure was also used in the trials that involved the mother of the infant. The use of the same infant in

more than one consecutive trial was avoided as much as possible by alternating the time or the date of the trials to minimise stress to the infants. For this and other reasons (e.g. availability of animals or cages), the order of the trials could not be in a strict order. Consequently, the trials with mothers were not always performed after those with the helpers. Animals in the experimental cage were video recorded throughout the trial by using four surveillance cameras (94mm (D) x 78mm (H), WIT1035SDW, WIT Security Technology Co., Ltd. Taoyuan, Taiwan R.O.C.) that were attached to the four corners of the experimental cage's ceiling to record the entire cage.

For the comparison between helpers and mothers, the total duration of time the focal animal spent carrying the infant was measured from the video footage for 30 minutes from the removal of the snake model. Infant-carrying behaviour was defined as when the four limbs of the infant were touching the carrier (and nowhere else). For the comparison between the trials with and without the predatory stimulus, infant-carrying time was measured for 30 minutes from the time the helper first took the infant. The video footages were not processed blind, relative to the treatment of trial (i.e. presence of the predatory stimulus). All behavioural observations were carried out by N. K. The experiment was performed between October 2010 and August 2011 and approved by the Monash Animal Ethics Committee (AEC number: BSCI/2010/13).

Statistical analyses

First, I examined the effects of perceived predation risk on alloparental infant-carrying behaviour by comparing the time spent carrying infant by helpers in trials with and without the predatory stimulus. I analysed a total of 62 observations from 31 helpers (13 males and 18 females) that were tested in the two treatments. Male helpers were on average younger than female helpers (mean age \pm se: male helpers = 16 ± 1.2 months; female helpers = 20 ± 1.3 months. Wilcoxon rank sum test: $W = 626$, $p < 0.05$). Within the 62 trials, 24 trials were performed using male infants and 38 trials were performed using female infants. Female infants were a few days younger than male infants on average (mean age \pm se: male infants = 35 ± 1.7 days; female infants = 30 ± 1.8 days. Wilcoxon rank sum test: $W = 315$, $p < 0.05$).

Second, I examined the relative propensity of helpers to defend infants by comparing the time spent carrying infant by helpers and mothers in trials with the predatory stimulus. I analysed a

total of 26 observations comprising 14 helpers (5 males and 9 females, mean age \pm se: 14 ± 2.5 months and 18 ± 2.4 months respectively) and 12 mothers (mean age \pm se: 60 ± 2.9 months) that were paired with the same infants. Of the 26 trials, 11 were performed using male infants (mean age \pm se: 37 ± 2.9 days) and 15 were performed using female infants (mean age \pm se: 33 ± 3.2 days).

To analyse the proportion of time that focal animals spent carrying the infants, I constructed generalized linear mixed models, using the lme4 package (Bates *et al.* 2012) in R 3.2.1 (R Core Team 2015). In the statistical models, I included focal animal ID and infant ID as random factors to control for pseudoreplication (the variance associated with the random factors was very small in all models, not shown). I used infant-carrying time (minutes) as the dependent variable. The infant-carrying time was combined by using the 'cbind' command with binomial totals of 30 (minutes). As independent variables, I included predatory stimulus in the comparison of trials with and without the predatory stimulus, and carrier (helper or mother) in the comparison of helpers and mothers. In both of the comparisons, infant age (days - centred and scaled to the mean and SD) and separation (whether the infant and helper had been separated prior to the study) were also included as independent variables. I also tested interactions between infant age and predatory stimulus, and between infant age and carrier by using the same models without the separation in the independent variables to increase the statistical power of the models.

Results

Predatory stimulus did not affect infant-carrying

I found no difference in times spent carrying infants by helpers between trials with and without predatory stimulus (Table 1a). Means of the time (minutes \pm se) spent carrying infants in the trials with and without predatory stimulus were 26 ± 1.3 (range: 7 - 30) and 28 ± 0.9 (range: 12 - 30) respectively (Figure 1a). The infant-carrying time was not affected by separation (Table 1a).

Infant-carrying did not differ between helpers and mothers

I found no difference in infant-carrying time between helpers (full siblings of the infants) and mothers in trials with the predatory stimulus (Table 1b). Means of the time (minutes \pm se) spent carrying infants by helpers and mothers were 25 ± 2.3 (range: 7 - 30 minutes) and $27 \pm$

1.3 (range: 18 - 30 minutes) respectively (Figure 1b). The infant-carrying time was not affected by separation (Table 1b).

Infant-carrying decreased with increasing infant age

Time spent carrying infants decreased with increasing infant age in both the trials with and without predatory stimulus (Tables 1a, Figure 2a), and helpers and mothers (Table 1b, Figure 2b). There was no interaction between infant age and predatory stimulus (GLMM: $z = -0.94$, $p = 0.35$), and between infant age and carrier (GLMM: $z = 1.54$, $p = 0.08$). In all trials, infants four weeks old or younger ($n = 27$) were generally carried for the entire duration of the trial (30 minutes), with the exception of two infants (27 and 28 minutes). In contrast, the carrying time for the infants older than four weeks ($n = 47$) ranged between 7 and 30 minutes (Figure 2a, b).

Discussion

I did not find any evidence for a trade-off between infant-carrying and antipredator behaviour in related helpers since helpers did not alter their contribution to infant-carrying under perceived predation risk. This persistent contribution of helpers to infant-carrying suggests that alloparental infant-carrying behaviour provides fitness benefits that compensate the increased predation risk of the helpers, or that carrying infants does not increase predation risk of helpers (Caine 1993; Tardif 1994; Bales *et al.* 2000).

Protecting infants by continuing to carry them under perceived predation risk may provide a variety of fitness benefits to the helpers. Assuming that carrying and protecting infants would increase their survival, this would be expected to help maintain and increase the size of the group (group augmentation: Kingma *et al.* 2014). As a result, the benefits of group living are preserved, such as its antipredator effects, through increased vigilance, dilution and confusion effects (Hamilton 1971). Maintaining group size and its antipredator effects become more beneficial for the group members under high predation pressure (Wilson 1975; Garay 2009). Therefore, although predation risk for the helpers may increase by carrying infants, protecting infants from predators might be still beneficial for the helpers in small primate species, such as common marmoset, which face higher predation pressure than larger primate species (Cheney & Wrangham 1987). Other benefits of being part of larger groups also exist. For marmosets and tamarins, a larger group size is advantageous in defending their territory

against neighbouring groups (Bales *et al.* 2000; Lazaro-Perea 2001). Moreover, younger subordinate group members may become helpers for older subordinate group members when the older subordinate group member establishes its own group (Lazaro-Perea *et al.* 2000; Sousa *et al.* 2009). Therefore, carrying and protecting younger group members from predators would also increase the future reproductive success of the helpers. In addition, since helpers are often also the older siblings of the infants in free-ranging groups of common marmosets (Nievergelt *et al.* 2000; Faulkes *et al.* 2009), protecting younger siblings from predators would increase the inclusive fitness of the helpers (Hamilton 1964). To disentangle these potential benefits and relative costs, more detailed investigations into the effects of alloparental infant-carrying on infant survival, on helpers' predation risk and the effects of group size on the fitness of helpers are required.

My observation that contributions to infant-carrying under perceived predation risk did not differ between the helpers and mothers suggests that the net fitness benefits of doing so are similar between related helpers and mothers. Carrying infants is likely to be energetically more costly for mothers compared to helpers. This is because mothers are under high energetic demand due to lactation, which is comparable to the energetic cost of somatic maintenance (Kirkwood & Underwood 1984). I showed in my previous study that the higher contribution of mothers to infant-carrying was associated with unsuccessful parturition in the subsequent breeding attempt (Chapter 2). Nevertheless, mothers may carry infants under perceived predation risk because this high cost is compensated by the high fitness benefit of the improved survival of their own young, in addition to the benefits associated with group augmentation (reviewed in Kingma *et al.* 2014). In contrast, although helpers are less energetically challenged than mothers, predation risks of infant-carrying are unlikely to be substantially different, and helpers gain less direct fitness benefits (compared to mothers) from the improved survival of the infant (Heinsohn & Legge 1999). Therefore, along with the observed persistent contribution of helpers to infant-carrying irrespective of perceived predation risk, the observed similarity in the contributions to infant-carrying between helpers and mothers also suggests that alloparental infant-carrying under perceived predation risk provides substantial fitness benefits to the related helpers to compensate for the high cost.

