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# THE EVOLUTION OF MALE PARENTAL CARE IN MAMMALS

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by

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# CONTENTS

# THESIS ABSTRACT

Males care for offspring across a diverse range of taxa. Why males give up mating opportunities and spend time and energy caring for offspring is unclear, especially when females already provide parental care. The evolutionary drivers for biparental care are currently uncertain, as are the evolutionary consequences of male care on female and offspring fitness. Using modern phylogenetic comparative methods, I test hypotheses on the evolution of biparental care in a sample of over 500 mammalian species while considering the diversity in parental care behaviours. Both male care and monogamy occur in species where levels of paternity are high, but only monogamy associates with reduced investment in sperm competition traits. Male care also has energetic benefits for females and offspring; females have higher fecundity and offspring faster growth in species with biparental care, in support of the 'load-lightening' hypothesis. I find strong support for the hypothesis that monogamy drives the evolution of male care but only for behaviours that provide fecundity benefits, while behaviours unrelated to female fecundity may either precede or follow monogamy. However, I find no support for the hypothesis that infanticide by males promotes the evolution of male care. Lastly, I investigate whether care by non-parental helpers exhibit similar associations with life history traits as male care and find that care by helpers associates with increased fecundity, but by influencing different times of the female reproductive cycle. Overall I identify a two-step process of evolution between male care and social monogamy, with care behaviours which do not confer fecundity benefits facilitating the evolution of social monogamy and higher paternity levels, which subsequently promote the evolution of further care behaviours with higher energetic benefits. Thus, this research demonstrates the importance of considering the care behaviour performed, the time of female reproduction at which it is performed, and the identity of the carer, in studies investigating the evolution of parental care.

# CHAPTER 1: AN INTRODUCTION TO MALE PARENTAL CARE

Behaviour can be an important evolutionary driver of diversity in morphology, physiology and ecology (Huey et al. 2003; Plotkin 1988). In the context of reproduction, behaviour can influence the evolutionary trajectory of several animal characteristics and can be responsible for large-scale differences between species. For example, the intensity of male-male competition and female choice help explain diversity in secondary sexually selected traits, such as horns across bovid species and colouration in birds (Bro-Jørgensen 2007; Emlen 2008; Dubuc et al. 2014; Emlen et al. 2005; Hill 1991). Likewise, competition between the sexes can help to explain the diversity in genital morphology (Hosken & Stockley 2004; Arnqvist & Rowe 2002; Brennan et al. 2007), and the evolution of male reproductive characteristics such as sperm morphology and testes mass (Fitzpatrick 2009; Soulsbury 2010; Møller 1988; Simmons & García-González 2008). Furthermore, the evolution of life history traits may also be affected by the intensity of parent-offspring conflict and sibling competition (Stockley & Parker 2002; Trivers 1972; Andersson 1994; Ricklefs 1993; Royle & Hartley 1999). Parental care, defined as any behaviour exhibited by a parent that increases the fitness of the offspring and has originated and/or is maintained for this function (Smiseth et al. 2012), is another important behaviour that may drive the evolution of interspecific diversity. By influencing the fitness of parents and offspring, parental care is at the centre of the cooperation and conflict between parents over which parent, and how long for, raises the offspring (Houston et al. 2005; Royle et al. 2010), cooperation and conflict between parents and offspring over parental allocation of resources to current and future offspring, as well as sibling competition over parental resources (Stockley & Parker 2002). The nature and duration of parental care, however, varies substantially both across species and between individuals of the same species (Balshine 2012). While in many species neither parent makes any substantial investment in offspring care, in others either or both parents devote a considerable amount of time and energy in raising the offspring and express a wide range of care behaviours (Balshine 2012; Kokko & Jennions 2012).

This project asks how the diversity of male parental care across mammal species relates to the diversity in female life history traits and male reproductive traits, and how it relates to other important behaviours such as mating system and parental care by other (non-parental) helpers (here 'alloparents'). A major advance of this project relative to previous studies is that it considers the diversity of care behaviours when investigating all the questions presented here. The definition of parental care is broad and encompasses a wide range of behaviours (Smiseth et al. 2012), yet each care behaviour is likely to entail different costs and benefits (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012). Most comparative research across species focuses on how parental care as a whole relates to species' reproductive and morphological characteristics, without explicitly considering either the diversity in care behaviours (Lukas & Clutton-Brock 2013; Opie et al. 2013) or carer identity, sometimes even classing male care together with allocare (Isler & van Schaik 2012). However, such diversity in both the type of behaviour and identity of the carer is likely key for fully understanding how and why parental care evolves.

Caring for the offspring is often costly. Parental care may entail substantial energetic costs leading to a remarkable loss of body mass and condition (Fietz & Dausmann 2003; Campbell et al. 2009; Reid 1987), increased predation risk and levels of parasitism (Schradin & Anzenberger 2001; Riguera & Gomendio 1999; Li & Jackson 2003; Nunn & Altizer 2006), reduced probability of survival (Descamps et al. 2009; Maynard Smith 1977), as well as opportunity costs such as missing mating opportunities. Costs may also differ between parents (Klug et al. 2012) and between parents and alloparents (Cant 2012). Thus, who cares and why is often an important source of conflict between individuals (Kokko & Jennions 2012; Taborsky 1985; Reyer 1986; Kutsukake & Clutton-Brock 2006). While many parental behaviours can be expressed by either sex, in many species, either one sex cares alone or, when biparental care occurs, one sex typically contributes more than the other (Balshine 2012). Theoretical models predict that the individual that makes the largest energetic contribution to reproduction should be the primary carer in order to protect their prior investment, while the parent who makes the lesser contribution should be the first to desert the offspring (Trivers 1972, but see: Dawkins & Carlisle 1976). Anisogamy, the differences in gamete size and the investment required to produce them, may represent the initial source of this asymmetry (Klug et al. 2012; Trivers 1972). This hypothesis proposes that females - the sex producing the larger gametes – should therefore be the primary carer (Balshine 2012; Klug et al. 2012; Trivers 1972). Yet among certain taxa, males are the sole carers of the offspring (Mank et al. 2005), and in many species of fish, amphibians, and birds, males are the primary carers (Balshine 2012). Recent mathematical models suggest that, rather than anisogamy, differences in adult mortality risk may determine which sex cares for the offspring (Klug et al. 2013). When male mortality is high, females mature faster and have greater juvenile survival, selection should favour care by males; while if female mortality is high, and males mature faster and have greater juvenile survival, care by females should be favoured (Klug et al. 2013). Other recent studies propose that intersexual selection may play a key role in the evolution of male only care; if females can determine which males might provide care, and preferentially mate with them, this should favour the evolution of male only care and lead to a high certainty of paternity for these caring males (Alonzo 2012; Kvarnemo 2005; Chemnitz et al. 2017).

While much research has focused on understanding the costs and benefits of parental care and the choice between caring or deserting the offspring, much less is known about why a parent provides additional care when the other already invests a substantial amount of energy, time and resources in raising the offspring, particularly at a large comparative scale across species. Biparental care occurs in several taxa, from insects to mammals (Balshine 2012; Gilbert & Manica 2015; Clutton-Brock 1991), and is the predominant form of care in birds (Balshine 2012). In insects, cichlid fish, and birds, biparental care appears to arise primarily through the initial evolution of female only care, with males subsequently joining caring females, leading to the evolution of biparental systems (Gilbert & Manica 2015; Remeš et al. 2015; Gonzalez-Voyer et al. 2008). However, why males should give up additional mating opportunities to help the female raising the offspring is currently unclear. Several theoretical models propose that care by one sex reduces the availability of this sex, altering the operational sex ratio (Queller 1997; Kokko & Jennions 2008), thus when the numbers of the caring sex that are available are limited, this may favour the evolution of additional care by the alternative sex. Empirical studies in a range of taxa, including insects, cichlid fish and birds, support this model and show that when additional mating opportunities for a male are limited, biparental care is more likely to evolve (Gilbert & Manica 2015; Remeš et al. 2015; Gonzalez-Voyer et al. 2008). However, because parental care is costly, males are unlikely to evolve the complex and costly care behaviours observed in nature without accruing some benefits to outweigh these costs. A lack of extra-pair mating opportunities is therefore unlikely to be the sole cause for the evolution of care by males.

Theoretical models predict that parents should invest more in offspring that they are related to (Trivers 1972; Queller 1997). Thus, much work on the evolution of male care has been on the relationship between male care and paternity (Alonzo 2010; Queller 1997; Møller & Birkhead 1993; Gross & Sargent 1985). High certainty of paternity should be essential for the evolution of male care, as caring for unrelated offspring reduces the benefits of care for a male (Alonzo & Klug 2012; Trivers 1972; Queller 1997). Thus, paternity represents an important constraint on the evolution of male parental care. Consistent with this hypothesis males in many species preferentially care for related offspring and plasticly reduce investment when paternity is uncertain (Alonzo 2010; Sheldon & Ellegren 1998; Lifjeld et al. 1998; Neff 2003; Hunt & Simmons 2002; Alonzo & Klug 2012; Griffin et al. 2013). However, it is unknown whether species with male care have an overall higher level of paternity than those without as predicted by these theoretical models, a question that I address in Chapter 2 of this thesis. This is important, because plasticity in parental care in response to paternity does not necessarily reflect selection over evolutionary time scales (Alonzo & Klug 2012). Furthermore, no study to date has investigated the consequence of the evolution of male care for male reproductive traits. Specifically, if male care evolves when males have higher certainty of paternity, we should also expect that this in turn affects the intensity of sperm competition. Males invest substantially in morphological traits, such as weapons or ornaments, and physiological traits, such as sperm production, which help increase their success in both pre- and post-copulatory male competition (Møller 1989; Gomendio & Roldan 2008; Emlen 2008; Parsons 1995). All these traits have high associated costs (Emlen 2008; Parsons 1995; Walther & Clayton 2005; Wedell et al. 2002; Olsson et al. 1997; Parker et al. 1996) and selection typically favours reductions in competitive traits when they are not necessary. Males of monogamous species, for example, have smaller weapons or are smaller and/or less colourful because intrasexual selection is typically less intense with monogamy (Bro-Jørgensen 2007; Dunn et al. 2001). Similarly, monogamous species invest less in sperm competition related traits (Iossa et al. 2008; Soulsbury 2010; Møller & Birkhead 1993). However, whether males that care for their offspring invest less in traits linked to sperm competition has not been studied. By investigating the inter-relationship between male care, levels of paternity, and traits linked to the intensity of sperm competition, Chapter 2 provides novel insights into the role of female promiscuity for the evolution of male parental care and its possible implications for males' investment into post-copulatory reproductive traits.

Most research on male parental care has focused on the costs and benefits of this behaviour for the male. By helping to raise the offspring, males should also provide important benefits to the offspring and the females, and in turn may benefit themselves. However, the potential implications of male care for these other individuals are little studied, particularly on a large scale. Beyond enhancing offspring survival, care by males may also increase offspring growth rates (Woodroffe & Vincent 1994; Oftedal & Gittleman 1989; Royle et al. 2006). Larger offspring often have higher probability of survival, so biparental care may have long-term benefits for the offspring survival. Care by males may also be beneficial to mothers (Woodroffe & Vincent 1994; Opie et al. 2013). In a few well-studied model biparental species, the presence of the male appears to allow females to raise more offspring (Jenkins et al. 2000; Gubernick & Teferi 2000; Cantoni & Brown 1997). Why this should be the case is unclear. Producing more offspring than the number a female can raise alone may also be a female strategy to solicit or retain male investment as this would require the additional support of the male (Smith & Härdling 2000; Royle 2016; Alonzo 2016). Alternatively, the help of a caring male may have direct energetic benefits for the female if, by reducing her investment in offspring care, she can then increase offspring production (Woodroffe & Vincent 1994; Crick 1992; Stockley & Hobson 2016). These hypotheses predict that biparental care influences the evolutionary trajectory of life history traits associated with fecundity and offspring growth, but no large-scale study has tested if this is the case. Furthermore, no study to date has investigated the benefits specific behaviours may have for female or offspring life histories. Chapter 3 addresses this question and does so while accounting for the diversity in male care behaviours in mammals.

A key behaviour often proposed as a driver for the evolution of male care is mating system. Previous studies suggest that a need for male care may act as an evolutionary driver for social monogamy, as selection should favour male-female associations if biparental care is vital for offspring survival (Birkhead & Møller 1996; Kleiman 1977; Wittenberger & Tilson 1980; Reichard & Boesch 2003; Burley & Johnson 2002; Ligon 1999). An alternative explanation is that monogamy is instead a key prerequisite for biparental care, a hypothesis supported by recent comparative studies (Lukas & Clutton-Brock 2013; Opie et al. 2013). However, these studies consider only two behaviours, carrying and provisioning of the offspring by males. These behaviours are often considered to be most energetically expensive than other care behaviours (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012), but they occur primarily in primates and carnivores (Nowak 1999). Thus, by neglecting to consider other behaviours, such as grooming and huddling, which may differ in their associated costs and benefits (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012; Campbell et al. 2009; Fietz & Dausmann 2003; Kenkel et al. 2014; Saltzman et al. 2015; Wynne-Edwards & Lisk 1989), and which are more prevalent in other orders (Nowak 1999), these studies may be biased towards certain groups. Given the differences in the costs and benefits of care behaviours, chapter 4 will therefore focus on the relationship between male care and social monogamy, investigating whether the specific male care behaviour in question alters the directionality of this relationship.

Behaviours do not occur in isolation; rather, specific behaviours tend to be present together. For example, species with male care may also exhibit infanticide or allocare. Male care and infanticide can be viewed as two sides of the same coin, because they are both male behaviours, sometimes expressed by the same individuals at different times (e.g. Elwood 1977; Elwood 1985; Gibber et al. 1984; Makin & Porter 1984) but they clearly affect the offspring in markedly different ways. Among several rodent species for example, where males are infanticidal towards pups, the act of mating and the presence of a pregnant female facilitates a behavioural switch from infanticidal behaviours to offspring care (Elwood 1977; Elwood 1985; Gibber et al. 1984; Makin & Porter 1984). Likewise in poison frogs (*Allobates femoralis*), territorial males often cannibalize all eggs prior to mating, but provide extensive care for any subsequent eggs laid in their territory (Ringler et al. 2017). A highly debated and long-standing hypothesis proposes that infanticide facilitates the evolution of male care because a high infanticide risk may select for the presence of caring males who can help to defend offspring from attack (Paul et al. 2000; van Schaik 2000; Agrell et al. 1998; Dunbar & van Schaik 1990). Like male care, infanticide should also affect the evolutionary trajectory of female life history traits (van Schaik 2000; Opie et al. 2013). While two recent comparative studies reached opposite conclusions with regard to whether male care and infanticide are evolutionary associated in mammals and primates respectively (Opie et al. 2013; Lukas & Clutton-Brock 2013), sparking debates on the evolutionary association between these behaviours (Opie et al. 2014; Lukas & Clutton-Brock 2014), no study to date has investigated how these two behaviours relate to species’ life history strategies at large comparative scale. Chapter 5 addresses this question while also re-evaluating the causal relationship between them.

Finally, older siblings and other non-parental helpers may also assist in raising the offspring (Isler & van Schaik 2012; Lukas & Clutton-Brock 2012a; Wisenden 1999; Cant 2012). Why these individuals care has been the subject of intensive study (Wisenden 1999; Cant

2012; Isler & van Schaik 2012; Lukas & Clutton-Brock 2012a), but the similarities and differences between allocare and care by males are much less well understood. While some consider both forms of care to be equivalent (Isler & van Schaik 2012), and many of the parental behaviours, such as provisioning, brooding, grooming or cleaning the young (Wisenden 1999; Lukas & Clutton-Brock 2012a; Brown 1987; Riedman 1982; Mitani & Watts 1997; Ridley & Raihani 2008; Santos & Macedo 2011), performed by males and alloparents are similar, the costs experienced by individual carers may not necessarily be the same. For example, among several bird species and some mammals where parents are aided by helpers, parents reduce their own investment in offspring care while helpers invest more (Hatchwell 1999; Clutton-Brock et al. 2004), suggesting that helpers face higher costs than parents do. Moreover, helpers are not always as closely related to the offspring as parents are, and in some species are totally unrelated (Dunn et al. 1995; Queller et al. 2000). Thus, the relative inclusive fitness gains of parental care may also differ depending on the identity of the carer and its relatedness to the offspring. As with the male in biparental species, alloparental helpers may bring substantial energetic benefits to the reproducing female, reducing the energetic costs of reproduction and enabling females to increase fecundity and reproductive success (Crick 1992). Although care by helpers associates with an increase in female fecundity in several single species studies (Riedman 1982; Mitani & Watts 1997; Meade et al. 2010), the generality of principles on the potential mechanism underlying this increase and whether this is the same as for male care, remains to be established. Chapter 6 investigates how the identity of the carer (the male or non-parental helpers) affects the relationship between care and life history traits, and investigates whether different allocare behaviours by helpers associate with different life history traits.

In this project, I consider parental care behaviours to be the following: food provisioning of the offspring (and/or pregnant or lactating females, as this indirectly benefits the offspring), carrying offspring, grooming offspring, or huddling with offspring for thermoregulatory purposes (Woodroffe & Vincent 1994). I exclude some behaviours, such as territoriality and teaching behaviours from my definition of male care, due to the difficulty of reliably classifying these behaviours in wild mammals (Thornton & McAuliffe 2006; Woodroffe & Vincent 1994). Classifying active protection of the young from predators by males as a form of care is difficult as these behaviours can be easily confused with general territorial behaviours, such as defensive behaviours against other males or groups (Woodroffe & Vincent 1994). As detailed above, it is important to consider a specific range of care behaviours because the differences in costs and benefits between the individual behaviours have the potential to alter the cost/benefit trade-offs underlying the evolution of parental care. Therefore, in all chapters I analyse the specific behaviours included within 'male care' individually, except in chapter 2, where limitations of sample size preclude this approach.

The aim of this thesis is to investigate the evolution of biparental care in mammals and how it relates to other behavioural, morphological and physiological traits, at a large comparative scale. A large-scale comparative approach is the most powerful tool for identifying general principles (Harvey & Pagel 1991). Here, I address questions on the evolutionary drivers for the evolution of biparental care; investigate how male care benefits males, females and offspring; and how male care relates to infanticide and care by other helpers. In doing so, I investigate the similarities and differences across behaviours and the identity of the carer. Because closely related species are expected to be more similar to each other than expected by chance due to their shared ancestry, I use modern phylogenetic comparative approaches that explicitly incorporate phylogeny into statistical models (Freckleton et al. 2002; Pagel 1999). Finally, chapter 7 brings the conclusions of all chapters together, and highlights how this work has advanced our understanding of the evolution of male parental care.

# CHAPTER 2: SOCIAL MONOGAMY, BUT NOT MALE CARE, ASSOCIATES WITH HIGHER PATERNITY AND LOWER LEVELS OF SPERM COMPETITION IN MAMMALS

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**Author contributions:** IC and HW designed the research, all authors designed the data collection protocols, HW and AB collected the data, HW conducted the analyses, HW and IC drafted the manuscript; all authors revised the draft.

## Abstract

Because parental care can be highly costly for males energetically and due to lost mating opportunities, males should care only when their certainty of paternity is high and/or when additional mating opportunities are unlikely. While many studies investigate male behavioural responses in care levels to paternity loss and the evolutionary association between male care and mating system, we still do not know whether species with male care achieve higher certainty of paternity than species without care, as predicted by theoretical models, and consequently invest less in traits influenced by sperm competition. Using phylogenetic comparative methods and data on over 500 mammalian species, we show that mammals with male care or social monogamy have higher certainty of paternity than species without these traits. However, social monogamy but not male care is evolutionarily associated with a reduction in traits related to high levels of sperm competition. These results, together with independent evidence that the evolution of social monogamy precedes the evolution of male care, indicate that monogamy increases paternity levels and reduces the intensity of sperm competition, and this in turn promotes the evolution of male parental care.

## Introduction

Parental care occurs in a wide range of taxa (Balshine 2012). Maternal care is generally more common, but in some groups, such as bony fish, it is the males that usually care for the offspring, and in birds both parents raise the offspring (Balshine 2012; Alonzo & Klug 2012). The physiological and morphological adaptations of gestation and lactation in mammals determine obligatory female care, yet males contribute to raising the offspring in about 10% of species (Woodroffe & Vincent 1994). Parental care involves substantial costs (Maynard Smith 1977; Alonso-Alvarez & Velando 2012) and should evolve when the benefits of caring, to the carer, outweigh these costs. Although both sexes spend considerable amounts of time and energy raising the offspring, males may also lose additional mating opportunities (Maynard Smith 1977). Moreover, while females typically have high certainty of maternity, particularly in internally fertilizing species, males generally have a lower certainty of paternity (Alonzo & Klug 2012). Theoretical models therefore predict that male care should evolve when a male's certainty of paternity is high (Trivers 1972; Queller 1997; Alonzo & Klug 2012). Although these models are centred on how male care evolves from a condition of no care, the majority of studies testing their predictions focus on the plasticity of male care behaviour to changes in certainty of paternity (e.g. Griffin et al. 2013; Møller & Cuervo 2000; Alonzo 2010). Therefore, whether levels of paternity are higher in species with male care than in species without, and whether a greater certainty paternity facilitates the evolution of male care, is currently unknown. Likewise, how mating system relates to both paternity levels and male care is unclear. Finally, if male care and monogamy evolve when certainty of paternity is higher, males should in turn reduce investment into traits typically associated with high levels of sperm competition (Iossa et al. 2008; Soulsbury 2010), a hypothesis that has yet to be tested. Here we address these questions and investigate how monogamy and male care relate to paternity and traits linked to sperm competition in mammals.

Male care should evolve when males have high certainty of paternity, as extra-pair young increase the costs of parental care for the cuckolded male without providing any fitness benefits (Trivers 1972; Alonzo & Klug 2012; Elwood 1994). This hypothesis is mostly tested by investigating how males respond to cuckoldry in species with male care (Alonzo 2010). In most such species, males reduce the amount of care in response to reduced paternity (Alonzo 2010; Griffin et al. 2013), supporting the idea that levels of paternity influence a male's decision to care. In a few species, however, there is no change in male care levels (Alonzo 2010). A comparative meta-analysis across birds, fish, mammals, and insects, reveals that males care less when cuckolded, but only when the costs of care are high, and proposes that, when costs are low, tolerant males that do not reduce care levels may outcompete males that desert the offspring (Griffin et al. 2013). However, these studies only consider male responses in species where males always provide at least some level of care, and so do not explicitly address the question of whether species with male care have a greater certainty of paternity than species without it.

A key and often overlooked issue in studies of plasticity in male care levels in response to low paternity is that behavioural and evolutionary timescales are not equivalent, so that behavioural responses within a species may not necessarily reflect the selective pressures driving the evolution of a trait (Kokko & Jennions 2012). In the context of male care evolution, this implies that a lack of behavioural responses to low paternity may indicate either that low paternity does not select for reduced levels (or the absence) of male care, or that there is insufficient selection for adaptive phenotypic plasticity in male care levels, which prevents males from detecting or responding to low paternity (Kokko & Jennions 2012). Therefore, male responses to uncertain paternity within species may not be informative of the evolutionary relationship between certainty of paternity and male parental care, and to investigate this issue paternity levels in species with and without male care should instead be compared.

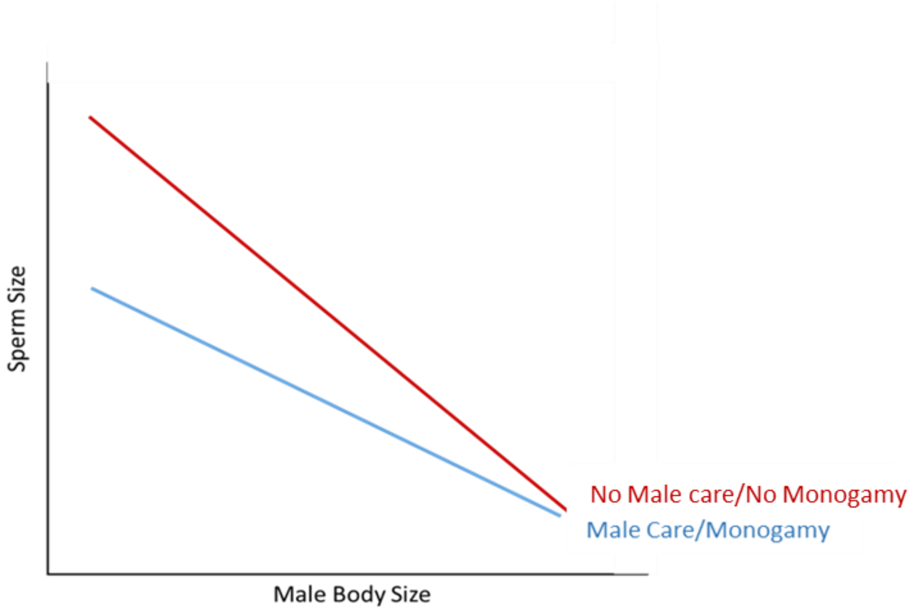
Interestingly, the evolution of male care follows the evolution of social monogamy across all mammals and within primates (Opie et al. 2013; Lukas & Clutton-Brock 2013). If social monogamy is necessary to secure high certainty of paternity, this may explain the direction of evolution between male care and social monogamy. Yet, social monogamy may not be indicative of genetic monogamy, such as in birds where over 90% of species are socially monogamous but less than 25% of them mate exclusively within the pair (Griffith et al. 2008). Social monogamy is less common in mammals, being present in approximately 5% of species (Lukas & Clutton-Brock 2013) and true genetic monogamy seems to be rare (Soulsbury 2010). Socially monogamous mammals only exhibit a marginally non-significant trend towards higher paternity than polygynous mammals (Clutton-Brock & Isvaran 2006) but have greater certainty of paternity than species with a multi-male mating system (Soulsbury 2010). No study to date, however, has examined the associations between male care, social monogamy, and certainty of paternity simultaneously, and specifically whether male care evolves in species with social monogamy to increase certainty of paternity, or whether male care is exchanged for certainty of paternity and in turn promotes the evolution of social monogamy.

Ultimately, if male care or social monogamy is associated with higher paternity levels, males should invest less in potentially costly traits associated with intense sperm competition, such as large ejaculates and large testes (Iossa et al. 2008; Soulsbury 2010). For a given body size, testes are larger with higher levels of female promiscuity and low certainty of paternity in many species (Iossa et al. 2008; Soulsbury 2010; Møller & Birkhead 1993), and so relative testes mass is often used as a proxy for the intensity of sperm competition. Larger testes probably reflect greater sperm production (Møller 1989). However, the costs of sperm production can be significant (Wedell et al. 2002; Olsson et al. 1997; Parker et al. 1996). For example, in adders (*Vipera berus*) the rate of mass loss due to sperm production is as high as the mass loss due to costly reproductive behaviours, such as male-male combat, mate searching, and courtship (Olsson et al. 1997), while spermatogenesis significantly reduces lifespan in nematodes (Parker et al. 1996). Therefore we predict that, if males care when their certainty of paternity is high (Trivers 1972; Queller 1997), they should no longer invest in high sperm production and larger testes.

Faster swimming speed also promotes success in sperm competition in many taxa (Gomendio & Roldan 2008). Because sperm length and mid-piece volume determine sperm swimming speed and fertilization success (Lüpold et al. 2009; Gomendio & Roldan 2008), under intense sperm competition, sperm are longer in birds, fish and insects (reviewed in: Gomendio & Roldan 2008), while mid-piece volume is larger in some passerine birds (Immler & Birkhead 2007). In mammals, small-bodied species under intense sperm competition have relatively larger sperm (Gomendio et al. 2011; Lüpold & Fitzpatrick 2015), while large-bodied species produce more, but not larger, sperm (Gomendio et al. 2011). These differences might be due either to metabolic constraints in larger mammals (Gomendio et al. 2011) or the size of the female reproductive tract (Lüpold & Fitzpatrick 2015). Regardless of what might explain differences among larger and smaller bodied mammals in sperm related traits, this evidence suggests that small-bodied mammals with male care or monogamy should have smaller sperm than expected for their size (Figure 1a), while large-bodied mammals with male care or monogamy should have fewer sperm (Figure 1b).

Using phylogenetic comparative approaches, we conduct the first comprehensive study of the evolutionary associations between paternity levels, traits associated with sperm competition, and male parental care in mammals. We test the hypothesis that male care is associated with increased certainty of paternity and lower levels of sperm competition. We therefore predict that the presence of male care is associated with lower levels of multiple paternity, smaller relative testes mass, and smaller or fewer sperm, while accounting for the potential confounding effects of social monogamy.

**a)**



**b)**

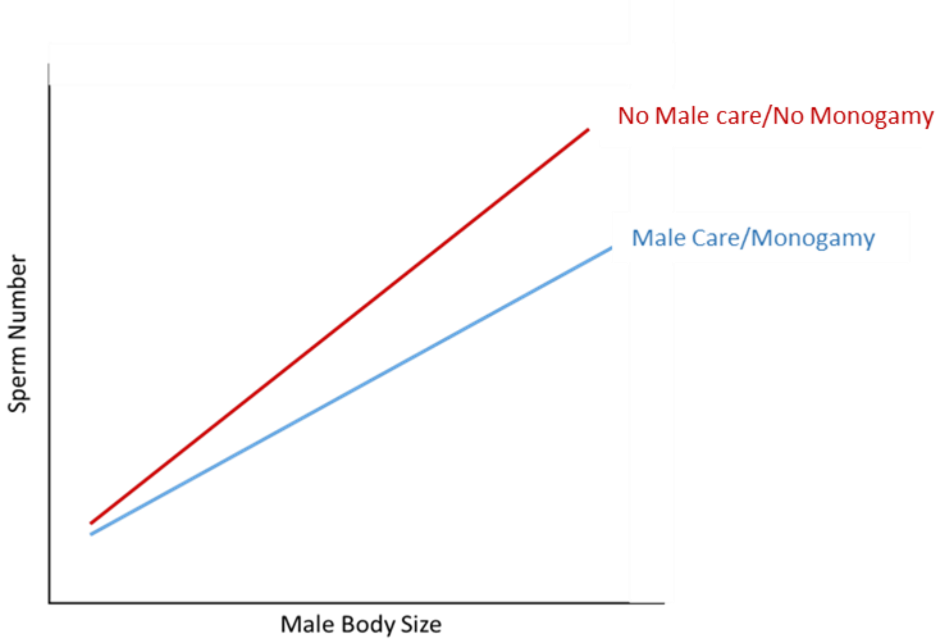


**Figure 1: Predicted associations between (a) sperm size and (b) sperm number, and body mass among species with and without male care or monogamy.** Among smaller species, those with male care or social monogamy should have smaller sperm than expected for their size when compared to species without male care, but no difference in sperm size is expected with increasing body size (a). Instead, large species, but not smaller species, with male care or monogamy should have fewer sperm for their size than those without male care (b). Blue lines indicate species with male care or social monogamy, while red lines indicate species without these traits.