In addition, it could be suggested that infant-carrying and antipredator behaviour are compatible with each other, allowing helpers to continue to carry infants under perceived predation risk. In several callitrichine species including common marmosets, individuals have

been noted to become inactive and inconspicuous while carrying infants irrespective of the presence of predators or any particular danger to the carriers (Goldizen 1987; Price 1992; Caine 1996; Digby & Barreto 1996; Sanchez *et al.* 1999; Lazaro-Perea 2001). It has been shown that, in captive cotton-top tamarins (*Saguinus oedipus*), carriers spend more time in concealed areas than when they are not carrying infants, suggesting that, because of their impeded mobility and decreased vigilance, carriers are implementing a cryptic strategy to reduce predation risk (Price 1992). In fact, predation on marmosets and tamarins by snakes have been observed in other studies when the monkeys were being active, such as while travelling, foraging and playing (Heymann 1987; Correa & Coutinho 1997; Tello *et al.* 2002; Ferrari & Beltrao-Mendes 2011). Therefore, it might be hypothesized that, while carrying infants, helpers are minimising their predation risk by being inconspicuous to avoid predators. This hypothesis could be tested by comparing the behaviour of helpers with and without infants under perceived predation risk or by comparing the conspicuousness and vulnerability of helpers to predators while carrying and not carrying infants.

It might be argued that the helpers persisted in carrying the infants in the trials with the model snake because the perceived predation risk was not critical enough for the helpers to drop the infant to decrease the risk of being attacked by the potential predator. For instance, the model snake may not have been close enough to the helpers or, alternatively, the helpers were aware that the snake was outside the cage and could not, therefore, attack them. However, the location of the potential predator at the initial sighting was not so important in this experiment since the helpers were expected to react to the increased perceived predation risk of a predator attacking from anywhere else, after losing sight of the predator. The fact that marmosets show antipredator reactions 12 hours after a potential predator has been sighted (Hankerson & Caine 2004) suggests that the helpers in this experiment would still be under increased perceived predation risk even after the disappearance of the potential predator. Therefore, it is still conceivable that, after a close sighting of a potential predator, the helpers could remain wary of a possible attack and refrain from carrying the infant to increase their chance of evading a future attack.

The results also suggest that helpers have a propensity to accommodate infants' needs to be carried since the contribution of helpers to infant-carrying decreased when the age of the infants increased. Helpers decreased their contribution to infant-carrying only when infants were older than four weeks, which is when the locomotive ability of infants is developed to

the stage where they start to leave the carriers and exploring the surroundings independently (Ingram 1977; Stevenson & Rylands 1988; Yamamoto 1993; Yamamoto *et al.* 2008). This propensity of helpers to accommodate the needs of infants to be carried was persistent under perceived predation risk further suggesting that infant-carrying is dictated by infant needs but not by the situation of the helper. Moreover, the propensity to provide sufficient carrying for the infants seems to be irrespective of the kinship (genealogical relationship) of the infant since the contribution to infant-carrying decreased with increasing infant age regardless of whether the carrier was the older sibling (helper) or the mother of the infant. Further investigation into the causes of the decreases in the contribution of helpers and mothers to carry infants may reveal the factors that could be driving the helpers to carry infants.

The decrease in the contribution of helpers to infant-carrying in my study might be due to the fact that the majority of older infants were carried by female helpers as past studies observed female helpers carried infants less than male helpers (Box 1977; Goldizen 1987; Ferrari 1992; Yamamoto & Box 1997; Zahed *et al.* 2010). However, my previous experiment showed that there was no sex difference in contribution to alloparental infant-carrying when there was no other group member to share the infant-carrying load (Chapter 3). Therefore, since there was no other group member to share the infant-carrying load for the helpers in the current study, the observed decrease in alloparental infant-carrying with increasing infant age was most likely a direct response to infant needs.

In conclusion, I found that the contribution of related helpers to infant-carrying is not influenced by perceived predation risk and is similar to it of the mothers of the infants. Also, helpers and mothers similarly decreased their contribution to infant-carrying when the infant age increased. The findings suggest that the infant-carrying behaviour likely to provide substantial fitness benefits to the helpers. Also, helpers seem to have a persistent propensity to accommodate the needs of infants to be carried, which is unaffected by perceived predation risk or the kinship with the infants. Further investigation into the effects of alloparental infant-carrying behaviour on the group size and the fitness consequence of increased group size to the helpers are required to evaluate the possible fitness benefits of alloparental infant-carrying behaviour through group augmentation. Understanding the causes of the decrease in the contribution of helpers to infant-carrying would indicate whether helpers have the propensity to accommodate the needs of infants to be carried.

Tables and Figures

Table 1. Results of generalized linear mixed models showing time spent carrying infant by **(a)** comparing between helpers ($n = 62$) in trials with and without the predatory stimulus (model snake presentation) and **(b)** comparing helpers ($n = 14$) and mothers ($n = 12$) in trials with the predatory stimulus. Models included focal animal ID and infant ID as random factors and infant-carrying time (minutes) as the dependent variable relative to binomial totals = 30 minutes (using ‘cbind’). Infant age was centred and scaled to the mean and SD.

(a)

	Estimate	SE	z	p
(Intercept)	-0.07	0.05	-1.37	0.17
Infant age (days)	-0.10	0.04	-2.69	0.01
Predatory stimulus	-0.04	0.07	-0.57	0.57
Separation	-0.12	0.09	-1.27	0.20

(b)

	Estimate	SE	z	p
(Intercept)	-0.16	0.09	-1.77	0.08
Infant age (days)	-0.13	0.06	-2.31	0.02
Mother ¹	0.07	0.12	0.60	0.55
Separation	-0.16	0.16	-0.98	0.33

¹ relative to helpers

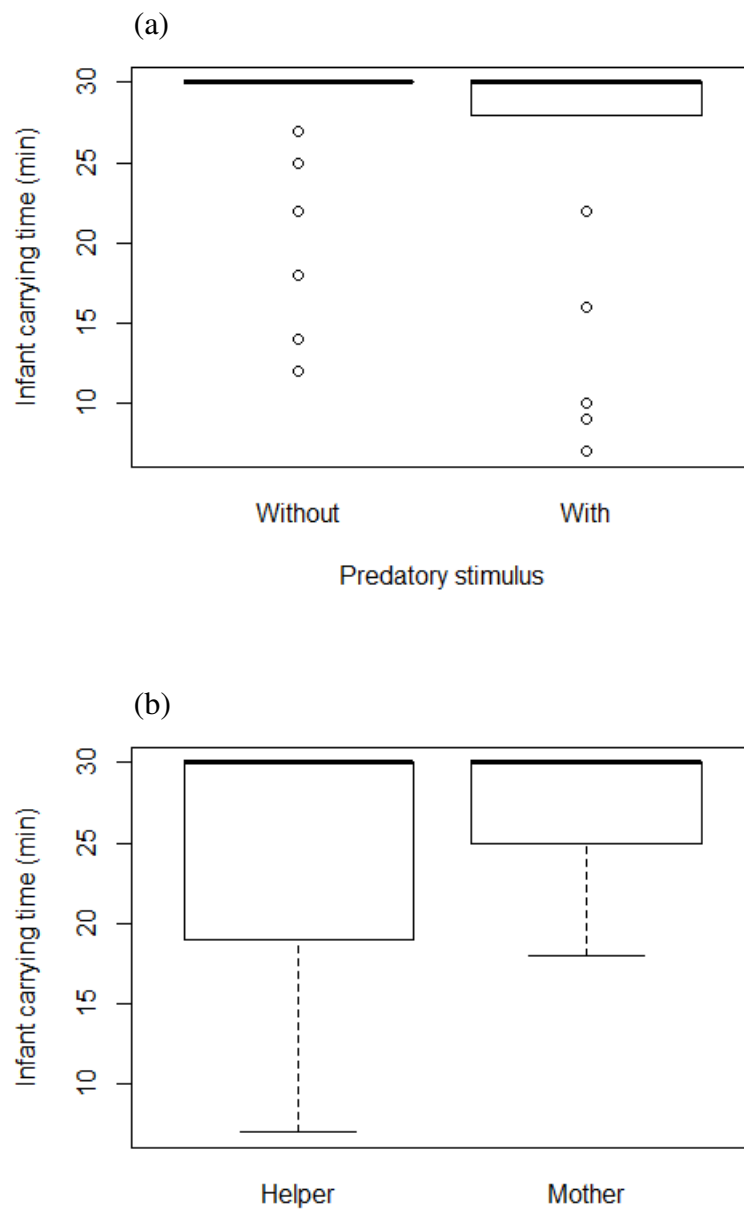


Figure 1. Box plots showing infant-carrying time (minutes) spent by **(a)** helpers in trials with and without the predatory stimulus, and by **(b)** helpers and mothers in the trials with the predatory stimulus.

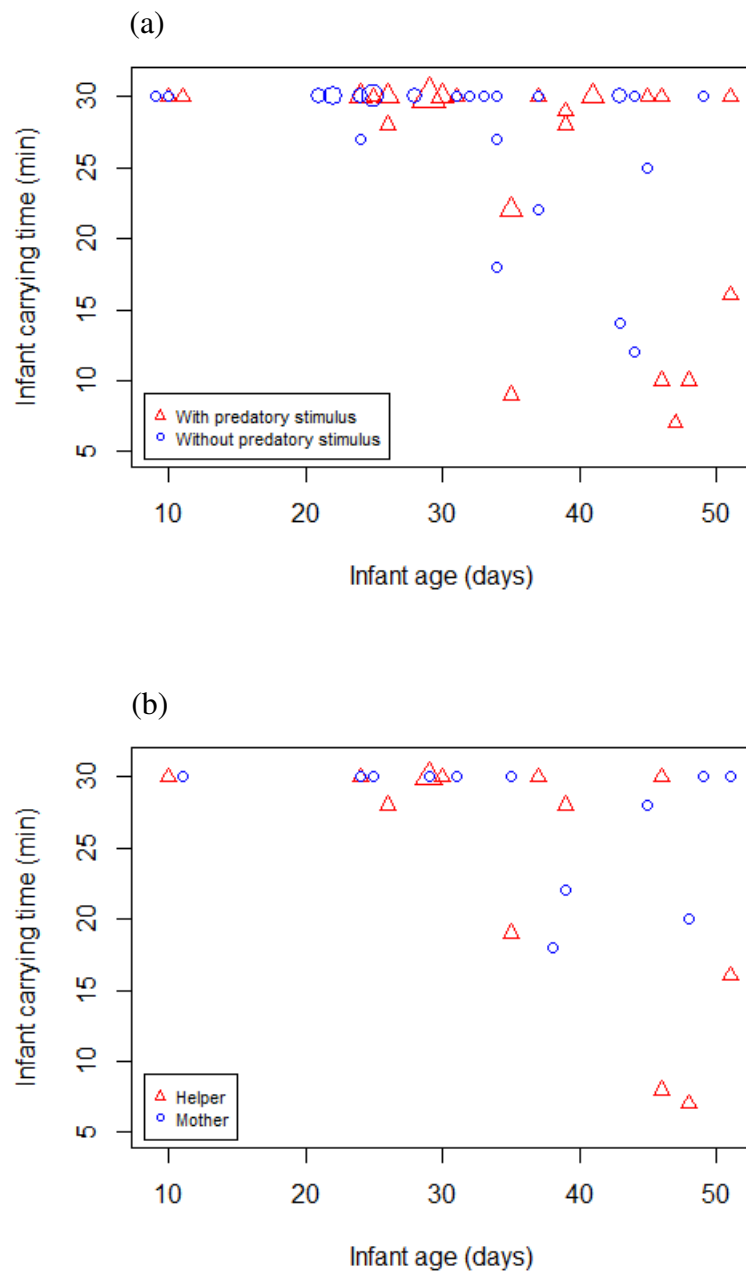


Figure 2. The infant-carrying time (minutes) spent by individual carriers with infants of various age (days) showing (a) helpers in trials with (Δ) and without (o) the predatory stimulus, and (b) helpers (Δ) and mothers (o) in trials with the predatory stimulus. The size of each data point corresponds to the number of overlapping data points.

References

- Alexander, R. D. (1974) The evolution of social behaviour. *Annual Review of Ecology and Systematics*, 5, 325-383.
- Animal Welfare Committee of the NHMRC (2003) Policy on the care and use of non-human primates for scientific purposes. 27th ed., The National Health and Medical Research Council.
- Arnold, K. E. (2000) Group mobbing behaviour and nest defence in a cooperatively breeding Australian bird. *Ethology*, 106, 385-393.
- Bales, K., Dietz, J., Baker, A., Miller, K. & Tardif, S. D. (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica*, 71, 27-38.
- Barros, M., Boere, V., Mello, E. L. & Tomaz, C. (2002) Reactions to potential predators in captive-born marmosets (*Callithrix penicillata*). *International Journal of Primatology*, 23, 443-454.
- Bates, D., Maechler, M. & Bolker, B. (2012) lme4: linear mixed-effects models using S4 classes. R package version 0.999999-0. <http://www.CRAN.R-project.org/package=lme4>.
- Blumstein, D. T., Steinmetz, J., Armitage, K. B. & Daniel, J. C. (1997) Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. *Animal Behaviour*, 53, 173-184.
- Box, H. O. (1977) Quantitative data on the carrying of young captive monkeys (*Callithrix jacchus*) by other members of their family groups. *Primates*, 18, 475-484.
- Brown, C. R. & Hoogland, J. L. (1986) Risk in mobbing for solitary and colonial swallows. *Animal Behaviour*, 34, 1319-1323.
- Cagni, P., Sampaio, A. C., Ribeiro, N. B. & Barros, M. (2011) Immediate, but no delayed, behavioral response to a snake model by captive black tufted-ear marmosets. *Behavioural Processes*, 87, 241-245.
- Caine, N. G. (1993) Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Caine, N. G. (1996) Foraging for animal prey by outdoor groups of Geoffroy's marmosets (*Callithrix geoffroyi*). *International Journal of Primatology*, 17, 933-945.
- Caperos, J. M., Morcillo, A., Pelaez, F., Fidalgo, A. & Sanchez, S. (2012) The effect of infant body mass on carrier travel speed in cotton-top tamarins (*Saguinus oedipus*). *International Journal of Primatology*, 33, 447-459.
- Caro, T. (2005) *Antipredator defenses in birds and mammals*, University of Chicago Press.
- Cheney, D. L. & Wrangham, R. W. (1987) Predation. IN Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds.) *Primates*. Chicago, IL, Chicago University Press.
- Clara, E., Tommasi, L. & Rogers, L. J. (2008) Social mobbing calls in common marmosets (*Callithrix jacchus*): Effects of experience and associated cortisol levels. *Animal Cognition*, 11, 349-358.
- Clode, D., Birks, J. D. S. & Macdonald, D. W. (2000) The influence of risk and vulnerability on predator mobbing by terns (*Sterna spp.*) and gulls (*Larus spp.*). *Journal of Zoology*, 252, 53-59.
- Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S. & Manser, M. (1999) Selfish sentinels in cooperative mammals. *Science*, 284, 1640-1644.

- Collier, T. C., Blumstein, D. T., Girod, L. & Taylor, C. E. (2010) Is alarm calling risky? Marmots avoid calling from risky places. *Ethology*, 116, 1171-1178.
- Correa, H. K. M. & Coutinho, P. E. G. (1997) Fatal attack of a pit viper, *Bothrops jararaca*, on an infant buffy-tufted ear marmoset (*Callithrix aurita*). *Primates*, 38, 215-217.
- Digby, L. J. & Barreto, C. E. (1993) Social organization in a wild population of *Callithrix jacchus*. I. Group composition and dynamics. *Folia Primatologica*, 61, 123-134.
- Digby, L. J. & Barreto, C. E. (1996) Activity and ranging patterns in common marmosets (*Callithrix jacchus*): Implications for reproductive strategies. IN Norconk, M., Rosenberger, A. & Garber, P. (Eds.) *Adaptive radiations of neotropical primates*. New York, Plenum Press.
- Dugatkin, L. A. & Godin, J.-G. J. (1992) Prey approaching predators: A cost-benefit perspective. *Annales Zoologici Fennici*, 29, 233-252.
- Elgar, M. A. (1989) Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society*, 64, 13-33.
- Emile, N. & Barros, M. (2009) Recognition of a 3D snake model and its 2D photographic image by captive black tufted-ear marmosets (*Callithrix penicillata*). *Animal Cognition*, 12, 725-732.
- Epple, G. (1968) Comparative studies on vocalization in marmoset monkeys (Hapalidae). *Folia Primatologica*, 8, 1-40.
- Faulkes, C. G., Arruda, M. F. & Monteiro da Cruz, M. A. O. (2009) Genetic structure within and among populations of the common marmoset, *Callithrix jacchus*: Implications for cooperative breeding. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Ferrari, S. F. (1992) The care of infants in a wild marmoset (*Callithrix flaviceps*) group. *American Journal of Primatology*, 26, 109-118.
- Ferrari, S. F. (2009) Predation risk and antipredator strategies. IN Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. K. & Strier, K. B. (Eds.) *South American primates: Comparative perspectives in the study of behavior, ecology, and conservation*. New York, Springer.
- Ferrari, S. F. & Beltrao-Mendes, R. (2011) Do snakes represent the principal predatory threat to callitrichids? Fatal attack of a viper (*Bothrops leucurus*) on a common marmoset (*Callithrix jacchus*) in the Atlantic Forest of the Brazilian Northeast. *Primates*, 52, 207-209.
- Ferrari, S. F. & Digby, L. J. (1996) Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, 38, 19-27.
- Forsman, J. T. & Monkkonen, M. (2001) Responses by breeding birds to heterospecific song and mobbing call playbacks under varying predation risk. *Animal Behaviour*, 62, 1067-1073.
- Foster, W. A. & Treherne, J. E. (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293, 466-467.
- Garay, J. (2009) Cooperation in defence against a predator. *Journal of Theoretical Biology*, 257, 45-51.
- Garay, J. & Varga, Z. (2011) Survivor's dilemma: Defend the group or flee? *Theoretical Population Biology*, 80, 217-225.
- Godin, J. (1986) Antipredator function of shoaling in teleost fishes: A selective review. *Le Naturaliste Canadien*, 113, 241-250.