## Methods

### Data collection

We define male care as any care behaviour by the male towards either the offspring or reproducing females and consider a species as exhibiting male care if any of the following behaviours is observed; food provisioning, carrying, grooming, or huddling (West & Capellini 2016). We consider males provisioning pregnant or lactating females as a form of male care, as this may have indirect benefits for the offspring. Our dataset includes 61 species with male care, of which 29 provision, 24 carry, 26 groom, and 19 huddle with the offspring, while 16 species also provide food to reproducing females. We group all male care behaviours as a single presence/absence variable for the majority of our analyses as in most cases sample sizes are too small (n<8) to test individual male care behaviours. However, we previously showed that carrying the offspring and provisioning the female associate with larger and more frequent litters, shorter lactations, and faster offspring growth, while huddling, grooming and provisioning of offspring do not associate significantly with life history traits (West & Capellini 2016). Based on this evidence, we combine behaviours associated with high benefits (carrying and provisioning females, n=37) for analysis on total sperm length where sample sizes for these two behaviours are too low to test individually.

Data on sperm competition related traits are taken from available datasets, supplemented with data from the primary literature, for the following variables: testes mass (g, n=274 species), total sperm length (um, n=218), sperm head length (um, n=202), sperm head width (um, n=113), mid-piece volume ($\mu m^3$, n=92), flagellum length (um, n=176), and sperm count per ejaculate (n=56). For this data collection we search ‘Web of Science’ by species common or scientific name and ‘sperm competition’ (date last accessed: 23/03/2015). All data are accepted only if they conform to detailed protocols for comparability (Appendix 1 (SI): Supplementary methods).

Certainty of paternity is generally measured as alpha paternity, extra-group paternity and multiple paternity (Soulsbury 2010). Data on alpha-paternity, defined as the proportion of all offspring sired by the alpha male in a social group, and extra-group paternity, defined as the proportion of all offspring sired by extra-group males, are limited to a few social species, and so sample sizes are too small for analyses. Multiple paternity is defined as the percentage of litters in a population sired by more than one male (Soulsbury 2010). Thus, a higher percentage of multiple paternity indicates lower certainty of paternity for a single male (Soulsbury 2010). By definition, however, multiple paternity can only be measured in polytocous species. We find data on multiple paternity for 71 species in our dataset (Supplementary methods). Species with larger litters appear to have higher levels of multiple paternity, and testes mass is higher in mammals with larger litters (Soulsbury 2010); thus we extract data from the literature on litter size (n=494; Supplementary methods) and include this variable in analyses on multiple paternity and testes mass. Finally, data on mating system are taken from West & Capellini (2016) where social monogamy is defined as a single male and female, which breed together, share a range or territory, and remain together for more than one breeding season.

The final dataset contains a total of 511 species, although data on paternity levels and sperm competition variables are not available for all species. All continuous data, except multiple paternity, are log-transformed for the analyses to normalize their distribution. Multiple paternity is arcsine transformed because this is the only transformation that successfully normalizes distribution of this variable. However, results are qualitatively similar to the ones reported here when using a logarithmic or logit transformation. The data for male care and mating system are coded as a binary variable, with 1 representing the presence of a trait and 0 its absence.

## Statistical Analysis

We use phylogenetic generalised least squares (PGLS) models (Freckleton et al. 2002) in the R package 'caper' (Orme 2013) to test whether multiple paternity and sperm competition traits are related to male care, while accounting for confounding variables (allometry, social monogamy and litter size). We use a comprehensive mammalian phylogeny (Fritz & Purvis 2010) to quantify the strength of phylogenetic signal in the data due to species' common evolutionary history. Caper uses a maximum likelihood approach to estimate PGLS model parameters, and the parameter lambda (λ) measures the magnitude of the phylogenetic signal in the model residuals (Freckleton et al. 2002). λ varies between 0, representing no phylogenetic signal, and 1, indicating that species similarity is directly proportional to the amount of shared evolution as expected under a Brownian motion model of evolution (Freckleton et al. 2002). We build PGLS models for a continuous dependent variable of interest, with male care as an independent binary variable, and male body mass to account for allometry where appropriate. Because intense sperm competition might affect several sperm traits simultaneously (Gomendio & Roldan 2008; Lüpold et al. 2009), we also include other traits related to sperm competition as predictors in models with a sperm competition variable as dependent variable. Similarly, we include litter size as additional independent variable in models for testes mass and multiple paternity. To evaluate the importance of male care and social monogamy as predictors of paternity and sperm related traits, we also assess the fit to the data of PGLS models with and without male care (or social monogamy) using the likelihood ratio (LR) test for nested models and Akaike Information Criterion (AIC) scores for non-nested models (Crawley 2007).

## Results

Multiple paternity is significantly lower in species with male care and in species with social monogamy, when these traits are tested separately (Table 1, Figure 2). When both traits are included as predictors in the same model, however, neither show any significant association with multiple paternity (Table 1), most likely because male care and monogamy are strongly evolutionarily associated (Lukas & Clutton-Brock 2013; Opie et al. 2013) and only few species in these models show male care without monogamy (n=3) or are monogamous without male care (n=3). We therefore use AIC scores to identify whether male care or monogamy better fit the data; however these models fit the data equally well (ΔAIC=0.27), so that it is not possible to determine whether male care or social monogamy has a stronger association with multiple paternity. Including litter size as a predictor in these models does not alter these conclusions, and litter size is not significantly associated with multiple paternity (Table S1 in Appendix 1: Supplementary tables). Among the sperm traits, sperm length, flagellum length and sperm head length are positively associated with higher levels of multiple paternity, while mid-piece volume, sperm head width, and sperm count are not, presumably because sample sizes of species with paternity and sperm data are small for the latter three traits (Table 2).

Contrary to predictions, testes mass is not relatively smaller in species with male care or with any specific individual care behaviour, with or without controlling for social monogamy (Table 1; Table S2, models 1-3; Figure 3a), and male care does not improve the fit to the data relative to a simple allometric model (any male care behaviour: $LR_1$=1.00, p=0.317; individual behaviours: $LR_5$=2.76, p=0.737). This conclusion does not change when litter size is added to the model (Table S2, models 4-7). Male care is also not associated to any of the morphological sperm traits (Tables S3-8) and does not improve model fit relative to models without it (Appendix 1: Supplementary results).

Conversely, socially monogamous species have significantly smaller testes for their size than species with promiscuous mating systems (Table 1, Table S2 model 8, Figure 3b; vs allometric model: $LR_1$=4.94, p=0.026), and mating system explains an additional 1.3% of variance. The inclusion of litter size as a predictor leads to qualitatively similar results (Table S2, model 9). Social monogamy is also associated with shorter flagella and a smaller mid-piece volume (Table 1, Table S4 model 3, Table S5 model 3, Figures 3c&d), explaining an extra 2% and 8% of variance respectively relative to models without it (flagellum length: $LR_1$=5.68, p=0.017; mid-piece: $LR_1$=7.38, p=0.007). Social monogamy is not significantly associated with total sperm length, sperm head length and width, or sperm numbers (Tables S3, S6-S8) and does not improve the fit of the model to the data (Supplementary results). Including both social monogamy and male care together in the models on sperm morphology does not alter any of these conclusions (Table 1 & Tables S3, S6-S8). Finally, these results do not differ across the range of body sizes; the interactions between male care, or monogamy, and body mass are all non-significant (Supplementary results).

**Table 1: PGLS models for multiple paternity, testes mass, flagellum length, and mid-piece volume with male care (any behaviour) and social monogamy.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$ and the model log-likelihood (Lh) and AIC score. The total sample size for models with multiple paternity is 70 species, of which 15 have male care and 15 are socially monogamous. The total sample size for testes mass is 263 species, of which 36 have male care and 40 are socially monogamous. The total sample size for flagellum length is 158 species, of which 17 have male care and 20 are socially monogamous. The total sample size for models with mid-piece volume is 78 species, of which 8 have male care and 9 are socially monogamous.

| | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Dependent Variable** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **R2** | **Lh** | **AIC** |
| **Multiple paternity** | Male Care | -13.7 | 5.6 | -2.4 | 0.018 | 0.23 | 0.08 | -300.24 | 604.49 |
| | Social Monogamy | -13.3 | 5.5 | -2.4 | 0.017 | 0.31 | 0.08 | -299.97 | 603.94 |
| | Male Care | -7.2 | 7.9 | -0.9 | 0.367 | 0.26 | 0.09 | -299.57 | 605.14 |
| | Social Monogamy | -8.7 | 7.6 | -1.2 | 0.253 | | | | |
| **Testes mass** | Male body mass | 0.7 | <0.1 | 17.8 | <0.001 | 0.86 | 0.56 | -113.05 | 234.11 |
| | Male Care | <0.1 | 0.1 | 0.1 | 0.887 | | | | |
| | Social Monogamy | -0.2 | 0.1 | -2.0 | 0.048 | | | | |
| **Flagellum length** | Male body mass | -<0.1 | <0.1 | -2.9 | 0.005 | 0.65 | 0.32 | 132.39 | -254.77 |
| | Sperm head length | 0.6 | 0.1 | 7.1 | <0.001 | | | | |
| | Male care | <0.1 | <0.1 | 0.6 | 0.567 | | | | |
| | Social Monogamy | -0.1 | <0.1 | -2.3 | 0.023 | | | | |
| **Mid-piece volume** | Sperm length | 0.4 | 0.3 | 1.5 | 0.136 | 0.75 | 0.14 | -3.58 | 15.15 |
| | Male care | <0.1 | 0.2 | <0.1 | 0.988 | | | | |
| | Social Monogamy | -0.3 | 0.1 | -2.2 | 0.029 | | | | |

**Table 2: PGLS models for all sperm traits and multiple paternity.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value and $R^2$).

| | | **Variable statistics** | | | | **Model statistics** | |
|---|---|---|---|---|---|---|---|
| **Dependent Variable** | **Sample n.** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** |
| **Total sperm length** | 33 | <0.1 | <0.1 | 2.4 | 0.025 | 1.00 | 0.15 |
| **Flagellum length** | 22 | <0.1 | <0.1 | 2.7 | 0.013 | 1.00 | 0.27 |
| **Mid-piece volume** | 12 | <0.1 | <0.1 | 1.0 | 0.321 | 0.00 | 0.10 |
| **Head length** | 29 | <0.1 | <0.1 | 3.0 | 0.006 | 0.86 | 0.24 |
| **Head width** | 16 | -<0.1 | <0.1 | -0.7 | 0.474 | 1.00 | 0.03 |
| **Sperm count** | 12 | -<0.1 | <0.1 | -1.4 | 0.207 | 1.00 | 0.17 |

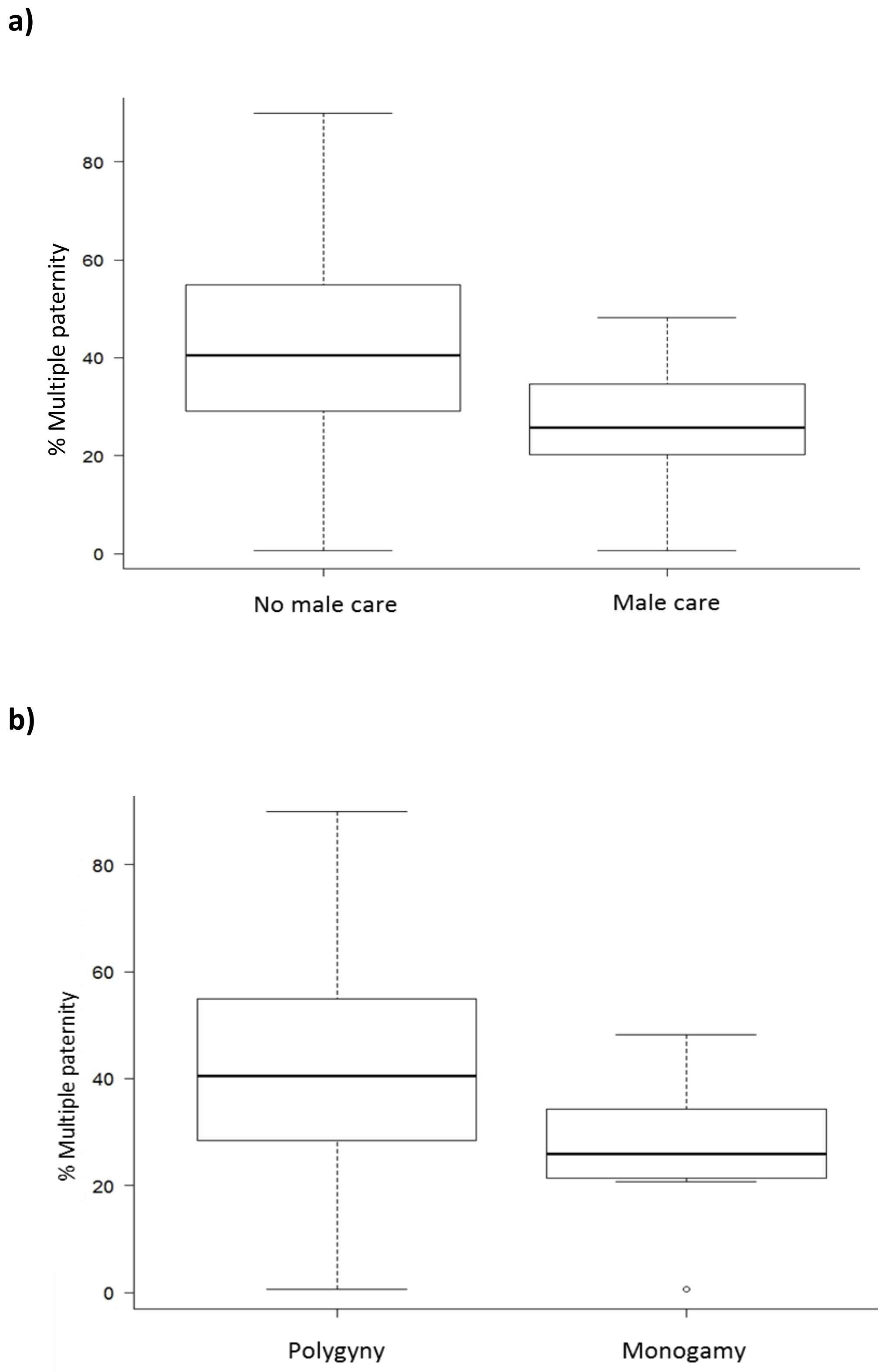
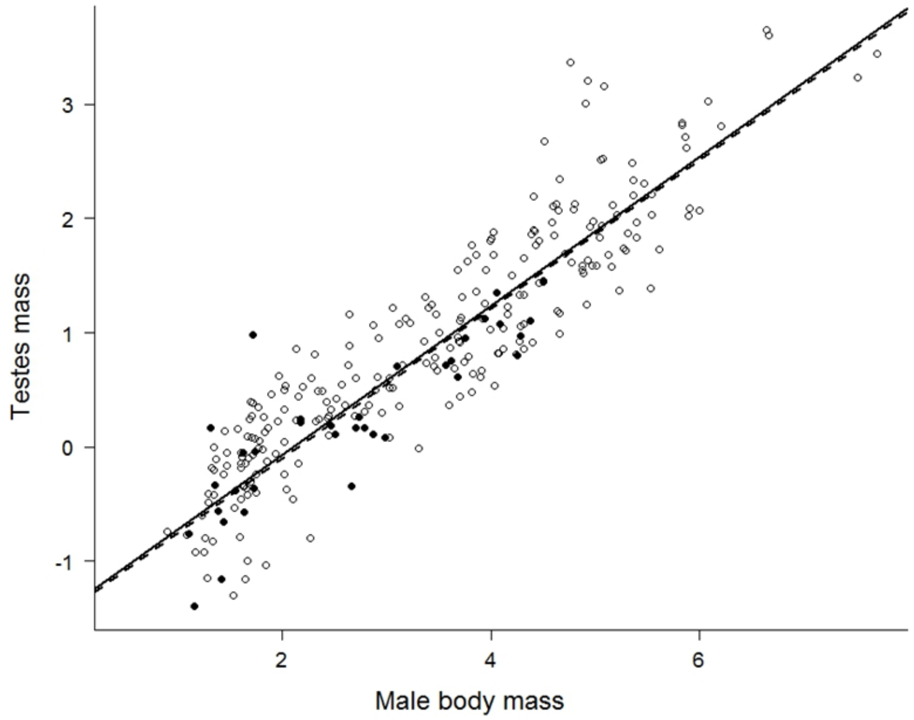
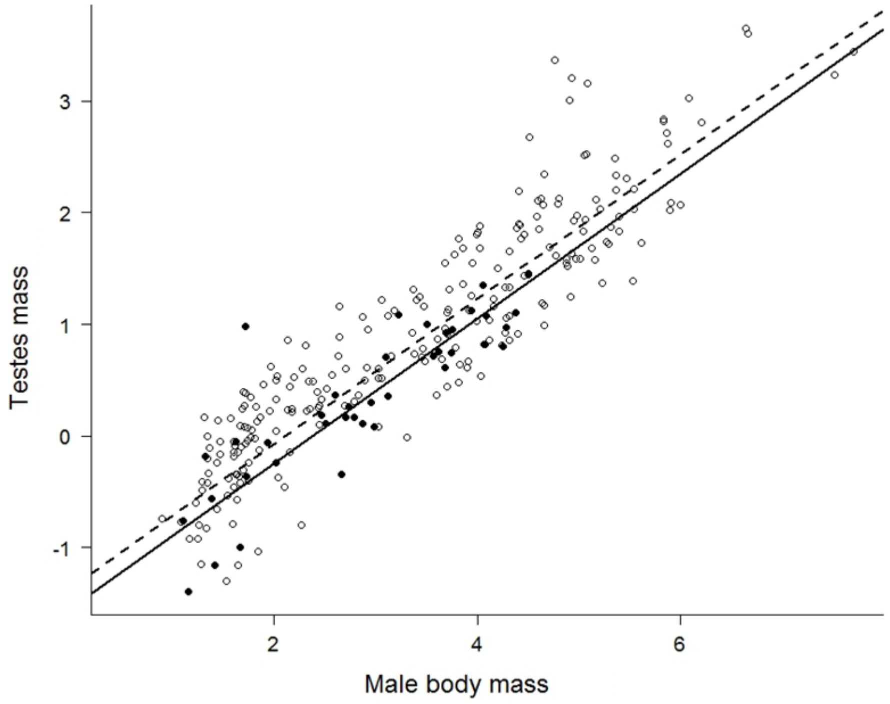


**Figure 2: Multiple paternity with (a) male care and (b) social monogamy.** Species with male care have lower levels of multiple paternity than species without male care (a), while monogamous species have lower levels of multiple paternity than polygynous species (b). Boxes represent the median with upper and lower quartiles, with 95% confidence intervals of the arcsine transformed percentage of multiple paternity (whiskers).

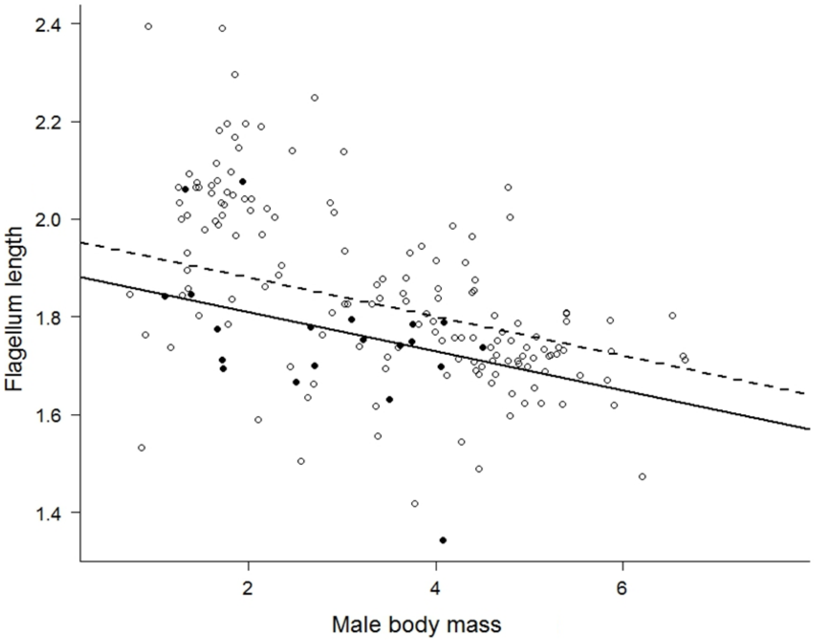
**a)**


Testes mass
3
2
1
0
-1
2
4
6
Male body mass

**b)**


Testes mass
3
2
1
0
-1
2
4
6
Male body mass

**c)**



**d)**

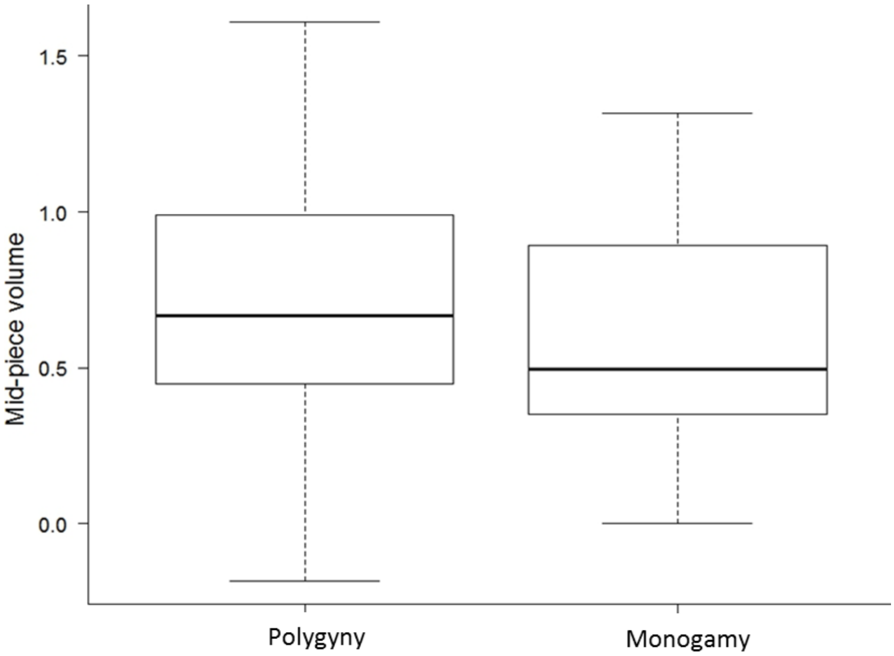


**Figure 3: Male care, social monogamy and sperm competition traits.** (a) The relationship between testes mass and male body mass does not differ between species with male care (filled circles, continuous line) and those without male care (open circles, dotted line). (b) For a given male body size, monogamous species (filled circles, continuous line) have smaller testes than polygynous species (open circles, dotted line). (c) Monogamous species (filled circles, continuous line) have shorter flagella for a given male body mass than polygynous species (open circles, dotted line). (d) Monogamous species have a smaller mid-piece volume than polygynous species. Boxes represent the median with upper and lower quartiles, with 95% confidence intervals (whiskers). All continuous variables are $\log_{10}$ transformed.

## Discussion

Certainty of paternity is expected to play an important role in promoting the evolution of male parental care (Trivers 1972) as extra-pair young should significantly reduce the benefits of care for the cuckolded male (Griffin et al. 2013; Trivers 1972; Elwood 1994). Here we show that male care and social monogamy in mammals are significantly associated with a higher certainty of paternity than species without either of these behaviours. However, social monogamy but not male care also associates with smaller testes, shorter sperm size (through shorter flagellum length), and a smaller mid-piece volume, indicating lower levels of sperm competition. Taken together, these results suggest that social monogamy in mammals is likely to increase certainty of paternity for males, allowing them to reduce investment in some, potentially costly, traits related to sperm competition. Because the evolution of social monogamy precedes the evolution of male care (Lukas & Clutton-Brock 2013; Opie et al. 2013) and it is associated with lower investment in traits promoting success in sperm competition (this study), we conclude that the association between high certainty of paternity and male care is indirect in mammals and mediated by the evolution of monogamy.

The evolution of male care and/or social monogamy should lead to a lower intensity of postcopulatory sexual selection (Alonzo & Klug 2012; Clutton-Brock & Isvaran 2006), and in turn to a corresponding reduction of investment in costly sperm competition traits. While certainty of paternity is higher with both monogamy and male care, only mating system associates with some sperm competition traits. Specifically, socially monogamous species have significantly smaller testes, for their size, than species with other mating systems. While we do not find similar reductions in all sperm morphological traits, socially monogamous species have significantly shorter flagella and a smaller mid-piece than promiscuous species, traits that promote success in sperm competition by increasing swimming speed (Anderson et al. 2005; Lüpold et al. 2009; but see Immler & Birkhead 2007). These differences are not affected by differential responses to sperm competition among species that differ in body size. Specifically, while we confirm previous findings (Lüpold & Fitzpatrick 2015; Gomendio et al. 2011) that sperm are shorter in larger mammals and sperm number increases with male body mass, we find no differences between large and small-bodied mammals in how sperm competition traits relate to male care or social monogamy. In support of the suggestion that longer sperm are an adaptive response to high levels of sperm competition (Gomendio & Roldan 2008), total sperm length, flagellum length, and sperm head length are positively associated with levels of multiple paternity. Altogether, these findings suggest that social monogamy, rather than male care, is the possible driver for the observed reduced levels of sperm competition and increased certainty of paternity. Thus, the relationship between male care and increased certainty of paternity may be mediated by the correlated evolution between male care and social monogamy (Lukas & Clutton-Brock 2013; Opie et al. 2013). However, we note that neither monogamy nor male care ensure 100% certainty of paternity as some levels of multiple paternity remain. We thus conclude that it may still be beneficial for males to maintain some investment in traits that promote success in sperm competition against sneak males or other alternative mating strategies, typical of less successful and younger males in mammalian societies (Kvarnemo 2005; Clutton-Brock & Isvaran 2006).

Alternatively, male care is unrelated to testes mass and sperm related traits because a greater certainty of paternity is a consequence of male care, as opposed to a requirement for its evolution, despite high levels of sperm competition. Kvarnemo (2005) proposes that care by males might help them enhance either current or future paternity levels through a range of possible mechanisms. Specifically, behaviours such as providing nuptial gifts or nest building may help males to achieve greater paternity by ensuring close proximity with either the female or her eggs (e.g. Svensson & Kvarnemo 2003). Alternatively, if females are choosy and prefer caring males, caring for unrelated offspring may help males increase their chance of siring future offspring with the mother (e.g. Freeman-Gallant 1996). Thus, if higher paternity can be gained by caring, male care may evolve initially when certainty of paternity is low, and males may even increase their care despite intense sperm competition (Kvarnemo 2005). Under this hypothesis, we expect caring males to maintain traits associated with success in sperm competition. Thus, selection for both male care and sperm competition traits may occur simultaneously, even among socially monogamous species. Under Kvarnemo's hypothesis (Kvarnemo 2005), therefore, the presence of male care may lead to a further increase in certainty of paternity for males without requiring a reduction of sperm competition.

The relationship between male care and certainty of paternity has been investigated extensively in empirical studies on male behavioural plasticity in care levels (Alonzo 2010; Griffin et al. 2013). Here we demonstrate that the evolution of male care in mammals is associated with higher certainty of paternity, but this association is likely mediated by the correlated evolution between male care and social monogamy. Alternatively, male care and male competition might be both maintained by female mate choice, low levels of female promiscuity and male alternative mating strategies (Kvarnemo 2005). Our results therefore highlight the importance of social monogamy in the evolution of male care among mammals. If certainty of paternity is enhanced by social monogamy, this may explain why social monogamy precedes the evolution of male care in mammals and allows males to partially reduce investment in costly sperm competition traits. However, the evolution of male parental care does not appear to lead to a further reduction in sperm competition traits, likely because promiscuity still persists in monogamous species, albeit at lower levels.

# CHAPTER 3: MALE CARE AND LIFE HISTORY TRAITS IN MAMMALS

**Authors:** Hannah E. R. West and Isabella Capellini

**Author contributions:** Both authors equally contributed to this study.

## Abstract

Male care has energetic and opportunity costs, and is more likely to evolve when males gain greater certainty of paternity or when future mating opportunities are scarce. However, little is known about the substantial benefits that males may provide to females and offspring. Using phylogenetic comparative methods and a sample of over 500 mammalian species, we show that mammals in which males carry the offspring have shorter lactation periods, which leads to more frequent breeding events. Provisioning the female is associated with larger litters and shorter lactation. Offspring of species with male care have similar weaning mass to those without despite being supported by a shorter lactation period, implying that they grow faster. We propose that males provide an energetic contribution during the most expensive time of female reproduction, lactation, and that different male care behaviours increase female fecundity, which in turn helps males offset the costs of caring.

The contents of this chapter are published as '*Male care and life history traits in mammals*' in the journal '*Nature Communications*' (See Appendix 6).

## Introduction

Parental care is any parental behaviour that benefits the offspring, frequently at the cost of survival or further mating opportunities for the carers (Smiseth et al. 2012); therefore, it should evolve when the carers' benefits outweigh the costs (Woodroffe & Vincent 1994). Parents provide no direct care in most species, yet females, males or both parents of different species across many lineages exhibit a great diversity of care behaviours (Alonzo 2010; Balshine 2012). The documented costs of male care in both vertebrates and invertebrates include increased risk of predation, parasitism or infection (Schradin & Anzenberger 2001; Riguera & Gomendio 1999; Li & Jackson 2003; Nunn & Altizer 2006; Descamps et al. 2009), reduced mobility and foraging time (Schradin & Anzenberger 2001), leading to loss of body mass and condition (Fietz & Dausmann 2003; Campbell et al. 2009; Reid 1987), loss of potential mating opportunities (Maynard Smith 1977), and in some species reduced survival (e.g. Getz & McGuire 2010). Given these costs, why do males care? Theoretical models and empirical studies show that males may trade off costly care for a greater certainty or degree of paternity, reducing the level of care when female promiscuity is high (Alonzo 2010; Kvarnemo 2005; Griffin et al. 2013; Møller & Birkhead 1993). Alternatively, when future mating opportunities are scarce, males might do better to care for their current offspring, regardless of paternity levels (Kokko & Jennions 2012). Most studies on the evolution of male care focus on the direct costs and benefits for the male, such as increased certainty of paternity, and the evolutionary relationship between male care and mating system (Lukas & Clutton-Brock 2013; Opie et al. 2013; Alonzo 2010; Queller 1997; Møller & Birkhead 1993; Gross & Sargent 1985). While males invest a considerable amount of time and energy in caring, whether and how this leads to possible benefits to females and offspring is much less well understood (Woodroffe & Vincent 1994), particularly in species where females already care for the offspring (i.e. biparental care). Quantifying these benefits, such as increased offspring survival and growth rates or female fecundity, is important because they could in turn increase the male's inclusive fitness and lead to evolutionary feedback between male care and life history traits (Alonzo

2010). Here we investigate hypotheses that relate life history traits and male care at a large comparative scale in mammals, a taxon with obligatory female care and in which male care is also present in approximately 10% of species (Lukas & Clutton-Brock 2013; Woodroffe & Vincent 1994).