- Goldizen, A. W. (1987) Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, 20, 99-109.
- Hamilton, W. D. (1964) The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, 7, 1-52.
- Hamilton, W. D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.
- Hankerson, S. J. & Caine, N. G. (2004) Pre-retirement predator encounters alter the morning behavior of captive marmosets (*Callithrix geoffroyi*). *American Journal of Primatology*, 63, 75-85.
- Heinsohn, R. & Legge, S. (1999) The cost of helping. *Trends in Ecology & Evolution*, 14, 53-57.
- Heymann, E. W. (1987) A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. *International Journal of Primatology*, 8, 193-195.
- Hollen, L. I. & Radford, A. N. (2009) The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, 78, 791-800.
- Ingram, J. C. (1977) Interactions between parents and infants, and development of independence in common marmoset (*Callithrix jacchus*). *Animal Behaviour*, 25, 811-827.
- Jensson, E. (2010) Monkey see, monkey hear but what monkey will do? Anti-predatory responses of common marmosets, *Callithrix jacchus*. School of Biological Sciences. Monash University. Clayton. Honours thesis.
- Kingma, S. A., Santema, P., Taborsky, M. & Komdeur, J. (2014) Group augmentation and the evolution of cooperation. *Trends in Ecology & Evolution*, 29, 476-484.
- Kirkwood, J. K. & Underwood, S. J. (1984) Energy requirements of captive cotton-top tamarins (*Saguinus oedipus oedipus*). *Folia Primatologica*, 42, 180-187.
- Kleiman, D. G. (1977) Monogamy in mammals. *The Quarterly Review of Biology*, 52, 39-69.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 187-196.
- Landeau, L. & Terborgh, J. (1986) Oddity and the confusion effect in predation. *Animal Behaviour*, 34, 1372-1380.
- Lazaro-Perea, C. (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. *Animal Behaviour*, 62, 11-21.
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araújo, A., Arruda, M. F. & Snowdon, C. T. (2000) Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology*, 48, 137-146.
- Maklakov, A. A. (2002) Snake-directed mobbing in a cooperative breeder: Anti-predator behaviour or self-advertisement for the formation of dispersal coalitions? *Behavioral Ecology and Sociobiology*, 52, 372-378.
- Nievergelt, C. M., Digby, L. J., Ramakrishnan, U. & Woodruff, D. S. (2000) Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *International Journal of Primatology*, 21, 1-20.
- Poiani, A. (1991) Antipredator behavior in the bell miner *Manorina melanophrys*. *Emu*, 91, 164-171.
- Powell, G. V. N. (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behaviour*, 22, 501-505.

- Price, E. C. (1992) The costs of infant carrying in captive cotton-top tamarins. *American Journal of Primatology*, 26, 23-33.
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>.
- Randall, J. A., Rogovin, K. A. & Shier, D. M. (2000) Antipredator behavior of a social desert rodent: Footdrumming and alarm calling in the great gerbil, *Rhombomys opimus*. *Behavioral Ecology and Sociobiology*, 48, 110-118.
- Reynolds, P. E., Reynolds, H. V. & Shideler, R. T. (2002) Predation and multiple kills of muskoxen by grizzly bears. *Ursus*, 13, 79-84.
- Ridley, A. R., Nelson-Flower, M. J. & Thompson, A. M. (2013) Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour*, 85, 137-142.
- Robinson, S. K. (1985) Coloniality in the yellow-rumped cacique as a defense against nest predators. *Auk*, 102, 506-519.
- Sanchez, S., Pelaez, F., Gil-Burmann, C. & Kaumanns, W. (1999) Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, 48, 99-111.
- Schradin, C. & Anzenberger, G. (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: An experimental analysis. *Animal Behaviour*, 62, 289-295.
- Shank, C. C. (1977) Cooperative defense by bighorn sheep. *Journal of Mammalogy*, 58, 243-244.
- Smith, R. J. F. (1992) Alarm signals in fishes. *Reviews in Fish Biology and Fisheries*, 2, 33-63.
- Sousa, M. B. C., Araújo, A., Yamamoto, M. E., Albuquerque, A. C. S. R. & Arruda, M. F. (2009) Emigration as a reproductive strategy of the common marmosets (*Callithrix jacchus*). IN Davis, L. C., Ford, S. M. & Porter, L. M. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Stevenson, M. F. (1976) Birth and perinatal behavior in family groups of common marmoset (*Callithrix jacchus jacchus*), compared to other primates. *Journal of Human Evolution*, 5, 365-381.
- Stevenson, M. F. & Poole, T. B. (1976) An ethogram of the common marmoset (*Callithrix jacchus jacchus*): General behavioural repertoire. *Animal Behaviour*, 24, 428-451.
- Stevenson, M. F. & Rylands, A. B. (1988) The marmosets, genus *Callithrix*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Tardif, S. D. (1994) Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant-care patterns. *American Journal of Primatology*, 34, 133-143.
- Tello, N. S., Huck, M. & Heymann, E. W. (2002) Boa constrictor attack and successful group defence in moustached tamarins, *Saguinus mystax*. *Folia Primatologica*, 73, 146-148.
- Torrez, L., Robles, N., Gonzalez, A. & Crofoot, M. C. (2012) Risky business? Lethal attack by a jaguar sheds light on the costs of predator mobbing for capuchins (*Cebus capucinus*). *International Journal of Primatology*, 33, 440-446.
- Verbeek, N. A. M. (1985) Behavioural interactions between avian predators and their avian prey: Play behaviour or mobbing? *Zeitschrift für Tierpsychologie*, 67, 204-214.
- Williams, G. C. (1964) Measurement of consociation among fishes and comments on the evolution of schooling. *Publications of the Museum, Michigan State University Biological Series*, 2, 349-384.
- Wilson, E. O. (1975) *Sociobiology: The new synthesis*, Cambridge, Harvard University Press.

- Wright, J., Berg, E., de Kort, S. R., Khazin, V. & Maklakov, A. A. (2001) Safe selfish sentinels in a cooperative bird. *Journal of Animal Ecology*, 70, 1070-1079.
- Yamamoto, M. E. (1993) From dependence to sexual maturity: The behavioural ontogeny of callitrichidae. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Yamamoto, M. E., Albuquerque, F. S., Lopes, N. A. & Ferreira, E. S. (2008) Differential infant carrying in captive and wild common marmosets (*Callithrix jacchus*). *Acta Ethologica*, 11, 95-99.
- Yamamoto, M. E. & Box, H. O. (1997) The role of non-reproductive helpers in infant care in captive *Callithrix jacchus*. *Ethology*, 103, 760-771.
- Zahed, S. R., Kurian, A. V. & Snowdon, C. T. (2010) Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology*, 72, 296-306.

Chapter Six

General discussion

The aim of my thesis was to contribute to an understanding of the evolution of alloparental infant-carrying behaviour in common marmosets. By exploiting the controlled environment of a captive colony, I explored possible fitness benefits of alloparental infant-carrying behaviour and the factors that influence the contribution of helpers to infant-carrying. I assessed the effect of helpers' contribution to infant-carrying within the breeding group on the infant-carrying loads of the breeders as well as parturition success in the subsequent breeding period of the breeding pairs (Chapter 2). I found that alloparental infant-carrying had no effect on either the parental infant-carrying loads or the parturition success of the breeding pairs in the subsequent breeding period. However, paternal infant-carrying decreased the maternal infant-carrying load, and higher paternal contribution to infant-carrying was associated with successful subsequent parturitions. The results indicate that alloparental infant-carrying does not benefit the breeding pairs but that the contribution of fathers to infant-carrying may still be important for the successful reproduction of common marmosets in a captive environment.

Because helper contributions in a group setting are determined by the motivations of individuals in combination with the behaviour of other group members, it is difficult to test evolutionary hypotheses explaining costly helping behaviour in such a setting. Therefore, I also investigated the helpers' contributions to infant-carrying while they were separated from the social group. Specifically, I tested the effects of three factors on the helpers' contribution: the sex of the helpers (Chapter 3), the presence of a social observer (i.e. either a dominant female from the helper's social group or an adult female from another social group. Chapter 4), and perceived predation risk (Chapter 5). I found that the contribution of helpers to infant-carrying was not affected by any of these factors, although infant-carrying did decrease with increasing infant age. Moreover, the helpers' contribution to infant-carrying was similar to the amount of carrying performed by the mothers of the infants.

Alloparental infant-carrying is driven by infants' needs

My findings suggest that one of the major functions of alloparental infant-carrying behaviour of common marmosets is to accommodate the carrying needs of the infant. Helpers contributed little to infant-carrying when they were in their social groups (Chapter 2). As most of the necessary infant-carrying was provided by the breeding pairs, infants did not need to be carried by the helpers. However, when the helpers were separated from the rest of the group, they carried infants as much as the infants' mothers did (Chapter 5). This indicates that helpers provide sufficient carrying of the infants when carrying cannot be provided by other members of the social group. Moreover, my findings indicate that a helpers' propensity to accommodate the infant's need for carrying was unaffected by the sex of the helpers, the presence of a social observer or perceived predation risk (Chapters 3, 4, 5). This is in agreement with infant-carrying being driven by infant need: if providing sufficient carrying for infants is the main driver of infant-carrying, factors related to characteristics of the helper or the external environment are not predicted to affect infant-carrying. For example, in a cooperatively breeding bird, the Arabian babbler (*Turdoides squamiceps*), the contribution of helpers to the provisioning of young increases the feeding rate and the number of young to fledge (Wright 1998). The provisioning behaviour of helpers is not influenced by the sex and/or dominant rank of the helper and the presence of group members (Wright 1997). This lack of influence on the provisioning behaviour from the social factors indicates that the function of provisioning behaviour of helpers is not to signal the quality of the helpers to other members of the group, as initially suggested by Zahavi (1995). Instead, the function of provisioning by the helpers would be to accommodate the needs of the young to increase the productivity of the breeders, which would benefit the helpers through group augmentation and kin selection (Wright 1998). Helping behaviour has also been observed to be influenced by the demand for help in various other taxa (e.g. *Pheidole* ants: Wilson 1984; meerkats, *Suricata suricatta*: Clutton-Brock *et al.* 2005; carrion crows, *Corvus corone corone*: Baglione *et al.* 2010; *Myrmica kotokui* ants: Hasegawa *et al.* 2016; *Temnothorax rugatulus* ants: Charbonneau *et al.* 2017). Similarly, my findings suggest that, the contribution of helpers to infant-carrying is determined by the needs of the infants to be carried. And like those other studies, this suggests that the benefits of alloparental infant-carrying are more likely to be delivered from increased productivity of the breeders through processes such as kin selection or group augmentation in common marmosets also.

The decrease in the contribution of helpers to infant-carrying with increasing infant age could also be interpreted to support the notion that a major function of alloparental infant-carrying behaviour is to meet the carrying needs of the infants: the decrease could be due to a reduction in the need to carry infants as a result of the progress in the infants' development, since infant-carrying only decreased when infants were older than four weeks (Chapters 3, 4, 5). This coincides with increased locomotive ability and the independence of the infants (Ingram 1977; Stevenson & Rylands 1988; Yamamoto 1993; Yamamoto *et al.* 2008). However, another possibility is that infant-carrying decreased because the increasing body weight of the infants makes it more costly for helpers to carry the infants. Carrying a 30-day-old infant has been estimated to cause a minimum 10% increase in the energetic cost of travelling compared to the cost of travelling without an infant (Tardif 1997). Also, it has been experimentally shown that carrying a 30-day-old infant with an average body weight of 64 g (Tardif & Bales 2004) would reduce the leaping ability of the carrier by 17%, which can be a considerable hindrance for the survival of small primates under high predation pressure (Schradin & Anzenberger 2001). On the other hand, my finding that helpers continue to invest similar amounts of effort into carrying infants regardless of perceived predation risk (Chapter 5) suggests that helpers accommodate the infant's need to be carried despite the increase in the potential costs. In this regard, further work is required to disentangle the effects of increased infant independence and body weight of the infants on helpers' contributions to infant-carrying. Moreover, if helpers are able to assess the needs of infant-carrying, then revealing how helpers assess the infant's need for carrying will tell us what proximate causes increase helpers' contributions to infant-carrying.

Participation of helpers in infant-carrying is regulated by social contexts of the groups

My findings support earlier suggestions that the actual participation of helpers in infant-carrying is regulated by the social contexts of the groups (Stevenson & Rylands 1988; Koenig & Rothe 1991; Rothe & Darms 1993; Yamamoto & Box 1997). Despite helpers carrying infants most of the time when separated from social groups (Chapters 3, 4, 5), when they were actually in their social group, helpers contributed very little to infant-carrying, with the parents carrying the infants most of the time (Chapter 2). This suggests that, in social groups, helper participation in infant-carrying was limited by parents' participation in infant-carrying. In social groups, it has been suggested that breeding pairs regulate the participation of the

group members in infant-carrying by maintaining close interaction with a few “qualified helpers”, which are often one or two of the oldest adult subordinate males in the groups (Koenig & Rothe 1991; Rothe & Darms 1993). In free-ranging groups of common marmoset, adult subordinate males within the group have been observed to perform most of the infant-carrying (Stevenson & Rylands 1988). Possibly, the observed small contribution of helpers to infant-carrying while in the social groups may be attributed to the lack of adult helpers in my study groups. Also, breeding females have been observed preventing adult subordinate females from carrying the infants by chasing the adult females away when they approached other helpers with the infants (Koenig & Rothe 1991; Albuquerque 1999 cited in Yamamoto *et al.* 2009). Such parental control over alloparental infant-carrying would be effective in avoiding harm to infants caused by individuals that are unskilled and unsuited to infant-carrying (Maestriperi 1994; Mitani & Watts 1997). Moreover, parental control over alloparental infant-carrying would prevent infanticide by other adult females who are potential reproductive competitors and have been observed to kill the infants of other members of the group in both captive and natural environments (reviewed in Digby & Saltzman 2009). Furthermore, there seems to be competition over infant-carrying among helpers, in which older helpers may have advantages over younger helpers. In free-ranging groups of common marmoset, younger individuals have been observed to be chastised by older individuals when they attempt to take infants from other group members (Stevenson & Rylands 1988). In captive groups, sub-adult helpers have been shown to participate less in infant-carrying, and for shorter bouts, than adult helpers, although the sub-adult helpers showed equal interest in infants as adult helpers (Yamamoto & Box 1997). Competition over infant-carrying among helpers has also been observed in captive groups of red-bellied tamarins (*Saguinus labiatus*) (Pryce 1988) and cotton-top tamarins (*Saguinus oedipus*) (Price 1991). In addition, infant-carrying is shared more among group members in demanding natural environments, rather than in benign captive environments (Yamamoto *et al.* 1996). Therefore, the accessibility of the infants, and the demand for alloparental infant-carrying seem to determine the extent of helpers’ involvement in infant-carrying in social groups in my study. Other studies have also shown that group members can prevent others from helping in various taxa (red foxes, *Vulpes vulpes*: silver-backed jackals, *Canis mesomelas*: wolves, *Canis lupus*: African wild dogs, *Lycaon pictus*: reviewed in Macdonald & Moehlman 1982; green woodhoopoes, *Phoeniculus purpureus*: Ligon & Ligon 1983; pied kingfishers, *Ceryle rudis*: Reyer 1986). Further studies into the influence of social factors in the

participation of helpers would be essential to clarify how the intrinsic propensity of helpers to carry infants is maintained.