By providing an energetic contribution towards offspring rearing through costly care, such as provisioning dependent offspring or carrying heavy offspring, care by helpers, including the male, may allow females to redirect more resources into reproduction and in turn increase female reproductive success and/or offspring growth rates (Woodroffe & Vincent 1994; Opie et al. 2013; Oftedal & Gittleman 1989). Males and additional carers may also enable females to spend more time foraging and gain more resources for current or future offspring (Woodroffe & Vincent 1994). The hypothesis that care by other individuals allows females to increase their reproductive output has been proposed mostly in the context of allocare (care by either the male or other individuals) for species with female care, such as birds and mammals ('load-lightening' hypothesis, Crick 1992; see also Woodroffe and Vincent for male care, Woodroffe & Vincent 1994). Support for this hypothesis in relation to male care specifically is found in burying beetles (*Nicrophorus sp.*), where caring males help provisioning the offspring, and allow females to reduce their parental effort in the current brood and greatly increase their future brood mass (Jenkins et al. 2000). Furthermore, female California mice (*Peromyscus californicus*) wean more offspring per reproductive bout and reproduce more frequently when males care (Gubernick & Teferi 2000; Cantoni & Brown 1997), indicating that females cannot meet the energetic demands of rearing more numerous and larger litters alone. Thus, it appears that the presence of male care has a 'load-lightening' effect similar to that observed in species, such as meerkats (*Suricata suricatta*) (Scantlebury et al. 2002) and grey crowned babblers (*Pomatostomus temporalis*) (Brown et al. 1978), where females helped by other carers can substantially increase their reproductive output (Crick 1992). However, whether male care is consistently associated with higher female fecundity across species is still poorly understood as the majority of studies addressing this question focus only on a few model species.

Large-scale comparative approaches are well suited to unravel the generality of patterns and processes (Harvey & Pagel 1991), but most comparative work on male care concerns primarily its evolutionary relationship with mating systems (e.g. Lukas & Clutton-Brock 2013; Opie et al. 2013). The few comparative studies that test, at least partially, the hypothesis that male care associates with female fecundity focus on mammals. These studies find that litters are larger in species where females are helped by alloparents (males and/or other individuals) (Isler & van Schaik 2012; Mitani & Watts 1997), and that breeding frequency is higher in socially monogamous mammals in which males provision or carry the offspring (Lukas & Clutton-Brock 2013), a result also found in primates with allocare (Isler & van Schaik 2012). However, it is unclear whether a larger litter associates specifically with male care or care by other individuals, as previous studies do not separate care according to the identity of the carer, although benefits and costs of care may differ between the male and alloparents. Likewise, it is important to identify at which stage of reproduction male care is more likely to associate with higher female fecundity. Lactation is the most energetically demanding period of reproduction for a female mammal, with daily energy expenditure increasing by up to four times (Speakman & McQueenie 1995; Hanwell & Peaker 1977; Gittleman & Thompson 1988). Male care may thus allow females to gain or save energy that can be (re)invested in more or better quality milk (Opie et al. 2013; Oftedal & Gittleman 1989), which in turn may result in a shorter lactation (Oftedal & Gittleman 1989; Woodroffe & Vincent 1994) and lead to shorter interbirth intervals; if so, the documented association between frequency of breeding and male care (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012) is mediated by a reduction in the duration of lactation (Woodroffe & Vincent 1994). Alternatively, by caring for the offspring post-weaning, males may allow females to invest more time foraging, regain body condition more quickly, and mate sooner, regardless of the duration of lactation (Cantoni & Brown 1997). Discriminating between these scenarios and identifying the relevant male care behaviour at a given stage of reproduction is fundamental because it helps to pinpoint the mechanism that underlies the evolutionary associations between male care and life history traits, and the possible evolutionary feedback between them.

Regardless of whether a higher frequency of breeding is achieved through male care post-weaning or by enabling females to wean the offspring sooner, higher female reproductive rates benefit the male only if he mates with the same female over more than one breeding event. This appears to be the case in mammals as recent comparative studies conclude that the evolution of social monogamy precedes the evolution of male care and is evolutionarily associated with it (Lukas & Clutton-Brock 2013; Opie et al. 2013). This evolutionary relationship may be especially relevant in long-lived species, as greater female fecundity over a longer lifespan could further help compensate for the loss of potential mating opportunities that should be experienced by monogamous caring males. Whether longer-lived species are more likely to exhibit male care is, however, unknown.

Like the care by other helpers, male care may also benefit the offspring by enhancing their survival to independence through protection against predators and/or by increasing offspring growth rates or size at independence (Woodroffe & Vincent 1994; Clutton-Brock 1991). Consistent with this hypothesis, zebra finch offspring (*Taeniopigia guttata*) have faster growth rate (Royle et al. 2006) and snow bunting fledglings (*Plectrophenax nivalis*) are larger (Lyon et al. 1987) when raised by two parents rather than one parent alone. Moreover, a non-phylogenetic study in carnivores finds that females have greater milk energetic output and offspring have higher growth rates in species where males or other individuals provision females and offspring (Oftedal & Gittleman 1989). However, we still do not know to what extent male care associates with greater offspring growth rates across mammals, and whether this leads to heavier offspring which enjoy greater survival.

Although comparative studies cannot rule out the possibility that male care evolves in species where female fecundity or offspring growth are higher, the limited available experimental and field evidence in mammals and other organisms suggests that the absence of males caring for the offspring can have detrimental effects on both female fecundity (e.g. Cantoni & Brown 1997; Jenkins et al. 2000) and offspring survival (Gubernick et al. 1993; Wright & Brown 2002; Bales et al. 2000; Wolf et al. 1988). Yet, we currently lack a clear and comprehensive picture of how life history traits associate specifically with male care in any animal taxon at a large comparative scale, which is necessary to help direct future efforts aimed at disentangling cause and effect of the evolution of male care. Furthermore, previous comparative studies often analyse male care together with care by other individuals, but to what extent male care and care by others exhibit the same costs and benefits, and associations with life history traits, is unknown. In addition, previous comparative work considers only a subset of all male care behaviours under the assumption that some are more costly (e.g. carrying and provisioning, most common in primates and carnivores) (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012). However, behaviours often regarded as less expensive, such as grooming and huddling with the offspring (most frequent in rodents), may entail substantial fitness costs for the male (Campbell et al. 2009; Fietz & Dausmann 2003; Kenkel et al. 2014; Saltzman et al. 2015), while allowing females to forage for longer periods and gain more resources for reproduction. Thus, identifying whose care – by the male or by other helpers – and which specific behaviour associates with life history traits is fundamental to understanding how and why male care evolves, as the benefits and costs of care are likely to vary in relation to the identity of the carer and the behaviour performed. Finally, assessing whether specific life history traits are evolutionarily associated with male care also requires that the correlated evolution between life history traits is accounted for, as ignoring it may lead to misleading conclusions (e.g. Barton & Capellini 2011; Capellini et al. 2015).

Here we compile the largest and most detailed dataset of male care behaviour in mammals to date (Figure 1) and test the hypothesis that increased female fecundity and offspring fitness related traits are associated with male care using phylogenetic comparative methods. From this hypothesis we test the predictions that species with male care exhibit (i) shorter lactation and/or gestation, (ii) more frequent and/or larger litters, and (iii) larger neonates and/or weanlings. We demonstrate that fecundity is higher in species with male care, but the way this is achieved is complex and varies across orders and the nature of male care. Litters are larger in species in which males provision reproducing females, especially carnivores, while frequency of breeding is higher in species with carrying, mostly primates, due to a reduction in lactation time. Lactation time is also shorter in carnivores where males provision reproducing females.

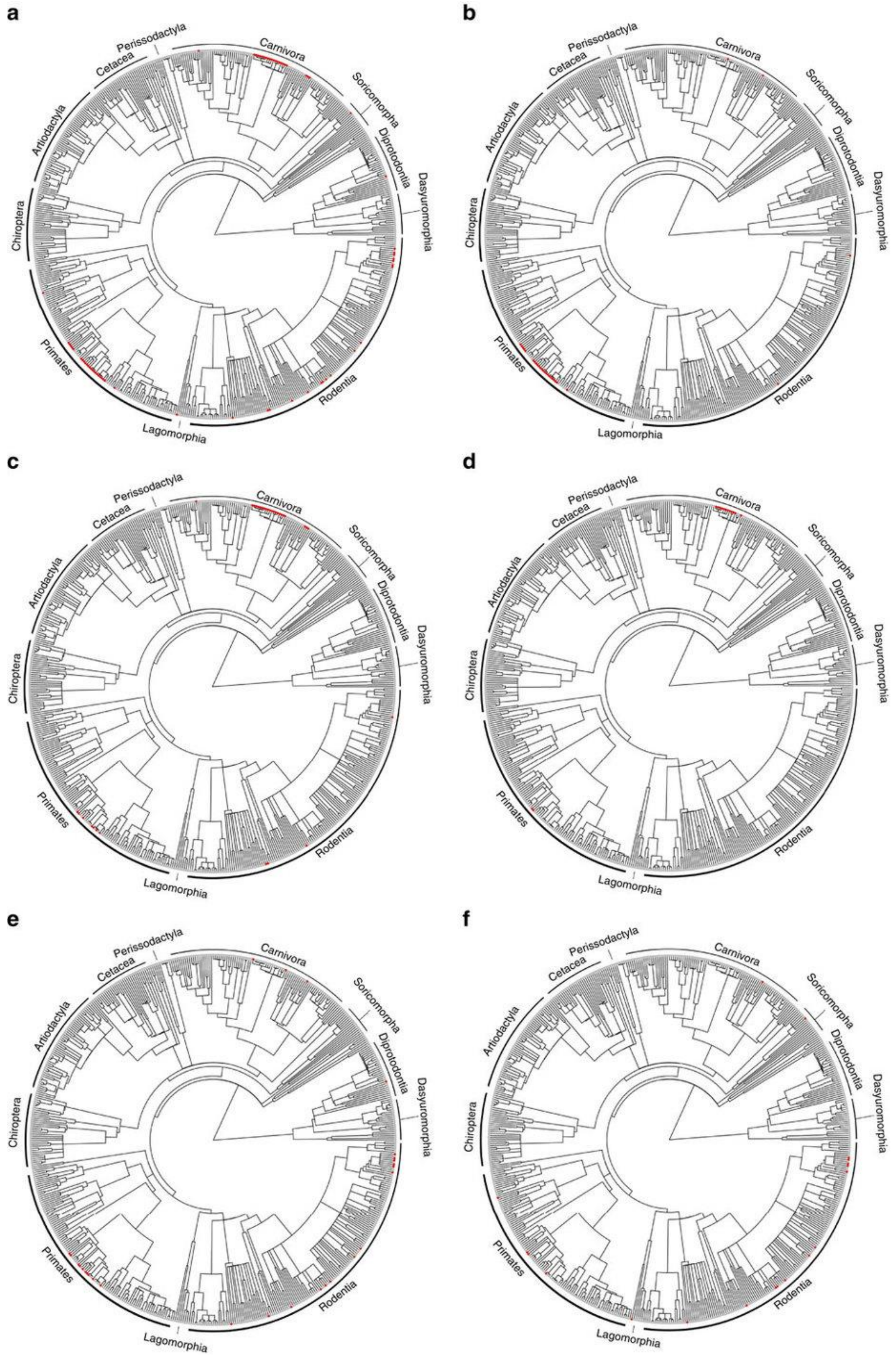


**Figure 1: Distribution of male care behaviours across the mammal phylogeny. (a) Male care (any behaviour, red dots) in mammals (65 species with and 464 species without any form of male care).** Species with biparental care (red dots) are indicated as follows: species with (b) carrying (n=27); (c) provisioning offspring (n=31); (d) provisioning reproducing females (n=15); (e) grooming (n=28); and (f) huddling with the offspring (n=19). In all panels, grey dots represent species without male care.

## **Methods**

### Data collection

We first identified species for which data were already available for at least two life history traits in existing large scale datasets (Appendix 2: Supplementary methods, Data collection). For these species we developed protocols for data comparability and collected data on male care, care by helpers, mating system and research effort, as indicated below. The total sample size in our dataset is 529 mammals with or without male care and includes species across all major orders. However, not all life history traits are available for all species. All continuous variables are $\log_{10}$-transformed to normalize their distribution. Typically, male care behaviours and care by helpers are described in the sources but there are no quantitative measures of the amount of care provided. Thus, we code all male care behaviours, care by helpers, and monogamy as binary variables, with 1 indicating the presence and 0 the absence of the trait.

We collected life history data for the following variables: female adult mass (g, n=467), lactation time (days, n=440), gestation time (days, n=461), weaning mass (g, n=262), neonatal mass (g, n=440), litter size (n=499), litters per year (n=433), and maximum lifespan (n=400). When both litters per year and interbirth interval were reported for a species, we used the former for the analysis. When only interbirth interval was available, we converted this into litters per year. We also calculated 'postnatal body mass increase' as the difference between weaning and neonatal body mass to investigate the association between male care and offspring growth postnatally. When multiple entries were found for a life history trait, we calculated the mean.

We define male care as any care behaviour by a male towards neonates or older dependent offspring (unweaned or weaned; Supplementary methods, Data collection). Following Woodroffe and Vincent (Woodroffe & Vincent 1994) we consider the following behaviours as evidence of male care: food provisioning (separating provisioning the offspring from provisioning the female), huddling with, grooming, and carrying the offspring. We investigate provisioning reproducing (pregnant or lactating) females as a form of male care because this behaviour may indirectly benefit the offspring, which could receive the additional resources that the mother has acquired. We exclude defence of the offspring from our definition of male care because this behaviour can be easily confused with general territorial behaviours (Woodroffe & Vincent 1994). Likewise, we do not consider babysitting and teaching behaviours as forms of male care because they are difficult to identify reliably across a large sample of widely different species (Thornton & McAuliffe 2006).

We extracted data from the literature on male care behaviours from a variety of primary and secondary sources for the species for which life history traits are available (Appendix 2: Supplementary References). We find data for 65 species; of which 31 provision, 27 carry, 28 groom, and 19 huddle with the offspring (Figure 1). Note that 40 species exhibit more than one male care behaviour. In 15 out of the 31 species that provision the offspring, males also provision pregnant or lactating females. We considered only species-specific descriptions of male care and excluded any entry for the whole genus or family, as closely related species may differ in the presence of male care behaviours (Nowak 1999). For example, male prairie voles (*Microtus ochrogaster*) and pine voles (*M. pinetorum*) groom and huddle with the offspring, while the closely related meadow vole (*M. pennsylvanicus*) shows no male care of the offspring (Oliveras & Novak 1986). We searched for additional information in Google Scholar and Web of Science using the keywords ‘male care’, ‘paternal care’ or ‘biparental care’, in conjunction with the species’ scientific or common name (Date last accessed: 22/05/2014) for both the species already known to have male care and for all species we had life history data for (see above). Furthermore, when using secondary sources, we checked all the information from these references against the original primary source and, when the cited primary sources were not available, we performed additional searches for new references as described above. When a source reported only that male care was present in a species without details of specific male behaviours, we discarded this information as ambiguous, since we could not assess whether male care conformed to our definition. If only ambiguous information was available for a species, we excluded the species from the dataset to avoid introducing any bias. As sources generally reported only observed behaviours rather than the absence of a behaviour from the behavioural repertoire of a species, we classified species as exhibiting 'no male care' if no mention was made of males provisioning, carrying, grooming, huddling with the offspring or provisioning reproducing females.

We define care by helpers as care towards neonates or older dependent offspring (unweaned or weaned) by any individuals other than the mother or (presumed) father of the offspring. We consider carrying, grooming, huddling with and provisioning the offspring, to be forms of care by helpers, and also include allonursing in our definition. Of the 529 mammals in our dataset 92 exhibit at least one of these behaviours. Data on care by helpers were extracted from a range of secondary sources that were checked against the original source whenever possible (Supplementary methods, Data collection).

Following Lukas and Clutton-Brock (Lukas & Clutton-Brock 2013), we define social monogamy as an association between a single breeding pair sharing a common range or territory over more than one breeding season. Data from Lukas and Clutton-Brock (Lukas & Clutton-Brock 2013), who compiled the largest and most recent dataset on mammalian monogamy, were then checked against primary sources and secondary sources (e.g. Nowak 1999), and the *Mammalian Species* monographs of the American Society of Mammalogy (Supplementary References), to ensure that the classification of mating system was at the species level rather than genus level for every species. In fact, as for male care behaviour, closely related species within a genus may vary in mating system (Nowak 1999; Valomy et al. 2015). Of the 529 species in our dataset, 78 are socially monogamous.

Finally, data for a behavioural trait, such as male parental care, may be absent from the literature because the behaviour is not exhibited in the species, or alternatively because the species is insufficiently studied for the behaviour to have been observed. In order to control for variation in research effort among species in our dataset, we include citation count as an additional independent variable in all models. Citation count is defined as the total number of papers on a species, hence the overall research effort on that species (Nunn et al. 2003). We collected data on citation count following Nunn et al.'s protocol (Nunn et al. 2003) for each species in our dataset, and specifically we extracted the total number of references published on each species since 1950 as reported in Web of Science, using the species' scientific name or common name as search parameters (Date last accessed: 02/11/2015).

### Statistical analysis

We use PGLS models (Freckleton et al. 2002; Pagel 1999), the R package 'caper' (Orme 2013), and a commonly used and comprehensive mammalian phylogeny (Fritz & Purvis 2010) that includes all mammals in our dataset, to account for species' shared ancestry and quantify the strength of phylogenetic signal in the data (Freckleton et al. 2002). Caper estimates PGLS model parameters in maximum likelihood (Orme 2013) and the parameter lambda (λ) quantifies the magnitude of the phylogenetic signal in the model residuals (Freckleton et al. 2002; Revell 2010). λ can vary between 0, indicating no phylogenetic signal, and 1, indicating that similarity between species is directly proportional to the amount of shared ancestry as expected under a Brownian motion model of evolution (Freckleton et al. 2002). We assess the association between a life history trait of interest, entered as the response variable, and male care, entered as the predictor variable, while also accounting for the following confounding variables in all models: other life history traits associated with the life history trait of interest (Bielby et al. 2007), social monogamy which is evolutionarily associated with male care in mammals (Lukas & Clutton-Brock 2013; Opie et al. 2013), care by helpers, and for research effort, measured as citation counts for a species. These PGLS models are conceptually analogous to ANCOVA models where parallel slopes with different intercepts are estimated for species with or without male care (Capellini et al. 2011), while accounting for the confounding effect of all other independent variables and phylogeny. We next use a model simplification procedure starting from 'full' models with all predictors and progressively eliminate the least significant predictors until only significant ones remain in the simplest statistically justifiable model ('reduced models') (Crawley 2007). We assess the model fit to the data of full versus reduced models, and reduced models with and without male care, using likelihood ratio (LR) test (Quinn & Keough 2002) with degrees of freedom equal the difference in number of predictors between two competing nested models. We carry out this procedure once when investigating the association between life history traits and male care classified as any behaviour, and once when investigating the association with all individual male care behaviours entered simultaneously as independent predictors.

Because life history traits in mammals covary along two life history axes, an 'output' axis and a 'timing' axis (Bielby et al. 2007), we generate variance inflation factors (VIF) to assess potential multicollinearity between all predictors in our models (Quinn & Keough 2002; Capellini et al. 2015). VIFs quantify how multicollinearity between predictors increases the variance of the model's parameters. We compute VIFs for all the independent variables in our models using non-phylogenetic generalized linear models. Including phylogeny in a statistical model generally reduces the strength of association between predictors (Freckleton et al. 2002), therefore our approach is conservative as VIFs are very likely to be higher in non-phylogenetic than in phylogenetic analyses. VIF scores higher than 5 indicate problematic multicollinearity in a model, and greater than 10 extremely problematic multicollinearity. We however find no evidence of problematic multicollinearity between predictors in any of our models as all VIFs are well below 5 (Appendix 2: Supplementary notes; Supplementary Tables 1-6).

Finally, by building a PGLS model as a phylogenetic t-test (Organ et al. 2007) we show that species with and without male care do not differ in research effort (Supplementary notes; Supplementary Table 14). All statistical tests are two-tailed with a $\alpha$-level of significance set at 0.05.

## Results

### Results across all mammals

Our analysis shows that lactation time is significantly shorter in mammals with male care (Table 1, Figure 2a), while accounting for allometry and gestation time (reduced model in Table 1), but is unrelated to all other predictors (full model 1 in Supplementary Table 1; likelihood ratio test for full vs reduced model: $LR_3$=1.9, p=0.585). The amount of variance explained by the reduced model with male care increases by 2% relative to a model without it ($LR_1$=6.1, p=0.013). When investigating individual behaviours, lactation time is shorter specifically in species where males carry the offspring while provisioning the female approaches significance (Table 1), but no other male care behaviour and no other predictor associates with lactation time (model 2 in Supplementary Table 1; full vs reduced model: $LR_6$=2.6 p=0.857).

Gestation time is not associated with male care, after accounting for allometry and lactation time across all mammals (models 1 & 2, Supplementary Table 2), individual male care behaviours (model 3, Supplementary Table 2). However, species with care by other helpers have a significantly longer gestation than species without (model 2, Supplementary Table 2).

Frequency of breeding is higher in mammals with male care (Figure 2b), with female body mass, care by helpers, lactation and gestation time being the only other predictors retained in the reduced model (Table 1; reduced model vs full model 1 in Supplementary Table 3: $LR_2$=0.8, p=0.664). The reduced model with male care explains an additonal 1% of variance compared to a model without it ($LR_1$=4.6, p=0.032). Among all care behaviours, grooming is the only significant predictor of litters per year, while accounting for allometry, the duration of maternal investment and care by helpers (Table 1, model 2 in Supplementary Table 3; full vs reduced model: $LR_6$=4.66 p=0.588). The lack of a significant association between litters per year and carrying or provisioning females across mammals may reflect the fact that lactation is shorter in species exhibiting these behaviours (see above), and so most of the variance in litters per year, which could be explained by these behaviours, is likely explained by lactation time when the latter is included in the model. To investigate this possibility further, we repeat the analysis with all behaviours but excluding the duration of maternal investment, and find that breeding frequency is higher in species with carrying (Table 1, model 3 in Supplementary Table 3).

Although there is no significant relationship between litter size and male care across all mammals (models 1 & 2 in Supplementary Table 4), litters are larger in species in which males provision reproducing females (Figure 2c, Table 1, reduced model vs full model 3 in Supplementary Table 4: $LR_6$=4.1, p=0.661). The reduced model with provisioning females and body size (Table 1) explains an additional 5% of variance in litter size than a model without it ($LR_1$=24.3, p<0.001).

Mass at birth and mass gain from birth to weaning are unrelated to male care and individual male care behaviours across all mammals (Supplementary Table 5). Maximum lifespan is unrelated to male care or any individual male care behaviour, after accounting for the duration of lactation and gestation, and the number of litters per year (Supplementary Table 6).

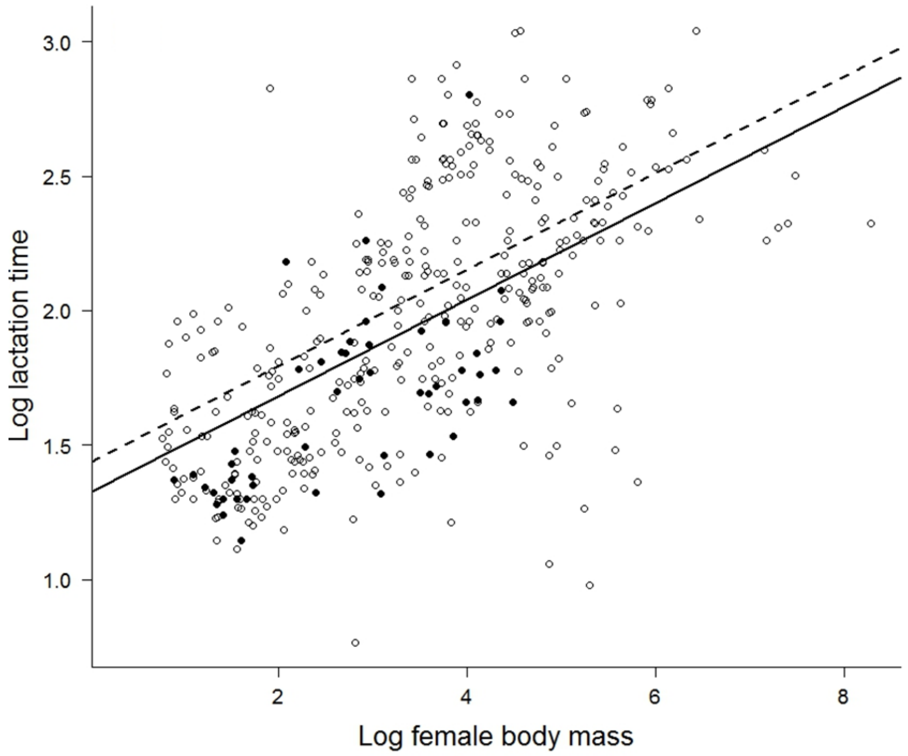
Finally, including litter size as an additional predictor of lactation time and litters per year does not alter our results since litter size is not a significant predictor of lactation or litters per year (Supplementary Table 7).

**Table 1. Reduced PGLS multi-predictor models for lactation time, litters per year and litter size with male care (any behaviour) and significant individual behaviours.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, R2 and the model log-likelihood (Lh). The total sample size for models with lactation is 390 species, of which 47 have male care (14 carrying, 24 provisioning, of which 12 also provision reproducing females, 18 huddling, and 23 grooming), while 80 exhibit care by helpers. The total sample size for litters per year is 370 species, of which 46 exhibit male care (14 carrying, 23 provisioning, 12 of which also provision reproducing females, 18 huddling, and 22 grooming), while 77 exhibit care by helpers. The total sample size for models with litter size is 448 species, of which 53 species exhibit male care, with 19 carrying, 26 provisioning, 13 of which also provision reproducing females, 18 huddling, and 25 grooming. Full models are reported in the Supplementary Tables 1, 3 & 4.

| | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Dependent Variable** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| Lactation | Female body mass | 0.13 | 0.02 | 6.3 | <0.001 | 0.81 | 0.26 | 45.78 |
| | Gestation time | 0.37 | 0.09 | 4.2 | <0.001 | | | |
| | Male care | -0.11 | 0.05 | -2.5 | 0.013 | | | |
| Lactation | Female body mass | 0.13 | 0.02 | 6.2 | <0.001 | 0.82 | 0.27 | 48.19 |
| | Gestation time | 0.36 | 0.09 | 4.1 | <0.001 | | | |
| | Carrying | -0.17 | 0.07 | -2.6 | 0.010 | | | |
| | Provisioning females* | -0.21 | 0.11 | -1.9 | 0.057 | | | |
| Litters per Year | Female body mass | -0.05 | 0.02 | -3.0 | 0.003 | 0.90 | 0.22 | 159.13 |
| | Lactation time | -0.15 | 0.04 | -3.9 | <0.001 | | | |
| | Gestation time | -0.23 | 0.07 | -3.3 | 0.001 | | | |
| | Male Care | 0.07 | 0.03 | 2.1 | 0.033 | | | |
| | Care by helpers | 0.06 | 0.02 | 2.5 | 0.013 | | | |
| Litters per Year | Female body mass | -0.05 | 0.02 | -2.9 | 0.004 | 0.90 | 0.22 | 159.10 |
| | Lactation time | -0.16 | 0.04 | -4.1 | <0.001 | | | |
| | Gestation time | -0.23 | 0.07 | -3.3 | 0.001 | | | |
| | Grooming | 0.08 | 0.04 | 2.2 | 0.035 | | | |
| | Care by helpers | 0.05 | 0.02 | 2.5 | 0.013 | | | |
| Litters per Year | Female body mass | -0.10 | 0.02 | -7.1 | <0.001 | 0.92 | 0.14 | 143.01 |
| | Carrying | 0.10 | 0.05 | 2.1 | 0.035 | | | |
| | Care by helpers | 0.06 | 0.02 | 2.6 | 0.010 | | | |
| Litter Size | Female body mass | -0.07 | 0.01 | -5.5 | <0.001 | 0.95 | 0.16 | 265.61 |
| | Provisioning females | 0.26 | 0.05 | 5.1 | <0.001 | | | |
| | Citation count | 0.05 | 0.01 | 6.2 | <0.001 | | | |

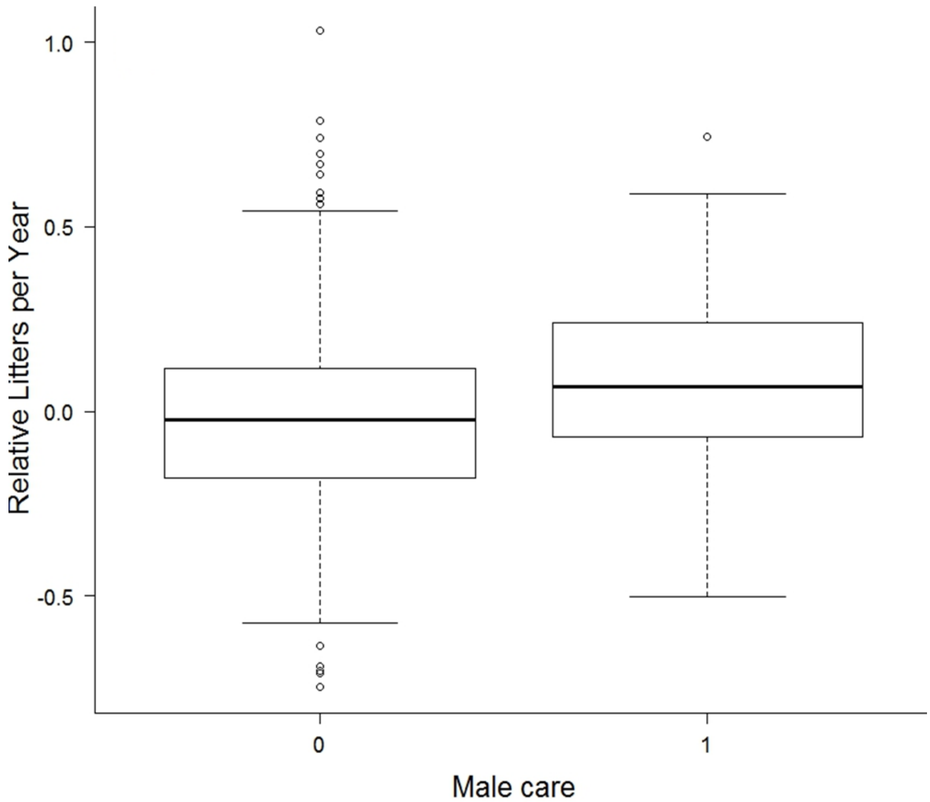
*For lactation time, the comparison between a full model with provisioning females (model 2, Supplementary Table 1) and a reduced model also without this predictor approaches significance (Likelihood ratio test: $LR_1$=3.66 p=0.056).

**a)**



Log lactation time
3.0
2.5
2.0
1.5
1.0
2
4
6
8
Log female body mass

**b)**



Relative Litters per Year
1.0
0.5
0.0
-0.5
0
1
Male care

**c)**

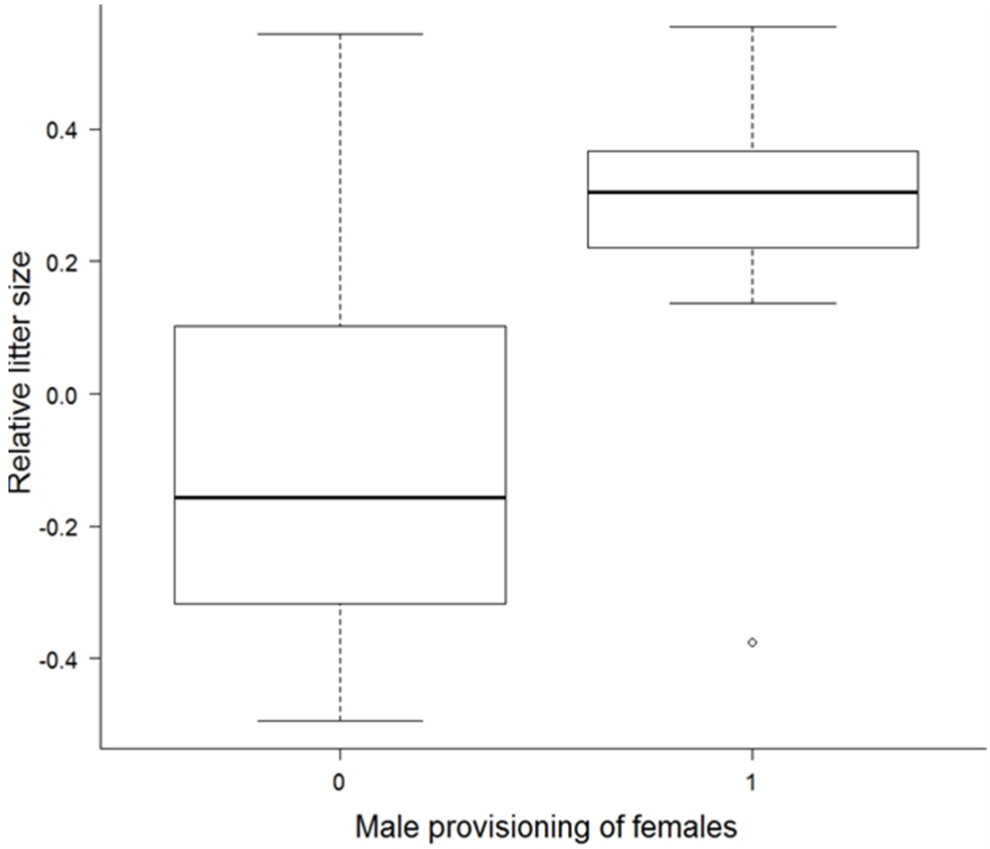


**Figure 2: Male care and female life history traits across all mammals.** (a) For a given female mass, lactation time is shorter in species with male care (filled circles) than species without it (open circles) (PGLS in Table 1: n=390). Best fitting line for species with male care in solid black, dashed line for species without male care. (b) The relative number of litters per year, after accounting for gestation time, lactation time and female mass, is higher in species with male care (coded as 1) than species without (coded as 0) (PGLS in Table 1: n=370). (c) Relative litter size, after accounting for female body mass, is larger in species where males provision reproducing females (coded as 1) than species without (coded as 0) (PGLS in Table 1: n=448). Figures in (b,c) report the median with upper and lower quartiles (boxes) and 95% confidence intervals (whiskers) of the residuals of litters per year (b) and litter size (c) computed from the reduced models in Table 1. All continuous data are $\log_{10}$-transformed.

## Order specific results

Within individual orders with sufficient sample sizes for care behaviours (Supplementary notes), the duration of lactation is reduced in primates with carrying and in carnivores where males provision reproducing females, but it is unrelated to male care behaviours most common in rodents; huddling and grooming (Table 2; Supplementary Table 8). Gestation time is not associated with male care, after accounting for allometry and lactation time, within orders (Supplementary Table 9). Frequency of breeding is higher in primates with carrying due to a reduction in lactation time (Table 2; Supplementary Tables 8 & 10), but litters per year is unrelated to any care behaviour in carnivores and rodents (Supplementary Table 10). Litter size is unrelated to male care in primates, while provisioning reproducing females is associated with larger litters in carnivores (Table 2; Supplementary Table 11). Litter size is larger in socially monogamous rodents but unrelated to male care behaviours in this order (Supplementary Table 11). Mass at birth and mass gain from birth to weaning are unrelated to individual male care behaviours within each order where sample sizes are sufficiently large for analysis (Supplementary Tables 12 & 13). However, neonates are larger in carnivores with care by helpers and smaller in socially monogamous rodents (Supplementary Table 12). Sample sizes are too small to investigate the associations between male care and longevity within orders, and post-natal body mass gain in primates and carnivores (Supplementary notes).

**Table 2. Reduced PGLS multi-predictor models for lactation time, litters per year and litter size with significant individual behaviours within orders.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$ and the model log-likelihood (Lh). Sample sizes are as follows: for lactation time 70 primate species of which 11 exhibit carrying behaviour and 80 carnivore species of which 12 provision reproducing females; litters per year in primates includes 63 species of which 10 with carrying and 33 with care by other helpers; litter size in carnivores includes 82 species, 12 with provisioning females. Full models are reported in the Supplementary Tables 8, 10 & 11.

| | | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Order** | **Dependent Variable** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| Primates | Lactation | Female body mass | 0.22 | 0.06 | 3.5 | 0.001 | 0.00 | 0.67 | 10.15 |
| | | Gestation | 1.21 | 0.33 | 3.7 | 0.001 | | | |
| | | Carrying | -0.23 | 0.08 | -2.8 | 0.007 | | | |
| Carnivores | Lactation | Female body mass | 0.16 | 0.05 | 3.0 | 0.003 | 0.86 | 0.16 | 4.15 |
| | | Provisioning females | -0.25 | 0.12 | -2.1 | 0.039 | | | |
| Primates | Litters per year | Female body mass | -0.21 | 0.05 | -4.2 | <0.001 | 0.87 | 0.49 | 37.16 |
| | | Carrying | 0.18 | 0.07 | 2.5 | 0.015 | | | |
| | | Care by helpers | 0.12 | 0.04 | 3.2 | 0.002 | | | |
| Carnivores | Litter size | Female body mass | -0.10 | 0.03 | -3.1 | 0.003 | 0.77 | 0.32 | 44.97 |
| | | Provisioning females | 0.31 | 0.07 | 4.4 | <0.001 | | | |
| | | Citation count | 0.09 | 0.03 | 3.3 | 0.002 | | | |

## Discussion

Male care should evolve when the benefits of caring outweigh the costs to males' inclusive fitness. Potential benefits of male care include increased female fecundity and/or offspring fitness, which in turn provide fitness benefits to the caring male (Woodroffe & Vincent 1994; Lukas & Clutton-Brock 2013; Opie et al. 2013; Oftedal & Gittleman 1989). Thus, species with male care are expected to have more frequent and larger litters, shorter durations of maternal investment and heavier or faster growing offspring (Woodroffe & Vincent 1994; Oftedal & Gittleman 1989). In support of this hypothesis, our comparative analysis reveals that male care is associated with increased female fecundity but differently across behaviours (Table 3). Specifically, litters are larger in species, mostly carnivores, where males provision reproducing females. Instead, a reduction in lactation time in species with carrying, mostly but not exclusively primates, increases the frequency of breeding. Lactation is also shorter among carnivores, where males provision the females. Paternal care is however unrelated to prenatal maternal investment and offspring size at birth and weaning, suggesting that offspring grow faster postnatally but do not achieve a larger size in species with carrying and provisioning. Finally, longer-lived species are not more likely to exhibit male care. Taken together these results suggest that male care benefits both parents through increased female productivity, and that greater fecundity, but not a longer lifespan, helps maintaining the evolutionary association between social monogamy and male care.

**Table 3. Summary of main results for male care and care by other helpers across all mammals, carnivores, primates and rodents.**

| Taxon | All mammals | Carnivores | Primates | Rodents |
|---|---|---|---|---|
| Male care | Shorter lactation with carrying<br>More litters per year with grooming (& carrying[1])<br>Larger litters with provisioning females | Shorter lactation with provisioning females<br>Larger litters with provisioning females | Shorter lactation with carrying<br>(More litters per year with carrying[1]) | No life history trait associated with any male care behaviour |
| Care by helpers | Longer gestation<br>More litters per year | Larger litters<br>Larger neonates | More litters per year | No life history traits associated with care by helpers |

[*] Mediated by a reduction in lactation time

By undertaking costly care or by caring for the offspring while the female forages for longer, males may help females meet the high energetic costs of lactation and allow them to invest more energy in milk production (Opie et al. 2013; Oftedal & Gittleman 1989). Consistent with this hypothesis, lactation time is shorter in mammals with male care; specifically with carrying the offspring or provisioning the females, behaviours most common in primates and carnivores respectively. Conversely, lactation time is unrelated to huddling and grooming, suggesting that, overall, these male care behaviours may not help females change activity budgets sufficiently to enhance milk energy output. Although male care explains a small additional amount of variance, the reduction in the duration of lactation in species with male care can be substantial. For example, we estimate from a simple PGLS model including only female body mass and male care that, for a 10kg mammal with biparental care, lactation is 31 days shorter (104 days) than that of a species of the same size without male care (135 days). While a previous study shows that allocare (including male care) in primates is associated with shorter lactation (Isler & van Schaik 2012), our analysis reveals that this effect is specifically linked to the presence of caring males, but not other helpers (Table 2). We propose that the lack of an association between care by other helpers and lactation is due to differences in the costs and benefits of care, and the associated trade-offs, for parents and non-breeding helpers across types of allocare. In species with a high reproductive skew within the social group, such as meerkats (*Suricata suricatta*), breeders reduce their care levels and divert energy towards future reproduction, while non-breeding helpers show high levels of postnatal offspring care, leading to greater offspring growth and survival (Clutton-Brock et al. 2004). Conversely, when reproductive skew is limited, such as in the banded mongoose (*Mungos mungo*), parents invest more in the current litter than non-breeding helpers, which instead conserve energy to reproduce themselves in the next reproductive bout (Gilchrist & Russell 2007). Future studies could thus investigate how reproductive skew influences the evolution of male care and female fecundity once data become available for a sufficient number of species, both with and without additional alloparents.

While previous studies do not discriminate between the specific care behaviours expressed by the male, our analysis identifies carrying and provisioning the female as the behaviours that associate specifically with a reduction in lactation time. Carrying appears to have evolved independently two or three times among primates, as well as at least twice in carnivores and twice in rodents (Figure 1b). The low incidence of carrying behaviours in non-primate species precludes us from testing comparatively whether a shorter lactation time is associated with the presence of male care in other orders, and should therefore be re-evaluated when more data become available. By supporting females directly through provisioning, as in some primates and canids (Oftedal & Gittleman 1989; Kleiman & Malcolm 1981), males provide additional valuable resources that allow females to wean their offspring sooner. Thus, while the behaviours expressed by males may differ between orders, the overall relationship is the same; a shorter lactation when males care. The lack of a significant association between the duration of lactation and provisioning the offspring may thus appear surprising. However, in most mammals (including carnivores, some rodents and primates), males provision the offspring post-weaning until independence, and so this behaviour is unlikely to influence female investment in milk production (Nowak 1999; Malcolm 1985).

An alternative hypothesis proposes that male care and a shorter lactation are counterstrategies against infanticide by males, as the former could evolve as a defence against competing males and the latter reduces the vulnerability of the offspring to infanticide risk (Opie et al. 2013; van Schaik 2000). In support of this hypothesis, social monogamy and male care in primates are associated with a reduction in weaning proportion, the relative duration of lactation to the overall period of maternal investment (Opie et al. 2013). However, Lukas and Huchard (Lukas & Huchard 2014) find little evidence that lactation time is shorter in species with higher infanticide risk.

Our study reveals that the previously documented increase in the frequency of breeding in species with male care (Lukas & Clutton-Brock 2013; Cantoni & Brown 1997) is mediated by a reduction in lactation time, such that females of species with male care wean the offspring earlier and consequently reproduce again sooner. Specifically, mammals with carrying by males produce more litters in a year than species without carrying, but this association becomes non-significant when the duration of lactation – which is shorter in species with carrying – is included in the model. Therefore, by accounting for the correlated evolution between life history traits, our study identifies lactation as the specific temporal stage of reproduction during which females may energetically benefit from the help of caring males. Conversely, we find that care by other helpers is significantly associated with frequency of breeding, but not lactation time. Altogether, these results suggest that care by the male and by other alloparents relate to female fecundity through fundamentally different mechanisms. Specifically, we suggest that male care may provide an important energetic contribution towards female reproduction during lactation, while care by other individuals is likely to be more important post-weaning and may allow females to regain body condition more quickly through mechanisms such as increased foraging time (Woodroffe & Vincent 1994).

When the duration of maternal investment (lactation and gestation) is accounted for, the number of litters produced in a year is positively associated with grooming behaviour. We suggest that producing frequent litters might require more grooming than females alone can provide to keep the offspring free of ectoparasites. Ticks, for example, can lead to high levels of infant mortality (e.g. up to 50% in Chacma baboons, *Papio ursinus*) as swelling around the muzzle due to tick infestation severely limits infant suckling (Brain & Bohrmann 1992). Therefore, frequent breeding may be the evolutionary cause for the evolution of offspring grooming by males.

Of all male care behaviours, only provisioning reproducing females is associated with larger litters. Among cooperatively breeding species, larger litter size appears to be an evolutionary prerequisite for the evolution of allocare, rather than an evolutionary consequence of it (Lukas & Clutton-Brock 2012a). Whether this is the case for male care too or whether a larger litter results from an energetic contribution by the male towards increased female fecundity, is currently unknown. However, single species studies show that, by providing protection against predators or provisioning the offspring, males directly enhance offspring survival (Gubernick et al. 1993; Wright 2006). Moreover, our analysis demonstrates that when care by helpers and provisioning of females by the male are tested together, litter size is significantly higher only in species with provisioning by the male. Altogether our study reveals that different care behaviours allow males to gain fitness benefits via increased female fecundity, and specifically when provisioning the female and supporting her in producing larger litters, most common in carnivores, or when carrying heavy offspring and allowing females to wean the offspring faster and breed again sooner, most common in primates. We propose that the observed differences among orders in the specific associations of life history traits with male care are likely due to how frequently and how long for each male care behaviour is expressed and the costs associated with it. Virtually nothing is currently known about the timing and energetic costs of different male care behaviours in wild mammals; quantifying how strongly costs of male care underlie the associations with life history traits revealed here across all mammals and within both the better studied orders – carnivores and primates – and the more neglected ones, will be an interesting venue for future research.

Mammals with male care or care by helpers do not have larger offspring, after accounting for the relevant duration of maternal investment. This, together with the finding that lactation time is shorter in species with biparental care, indicates that offspring grow faster postnatally in species with male care, as they reach the same size at weaning as offspring of species without it but in a shorter time. Our results support suggestions that allocare, including male care, associates with greater milk energetic output and faster offspring growth (Oftedal & Gittleman 1989). Finally, we find no evidence that long-lived species are more likely to exhibit male care behaviours. Thus, unlike increased female fecundity, a longer lifespan does not seem to help males compensate for the likely loss of additional mating opportunities associated with caring.

Most studies on the evolution of male care focus on the costs and benefits of this behaviour for the male, in relation to lost mating opportunities and increased certainty of paternity (Kvarnemo 2005; Alonzo 2010). Here we demonstrate that the evolution of male care in mammals has appreciable benefits for both males and females through increased female breeding frequency, mediated by a reduction in lactation time, and increased litter size. Our study thus reveals that male care may provide a major energetic contribution specifically during the most expensive time of female reproduction, lactation. While an increased certainty of paternity may promote the evolution of male care (Woodroffe & Vincent 1994; Alonzo 2010), higher female fecundity, but not a longer lifespan, contributes to reduce the energetic and opportunity costs of caring for the males. This can also help to explain why male care evolves more easily – but not exclusively - among socially monogamous species (Lukas & Clutton-Brock 2013; Opie et al. 2013), and suggests that male care is likely under strong selection to help reduce the costs of social monogamy. As a result, the association between increased female fecundity and male care may lead to a positive evolutionary feedback between the two. Our results demonstrate that the association between male care and increased female fecundity is underappreciated and should be considered when investigating the benefits and costs of evolution of parental care by males.

# CHAPTER 4: THE EVOLUTIONARY RELATIONSHIP BETWEEN MALE CARE AND SOCIAL MONOGAMY IN MAMMALS

**Authors:** Hannah E. R. West and Isabella Capellini

**Author contributions:** IC and HW designed the research and data collection protocols; HW collected the data, conducted the analyses, and drafted the manuscript; IC and HW revised the draft.

## Abstract

The evolution of biparental care is a topic of much debate in the field of biology. One hypothesis, supported by recent studies in mammals, is that male care evolves in socially monogamous species, as males should preferentially care for offspring that they have sired. Alternative theoretical models suggest instead that male care may precede the evolution of a socially monogamous mating system if male care is an important factor for offspring survival. Previous studies addressing this question however, give little consideration to the different forms of care behaviours exhibited by male mammals. Using phylogenetic comparative methods, we investigate whether social monogamy precedes or follows the evolution of individual male care behaviours in a sample of over 500 mammalian species. We find that provisioning and carrying behaviours by males follow the evolution of social monogamy. In contrast, grooming and huddling behaviours appear to precede the evolution of social monogamy. We conclude that the evolution of low-reward and presumably low-cost male care behaviours promotes the evolution of social monogamy, which in turn promotes the evolution of high-reward, high-cost male care behaviours. By accounting for all the diversity in male care behaviours, we thus reveal that the correlated evolution of monogamy and male care in mammals has followed a complex, two-step, feedback process, and we suggest similar results may be found in other lineages.

## Introduction

Parental care has been studied in a wide range of species, but identifying the social or ecological drivers that promote the evolution of this behaviour has been challenging (Burley & Johnson 2002; Wesołowski 2004; Brown et al. 2010). Within this broad question, understanding why biparental care evolves is even more puzzling, given the documented high costs of male care in many species where females already invest heavily in raising the offspring (Sánchez et al. 1999; Schradin & Anzenberger 2001; Reid 1987; Descamps et al. 2009; Townsend 1986; Campbell et al. 2009; Fietz & Dausmann 2003; Saltzman et al. 2015). Several authors propose that biparental care is evolutionarily associated with social monogamy (Reichard & Boesch 2003; Burley & Johnson 2002; Ligon 1999; Lukas & Clutton-Brock 2013; Opie et al. 2013), but they strongly disagree on which of these behaviours evolves first and potentially facilitates the evolution of the other (Reichard & Boesch 2003). A major shortcoming of previous studies, however, is that they do not consider the importance and implications of the diversity in care behaviours that males exhibit (Lukas & Clutton-Brock 2013; Gilbert & Manica 2015; Opie et al. 2013). This is problematic because different care behaviours may entail both different costs (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012) and different benefits (West & Capellini 2016). Here we exploit the diversity in male care behaviour, including two high-benefit and two low-benefit behaviours, and investigate the directionality of the correlated evolution between social monogamy and male care in a sample of over 500 mammals.

The most commonly proposed hypothesis suggests that male care precedes the evolution of social monogamy because additional parental care is essential to support offspring growth and survival (Reichard & Boesch 2003; Burley & Johnson 2002; Ligon 1999; Gowaty 1996). Proponents of this idea suggest that if offspring survival is heavily dependent on parental care such that one parent cannot raise the offspring, male care should evolve first. Thus, when females vary substantially in their ability to raise offspring and high-quality females may be able to successfully raise offspring alone, additional help by males may be essential for offspring survival of lower-quality females (Gowaty 1996). A theoretical model also suggests that the evolution of biparental care is promoted when parental care has low costs for the male but substantially enhances offspring survival (Burley & Johnson 2002). Care by males may also reduce the risk of infanticide, as proposed by several studies in primates (Paul et al. 2000; Agrell et al. 1998; Dunbar & van Schaik 1990). Once evolved, male care may in turn facilitate the evolution of social monogamy as the best reproductive strategy to maximize both male and female fitness (Birkhead & Møller 1996; Kleiman 1977; Wittenberger & Tilson 1980). Several single species studies support this suggestion and show that the removal of the male drastically reduces offspring survival (Townsend et al. 1984; Wolf et al. 1988; Markman et al. 1996; Gubernick et al. 1993; Gubernick & Teferi 2000; Wright 2006). For example, chicks in the dark-eyed junco (*Junco hyemalis*) raised by one parent alone are more likely to die from starvation and exposure to low temperatures, compared to broods supported by both parents (Wolf et al. 1988), while male care is vital for protection against infanticidal intruders in the orange-tufted sunbird (*Nectarinia osea*) (Markman et al. 1996). This is not limited to birds, studies in mammals also demonstrate a positive relationship between male care and offspring survival (Gubernick et al. 1993; Gubernick & Teferi 2000; Wright 2006). Offspring survival is reduced by nearly 50% following removal of the father in the Djungarian hamster (*Phodopus campbelli*), particularly when ambient temperature is low (Wynne-Edwards & Lisk 1989). Other studies propose that the presence of male care may also inform female choice, with females preferentially mating with caring males (Kvarnemo 2005); another route by which male care may promote the evolution of monogamy. If females preferentially mate with caring males, and if care is costly so that males can care only for one female's offspring, then this should favour the evolution of social monogamy. However, in many species, including mammals, social monogamy is more common than male care and often occurs without additional male care, suggesting that the evolutionary pathway leading to the presence of both behaviours in the same species may not be the same in all cases.

The alternative scenario is that social monogamy promotes the evolution of biparental care. Caring for the offspring is costly, not only in terms of energy expenditure but also because of lost mating opportunities, thus parents should only care when the benefits of doing so outweigh the costs (Trivers 1972; Klug et al. 2012). The costs of care should also vary between males and females (Klug et al. 2012; Kokko & Jennions 2012). While both sexes may pay substantial energetic and opportunity costs, males of internally fertilizing species often lose reproductive benefits due to potential female promiscuity reducing levels of paternity and increasing uncertainty of paternity (Maynard Smith 1977). Thus, males should be under intense selection to care only for offspring they are more certain of having sired (Alonzo & Klug 2012; Griffin et al. 2013). The relationship between biparental care and monogamy may therefore be dependent on a male's certainty of paternity (Chapter 2) and, if monogamy is associated with a high certainty of paternity, it may facilitate the evolution of costly care by males. Large-scale comparative studies in mammals find support for this hypothesis. Among mammals as a whole and primates specifically, the evolution of male care appears to follow the evolution of a social monogamy (Lukas & Clutton-Brock 2013; Opie et al. 2013). Although social monogamy is not always indicative of genetic monogamy as many socially monogamous species mate promiscuously outside of their pairs, particularly in birds (Griffith et al. 2008), social monogamy in mammals associates with an increased certainty of paternity when compared to other mating systems (Chapter 2; Soulsbury 2010). Thus, the high certainty of paternity resulting from social monogamy may potentially drive the evolution of costly male parental care in mammals. As a result, the benefits associated with male care in mammals, notably increased female fecundity (Chapter 3; West & Capellini 2016), are likely to be more beneficial among monogamous mammals, where males mate with the same female over multiple breeding attempts, and may provide a positive evolutionary feedback in the association between monogamy and male care.

One major limitation of previous empirical studies in many lineages is that they focus on a limited number of male care behaviours, and often class them together (Gilbert & Manica

2015; Summers et al. 2006; Remeš et al. 2015), even though costs and benefits are likely to vary across care behaviours. Recent work in insects for example considers guarding, carrying, provisioning and cleaning behaviours together (Gilbert & Manica 2015), while studies in frogs class all forms of care to be equivalent, regardless of the sex providing them and the behaviour performed (Summers et al. 2006). Likewise, mammal species are often considered biparental if the male either provisions or carries the offspring, because these behaviours are believed to be energetically more expensive than others such as grooming and huddling (Isler & van Schaik 2012; Lukas & Clutton-Brock 2013). Little is known about the relative costs of individual care behaviours but available evidence indicates that even behaviours typically considered less demanding can be very expensive (Campbell et al. 2009; Fietz & Dausmann 2003; Kenkel et al. 2014; Saltzman et al. 2015). For example, in prairie voles (*Microtus ochrogaster*) where the primary form of care by males is grooming and huddling with the offspring, caring males experience a significant loss in weight and fat stores (Kenkel et al. 2014). Crucially, we have recently shown that male care behaviours differ in benefits (West & Capellini 2016). Specifically, mammals in which males either carry the offspring or provision reproducing females have higher female fecundity and faster offspring growth, while grooming and huddling do not appear to confer substantial benefits in relation to life history traits (West & Capellini 2016). Rather than increasing female fecundity or offspring growth, grooming and huddling may be important for offspring survival (Wynne-Edwards & Lisk 1989). Thus, the evolutionary association between male care behaviours and social monogamy may vary across behaviours.

Using modern phylogenetic comparative approaches and considering the great diversity in mammalian male care behaviours, we investigate correlated evolution between social monogamy and each male care behaviour individually – carrying, provisioning, huddling and grooming. Under the hypothesis that all male care behaviours are essential for offspring survival, we predict all behaviours to precede the evolution of monogamy. Alternatively, if males care only for offspring they have sired, monogamy should precede the evolution of all male care behaviours. If behaviours differ in costs and benefits, a third possibility is that some behaviours precede and some follow the evolution of male care.

## Methods

### Data collection

We consider four male care behaviours; carrying the offspring, provisioning either the offspring or the reproducing female, grooming, and huddling with the offspring. Data on each of these male care behaviours are taken from West and Capellini (2016), and have been extracted from a variety of primary and secondary sources (full details in Chapter 3; West & Capellini 2016). Of the total sample of 536 mammals in this study, 67 species exhibit one or more forms of male care and specifically 33 provision (both the offspring and the female), 27 carry, 28 groom, and 19 huddle with the offspring. Note that 40 species exhibit more than one male care behaviour. Data on mating system are also taken from West and Capellini (2016), where social monogamy is defined as an association between a single breeding pair sharing a common range or territory over more than one breeding season. In this dataset 78 species are socially monogamous. We code all male care behaviours and social monogamy as binary variables, with 1 indicating the presence and 0 the absence of the trait.

### Statistical analysis

We use Pagel's method to investigate the correlated evolution of binary traits (Pagel 1994; Pagel 1999), here male care and social monogamy, in a Bayesian framework using the program BayesTraits (Pagel et al. 2004). To account for species' shared ancestry (Pagel 1999) we use a comprehensive mammalian phylogeny (Fritz & Purvis 2010) that includes all mammals in our dataset. Pagel's method is based on a continuous time Markov model of evolution for discrete traits and estimates the instantaneous rate of change between the states (presence/absence) of binary traits along the branches of a tree (Pagel 1994; Pagel 1999). We first calculate the relative fit to the data of two alternative models of evolution, one where the two traits evolve independently of one another ('Independent model'), and the other where they evolve in a correlated fashion ('Dependent model'). Specifically, the independent model of evolution allows the two binary traits to evolve independently of each other and calculates the rates of transition between states (α, 0 to 1, and β, 1 to 0) for each of the two traits (Pagel 1999). The 'α' transitions represent the gain and the 'β' transitions the loss of a character state, so that four parameters are required for two traits evolving independently (Figure 1a). The dependent model instead considers the four possible combinations of character states that the two discrete traits can jointly take - (0, 0), (1, 1), (0, 1) and (1,0) - and estimates eight possible transition rates (qij) (Pagel 1999) (Figure 1b). Under a dependent model of evolution, the two traits are not allowed to change simultaneously, so by examining the transition rates in this model we can determine the order of evolution for the relationship between two discrete traits (Pagel 1999).

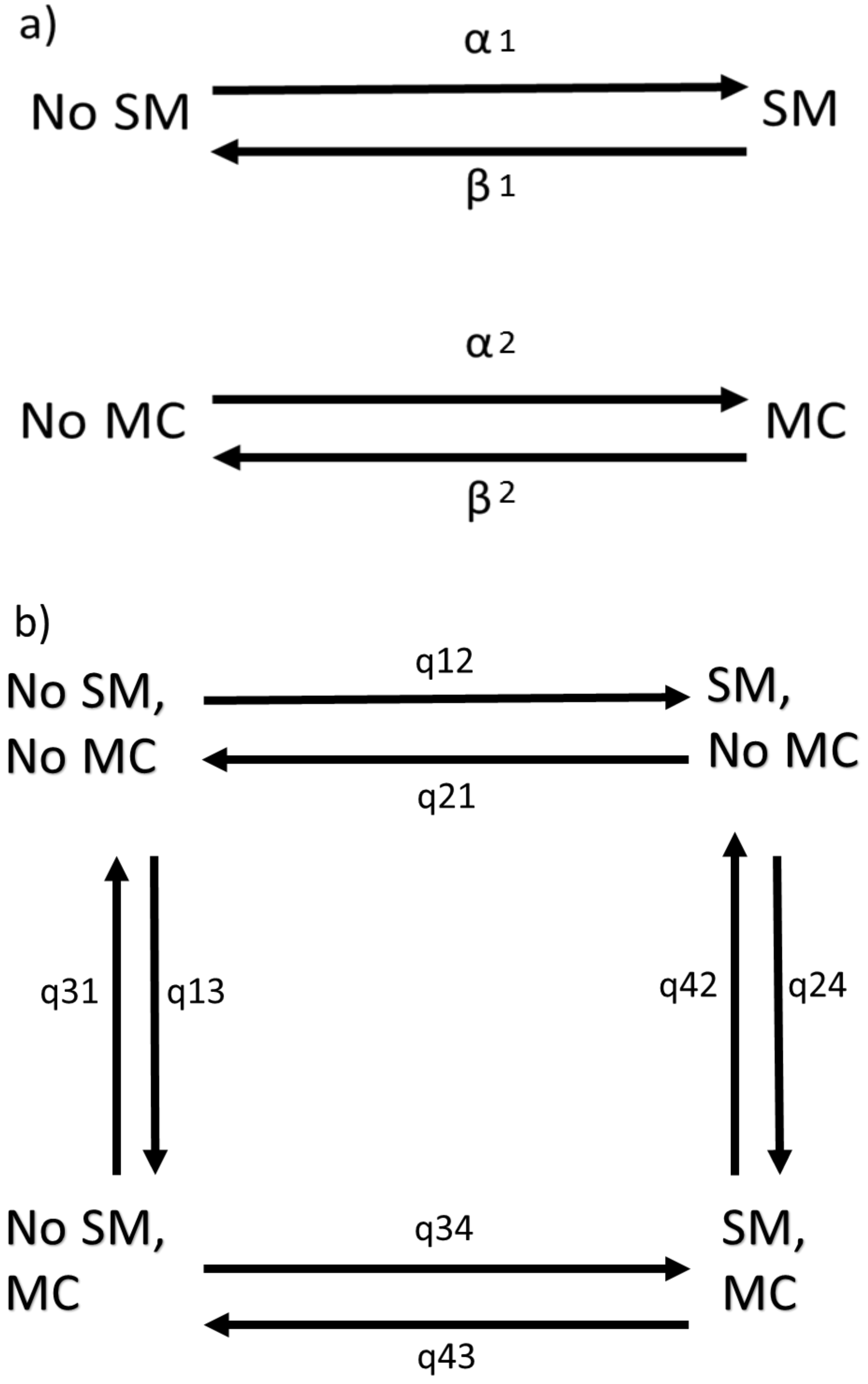


**Figure 1: Rates of transitions for (a) the independent model of evolution (4 transition rates), and (b) the dependent model of evolution (8 transition rates) for male care and social monogamy.** The arrows represent the direction of the evolutionary transitions. SM = social monogamy, MC = male care.