It would also be of value to investigate whether social contexts affect the helpers' motivation for carrying infants. In the current study, I deliberately isolated focal individuals from other potential helpers. However, the presence of other potential carriers might decrease the motivation of helpers to carry infants since it would be beneficial for helpers to share the costs of carrying infants without losing the benefits from increased survival of the infants through processes, such as, kin selection and group augmentation (Hamilton 1964; Wright 1998; Kokko *et al.* 2001). Alternatively, the presence of other potential carriers might increase the motivation of helpers to carry infants. For instance, the motivation of helpers to carry infants might be increased to prevent others from carrying the infants in order to retain the opportunity for the helper to improve their own infant care skills (Tardif 1997; Snowdon & Ziegler 2007) or to protect the infants from being injured by other carriers who may be unskilled or unreliable (Maestripieri 1994; Mitani & Watts 1997; Digby & Saltzman 2009). Such effects could be explored experimentally. However, experiments would have to be performed using individuals within the group that are similar in age and hierarchy since older or higher ranked individuals seem to be more adept in competing for infant-carrying opportunities (Stevenson & Rylands 1988; Yamamoto & Box 1997). Similarly, in future, more detailed behavioural observations could measure, not only the infant-carrying time, but also behaviours, such as attempts to retrieve or dislodge the infants, in order to fully understand the motivation of helpers to carry infants (Yamamoto & Box 1997; Zahed *et al.* 2008; Saito *et al.* 2011b). Such investigations could be useful in revealing proximate mechanisms that motivate helpers to carry infants, which would provide valuable insights into the function and, hence, the benefits of alloparental infant-carrying behaviour.

Possible fitness benefits of alloparental infant-carrying behaviour

Given the findings of my thesis, there are three possible reasons that might underpin the existence of alloparental infant-carrying behaviour in common marmosets. The first is that alloparental infant-carrying behaviour may provide indirect fitness benefits by increasing the reproductive success of breeding pairs that are genetically related to the helpers (Hamilton 1964). Although my research showed that the helpers' contribution to infant-carrying was not substantial enough to reduce parental infant-carrying loads, and may not be necessary for the

successful reproduction of breeding pairs in captive environments, this absence of the load lightening effect in alloparental infant-carrying behaviour may be due to the fact that my sample lacked adult helpers (Chapter 2), which have been suggested to play an important role in reducing parental infant-carrying loads (Koenig & Rothe 1991; Rothe & Darms 1993; Yamamoto & Box 1997). Also, the importance of fathers' contributions to infant-carrying for successful reproduction, as evidenced by the higher success in parturition during subsequent breeding (Chapter 2), even in the benign captive environment, suggests that alloparental, as well as paternal infant-carrying, may be important for the successful reproduction of common marmosets in natural environments where reproduction would be more challenging. This suggestion is supported by field observations of free-ranging callitrichines in which lone breeding pairs without alloparents are rarely successful in raising their young (Goldizen 1988; Koenig 1995; Bales *et al.* 2000). Therefore, the contribution of alloparents seems to be essential for successful reproduction. Moreover, the association of longer reproductive tenure of male breeders with a greater number of helpers in the groups of free-ranging golden lion tamarins (*Leontopithecus rosalia*) suggests the possible positive effect of alloparental infant-carrying on the lifetime reproductive opportunities of the breeding pairs (Bales *et al.* 2000). In free-ranging groups of common marmosets, alloparents are often the offspring of the breeding pairs (Digby & Barreto 1993; Ferrari & Digby 1996; Nievergelt *et al.* 2000) and some immigrant alloparents have been shown to be the maternal relatives of the dominant breeders (Faulkes *et al.* 2009). Therefore, alloparental infant-carrying behaviour in demanding natural environments may provide indirect fitness benefits by improving the reproductive success of the breeding pairs by lightening the parental infant-carrying loads and reducing the energetic costs of reproduction. Future studies, in this regard, should explicitly test whether alloparental infant-carrying does, indeed, confer positive effects on the reproductive success of parents.

The second reason is that alloparental infant-carrying may provide fitness benefits to the helpers through group augmentation. My findings suggest that alloparental infant-carrying behaviour is likely to fulfil one of the preconditions for group augmentation, namely that helpers increase group size, in which larger group size would be beneficial for the helpers (Kokko *et al.* 2001). The result that helpers also carried infants most of the time under perceived predation risk (Chapter 5) suggests that alloparental infant-carrying could increase group size by increasing infant survival and the reproductive success of the breeding pairs. This increased group size would benefit the helpers by reducing predation risk through

increased vigilance and the antipredator defence of the groups (Hamilton 1971; Wilson 1975; Garay 2009). Vigilance behaviour of individuals has been shown to decrease with increase in group size in free-ranging moustached tamarins (*Saguinus mystax*) (Stojan-Dolar & Heymann 2010) and captive common marmosets (Gosselin-Ildari & Koenig 2012), suggesting increased safety in larger groups. Moreover, in captive red-bellied tamarins, the total amount of visual monitoring of a threatening object has been shown to increase with group size, indicating increased antipredator defence in larger groups (Caine 1986). These antipredator effects of group size would be especially vital for the survival of small-bodied animals under high predation pressure, such as common marmosets (Cheney & Wrangham 1987; Caine 1993; Ferrari 2009). The increased group size would also benefit the helpers in defending their territory in conflicts with neighbouring groups. In free-ranging common marmosets, a smaller group was more likely to be invaded by a larger neighbouring group and lose their territory (Lazaro-Perea 2001). It has also been observed that newly established groups of free-ranging golden lion tamarins, which are smaller in size and tend to occupy territories that are difficult to defend, have lower survivorship compared to more established groups (Baker *et al.* 1993). Also, a larger group size with more numbers of younger members in the group can potentially increase the future reproductive success of the helpers, since the younger group members may disperse with the helpers and become helpers when the former helpers become breeders. In free-ranging common marmosets, younger group members can assume the role of subordinate members for adult helpers that subsequently become the dominant breeders in newly formed groups (Lazaro-Perea *et al.* 2000). Formation of new groups by a coalition of former group members have also been observed in free-ranging groups of other callitrichines (buffy-headed marmosets, *Callithrix flaviceps*: Ferrari & Lopes Ferrari 1989; cotton-top tamarins: Savage *et al.* 1996; moustached tamarins: Heymann 1998). Since the contribution of alloparents to infant care seems to be crucial for the successful reproduction of callitrichines in natural environments (Goldizen 1988; Koenig 1995; Bales *et al.* 2000), raising younger group members as future allies would be important for the reproductive success of helpers when they become breeders. In order to evaluate the possible role of alloparental infant-carrying in group augmentation, the effects of group size in the survival and future reproductive success of the helpers, as well as the effects of alloparental infant-carrying behaviour on the reproductive success of breeding pairs, need to be assessed further in future studies.

The third reason that could explain the existence of alloparental infant-carrying behaviour is that such behaviour may be associated with the learning of important skills that can help to increase the future reproductive success of the helpers. Experience in alloparental care has been suggested to improve the future reproductive success of the helpers. In some callitrichine species, including common marmosets, survival of the first litter has been reported to be higher in individuals who have had prior experience engaging in alloparental infant care compared to individuals without any alloparental experience (Epple 1978; Hoage 1978; Ingram 1978; Tardif *et al.* 1984; Snowdon *et al.* 1985; Pryce 1988; Baker & Woods 1992; Pryce 1993; reviewed in Tardif 1997; but see Zahed *et al.* 2010). I showed that the contribution of male and female parents to infant-carrying is important for successful parturition by the breeding females in a subsequent breeding attempt (Chapter 2). This indicates that skills in infant care would be important to both parents for the successful reproduction. Therefore, learning how to care for infants through experience in alloparental infant-carrying could potentially be important for male and female helpers in terms of their future reproductive success as breeders. This is also concordant with the finding that contributions to infant-carrying did not differ between male and female helpers (Chapter 3), which suggests that male and female helpers are similarly interested in practising their infant care skills. However, it has been suggested that the positive effect of helper experience on their future reproductive success could be due to being exposed to infants *per se* rather than actual participation and experience in infant care (Baker & Woods 1992; Tardif *et al.* 1992; Zahed *et al.* 2010). Therefore, although experience in alloparental infant care seems to be important for the future reproductive success of the helpers, further work is required to test whether alloparental infant-carrying behaviour has skill learning effects, and how helper experience in alloparental infant-carrying actually improves the reproductive success of the helpers.