We run the analysis in a Bayesian framework for both the independent and dependent models of evolution. Specifically, we use Markov Chain Monte Carlo (MCMC) method to explore parameter space for the possible transition rates under a given model of evolution (dependent or independent) and derive a posterior distribution of transition rate parameters based on the model's likelihood given the data; models that fit the data better are sampled more frequently (Currie & Meade 2014). We use exponential priors for all rate parameters, with a uniform hyperprior from which the proposed mean and variance of the prior are drawn at each iteration. Using a hyperprior instead of setting the prior manually allows the model to sample across a larger range of possible values for a given prior distribution. This procedure therefore substantially limits the uncertainty and arbitrariness in the choice of prior values (Pagel & Meade 2006). We set a uniform hyperprior to range between 0 and 5 for all models, with the exception of the dependent model for carrying and social monogamy that performs best with a uniform hyperprior ranging between 0 and 2. We also employ a reversible jump procedure for all models (both dependent and independent), which sets certain qij transition rates to zero at some iterations (Pagel & Meade 2006). Reversible jump can help reduce model complexity and over-parameterisation, and helps identifying which transitions are unlikely to occur. All chains are run to convergence for 50 million iterations, sampling every 2000 iterations, and with a burn-in period of 500000. The resulting effective sample sizes (ESS) for all model parameters are greater than the minimum recommended value of 1000. Following standard practice using the diagnostics tools in Tracer (Rambaut et al. 2014), we confirm that the chains reach convergence, have a good mixing and that the effective sample sizes are over 1000 with these specifications. These analyses are repeated three times and results do not differ qualitatively across runs.

We compare the fit to the data of independent and dependent models of evolution using Bayes factors (BF) (Currie & Meade 2014). A Bayes factor is a ratio of the posterior probabilities of two competing models (Currie & Meade 2014), and are calculated as twice the difference between the harmonic means of alternative models, here the dependent and independent models of evolution (Pagel & Meade 2006), where the model with the higher harmonic mean first the data better. Bayes factors greater than 2 are considered positive evidence for the model with the higher Harmonic mean, greater than 5 as strong evidence, while values over 10 as very strong evidence (Pagel & Meade 2006).

## Results

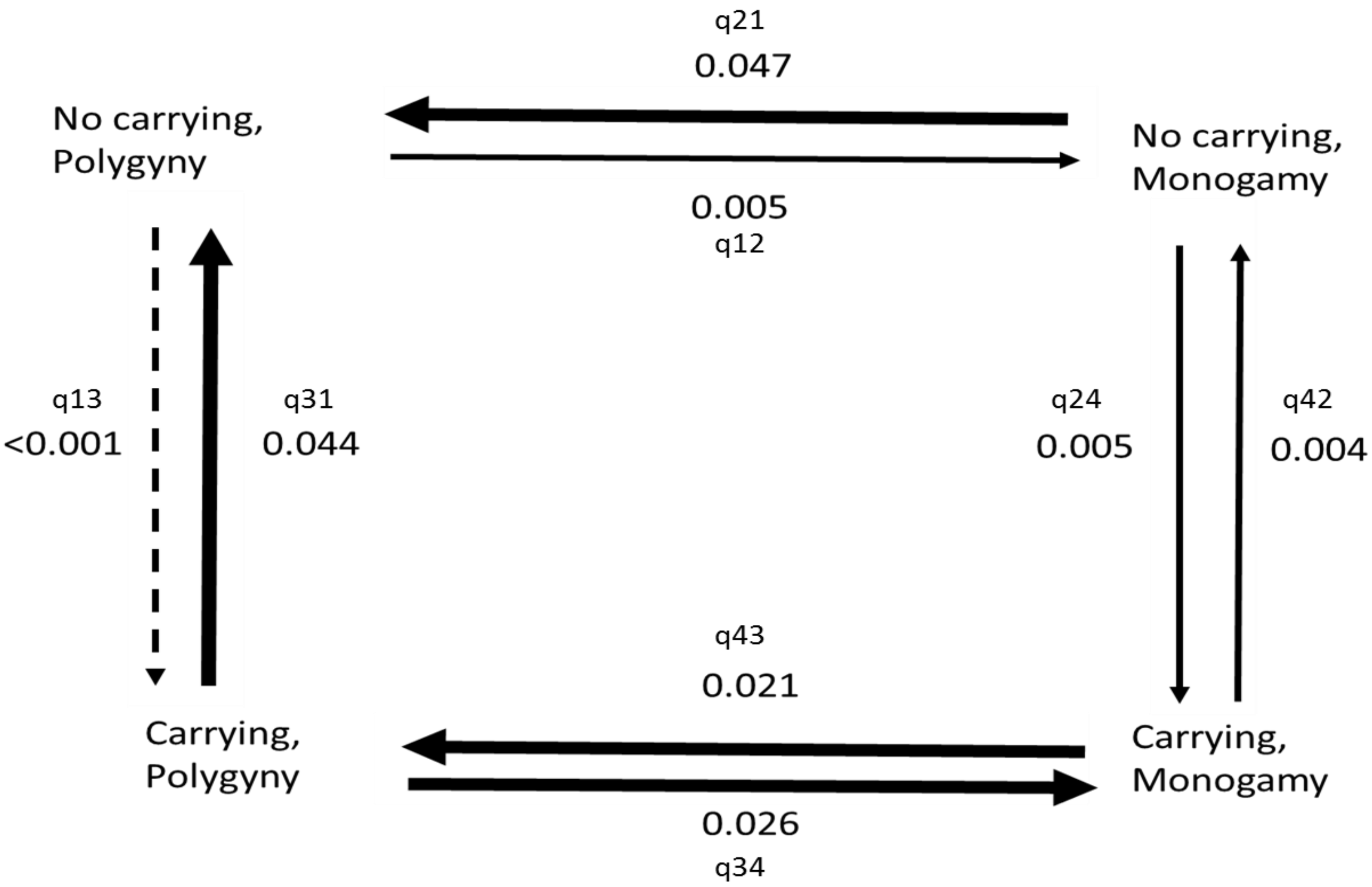
We find very strong evidence in support of the model of correlated evolution between social monogamy and all four male care behaviours here considered. In all cases the dependent model of evolution provides a far better fit to the data than the independent model (carrying: BF=17.88; provisioning: BF=27.58; grooming: BF=14.08; huddling: BF=15.1). However, directionality and order of evolution between male care and social monogamy differ across behaviours.

Specifically, carrying and provisioning follow the evolution of monogamy (Figure 2). From a condition of polygyny without carrying, monogamy is more likely to evolve in the absence of male care than carrying is to evolve with polygyny (mean $q_{12}$=0.005, $q_{13}$<0.001). Once social monogamy evolves, it is either rapidly lost ($q_{21}$=0.047), or carrying by males evolves next ($q_{24}$=0.005). Carrying with polygyny is an evolutionarily unstable state, more likely to be gained through the loss of monogamy ($q_{43}$=0.021), and leading to either the rapid loss of carrying ($q_{31}$=0.044) or the gain of monogamy ($q_{34}$=0.026). Thus, while monogamy is more likely to evolve in the presence of carrying ($q_{34}$=0.026) than in its absence ($q_{12}$=0.005), carrying is very unlikely to evolve with polygyny ($q_{13}$<0.001) and more likely to evolve with monogamy ($q_{24}$=0.005). Results are similar for social monogamy and provisioning by the male (Figure 3) and indicate that provisioning can only evolve after monogamy ($q_{12}$=0.004 followed by $q_{24}$=0.019), but does not evolve with polygyny ($q_{13}$=0). Provisioning with polygyny thus evolving from losing monogamy ($q_{43}$=0.019), and is evolutionarily unstable since is either provisioning is quickly lost ($q_{31}$=0.012), or monogamy is regained ($q_{34}$=0.013). When we consider carrying and provisioning together in a ‘high-benefit male care’ variable, high-benefit care behaviours by the male only evolve after monogamy (Appendix 3: Supplementary results).

Low benefit behaviours instead show a more dynamic picture (Figures 4 & 5). From a condition of polygyny without grooming, either grooming or social monogamy can evolve first at similar but low rates ($q_{12}$=0.004, $q_{13}$=0.001; Figure 4). Once either behaviour has evolved, the other soon follows. Specifically, monogamy evolves far more readily in the presence ($q_{34}$=0.159) than in the absence of grooming ($q_{12}$=0.004) and grooming evolves much more rapidly with ($q_{24}$=0.111) than without monogamy ($q_{12}$=0.001). However, from a condition of grooming with social monogamy, losses of either trait occur slightly faster than gains ($q_{42}$=0.113, $q_{43}$=0.170). Likewise, grooming with polygyny can be easily lost ($q_{31}$=0.181). Similar patterns are observed for huddling behaviours (Figure 5) with the difference that huddling evolves at similar rates with polygyny ($q_{13}$=0.003) and monogamy ($q_{24}$=0.005) but monogamy is far more likely to evolve when huddling is present ($q_{34}$=0.116) than when it is absent ($q_{12}$=0.003). Finally, a model combining both grooming and huddling behaviours shows a similar pattern of correlated evolution between these behaviours and social monogamy, with these care behaviours evolving before a socially monogamous mating system (Supplementary results).

Given that our results suggest that grooming and huddling, precede the evolution of social monogamy followed next by the evolution of carrying and provisioning, we also test the pattern of correlated evolution between the male care behaviours. We find that high-benefit (carrying and provisioning) and low-benefit (grooming and huddling) male care behaviours (Figure 6) are evolutionarily associated (BF=26.53). Low-benefit behaviours are more likely to evolve before high-benefit behaviours from a condition of the absence of both ($q_{12}$=0.003, $q_{13}$<0.001) and, crucially, high-benefit behaviours are more likely to evolve in the presence of low-benefit behaviours ($q_{24}$=0.062) than in their absence ($q_{12}$<0.001). Low-benefit male care alone is either lost ($q_{21}$=0.067), or high-benefit male care evolves next ($q_{24}$=0.062). When high and low-benefit behaviours occur in conjunction either can be lost at a similar rate ($q_{42}$=0.055, $q_{43}$=0.067), but they can both also be rapidly regained ($q_{24}$=0.062, $q_{34}$=0.067).

a)


q21
0.047
No carrying,
Polygyny
No carrying,
Monogamy
0.005
q12
q13
<0.001
q31
0.044
q24
0.005
q42
0.004
q43
0.021
Carrying,
Polygyny
Carrying,
Monogamy
0.026
q34

**b)**

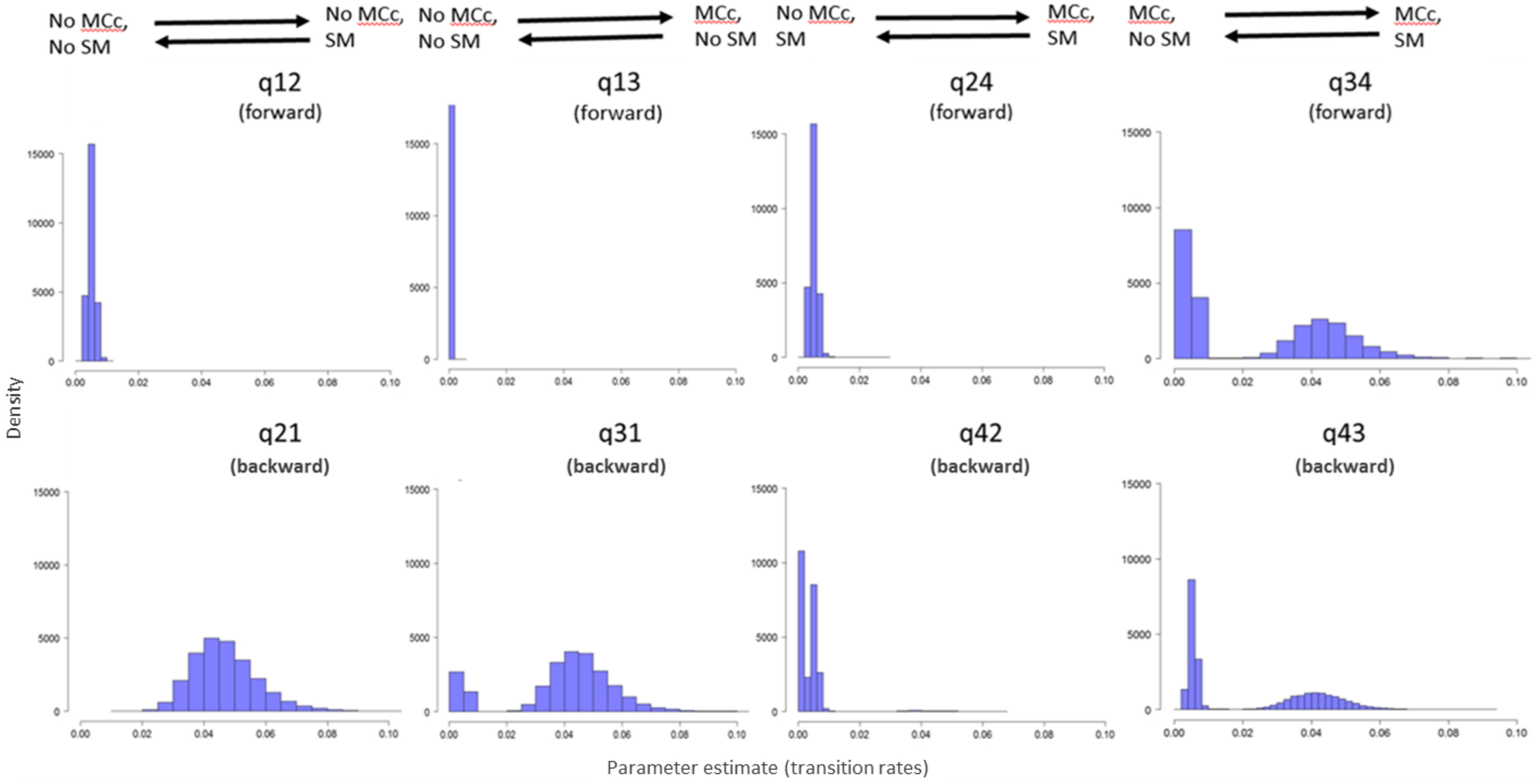
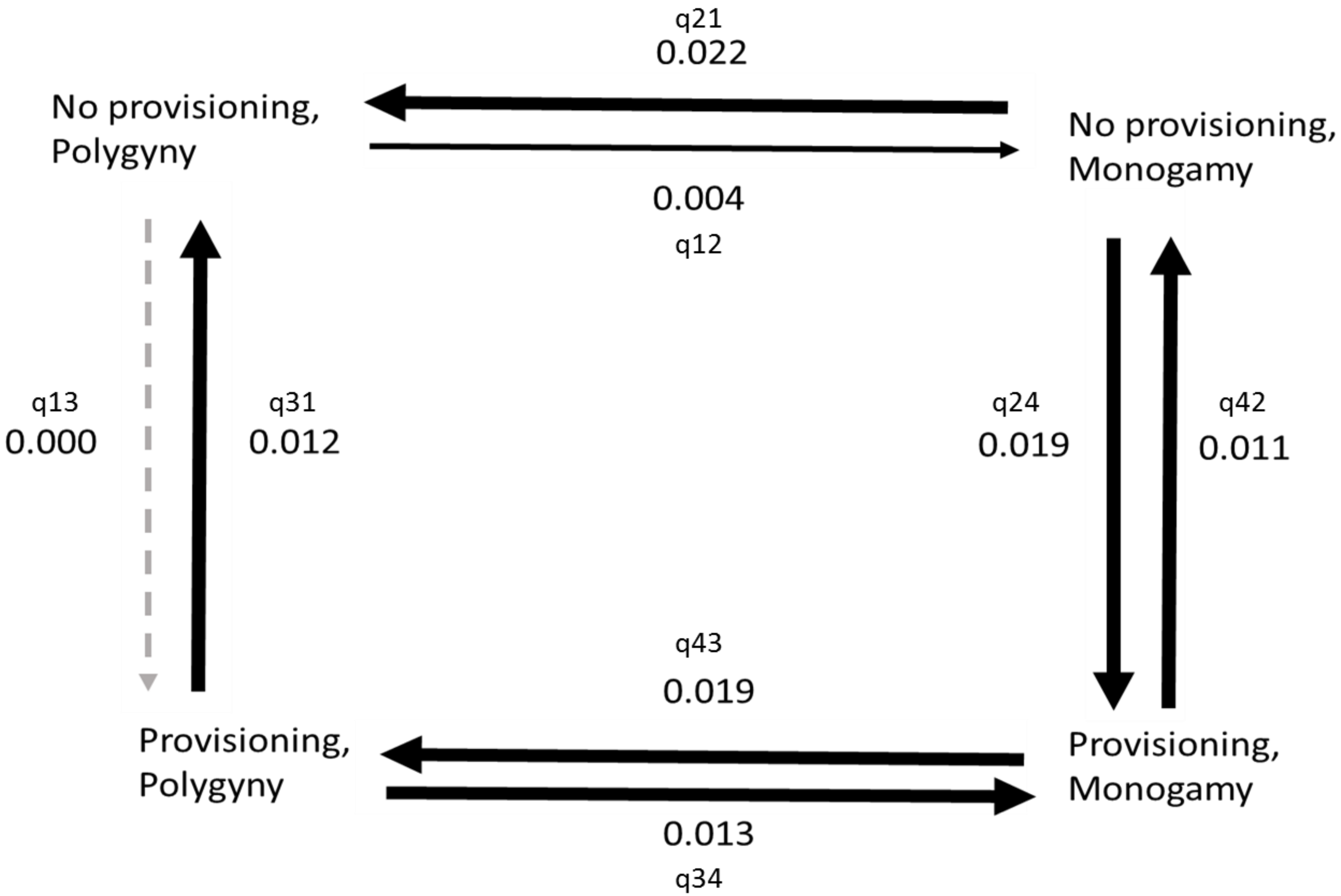


**Figure 2: The dependent model of evolution between male care (carrying) and social monogamy (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions, and dashed arrows representing unlikely transitions. The arrow labels represent the mean rate for each transition taken from the posterior distribution of the dependent model of evolution. MCc = carrying by males, SM = social monogamy.

**a)**


q21
0.022
No provisioning,
Polygyny
No provisioning,
Monogamy
0.004
q12
q13
0.000
q31
0.012
q24
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q42
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0.019
Provisioning,
Polygyny
Provisioning,
Monogamy
0.013
q34

**b)**

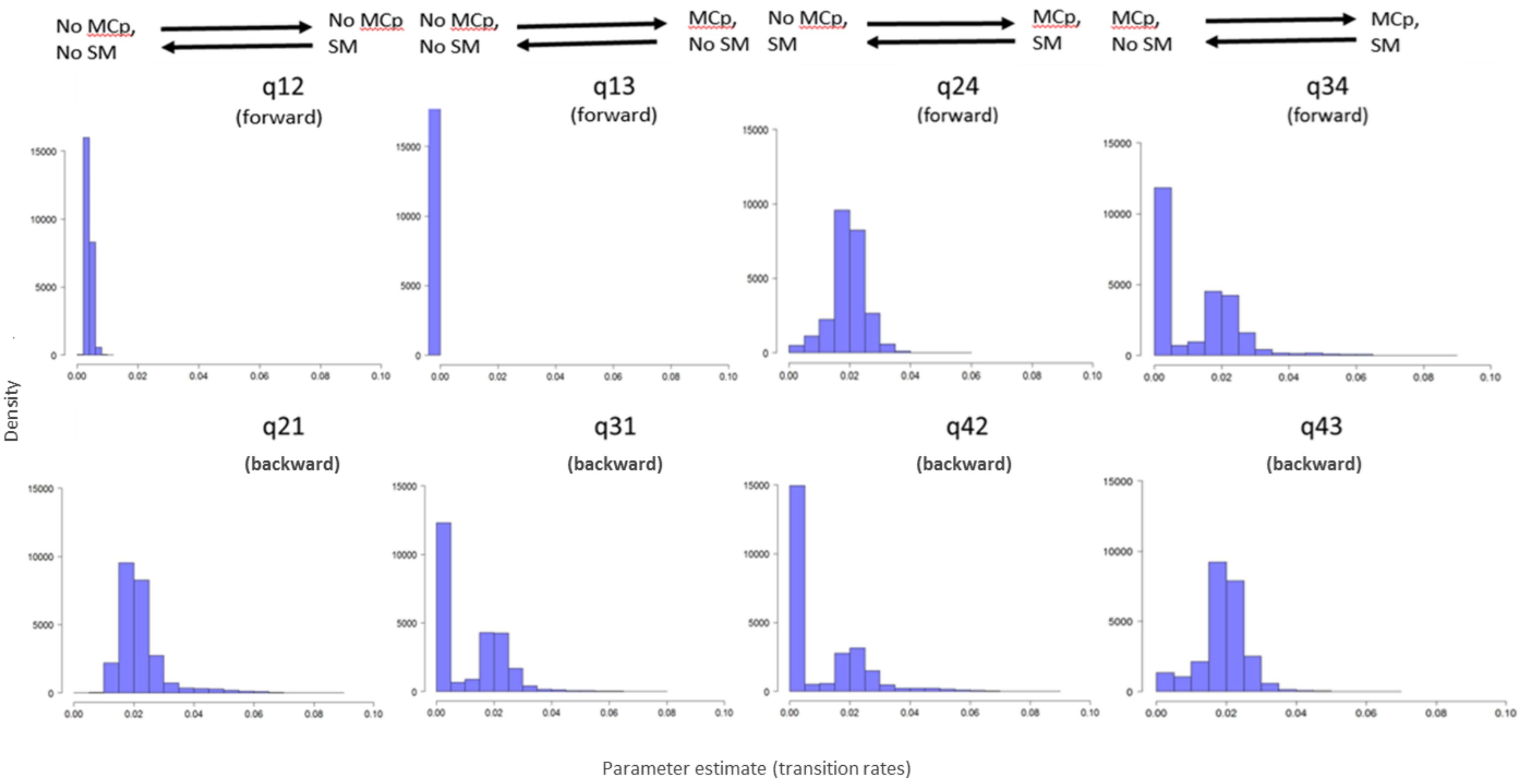
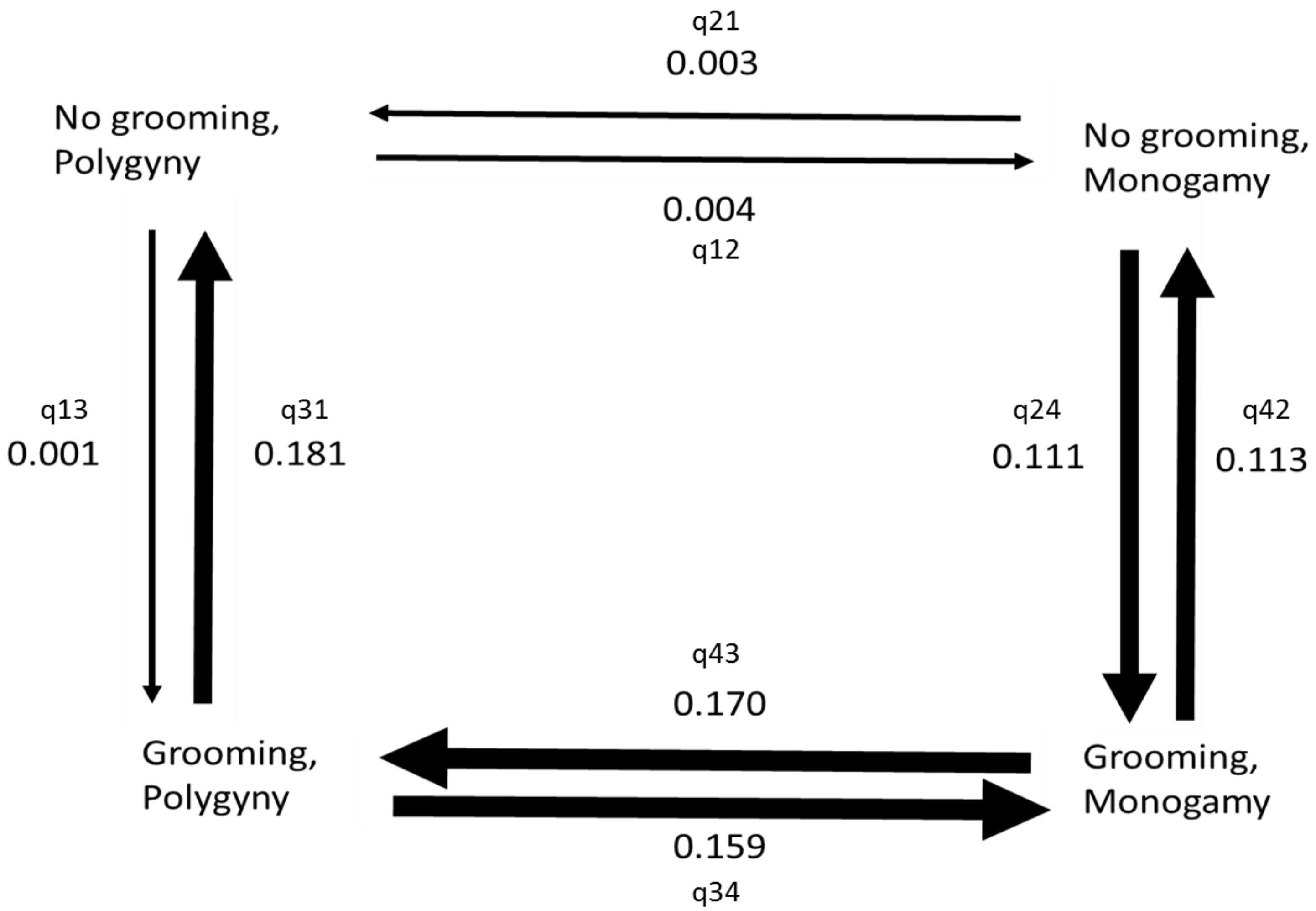


**Figure 3: The dependent model of evolution between male care (provisioning) and social monogamy (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions, and dashed arrows representing unlikely transitions. Greyed out transitions never occur within the model. The arrow labels represent the mean rate for each transition taken from the posterior distribution of the dependent model of evolution. MCp = provisioning by males, SM = social monogamy.

**a)**


q21
0.003
No grooming,
Polygyny
No grooming,
Monogamy
0.004
q12
q13
0.001
q31
0.181
q24
0.111
q42
0.113
q43
0.170
Grooming,
Polygyny
Grooming,
Monogamy
0.159
q34

**b)**

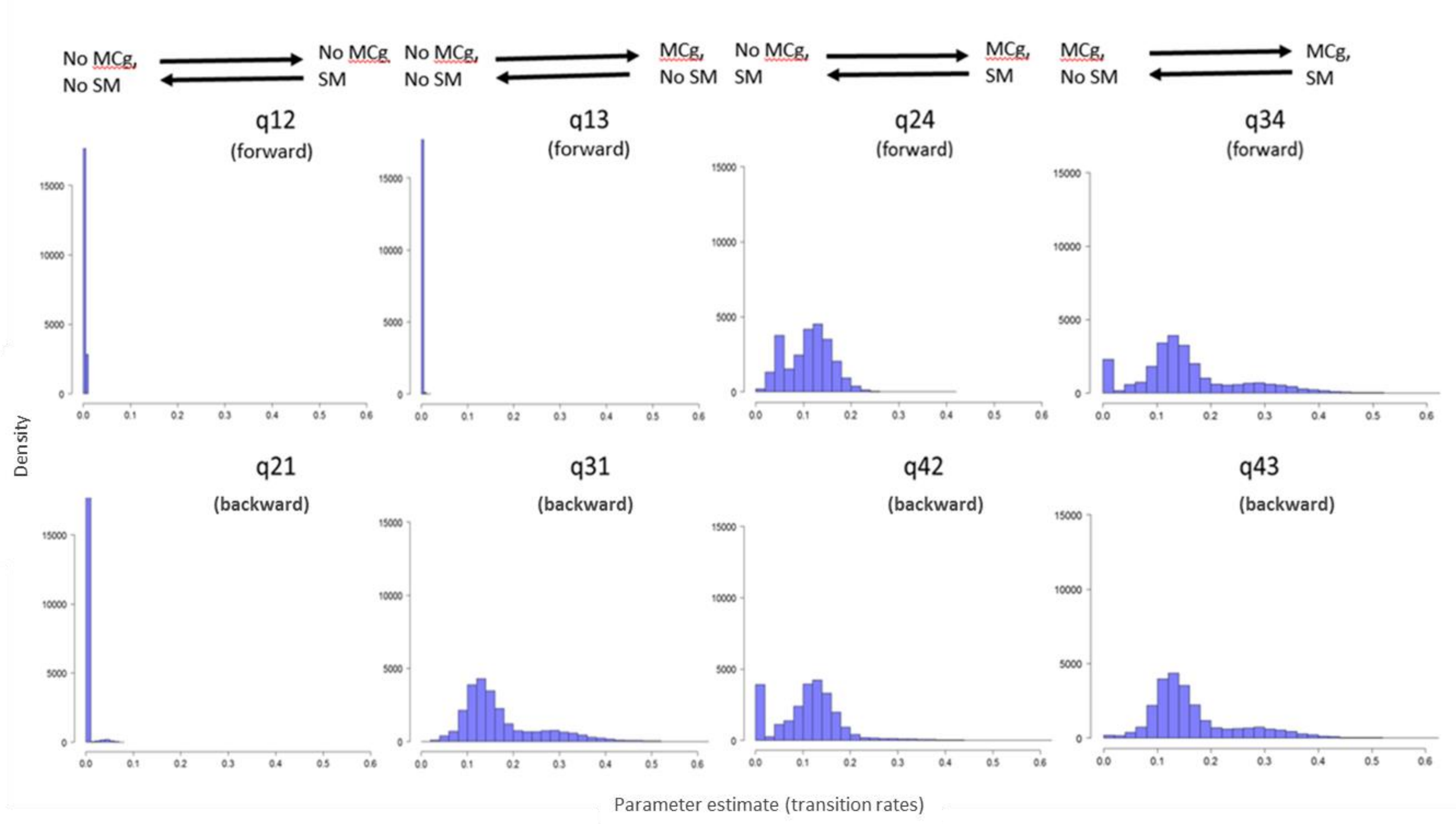
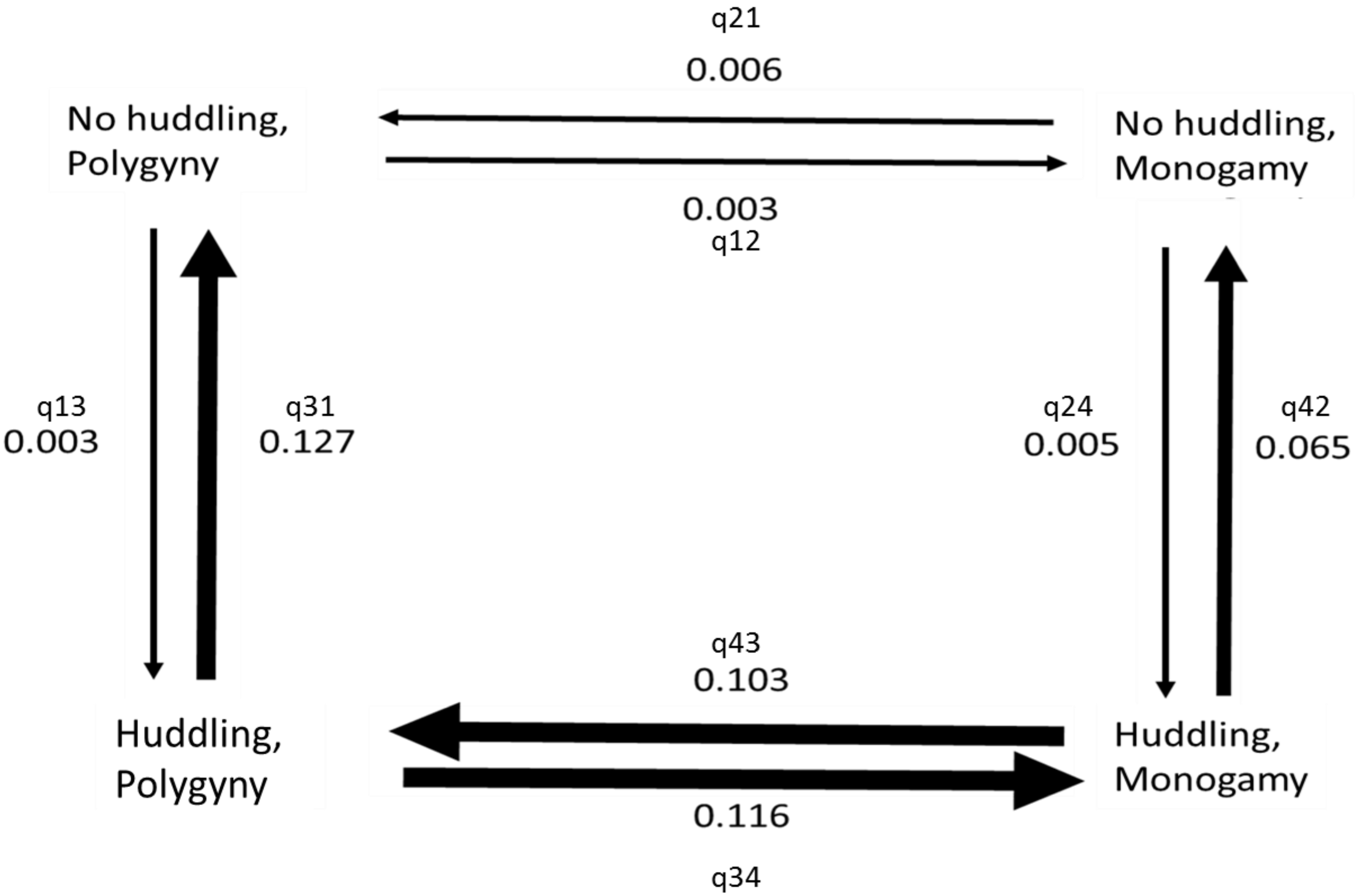


**Figure 4: The dependent model of evolution between male care (grooming) and social monogamy (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions, and dashed arrows representing unlikely transitions. The arrow labels represent the mean rate for each transition taken from the posterior distribution of the dependent model of evolution. MCg = grooming by males, SM = social monogamy.

**a)**


q21
0.006
No huddling,
Polygyny
No huddling,
Monogamy
0.003
q12
q13
0.003
q31
0.127
q24
0.005
q42
0.065
q43
0.103
Huddling,
Polygyny
Huddling,
Monogamy
0.116
q34

**b)**

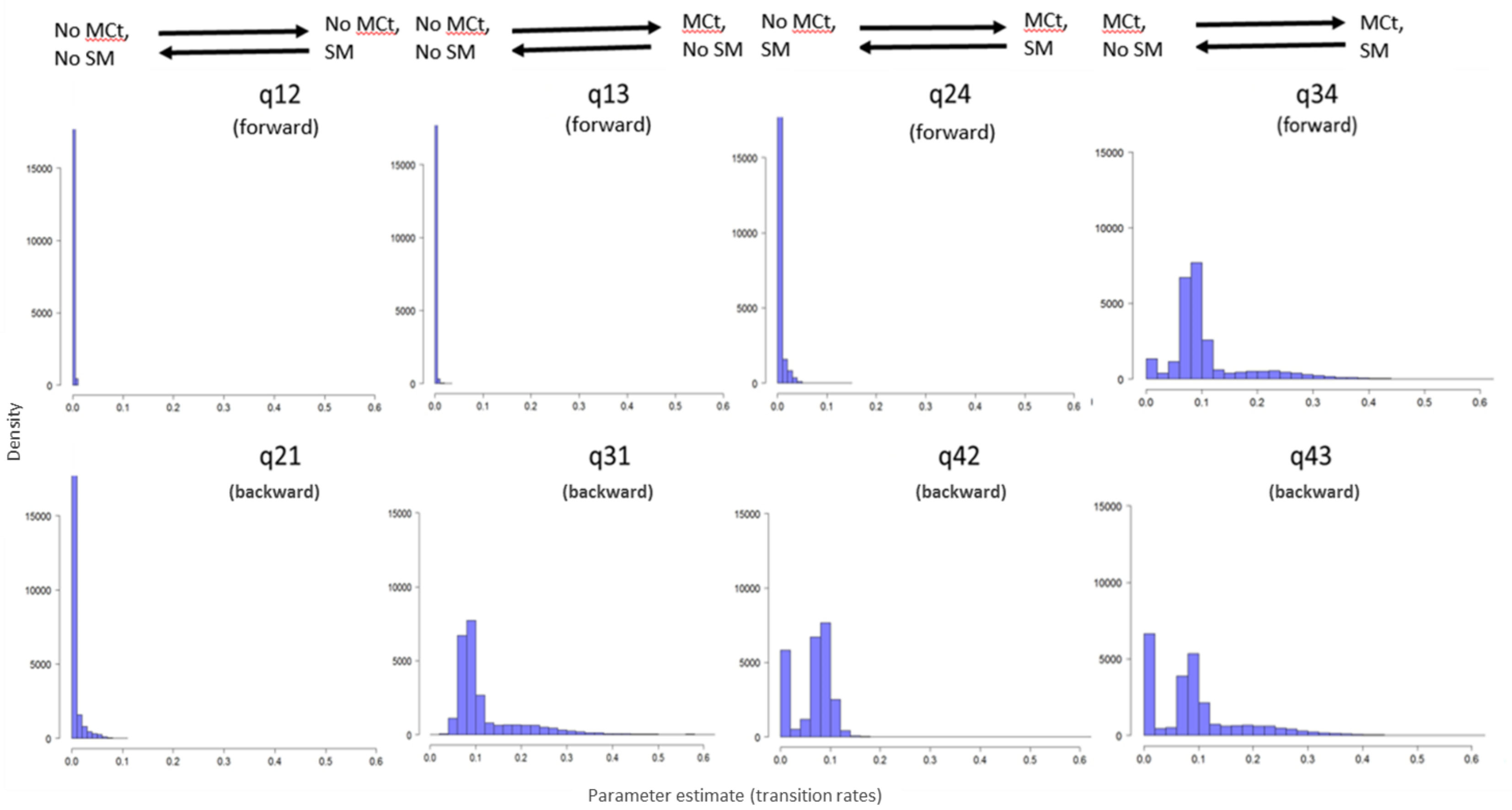
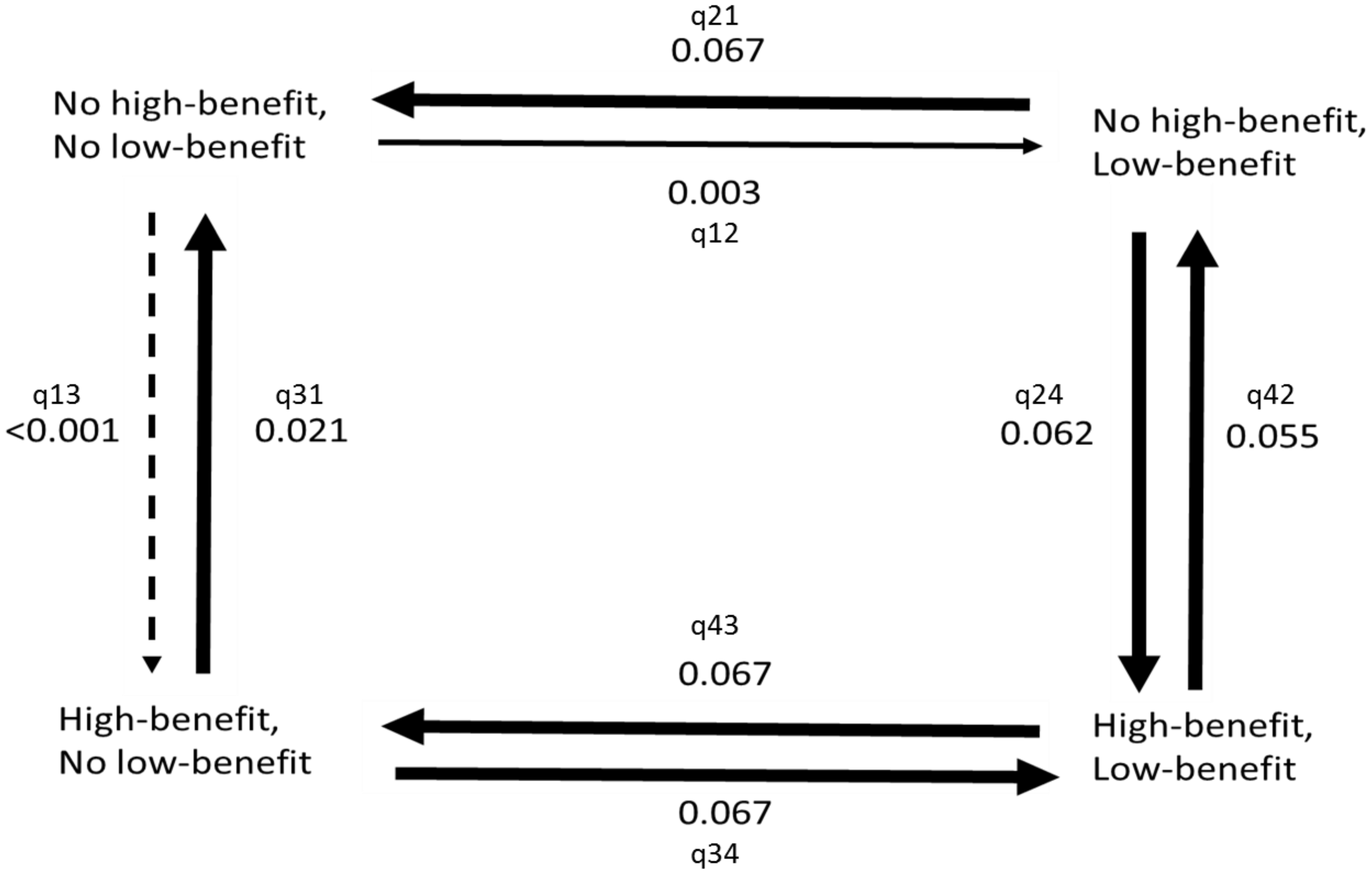


**Figure 5: The dependent model of evolution between male care (huddling) and social monogamy (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions, and dashed arrows representing unlikely transitions. The arrow labels represent the mean rate for each transition taken from the posterior distribution of the dependent model of evolution. MCt = huddling by males, SM = social monogamy.

**a)**


q21
0.067
No high-benefit,
No low-benefit
No high-benefit,
Low-benefit
0.003
q12
q13
<0.001
q31
0.021
q24
0.062
q42
0.055
q43
0.067
High-benefit,
No low-benefit
High-benefit,
Low-benefit
0.067
q34

**b)**

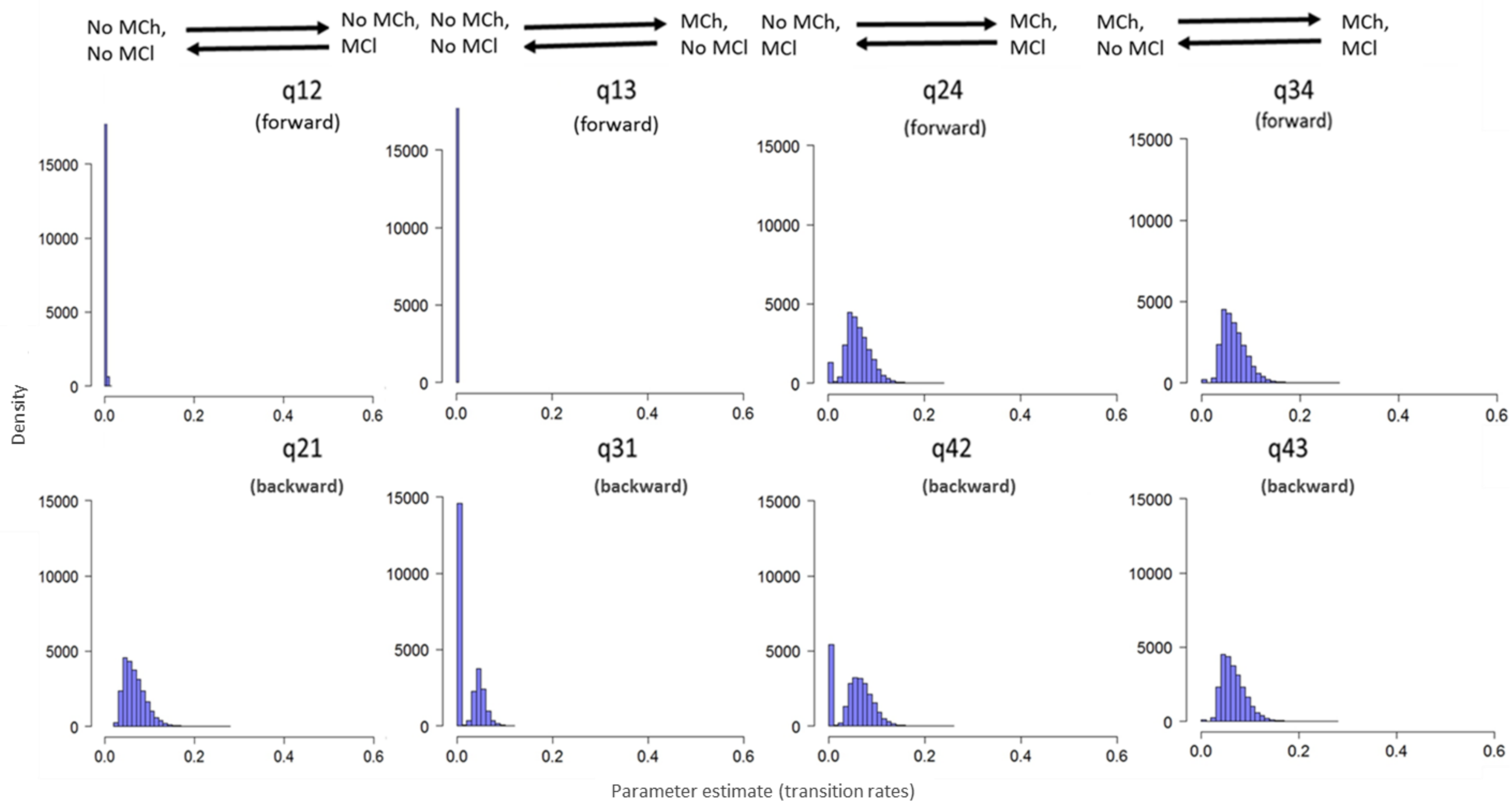


**Figure 6: The dependent model of evolution between high-benefit and low-benefit male care (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions, and dashed arrows representing unlikely transitions. The arrow labels represent the mean rate for each transition taken from the posterior distribution of the dependent model of evolution. MCh = high-benefit care behaviours (carrying and provisioning), MCl = low-benefit male care (grooming and huddling).

## Discussion

While the relationship between biparental care and social monogamy has been previously investigated (Lukas & Clutton-Brock 2013; Opie et al. 2013), little consideration has been given to the specific behaviours that make up ‘male care’. Here we show that different care behaviours associate with social monogamy in markedly different ways. Carrying and provisioning, behaviours that bring substantial fitness benefits to both parents (West & Capellini 2016) and are considered more costly to perform (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012), follow the evolution of a social monogamy. Conversely, grooming and huddling, which are considered less costly (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012), are unrelated to female fecundity, but are probably important for offspring survival (West & Capellini 2016; Gubernick & Teferi 2000; Wright 2006; Wynne-Edwards & Lisk 1989), both follow and precede the evolution of a monogamy. These results, together with our findings that low-benefit behaviours facilitate the evolution of high-benefit behaviours, suggest a two-step process, in which low-benefit behaviours promote the evolution of social monogamy and in turn the evolution of high-benefit male care behaviours.

The pattern of correlated evolution between social monogamy and male care differs across forms of male care, with low-benefit behaviours more likely to facilitate the evolution of social monogamy which in turn precedes the evolution of high-benefit behaviours. The differences in the energetic and opportunity costs and benefits among care behaviours may provide a potential explanation for their diverse relationship with social monogamy. Specifically, if carrying and provisioning are more costly than other care behaviours, such as huddling and grooming, as some assume (Isler & van Schaik 2012; Lukas & Clutton-Brock 2013), their costs may explain why these behaviours only evolve in the presence of monogamy as males should only invest heavily in parental care if their certainty of paternity is high (Trivers 1972). In chapter 2 we demonstrate that social monogamy associates with an increased certainty of paternity, which may potentially compensate for the costs the more energetically expensive carrying and provisioning male care and promote the evolution of further male investment through such behaviours. Furthermore, once evolved carrying and provisioning are associated with greater female fecundity (Chapter 3; West & Capellini 2016), which should be particularly important in monogamous species. Monogamous mammals are typically solitary or pair-living (Lukas & Clutton-Brock 2013). Therefore, monogamous males that remain with the female and her offspring achieve a higher certainty of paternity (Chapter 2), but are far less likely to gain extra-pair matings. If carrying and provisioning behaviours allow females to increase their reproductive output (West & Capellini 2016), these behaviours, and their associated benefits, should be under strong selection particularly in monogamous species where males are likely to sire fewer offspring per reproductive season in total than in polygynous species. Conversely, grooming and huddling behaviours provide no substantial fecundity benefits (West & Capellini 2016), and should be under less intense selection to evolve with monogamy. In other taxa, a similar relationship between a scarcity of mating opportunities or high mate fidelity leading to high genetic monogamy, and male care behaviours in turn increasing female fecundity may also occur, however because social monogamy may not be indicative of genetic monogamy, the relationship between male care and mating system may differ. In support of this idea, studies in birds and insects identify fecundity benefits associated with male care (Jenkins et al. 2000; Wolf et al. 1991), and suggest that biparental care evolves when mating opportunities are scarce in these and other groups (Gilbert & Manica 2015; Remeš et al. 2015; Gonzalez-Voyer et al. 2008). However, no study to date have identified the specific care behaviours associated with increased fecundity in these taxa, or investigated the evolutionary feedbacks between male care, paternity and mating systems.

The evolutionary relationship between social monogamy and grooming and huddling is more dynamic; both male care and monogamy can evolve first, but social monogamy evolves more readily in the presence of grooming and huddling than in their absence. A more dynamic pattern of correlated evolution between male care and mating system is not surprising when the relative costs and benefits of huddling and grooming behaviours, compared to carrying and provisioning, are considered. Grooming and huddling behaviours are generally thought to be less costly than other care behaviours such as provisioning and carrying the offspring (Isler & van Schaik 2012; Lukas & Clutton-Brock 2013). If this assumption is generally correct, a male should lose less if he directs these behaviours towards offspring that are not his own. In support of this suggestion, recent a meta-analysis across mammals, birds, fish, and insects, shows that, unless parental care is very costly as measured through an associated reduction in a male's future reproductive success, males will care for unrelated offspring even when cuckolded (Griffin et al. 2013). In mammals, as well as other groups, little research has directly investigated the energetic costs of different care behaviours, but a few studies in rodents and one in dwarf lemurs (*Cheirogaleus medius*) do demonstrate substantial costs to grooming and huddling behaviours (Townsend 1986; Campbell et al. 2009; Fietz & Dausmann 2003; Saltzman et al. 2015). Whether costs of grooming and huddling are generally high in other species, rather than being particularly expensive only in the few currently studied taxa, remains to be established. Furthermore, the fundamental and still unanswered issue is whether the energetic costs of huddling and grooming are fewer than or similar to those of other care behaviours, such as carrying and provisioning.  Finally, although we find very limited evidence that grooming and huddling associate with life history traits in mammals (Chapter 3; West & Capellini 2016), these behaviours can substantially improve offspring survival in at least some species (Wynne-Edwards & Lisk 1989; Gubernick et al. 1993; Schradin 2004). This effect seems to be particularly evident in harsh environments (Wynne-Edwards & Lisk 1989), implying that grooming and huddling may be more likely to evolve in less favourable environments, a hypothesis that remains to be tested.

While social monogamy evolves more readily in the presence of low-benefit male care behaviours, biparental care is unlikely to be the sole driver for the evolution of this mating system. Among amphibians, for example, both biparental care and monogamy appear to occur in response to environmental stochasticity, with both behaviours being present in species that occupy ephemeral water bodies (Brown et al. 2010). A recent large scale study in mammals instead finds that social monogamy is favoured when females are solitary and sparsely distributed, such that males cannot defend multiple females simultaneously (Lukas & Clutton-Brock 2013). Among primates, however, the main driver of monogamy appears to be the defence of the offspring against infanticidal conspecifics (Opie et al. 2013), although this is subject to debate (Opie et al. 2014; Lukas & Clutton-Brock 2014). Thus, the evolution of social monogamy in mammals is likely promoted by a combination of social and environmental factors, including certain male care behaviours that help increase offspring survival, such as grooming and huddling. Whether biparental care, and its benefits for offspring survival, play a similar role in the evolution of social monogamy in other groups is unclear however. Although several studies in birds propose that increased survival benefits for the offspring may be a key driver for the evolution of biparental care in this group (Burley & Johnson 2002; Reichard & Boesch 2003), and certain studies do demonstrate a positive relationship between male care and offspring survival (Townsend et al. 1984; Wolf et al. 1988; Markman et al. 1996; Gubernick et al. 1993; Gubernick & Teferi 2000; Wright 2006), the directionality of this relationship remains uncertain.

Similarly, the initial evolution of male parental care behaviours is unlikely to be driven by one single factor. In many groups, including insects, fish, and birds, biparental care appears to evolve when additional mating opportunities for the male are limited (Gilbert & Manica 2015; Remeš et al. 2015; Gonzalez-Voyer et al. 2008). In mammals, a solitary social system, and potentially fewer mating opportunities, appears to favour the evolution of social monogamy (Lukas & Clutton-Brock 2013), and subsequently – through an increased certainty of paternity - carrying and provisioning by males (Chapter 2 and here). Grooming and huddling behaviours, which precede the evolution of both monogamy and high-benefit care behaviours (carrying and provisioning), appear to have different evolutionary drivers. Selection is proposed to favour parental care when offspring survival is low in the absence of care (Klug et al. 2012). Support for this prediction can be found in a number of species; in sun skinks (*Eutropis longicaudata*) for example, a species that usually provides no parental care, high predation risk by egg-eating snakes (*Oligodon formosanus*) can drive the evolution of nest guarding by females (Pike et al. 2016). In mammals, aridity can promote the evolution of alloparental care by non-breeding helpers in cooperatively breeding species (Lukas & Clutton-brock 2017). Although this latter study does not differentiate between different care behaviours it suggests that additional care in mammals may occur in response to high levels of environmental harshness. Regarding grooming and huddling experimental studies in a range of rodent species show that these behaviours have a strong positive effect on offspring survival in cold conditions (Wynne-Edwards & Lisk 1989; Gubernick et al. 1993; Schradin 2004), which may explain why we find that these behaviours precede the evolution of social monogamy. Huddling for thermoregulatory purposes may be vital in species with highly altricial offspring, where the presence of a second parent is key for keeping the offspring warm while the other parent is away from the nest. Alternatively, altriciality may represent a female strategy to induce males to care, in a similar way to female birds producing brightly coloured eggs that induce male brooding (Hanley et al. 2010).

In conclusion, we find strong evidence for a two-step process of evolution when considering the relationship between social monogamy and male care. Grooming and huddling help to promote the evolution of social monogamy in mammals, possibly by improving offspring survival under unfavourable environmental conditions. Social monogamy then provides a higher certainty of paternity for males (Chapter 2), facilitating further male investment in more costly care behaviours – carrying and provisioning – which in turn increase female fecundity (Chapter 3; West & Capellini 2016) that further helps to outweigh the costs of monogamy. This study is thus the first to unravel evolutionary feedbacks by considering the diversity of care behaviours males express and highlights the importance of considering the diversity of a behavioural or phenotypic trait when investigating patterns of correlated evolution. A similar approach to the one used here can thus be invaluable in evolutionary biology where we observe diversity in phenotypes that may help unravel positive or negative feedbacks, such as evolutionary arms races or other competitive situations. For example, various components of placental morphology are known to influence offspring growth and levels of female investment (Capellini et al. 2011) which may reflect a combination of both cooperation and conflict between mother and offspring. However, no study has considered the whole diversity in placental structure and female investment to identify the directionality of evolutionary relationships between these traits. Likewise, the complexity of male and female reproductive organs, as observed in waterfowl (Brennan et al. 2007) and water striders (Fairbairn et al. 2003) for example, can unravel complex negative feedbacks in species with intense sexual conflict. Thus, by considering individual aspects of complex traits, rather than relying on the commonly used approach of clustering characteristics, we can identify where in an evolutionary pathway specific relationships occur, and how they individually relate to evolutionary processes.

# CHAPTER 5: ENERGETIC CONTRIBUTIONS BY MALES, NOT INFANTICIDE RISK, ASSOCIATE WITH A SHORTER LACTATION IN MAMMALS

**Authors:** Hannah E. R. West and Isabella Capellini

**Author Contributions**: IC and HW designed the research and data collection protocols; HW collected the data, conducted the analyses, and drafted the manuscript; IC and HW revised the draft.

## Abstract

The limitations on an organism's time and energy lead to a wide diversity of life history strategies to allow individuals to maximise their lifetime fitness. Behaviour, particularly parental care, is inherently linked to the trade-offs that are key to the evolution of life history traits. Male parental care promotes offspring survival and fitness in many species and is associated with greater female fecundity. In mammals, the shorter duration of lactation in species where males carry the offspring and provision the mother supports the hypothesis that males may provide an energetic contribution towards offspring rearing during the most expensive period of female reproduction. However, an alternative hypothesis suggests that a shorter lactation evolves as a counter strategy against infanticide by males to limit the period of greater offspring vulnerability. We test these alternative hypotheses using phylogenetic comparative methods and a sample of over 400 mammalian species. We show that a shorter lactation is specific to species with male care, which allows females to reduce their lactation irrespective of gestation. We find no evidence that a short lactation (relative to gestation) is linked to infanticide risk; there is no direct association, and correlated evolution models show that male care and infanticide are mutually exclusive and are rarely present in the same species. Thus, these results support the hypothesis that male care helps females meet the high

energetic costs of lactation, and provide no evidence that infanticide risk shapes the life history strategy of mammal species or promotes the evolution of care by males.

## Introduction

Because organisms have a limited amount of time and energy to invest in reproduction, life history theory explains the diversity of life history strategies in nature as trade-offs that maximise individual fitness given the mortality rates of adults and juveniles (Edward & Chapman 2011). Behaviour is one potential evolutionary driver of the diversity in life history strategies among species as it can help resolve or alter these trade-offs (Trivers 1972; Andersson 1994). In this context, parental care is particularly relevant because it directly relates to reproductive investment (Royle et al. 2012). Female or male parental care is generally present in species in which females invest more resources into the offspring, such as larger eggs (Summers et al. 2006; Kolm & Ahnesjö 2005), leading to greater offspring survival (Clutton-Brock 1991; Shine 1978; Gross & Sargent 1985; Townsend et al. 1984). Additional alloparents that help raise the offspring, including the male, may also provide an energetic contribution towards female reproductive costs (‘load-lightening’ effect: Crick 1992; Isler & van Schaik 2012), which may in turn shorten the duration of maternal investment (West & Capellini 2016), allow females to speed up reproduction (Woxvold & Magrath 2005; Blackmore & Heinsohn 2007; West & Capellini 2016), or increase breeder’s survival (Cockburn et al. 2008; Koenig & Mumme 1987). Infanticide and egg cannibalism, instead, lie at the opposite end of the spectrum of behaviours towards the offspring (Ebensperger 1998; Paul et al. 2000) and are also potentially related to life history traits (Elgar & Crespi 1992). Infanticide should be advantageous to males if killing the offspring reduces the time needed for a female to resume reproduction (Ebensperger 1998; van Schaik 2000). Infanticide should however promote the evolution of counterstrategies, such as male care as protection against rival infanticidal males and shorter period of offspring dependency to limit offspring vulnerability (van Schaik 2000; Opie et al. 2013; Ebensperger 1998), and thus influence the trajectory of life history evolution. No study to date, however, has considered simultaneously how drastically different behaviours such as male care and infanticide relate to life history evolution, despite the fact that these behaviours may select for similar evolutionary responses in similar life history traits. We address this question in mammals, an ideal model system as male care and infanticide are observed in several species.