Potential limitations of the study

My study took place using a captive colony of marmosets. While this enabled me to use experimental approaches and achieve sample sizes comparable to, or greater than, similar studies in the published literature (Price 1992a, b; Schradin & Anzenberger 2001; Cronin *et al.* 2005; Burkart *et al.* 2007; Zahed *et al.* 2008; Burkart *et al.* 2009; Saito *et al.* 2011a, b), two main artefacts of captivity might have affected the study outcomes. Those artefacts are

(1) handling stress to carriers and infants and (2) other experiments performed in the colony. I will discuss each of these, in turn.

Effects of stress from handling on the behaviour of animals

I consider it unlikely that handling of animals just prior to the experiment resulted in stress that might have significantly affected their behaviour during the experiments. First, the effects of handling on the animals would be minimal: animals in this captive population have been extensively captured and handled by the station staff since they were born (e.g. hand-feeding, weighing, health check and relocation of the animals) and are therefore accustomed to be handled by humans. Second, the animals used in the experiments were frequently monitored by the station staff before, during and after the experiment throughout the day to ensure that the animals were not stressed. Third, I did not observe a reduction in infant-carrying behaviour of the focal animals as a result of stress. Infants aged between 19 to 25 days old were mostly carried full time during the one-hour observation periods while they were in the social groups (Chapter 2). In the experiments, infants of similar age were generally carried full time during the 30-minutes trials (Chapters 3, 4, 5). Lastly, the experiments were designed to standardise the potential stress level the animals experience by ensuring that all the animals underwent similar levels of handling and separation from the social group. Similarly, the distress to infants from handling or separation from the mother, or a lack of nursing was minimised by keeping infants with their mothers in the home cage until they were moved for the trials (Chapters 3, 4, 5). Therefore, infants had the opportunity to be nursed before being separated for the trials. Also, the separation of an infant from the mother for the trials was limited to 40 minutes (i.e. the duration of the trial) except for one infant that was used in two consecutive trials but was briefly return to the social group (approximately ten minutes) between trials. Therefore, infants were not prevented from nursing for a prolonged time. In addition, when the infant was found to be nursing before a planned trial, the trial was postponed until the infant finished nursing.

Effects of experiments performed in the colony by other researchers

I also consider it unlikely that the behaviour of animals in my study may have been affected significantly by experiments that were performed in the colony by other researchers. First, potential effects of the other experiments on my study were inherently minimal. The primary function of the marmoset colony was to breed common marmosets for medical research. Hence, in general, medical experiments on the animals are not performed at the colony *per se*,

but are, instead, sent out to other research institutes. Second, I made every effort to avoid confounding effects of the other experiments on my study. Although some animals within the colony underwent surgery for (unrelated) medical experiments, and were temporally kept in the colony, marmoset families with the operated animals were not involved in the observational study (Chapter 2). Some families with operated animals, however, were involved in the manipulative experiments (Chapters 3, 4, 5). In those instances, operated animals were not used in experiments. As described in the Methods sections of the relevant chapters, the subordinate members (helpers) of groups with operated infants were separated from the operated infant, other infants from the same litter and the parents for two weeks after surgery. The experiments on the animals from these groups were performed after the group members were reunited for at least one week to ensure that the infants were familiar with the helpers.

Conclusions

My thesis showed that, in captive common marmoset groups, helpers' contribution to infant-carrying was quite minimal when the helpers were in the social groups. However, when helpers were separated from the social groups, they carried infants as much as the mothers of the infants. This contribution of helpers to infant-carrying was not influenced by the sex of the helpers, the presence of a social observer or perceived predation risk, but it only decreased as infant age increased. The results suggest three fundamental features underpinning alloparental infant-carrying behaviour: (1) its function in accommodating the carrying need of the infant, (2) social restraints over the helpers' participation in infant-carrying in the groups, and (3) substantial fitness benefits to the helpers. Future studies should, in turn, investigate the causes of the variation in helpers' contributions to infant-carrying, which would be important in revealing the factors that influence helpers' motivation to help, as well as the motivation driving the helping behaviour. Also, the fitness effects of alloparental infant-carrying behaviour for the helpers and the recipients need to be quantified in order to understand how this behaviour is maintained in a population. Further insights into the proximate and ultimate causes of alloparental infant-carrying behaviour have important implications for understanding the evolution of helping behaviour in general. It may provide clues to the evolutionary root of helping behaviour, and environmental conditions and factors that may have facilitated the evolution of helping behaviour in different species, including our own.

References

- Albuquerque, F. S. (1999) Cuidado cooperativo à prole em *Callithrix jacchus*: Dinâmica em ambiente natural. the Universidade de São Paulo. São Paulo, Brazil. PhD thesis.
- Baglione, V., Canestrari, D., Chiarati, E., Vera, R. & Marcos, J. M. (2010) Lazy group members are substitute helpers in carrion crows. *Proceedings of the Royal Society B-Biological Sciences*, 277, 3275-3282.
- Baker, A. J., Dietz, J. M. & Kleiman, D. G. (1993) Behavioral evidence for monopolization of paternity in multimale groups of golden lion tamarins. *Animal Behaviour*, 46, 1091-1103.
- Baker, A. J. & Woods, F. (1992) Reproduction of the emperor tamarin (*Saguinus imperator*) in captivity, with comparisons to cotton-top and golden lion tamarins. *American Journal of Primatology*, 26, 1-10.
- Bales, K., Dietz, J., Baker, A., Miller, K. & Tardif, S. D. (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica*, 71, 27-38.
- Burkart, J. M., Fehr, E., Efferson, C. & van Schaik, C. P. (2007) Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 19762-19766.
- Burkart, J. M., Strasser, A. & Foglia, M. (2009) Trade-offs between social learning and individual innovativeness in common marmosets, *Callithrix jacchus*. *Animal Behaviour*, 77, 1291-1301.
- Caine, N. G. (1986) Visual monitoring of threatening objects by captive tamarins (*Saguinus labiatus*). *American Journal of Primatology*, 10, 1-8.
- Caine, N. G. (1993) Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Charbonneau, D., Sasaki, T. & Dornhaus, A. (2017) Who needs 'lazy' workers? Inactive workers act as a 'reserve' labor force replacing active workers, but inactive workers are not replaced when they are removed. *PLoS ONE*, 12.
- Cheney, D. L. & Wrangham, R. W. (1987) Predation. IN Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds.) *Primates*. Chicago, IL, Chicago University Press.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L. & Jordan, N. R. (2005) 'False feeding' and aggression in meerkat societies. *Animal Behaviour*, 69, 1273-1284.
- Cronin, K. A., Kurian, A. V. & Snowdon, C. T. (2005) Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). *Animal Behaviour*, 69, 133-142.
- Digby, L. & Saltzman, W. (2009) Balancing cooperation and competition in callitrichid primates: Examining the relative risk of infanticide across species. IN Davis, L. C., Ford, S. M. & Porter, L. M. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Digby, L. J. & Barreto, C. E. (1993) Social organization in a wild population of *Callithrix jacchus*. I. Group composition and dynamics. *Folia Primatologica*, 61, 123-134.
- Epple, G. (1978) Reproductive and social behavior of marmosets with special reference to captive breeding. *Primates in Medicine*, Vol. 10, 50-62.
- Faulkes, C. G., Arruda, M. F. & Monteiro da Cruz, M. A. O. (2009) Genetic structure within and among populations of the common marmoset, *Callithrix jacchus*: Implications for cooperative breeding. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest*

- anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Ferrari, S. F. (2009) Predation risk and antipredator strategies. IN Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. K. & Strier, K. B. (Eds.) *South American primates: Comparative perspectives in the study of behavior, ecology, and conservation*. New York, Springer.
- Ferrari, S. F. & Digby, L. J. (1996) Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, 38, 19-27.
- Ferrari, S. F. & Lopes Ferrari, M. A. (1989) A re-evaluation of the social organization of the callitrichidae, with reference to the ecological differences between genera. *Folia Primatologica*, 52, 132-147.
- Garay, J. (2009) Cooperation in defence against a predator. *Journal of Theoretical Biology*, 257, 45-51.
- Gardner, A., West, S. A. & Wild, G. (2011) The genetical theory of kin selection. *Journal of Evolutionary Biology*, 24, 1020-1043.
- Goldizen, A. W. (1988) Tamarin and marmoset mating systems - unusual flexibility. *Trends in Ecology & Evolution*, 3, 36-40.
- Gosselin-Ildari, A. D. & Koenig, A. (2012) The effects of group size and reproductive status on vigilance in captive *Callithrix jacchus*. *American Journal of Primatology*, 74, 613-621.
- Hamilton, W. D. (1964) The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, 7, 1-52.
- Hamilton, W. D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.
- Hasegawa, E., Ishii, Y., Tada, K., Kobayashi, K. & Yoshimura, J. (2016) Lazy workers are necessary for long-term sustainability in insect societies. *Scientific Reports*, 6.
- Heymann, E. W. (1998) Sex differences in olfactory communication in a primate, the moustached tamarin, *Saguinus mystax* (Callitrichinae). *Behavioral Ecology and Sociobiology*, 43, 37-45.
- Hoage, R. J. (1978) Parental care in *Leontopithecus rosalia rosalia*: Sex and age differences in carrying behavior and the role of prior experience. IN Kleiman, D. G. (Ed.) *The biology and conservation of the callitrichidae: A symposium held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, August 18-20, 1975*. Smithsonian Institution Press.
- Ingram, J. C. (1977) Interactions between parents and infants, and development of independence in common marmoset (*Callithrix jacchus*). *Animal Behaviour*, 25, 811-827.
- Ingram, J. C. (1978) Preliminary comparisons of parental care of wild-caught and captive-born common marmosets. IN Rothe, H., Wolters, H. J. & Hearn, J. P. (Eds.) *Biology and behaviour of marmosets*. Göttingen, West Germany, Eigenverlag.
- Koenig, A. (1995) Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 35, 311-317.
- Koenig, A. & Rothe, H. (1991) Social relationships and individual contribution to cooperative behavior in captive common marmosets (*Callithrix jacchus*). *Primates*, 32, 183-195.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268, 187-196.

- Lazaro-Perea, C. (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. *Animal Behaviour*, 62, 11-21.
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araújo, A., Arruda, M. F. & Snowdon, C. T. (2000) Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology*, 48, 137-146.
- Ligon, J. D. & Ligon, S. H. (1983) Reciprocity in the green woodhoopoe (*Phoeniculus purpureus*). *Animal Behaviour*, 31, 480-489.
- Macdonald, D. W. & Moehlman, P. D. (1982) Cooperation, altruism, and restraint in the reproduction of carnivores. IN Bateson, P. P. G. & Klopfer, P. H. (Eds.) *Ontogeny*. Boston, MA, Springer US.
- Maestriperi, D. (1994) Social structure, infant handling, and mothering styles in group-living old world monkeys. *International Journal of Primatology*, 15, 531-553.
- Mitani, J. C. & Watts, D. (1997) The evolution of non-maternal caretaking among anthropoid primates: Do helpers help? *Behavioral Ecology and Sociobiology*, 40, 213-220.
- Nievergelt, C. M., Digby, L. J., Ramakrishnan, U. & Woodruff, D. S. (2000) Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *International Journal of Primatology*, 21, 1-20.
- Price, E. C. (1991) Competition to carry infants in captive families of cotton-top tamarins (*Saguinus oedipus*). *Behaviour*, 118, 66-88.
- Price, E. C. (1992a) The benefits of helpers: Effects of group and litter size on infant care in tamarins (*Saguinus oedipus*). *American Journal of Primatology*, 26, 179-190.
- Price, E. C. (1992b) The costs of infant carrying in captive cotton-top tamarins. *American Journal of Primatology*, 26, 23-33.
- Pryce, C. R. (1988) Individual and group effects on early caregiver-infant relationships in red-bellied tamarin monkeys. *Animal Behaviour*, 36, 1455-1464.
- Pryce, C. R. (1993) The regulation of maternal behavior in marmosets and tamarins. *Behavioural Processes*, 30, 201-224.
- Reyer, H. U. (1986) Breeder-helper-interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour*, 96, 277-303.
- Rothe, H. & Darms, K. (1993) The social organization of marmosets: A critical evaluation of recent concepts. IN Rylands, A. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Saito, A., Izumi, A. & Nakamura, K. (2011a) Development of infant common marmosets' (*Callithrix jacchus*) preference for their parents over adults from another group. *Primates*, 52, 43-50.
- Saito, A., Izumi, A. & Nakamura, K. (2011b) Fathers have higher motivation for parenting than mothers in common marmoset (*Callithrix jacchus*). *Behaviour*, 148, 1199-1214.
- Savage, A., Giraldo, K. H., Soto, K. H. & Snowdon, C. T. (1996) Demography, group composition, and dispersal in wild cotton-top tamarin (*Saguinus oedipus*) groups. *American Journal of Primatology*, 38, 85-100.
- Schradin, C. & Anzenberger, G. (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: An experimental analysis. *Animal Behaviour*, 62, 289-295.
- Snowdon, C. T., Savage, A. & McConnell, P. B. (1985) A breeding colony of cotton-top tamarins (*Saguinus oedipus*). *Laboratory Animal Science*, 35, 477-480.
- Snowdon, C. T. & Ziegler, T. E. (2007) Growing up cooperatively: Family processes and infant care in marmosets and tamarins. *Journal of Developmental Processes*, 40-66.

- Stevenson, M. F. & Rylands, A. B. (1988) The marmosets, genus *Callithrix*. IN Mittermeier, R. A., Rylands, A. B., Coimbra-Filho, A. F. & de Fonseca, G. A. B. (Eds.) *Ecology and behavior of neotropical primates*. Washington DC, World Wildlife Fund.
- Stojan-Dolar, M. & Heymann, E. W. (2010) Vigilance in a cooperatively breeding primate. *International Journal of Primatology*, 31, 95-116.
- Tardif, S. D. (1997) The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. IN Solomon, N. G. & French, J. A. (Eds.) *Cooperative breeding in mammals*. Cambridge, Cambridge University Press.
- Tardif, S. D. & Bales, K. L. (2004) Relations among birth condition, maternal condition, and postnatal growth in captive common marmoset monkeys (*Callithrix jacchus*). *American Journal of Primatology*, 62, 83-94.
- Tardif, S. D., Carson, R. L. & Gangaware, B. L. (1992) Infant-care behavior of nonreproductive helpers in a communal-care primate, the cotton-top tamarin (*Saguinus oedipus*). *Ethology*, 92, 155-167.
- Tardif, S. D., Richter, C. B. & Carson, R. L. (1984) Effects of sibling-rearing experience on future reproductive success in two species of callitrichidae. *American Journal of Primatology*, 6, 377-380.
- Wilson, E. O. (1975) *Sociobiology: The new synthesis*, Cambridge, Harvard University Press.
- Wilson, E. O. (1984) The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera, Formicidae). *Behavioral Ecology and Sociobiology*, 16, 89-98.
- Wright, J. (1997) Helping-at-the-nest in Arabian babblers: Signalling social status or sensible investment in chicks? *Animal Behaviour*, 54, 1439-1448.
- Wright, J. (1998) Helping-at-the-nest and group size in the Arabian babbler *Turdoides squamiceps*. *Journal of Avian Biology*, 29, 105-112.
- Yamamoto, M. E. (1993) From dependence to sexual maturity: The behavioural ontogeny of callitrichidae. IN Rylands, A. B. (Ed.) *Marmosets and tamarins: Systematics, behaviour and ecology*. London, Oxford University Press.
- Yamamoto, M. E., Albuquerque, F. S., Lopes, N. A. & Ferreira, E. S. (2008) Differential infant carrying in captive and wild common marmosets (*Callithrix jacchus*). *Acta Ethologica*, 11, 95-99.
- Yamamoto, M. E., Arruda, M. d. F., Alencar, A. I., de Sousa, M. B. C. & Araújo, A. (2009) Mating systems and female-female competition in the common marmoset, *Callithrix jacchus*. IN Ford, S. M., Porter, L. M. & Davis, L. C. (Eds.) *The smallest anthropoids: The marmoset/callimico radiation*. New York, Springer Science+Business Media.
- Yamamoto, M. E. & Box, H. O. (1997) The role of non-reproductive helpers in infant care in captive *Callithrix jacchus*. *Ethology*, 103, 760-771.
- Yamamoto, M. E., Box, H. O., Albuquerque, F. S. & Arruda, M. D. (1996) Carrying behaviour in captive and wild marmosets (*Callithrix jacchus*): A comparison between two colonies and a field site. *Primates*, 37, 297-304.
- Zahavi, A. (1995) Altruism as a handicap - the limitations of kin selection and reciprocity. *Journal of Avian Biology*, 26, 1-3.
- Zahed, S. R., Kurian, A. V. & Snowdon, C. T. (2010) Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. *American Journal of Primatology*, 72, 296-306.
- Zahed, S. R., Prudom, S. L., Snowdon, C. T. & Ziegler, T. E. (2008) Male parenting and response to infant stimuli in the common marmoset (*Callithrix jacchus*). *American Journal of Primatology*, 70, 84-92.