The 'male energetic contribution' hypothesis proposes that caring males help females reduce the costs of reproduction by contributing towards offspring rearing and costly care behaviours (Crick 1992; West & Capellini 2016; Opie et al. 2013). Lactation is the most costly period of female reproduction in mammals, with the daily energy expenditure of lactating females being up to four times that of non-reproducing females (Speakman & McQueenie 1995). If males contribute to offspring care this could potentially reduce the costs of lactation for females (West & Capellini 2016) through a load-lightening mechanism (Crick 1992). Although male care in mammals is relatively rare, being present in about 10% of species, it is highly diverse. Males of some carnivore species bring food to pregnant or lactating females (Nowak 1999; Kleiman & Malcolm 1981), presumably allowing them to gain extra energy and possibly conserve the energy that they would have otherwise spent hunting or foraging. In many callitrichid primates males carry heavy offspring until weaning (Wright 1990), a behaviour that significantly reduces male body mass by the end of reproductive cycle and increases the male's risk of predation (Schradin & Anzenberger 2001). Finally, in some rodents males groom or huddle with the offspring (Nowak 1999), presumably allowing the female to spend more time foraging for herself (Woodroffe & Vincent 1994; Cantoni & Brown 1997). Each of these behaviours could potentially allow females to either save or build up energy reserves that can then be (re)invested in producing a greater quantity of and/or more nutritious milk. As a result, females may wean the offspring earlier in species with care by males. In support of this mechanism, we previously found that lactation time is shorter, breeding frequency is higher, offspring growth rates are greater, and litter sizes are larger in mammals in which males carry the offspring and provision lactating females, but huddling and grooming are unrelated to female reproductive investment (West & Capellini 2016). Moreover, we found that no male care behaviours are related to gestation time, suggesting that male load lightening is limited to the most expensive period of female reproduction (West & Capellini 2016).

A still untested prediction of the male energetic contribution hypothesis is that the well-documented evolutionary association between lactation and gestation times across mammals should be weakened in species with male care. Mammalian life history traits covary along a slow fast continuum, also known as the 'pace of life' (Bielby et al. 2007; Harvey & Clutton-Brock 1985; Read & Harvey 1989). Thus, lactation time is longer in species with longer gestation, even after accounting for allometric effects (Bielby et al. 2007; Harvey & Clutton-Brock 1985). Therefore, if male care helps females meet the energetic costs of lactation, lactation and gestation time should be either unrelated, or more weakly but still positively correlated in species with male care than in species without male care, after accounting for allometry (Figure 1a).

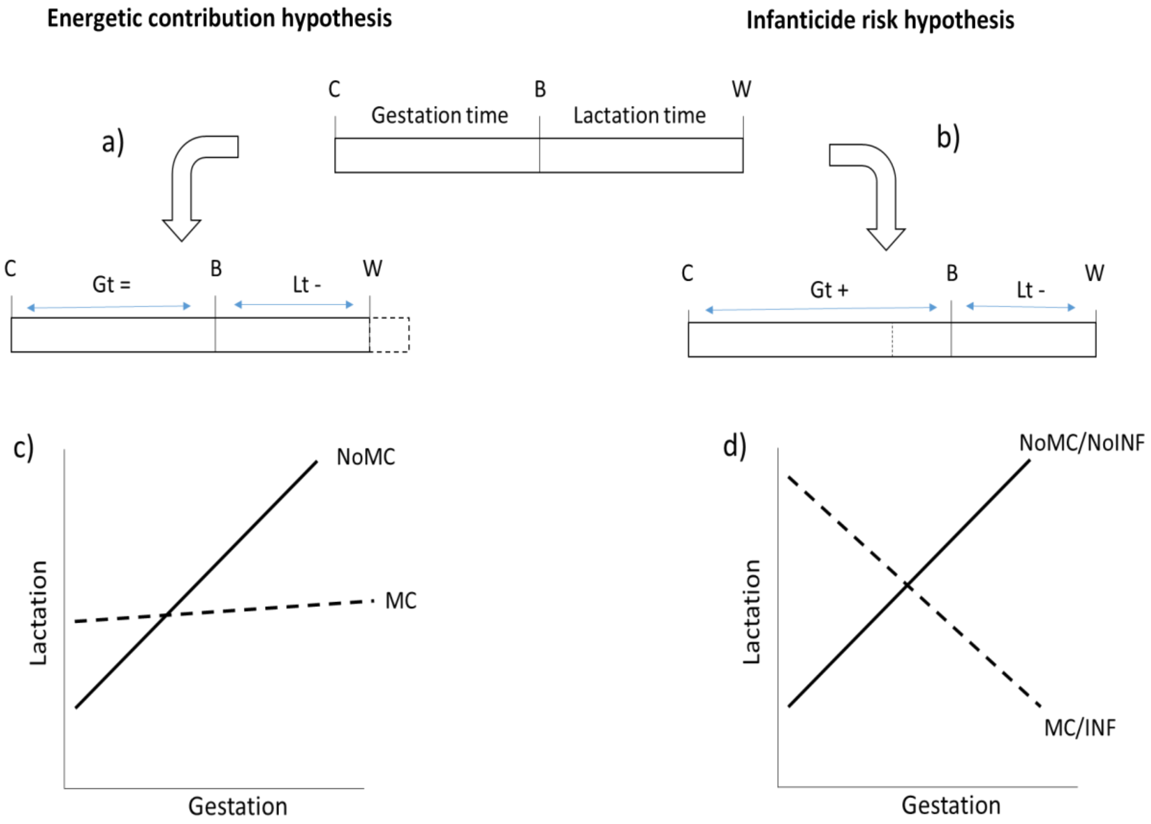


**Figure 1: The predictions of the male energetic contribution hypothesis (a&c), and the infanticide risk hypothesis (b&d)**. Under the male energetic contribution hypothesis (a), lactation time (LT) is reduced but gestation time (GT) is unaltered, leading to a weaker association across species between the durations of gestation and lactation in species with male care than in species with infanticide, after allometry is accounted for (c). Under the infanticide risk hypothesis, lactation time is reduced while gestation time increases (b) leading to a negative association between relative gestation and lactation times in species with male care and infanticide, after accounting for allometry (d). In (a) and (b) events are indicated as follows: C= conception, B=birth, W=weaning; GT= gestation time; LT= lactation time. A '+' indicates an increase in the duration of a given period, while a '-' indicates a reduction, and an '=' indicates no change. In (c) and (d) the statistical predictions regarding the direction of the association between gestation and lactation times derived from the two hypotheses. The expected direction for the association between lactation and gestation times in species with male care (MC) or infanticide (INF) are indicated by the dotted line, and in species without male care (NoMC) and without infanticide (NoINF) in continuous line.

Infanticide is also predicted to influence the evolution of female reproductive strategies and life history traits, as well as promote the evolution of male care (van Schaik 2000; Paul et al. 2000; Opie et al. 2013). Males may commit infanticide in species where the loss of a current litter induces a rapid return to oestrus in the mother (van Schaik 2000; Ebensperger 1998). Therefore, killing unrelated offspring can lead to significant benefits for the infanticidal male, if he can subsequently mate with the female that has lost her offspring (van Schaik 2000), as in lions (*Pantheria leo*) (Pusey & Packer 1994a) and hanuman langurs (*Presbytis entellus*) (Sommer 1994). Lactation is the period during which the offspring are smaller and most vulnerable to infanticidal attacks, as well as still being heavily dependent on the mother (van Schaik 2000; Opie et al. 2013). For example, neonates and very young offspring of hanuman langurs and red howler monkeys (*Alouatta seniculus*) are much more likely to die in an infanticidal attack than older individuals closer to weaning age (Sommer 1994; Crockett & Sekulic 1984). The 'infanticide risk’ hypothesis proposes that a high risk of infanticide should (i) promote the evolution of male care so that the father can better protect his own offspring from rival males (Paul et al. 2000; Agrell et al. 1998; Dunbar & van Schaik 1990), and (ii) select for shorter lactation time and an extended gestation that results in more precocial, less vulnerable offspring, to reduce the period of offspring vulnerability to infanticide (van Schaik 2000; Opie et al. 2013) (Figure 1b). Therefore, infanticide risk should lead to the evolution of two separate, sex-specific evolutionary responses. Under this scenario, the documented association between male care and a short lactation across species (West & Capellini 2016) may reflect instead the association of each of them with infanticide risk. Support for the infanticide risk hypothesis is found particularly within primates where infanticide appears to occur in species with long lactation for their gestation time (van Schaik 2000), and where species with male care have a shorter weaning proportion - the ratio of the duration of lactation to that of gestation (Opie et al. 2013). However, a recent comparative study across mammals (Lukas & Huchard 2014) finds no evidence that weaning proportion is shorter in species where infanticide by males occurs. No study to date, however, has tested directly the predictions of this hypothesis (Figure 1b & d) that (i) gestation time increases proportionally to a reduction in lactation time in species with male care and in species with high infanticide risk, and that (ii) infanticide risk is evolutionarily associated with and precedes the evolution of male care.

Here we test the markedly different predictions of the energetic contribution hypothesis and the infanticide risk hypothesis with regards to the association between male care, infanticide risk and female life history traits. The male energetic contribution hypothesis predicts that species with male care have a shorter lactation time, irrespective of the duration of gestation (Figure 1a). Therefore, we expect either a weaker positive or a non-significant relationship between lactation and gestation in species with male care, after accounting for allometric effects (Figure 1c). In contrast, the infanticide risk hypothesis predicts that species with high rates of infanticide extend gestation and reduce lactation (Figure 1b), and so the durations of lactation and gestation are proportionally negatively associated with one another among species with either male care or infanticide, after allometric effects have been accounted for (Figure 1d). Under the infanticide risk hypothesis the presence of infanticide should also be correlated with and precede the evolution of both male care, and precocial offspring. Because the infanticide risk hypothesis is believed to apply particularly to primates, we test these predictions both across all mammals and across primates only.

## Method

### Data collection

We extract life history data from available comprehensive datasets (Jones et al. 2009; Capellini et al. 2011; Silva & Downing 1995; Bielby et al. 2007; Barton & Capellini 2011) for the following variables; female adult body mass (g), lactation time (days), and gestation time (days). In total, our dataset contains 459 species for which we have data on all of these three variables. We also collect data on age at eye opening (days, n=409), which is used as a measure of precociality (Jones et al. 2009) and we convert into a discrete variable, with species with eyes open at birth classified as precocial and those which open the eyes after birth classified as altricial (Barton & Capellini 2011). All continuous data for the analyses are log-transformed in order to normalise their distribution. Male care, infanticide and precociality are coded as binary variables, with 1 representing the presence of the trait and 0 its absence.

We define male care as any care behaviour by a male towards dependent offspring, or towards a reproducing female (as this indirectly benefits the offspring). Because we previously show that lactation time is shorter and fecundity higher in species where the male either provisions the females, or carries the offspring, but not in species where the males huddles with or grooms the offspring (West & Capellini 2016), here we consider as evidence of male care only species where these behaviours are expressed and lead to high benefits; we call this variable 'Male Care (high)'. Therefore, in analyses using 'Male Care (high)', we class as having no male care species that only huddle, groom, or provision the offspring. However, results are qualitatively similar to those presented here if we instead consider as having male care any species in which males exhibit any care behaviour (carrying, provisioning the female, provisioning the offspring, huddling with and grooming), a variable we call 'Male care (all)' (West & Capellini 2016). Following previous studies (Woodroffe & Vincent 1994; Lukas & Clutton-Brock 2013; Opie et al. 2013; Isler & van Schaik 2012) we exclude male defence of the offspring from our definition of male care as it is difficult to reliably quantify whether defence is specifically aimed at protecting the offspring or whether offspring protection is a side effect of male territorial defence. While males defending a territory may have indirect benefits for his dependent offspring, especially keeping infanticidal conspecifics away from the offspring (reviewed in: Ebensperger 1998; Paul et al. 2000), territorial males in other species, such as in red howler monkeys (*Alouatta seniculus*) and sifakas (*Propithecus diadema*) (Izawa & Lozano 1991; Wright 1995), may make little to no active offspring defence against an infanticidal attack. Data on male care behaviours are extracted from the primary literature and are available from West & Capellini (West & Capellini 2016). Of the species for which life history traits are available (gestation, lactation, female mass; n=459), 25 species exhibit either carrying or provisioning behaviours (male care (high)), of which 12 provision the female and 14 carry the offspring. A further 23 species either provision only the offspring (n=8), or groom (n=14) or huddle (n=12) with the offspring, which are only included in our 'male care (all)' analyses. Note that some species exhibit more than one male care behaviour. As a result, the sample size of 'Male care (high)' is 25 species and 'Male care (all)' is (n=48) species.

Data on the presence of infanticide by males are extracted from (Lukas & Huchard 2014) and supplemented with data from a range of primary and secondary sources (van Schaik 2000; Cížková et al. 2011; Wilson et al. 1993; Arvola et al. 1962; Semb-Johansson et al. 1979; Hiraiwa-Hasegawa & Hasegawa 1994; Ebensperger & Blumstein 2007; Blumstein 2000; Ebensperger 1998) following Lukas & Huchard's (2014) protocol. Specifically, we include in our dataset only species for which observations on females and juveniles in wild populations are available over three or more reproductive seasons, and classify species as exhibiting infanticide if at least one observation of infanticide is reported and the killer can be unambiguously identified. Non-infanticidal species are those for which no occurrence of infanticide is reported in wild populations over three or more reproductive seasons. Altogether infanticide data are available for 197 species, of which 84 exhibit male infanticide and 113 have no reported instances of infanticide according to the criteria here defined.

### Statistical analysis

We test whether the evolutionary association between lactation and gestation times varies in species with and without male care or infanticide, after accounting for allometry, using phylogenetic least squares (PGLS) models that account for species' shared ancestry and quantify the strength of the phylogenetic signal in the data (Freckleton et al. 2002; Pagel 1999). We build PGLS models using the R package 'caper' (Orme 2013) and a comprehensive mammalian phylogeny (Fritz & Purvis 2010). Model parameters are estimated in maximum likelihood, and the parameter lambda (λ) quantifies the magnitude of phylogenetic signal in the model residuals (Revell 2010; Freckleton et al. 2002). λ varies between 0 and 1, with 0 representing no phylogenetic signal, and with 1 indicating that species similarity is directly proportional to the time of shared evolutionary history as expected under a Brownian motion model of evolution (Freckleton et al. 2002; Pagel 1999). For all PGLS analyses, polytomies in the phylogeny are randomly resolved and assigned a 0 value for any resolved branch length, and so treated as soft polytomies.

Lactation is the dependent variable in all PGLS models, male care or infanticide are independent binary variables, female body mass is the covariate to account for allometric effects. In these models we also include gestation time and the interaction terms between both categorical variables (male care and infanticide) and gestation time to investigate how lactation time and gestation time relate to one another as predicted by the male energetic contribution hypothesis and the infanticide risk hypothesis (Figure 1). The inclusion of the interaction term in the model allows us to fit separate lines for the relationship between lactation and gestation time for each level of the categorical variable (presence/absence of male care or infanticide) (Crawley 2007; Dalgaard 2002). A significant interaction between a categorical variable and continuous variable therefore indicates a significant difference in model slopes. Thus, under the male energetic contribution hypothesis we expect that the slope of the group of species with male care, modelled by the interaction term, is positive but weaker than that of the group of species without male care (Figure 1c). Under the infanticide risk hypothesis the slope of species with either male care or infanticide should be negative, and the slope of species without these behaviours should be positive (Figure 1d). Finally, we assess the fit to the data of alternative nested models, with or without the interaction term, using the likelihood ratio (LR) test with degrees of freedom (Quinn & Keough 2002).

We use Pagel's method of correlated evolution between binary traits (Pagel 1994; Pagel 1999) to investigate the correlated evolution between male care and infanticide, and infanticide and precociality. This approach relies on a continuous time Markov model to estimate the instantaneous rate of change between the states (presence/absence) of binary traits along the branches of a tree (Pagel 1994; Pagel 1999). Only the infanticide risk hypothesis explicitly predicts a significant association between the variables here tested, and specifically that infanticide precedes the evolution of both male care and precociality. We first compare the fit to the data of two alternative evolutionary models (Figure 2), one where the two traits are allowed to evolve independently of one another, and one where they evolve in a correlated fashion (Pagel 1994; Pagel 1999). The independent model of evolution (Figure 2a) estimates two transition rates for each trait; α is the gain of a trait (from 0, absence, to 1, presence) and β the loss (from 1 to 0). The dependent model (Figure 2b) estimates eight possible transition rates (qij) by considering the four possible combinations of character states of the two discrete traits: 0 and 0 (state 1, absence of both), 0 and 1 (state 2), 1 and 0 (state 3), 1 and 1 (state 4, presence of both). In all models of character evolution for the discrete traits (dependent and independent) polytomies are treated as hard and not resolved because 0 branch lengths imply changes occur over 0 time, leading to inaccurate parameters for the rates of change.

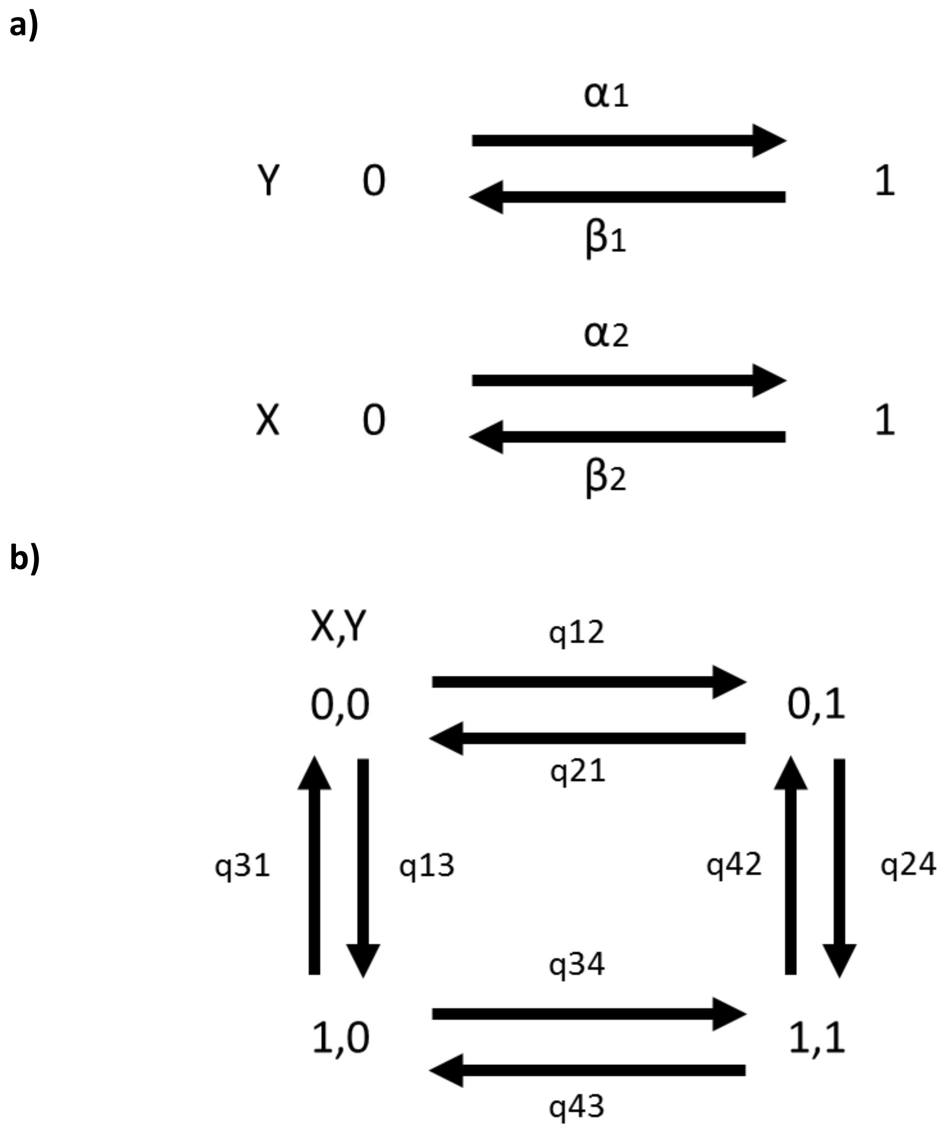


**Figure 2: The (a) independent and (b) dependent models of trait evolution.** X and Y represent the two traits in question, in this case either male care, infanticide, or precociality, with 1 representing the presence of the trait and 0 representing absence. The arrows represent evolutionary transitions with the $q_{ij}$ values representing the rate of transitions.

We implement all models in a Bayesian framework with Markov chain Monte Carlo (MCMC) in BayesTraits (Pagel et al. 2004). In all models we use exponential priors for estimating all rate parameters, with a uniform hyperprior from which the proposed mean and variance of the prior are drawn at each iteration; we set uniform hyperpriors to range between 0 and 5. Using hyperpriors allows the model to sample across a large range of possible prior values for a given prior distribution, rather than fixing them, so that we limit the uncertainty and arbitrariness in the choice of prior values (Pagel & Meade 2006). We run the chains for 50 million iterations, with an additional half a million as burn-in to allow the chain to reach convergence, and sample every 2000 to minimize autocorrelation and ensure an effective sample size of well over the recommended threshold of 1000 is reached for each estimated parameter. In all models (dependent and independent), we also employ a reversible-jump MCMC procedure that explores how alternative models, in which some qij transition rates are set equal to zero, fit the data and visits all possible alternative models in direct proportion to their posterior probabilities (Pagel & Meade 2006). Therefore, reversible-jump reduces model complexity and over-parameterisation. We confirm that the chains reach convergence, have a good mixing and that the effective sample sizes are over 1000 using the diagnostics in Tracer (Rambaut et al. 2014). These analyses are repeated three times and results do not differ qualitatively across runs.

We compare the alternative nested independent and dependent models of character evolution described above using Bayes factors (BF). A Bayes factor is the ratio of the marginal likelihoods of two competing models, where the marginal likelihood is the model likelihood scaled by the prior probabilities integrated across all parameter values (Currie & Meade 2014). Bayes factors thus represent how much the evidence of the observed data favours one model over another, and are calculated as twice the difference between the marginal likelihoods of the dependent and independent models of evolution (Pagel & Meade 2006). The larger the value of the Bayes factor the stronger the support for the model with the higher harmonic mean; Bayes factors 2-5 are considered positive evidence for a given model, greater than 5 strong evidence (Pagel & Meade 2006).

## Results

We first confirm our previous finding that mammals in which males exhibit high cost/benefit care behaviours (defined as either carrying the offspring or provisioning the female; 'Male care (high)') (Table 1, model 1) have a shorter lactation than those without. As predicted by the male energetic contribution hypothesis there is also a significant interaction between gestation time and male care (high) (Table 1, model 2), indicating that, while lactation increases with gestation in species without male care, it is unrelated to gestation in species with biparental care (slope for species with male care: $t_{413}$=-0.2, p=0.867, Figure 3). A full model with male care and the interaction between male care and gestation explains an additional 3% of variance compared to a model without male care ($LR_2$=14.78, p<0.001).

Contrary to the infanticide risk hypothesis there is no significant association between the presence of male infanticide and the duration of lactation (Table 1, model 3), and the inclusion of infanticide does not improve the model fit compared to a model without it ($LR_1$=0.14, p=0.708). Crucially, the interaction between the presence of infanticide and gestation time is also not significant (Table 1, model 4, Figure 4).

Male care (high) and infanticide are evolutionarily correlated, as the dependent model of evolution fits the data substantially better than the independent model of evolution (BF=8.0). Contrary to the infanticide risk hypothesis, these behaviours are almost mutually exclusive (Figure 5). Specifically, the dependent model of evolution (Figure 5) estimates that the ancestral combination of character states in mammals is most likely to have been no male care with no infanticide (39%), while estimates for other combinations are lower (infanticide without male care, 20%; male care without infanticide, 22%; male care and infanticide, 18%). From a state of no male care and no infanticide (0,0), infanticide evolves more readily than male care (transition rate mean: $q_{12}$=0.013, $q_{13}$<0.001). Male care in the absence of infanticide (1,0) and infanticide without mare care (0,1) revert back to the absence of both behaviours more quickly or as quickly as they are gained (transition rate mean $q_{31}$=0.013; $q_{21}$=0.013).

Gaining male care in infanticidal species and gaining infanticide in species with male care occur at the same rate (transition rate mean $q_{24}$=0.013; $q_{34}$=0.013). Furthermore, the presence of both infanticide and male care (1,1) appears to be an unstable condition as it is very rapidly lost either back to a state of infanticide without male care (mean $q_{42}$=1.443), or to a state with male care only (mean $q_{43}$=0.1.276). The evolution of the combination infanticide with male care (1,1) therefore occurs at a much lower rate than the transitions away from this state. Overall these results indicate that male care and infanticide are evolutionarily associated but that the coexistence of these two behaviours in the same species is extremely rare, and represents an unusual and evolutionarily unstable condition.

For our analyses including male care (high) we also re-ran the analyses including all male care behaviours (male care (all)). The results of these analyses do not differ substantially from the analyses presented here; the presence of male care decouples the relationship between lactation and gestation times, and while we find evidence for correlated evolution between male care and infanticide the two behaviours remain mutually exclusive (Appendix 4; Supplementary results, Figure S1). We also re-run all analyses in primates, because certain studies suggest that the evolution of infanticide in primates might differ from other mammals due to the prevalence of monogamy in this group (Opie et al. 2014), but again find no evidence that infanticide drives the reduction in lactation time associated with male care (Supplementary results).

A longer gestation should also lead to the production of more developed offspring. However while precociality is evolutionarily associated with the presence of male infanticide (BF=11.3), the directionality of the relationship does not support the infanticide risk hypothesis (Figure 6). The dependent model estimates the ancestral state in mammals is either altriciality without infanticide (35%) or infanticide and altricial offspring (40%), with other combinations having a substantially lower probability (precociality without infanticide 8%; infanticide and precociality, 17%). In contrast to the predictions made by the infanticide risk hypothesis, the model indicates that precociality is very unlikely to evolve in response to infanticide by males (mean $q_{34}<0.001$). From a condition of altriciality without infanticide, the evolution of either precociality or infanticide occurs at a similar rate (transition rate mean $q_{12}=0.012$; $q_{13}=0.013$). However, while infanticide with altriciality is unstable and quickly reverts to an absence of both traits (transition rate mean $q_{31}=0.016$), precociality without infanticide is very unlikely to revert to altriciality without infanticide (transition rate mean $q_{21}<0.001$). Infanticide evolves readily among precocial species (transition rate mean $q_{24}=0.015$), but a state of both infanticide and precociality is unstable, and either infanticide or precociality is quickly lost (transition rate mean $q_{43}=0.016$; $q_{42}=0.016$). Overall, this indicates that precociality does not evolve in response to infanticide, and that infanticide can evolve in either altricial species or follow – but not precede – the evolution of precociality. The correlated evolution between male care, infanticide and precociality cannot be investigated in primates, as the sample sizes for these models are too low (n=<10).

**Table 1: Best fitting PGLS models for the duration of lactation with male care and infanticide across all mammals.** For each independent variable in each model we report the β-values, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$ and the model log-likelihood (Lh). The total sample size for models with male care is 413 species, of which 25 have male care. The total sample size for models including infanticide is 197 species, of which 84 species exhibit male infanticide.

| **Lactation time** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1** | Female body mass | 0.13 | 0.02 | 6.6 | <0.001 | 0.82 | 0.27 | 54.13 |
| | Gestation time | 0.34 | 0.09 | 4.0 | <0.001 | | | |
| | Male care (high) | -0.21 | 0.06 | -3.6 | <0.001 | | | |
| **2** | Female body mass | 0.13 | 0.02 | 6.6 | <0.001 | 0.82 | 0.28 | 56.62 |
| | Gestation time | 0.35 | 0.09 | 4.1 | <0.001 | | | |
| | Male Care (high) | 0.52 | 0.33 | 1.6 | 0.120 | | | |
| | Gestation:Male Care (high) | -0.38 | 0.17 | -2.2 | 0.026 | | | |
| **3** | Female Body mass | 0.20 | 0.04 | 5.2 | <0.001 | 0.89 | 0.24 | -15.84 |
| | Gestation time | 0.26 | 0.15 | 1.7 | 0.084 | | | |
| | Infanticide | -0.02 | 0.04 | -0.4 | 0.659 | | | |
| **4** | Female body mass | 0.20 | 0.04 | 5.3 | <0.001 | 0.89 | 0.24 | -15.46 |
| | Gestation time | 0.27 | 0.15 | 1.8 | 0.069 | | | |
| | Infanticide | 0.14 | 0.19 | 0.8 | 0.456 | | | |
| | Gestation:Infanticide | -0.08 | 0.09 | -0.9 | 0.389 | | | |

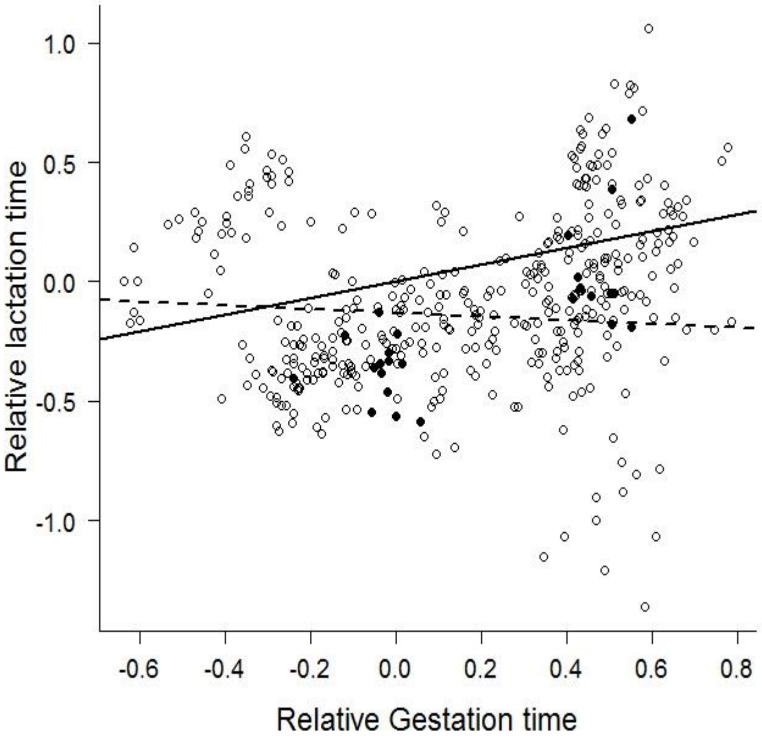


**Figure 3: Relative lactation time and gestation time (while accounting for female body mass) in species with male care (high) (filled circles) and in species without (open circles).** After removing allometric effects, lactation is unrelated to gestation time in species with male care (high) (dotted line), but in species without male care lactation and gestation are positively associated (solid line) (Table 1).

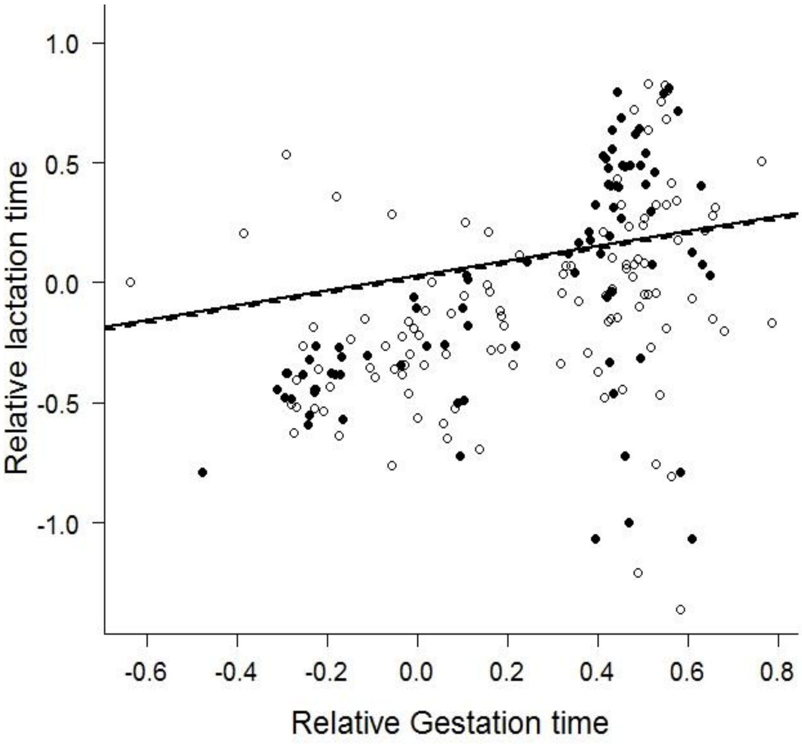
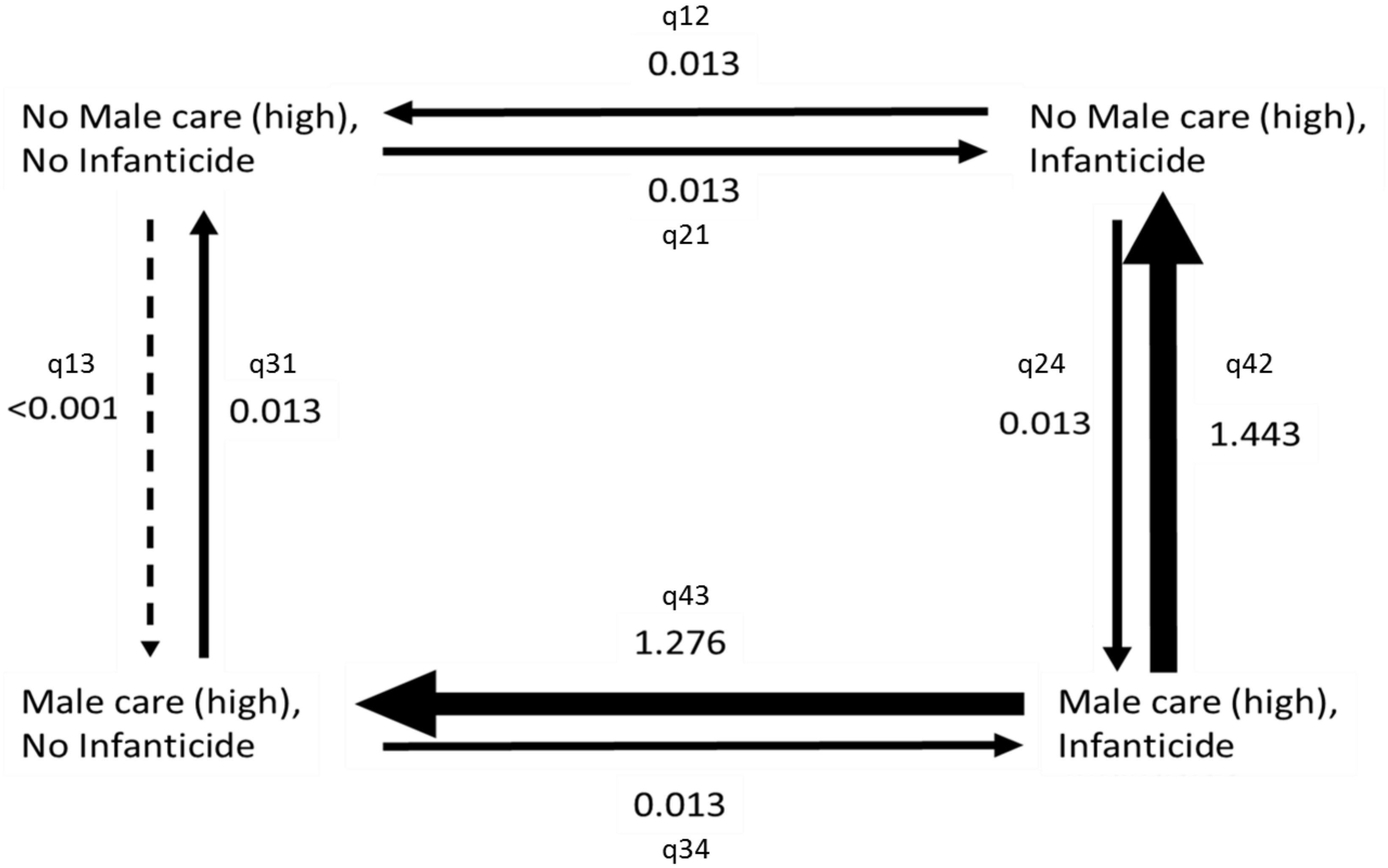


**Figure 4: The relationship between male infanticide, lactation time, and gestation time (while accounting for female body mass) in species with (filled points) and without (open circles) male infanticide.** After removing allometric effects, the slope of the relationship between lactation and gestation does not differ significantly between species with male infanticide (dotted line) and those without (solid line) (Table 1).

a)


q12
0.013
No Male care (high),
No Infanticide
No Male care (high),
Infanticide
0.013
q21
q13
<0.001
q31
0.013
q24
0.013
q42
1.443
q43
1.276
Male care (high),
No Infanticide
Male care (high),
Infanticide
0.013
q34

**b)**

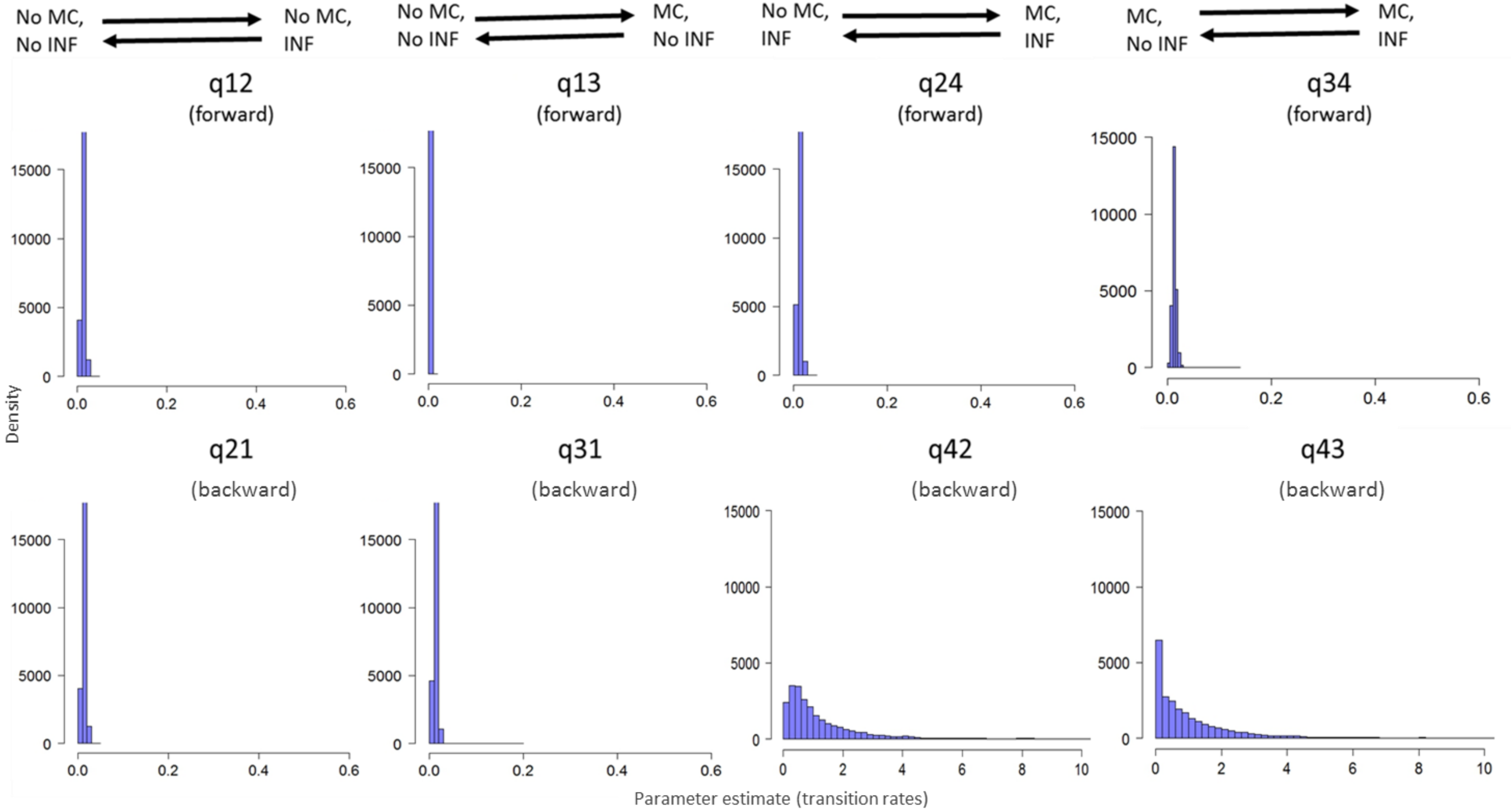
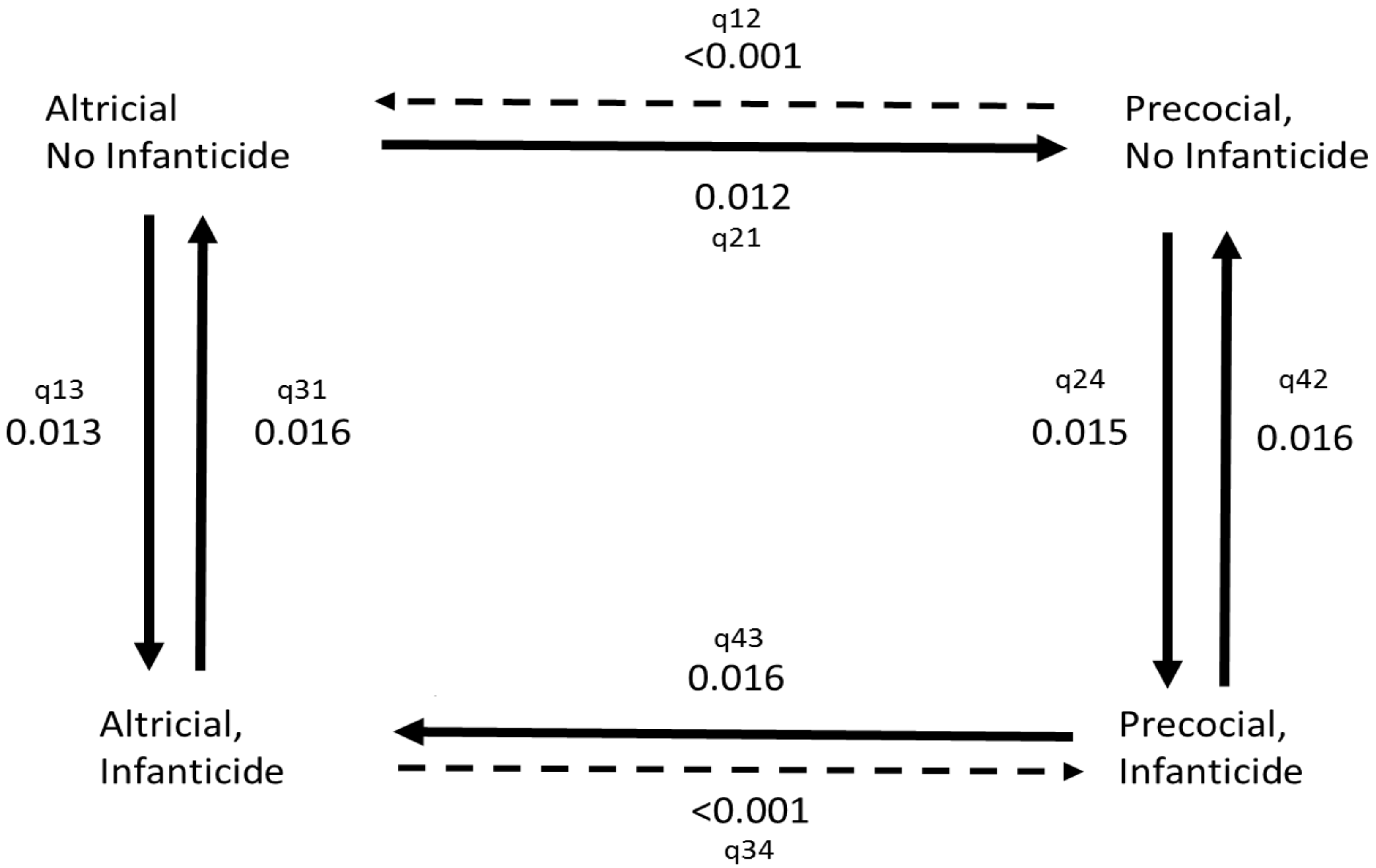


**Figure 5**: **The dependent model of evolution between male care (high) and infanticide by males (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions. The arrow labels represent the mean rate for each transition. MC=male care (high), INF=infanticide.

**a)**


q12
<0.001
Altricial
No Infanticide
Precocial,
No Infanticide
0.012
q21
q13
0.013
q31
0.016
q24
0.015
q42
0.016
q43
0.016
Altricial,
Infanticide
Precocial,
Infanticide
<0.001
q34

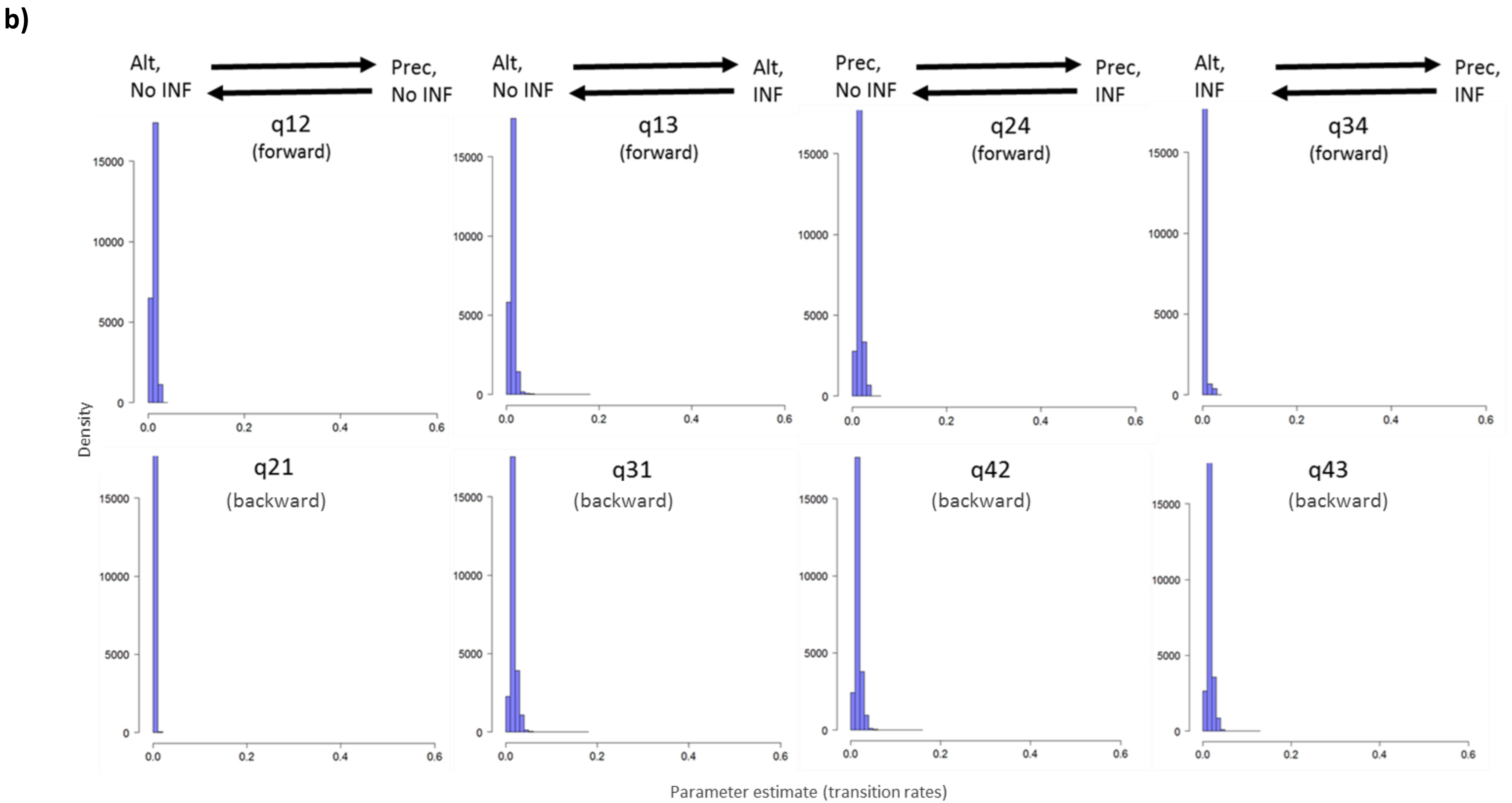


**Figure 6**: **The dependent model of evolution between male infanticide and precociality (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions. The arrow labels represent the mean rate for each transition. Prec=precocial, Alt=altricial, INF=infanticide.

## Discussion

In this study we investigate how two drastically different behaviours towards the offspring, male care and infanticide, may influence the evolutionary trajectory of life history traits in mammals, and whether they are evolutionarily associated. While male care and infanticide may theoretically lead to similar associations with the duration of lactation, which we previously show is shorter in mammals with carrying and provisioning (West & Capellini 2016), these behaviours should alter the patterns of covariation between life history traits differently. In support of the energetic contribution hypothesis, we find that lactation and gestation times are unrelated in species with male care. Contrary to the infanticide risk hypothesis, infanticide is unrelated to lactation time, and does not extend gestation and shorten lactation. Moreover, male care and infanticide are evolutionarily associated but almost entirely mutually exclusive; the combination of male care and infanticide is an evolutionarily unstable state. Likewise, precociality is unlikely to be an evolutionary response to infanticide risk as it does not follow the evolution of infanticide. Altogether, our results provide strong support for the hypothesis that a reduction in lactation time is driven by energetic benefits to female reproduction that male care provides, and suggest that male parental care can not only affect offspring fitness and survival, but reduces female reproductive costs.

The costs of reproduction for females can be very high. For example, egg production and brood care among birds and reptiles is often associated with a significant loss of body mass or reduced survival (Landwer 1994; Kalmbach & Griffiths 2004; Cox et al. 2010; Golet et al. 2004). Lactation is the most demanding period of reproduction in mammals and females substantially increase their energetic intake prior and/or during lactation (Gittleman & Thompson 1988; Oftedal & Gittleman 1989) in order to match the greater requirements of the growing offspring (Bowen et al. 2001; Oftedal & Gittleman 1989). Furthermore, milk composition changes over the course of lactation (Oftedal & Gittleman 1989), with the percentage of fats and sugars generally increasing towards weaning age and milk energy output peaking at the time of maximal milk intake and offspring growth rate (Brennan et al. 2007; Riek 2008; Speakman & McQueenie 1995). By undertaking costly care behaviours, males may help females meet the costs of reproduction and allow them to increase their reproductive output (e.g. litter or clutch size) or reproduce faster (Cantoni & Brown 1997; Scantlebury et al. 2002; Brown et al. 1978). Many male care behaviours in mammals are in fact very expensive; for example carrying the offspring leads to a substantial loss of paternal body mass and condition as well as reducing mobility and increasing predation risk (Schradin & Anzenberger 2001), while provisioning the offspring increases hunting or foraging costs. Without having to face these costs, female mammals can divert more energy towards producing more nutritious and/or a larger quantity of milk (Lappan 2009) which in turn should benefit the offspring as higher milk energy output increases offspring growth rate and weaning mass (Riek 2008; Mellish et al. 1999; Iverson et al. 1993). Consistent with this prediction, we previously found that offspring grow faster, but not to a larger size, in mammals with biparental care (West & Capellini 2016). Here we show that a second key prediction of the male energetic contribution hypothesis is also supported; the positive relationship between the durations of lactation and gestation across species is weakened – in fact non-significant - in species with biparental care (Figure 3). Therefore, the presence of male care leads to an evolutionary decoupling between lactation and gestation across biparental mammal species.

The male energetic contribution hypothesis makes additional still untested predictions. Specifically, future studies should quantify energetic costs of care behaviours in a larger sample of species as these are primarily available in primates at present (Sánchez et al. 1999; Altmann & Samuels 1992; Wright 1990; Schradin & Anzenberger 2001), and a single rodent species (Saltzman et al. 2015; Campbell et al. 2009). Likewise, estimates of milk energetic output and corresponding growth rates across a range species with and without male care are needed to quantify how much females benefit energetically from males' help and how this translates into better support offspring growth. At present, too few data are available, particularly on offspring growth rates, for a comparative analysis testing the direct associations between male care, milk energy intake and offspring growth rate. However, both growth rate and milk energy intake appear to be greater in carnivore species with biparental care than in species without male care (Oftedal & Gittleman 1989).

More broadly, our findings are consistent with comparative and empirical evidence that care of the offspring provided by the male or other helpers enable females to reduce the costs of reproduction (‘load-lightening’ effect: Crick 1992; Isler & van Schaik 2012). Female meerkats (*Suricata suricatta*), for example, who raise offspring supported by helpers that either allonurse or ‘babysit’ pups, have a lower daily energy expenditure than females who raise the offspring alone (Scantlebury et al. 2002). Helpers in meerkats may therefore allow the reproducing female to save energy, reducing the quality or quantities of milk she would need to produce to raise each litter, and allow her to spend more time away from the offspring and gain energy through hunting or foraging (Scantlebury et al. 2002; Sharp et al. 2012). Similarly helpers allow female carrion crows (*Corvus corone*) to save energy by reducing investment in egg size, without compromising offspring size or survival at independence (Canestrari et al. 2011). Yet, while current studies show how female reproductive output varies with and without additional helpers, we also need estimates of how female activity budget changes accordingly in species with and without male care.

Our results are not consistent with the alternative hypothesis that both male care and a shorter lactation are counter-strategies against high infanticide risk (Paul et al. 2000; Opie et al. 2013; van Schaik 2000). Under this hypothesis, male care evolves as a defence against infanticidal males, while a shorter lactation time and a longer gestation allow females to produce more precocial offspring and reduce the period of time during which the offspring are at the highest risk of infanticide. Crucial to this idea is the relative increase in gestation accompanied by a reduction in lactation (Figure 1b). Yet we find no support for this mechanism; a shorter lactation in species with male care is not accompanied by a proportional evolutionary increase in gestation time, nor is there any association between the presence of infanticide risk and the relative durations of lactation and gestation. These conclusions do not change if only primates are considered, contrary to suggestions that primates have a higher risk of infanticide than other mammals (Opie et al. 2014) because they require relatively longer lactation to support the development of their larger brains (Barton & Capellini 2011). Furthermore, precociality does not follow the evolution of infanticide; rather, it evolves only in the absence of infanticide. Therefore, our study confirms previous findings that infanticide risk is unrelated to female life history traits (Lukas & Huchard 2014), but also demonstrates that there is no expected shift forward in the timing of birth, core to this hypothesis. We conclude that species with a longer lactation relative to gestation time do not necessarily have a greater risk of infanticide than other species and 'weaning proportion', the relative duration of gestation to the total duration of maternal investment, cannot be used as an indirect measure of infanticide risk. We do however find that the presence of infanticide is associated with a more developed state at birth, but not in the direction predicted by the infanticide risk hypothesis. While infanticide is equally likely to evolve among altricial and precocial species (Figure 6; $q_{13}$=0.013, $q_{24}$=0.015), precociality appears never to evolve in the presence of infanticide (Figure 6; $q_{34}$<0.001). Thus, it appears that rather than precociality evolving among females as a counterstrategy to infanticide (Ebensperger 1998; van Schaik 2000), infanticide by males may evolve as an adaptive response to precociality. Among certain species with high levels of male infanticide, the killing of dependent offspring causes females to resume reproduction early (van Schaik 2000; Pusey & Packer 1994a; Sommer 1994), thus, if females produce precocial offspring, which typically involves long-term investment on the part of the female (Hennemann 1984), males might be selected to increase their own reproduction by killing unrelated offspring.

Although male care and infanticide are evolutionarily correlated, these two behaviours appear mutually exclusive, and species with both male parental care and infanticide are extremely rare (although they do occur, see Elwood 1977; Elwood 1985). Although the correlated evolution model shows that the evolution of male care without infanticide is rare and infanticide may precede the evolution of male care, faster transitions away from a state where a species has both male care and infanticide suggests that male care with infanticide is an evolutionarily unstable state (Figure 5), and that either male care or infanticide alone is a far more beneficial strategy for males. We therefore suggest that the evolution of monogamy (Lukas & Clutton-Brock 2013) is a better predictor for the evolution of male care than infanticide, and the underlying driver of the pattern documented here. Altogether, our results do not support the predictions of the infanticide risk hypothesis that male care evolves as a counter-strategy to high risk of infanticide. One reason why male care and infanticide are rarely found in the same species is the potential for overlap in the hormonal controls of these behaviours. At a proximate level both care by males and infanticide may be dependent on the same hormones, but at different levels of expression. Vasopressin in vole species (*Microtus sp.*) for example is known to mediate the expression of parental behaviour (Wang et al. 1999), while high levels of prolactin are also associated with male care in both rodents, callitrichid primates and birds (Ziegler 2000). Less is known about the specific hormonal mechanisms for infanticide, but high levels of testosterone are typically associated with male aggression, which may include infanticidal behaviours (Wingfield et al. 1990; Wingfield et al. 1987; Hau 2007). On the other hand, low levels of testosterone are associated with parental behaviours in both rodents and birds (Ziegler 2000). Thus, if both behaviours are present in the same species males risk killing when they should care and vice versa, if the hormonal controls behind these behaviours are similar and switching between them requires complex regulatory mechanisms. Therefore, selection should not favour the occurrence of both behaviours simultaneously.

The importance of behaviour in driving life history strategies is a key question in studies of animal behaviour (Trivers 1972; Andersson 1994). Understanding the relationship between parental care and reproductive investment is vital, but very few studies have examined the potential effect of male care on female reproductive success in biparental species. While we have empirical evidence that male care may reduce female parental effort in some bird and insect species (Curlee & Beissinger 1995; Richmond 1978; Martin et al. 1985; Jenkins et al. 2000), our comparative study is consistent with the hypotheses that females of biparental species gain energetic benefits from male care that allow them to reduce the costs of reproduction. We show that the presence of male care decouples the evolutionary association between gestation and lactation and suggest that males taking over energetically costly parental care behaviours have a load-lightening effect on the female allowing her to divert more energy towards milk production (Crick 1992). Future studies could quantify the energetic contribution of male care towards female reproduction, milk production and maternal activity budget across and within species. While lactation is a unique reproductive feature of female mammals, the energetic benefits to male care are likely to be substantial in many other species where females face high reproductive costs. Finally, we find no evidence that the presence of infanticide by males generates any selective pressure on the evolution of male parental care, or female life histories.

# CHAPTER 6: THE IMPORTANCE OF DIVERSITY IN ALLOCARE BEHAVIOUR FOR MAMMALIAN LIFE HISTORY STRATEGIES.

**Authors:** Hannah E. R. West and Isabella Capellini

**Author contributions:** IC and HW designed the research and data collection protocols; HW collected the data, conducted the analyses, and drafted the manuscript; IC and HW revised the draft.

## Abstract

While parents of many species provide extensive care for their offspring, in some species they are also assisted by related and/or unrelated 'alloparents' that perform a diverse range of parental duties. Like male parental care, allocare is predicted to reduce the energetic costs of reproduction through 'load-lightening' effects and increase maternal reproductive output. Although distinct allocare behaviours should entail different costs and benefits, which behaviours have load-lightening effects at which stage of female reproduction, is currently unknown. To test the load-lightening hypothesis, we investigate the evolutionary associations of individual allocare behaviours with life history traits in over 500 mammals, using modern phylogenetic comparative methods. As predicted, mammals in which helpers carry the offspring have more frequent breeding events, but unlike male offspring carrying, this is not determined by a reduction in lactation time. We suggest that, while male offspring carrying is likely to reduce the heavy energetic costs of lactation, allo-carrying most likely speeds up females' post-weaning recovery. Mammals in which helpers provision the offspring have larger litters, suggesting that the additional resources that helpers provide allow females to produce more offspring than they could raise alone. We conclude that while both male care and care by helpers are evolutionarily associated with higher fecundity in mammals, they influence different times of females' reproductive cycle. Future theoretical models on the evolution of parental care should consider both the identity of the carer and its relatedness to the

offspring, as well as the costs and benefits of different behaviours to the carer, mothers and offspring.

## Introduction

In a wide range of species, some individuals perform many of the same care behaviours that parents show towards the offspring (Wisenden 1999; Lukas & Clutton-Brock 2012a; Brown 1987). By caring for offspring that are not their own, helpers face substantial energetic and opportunity costs, since they do not directly invest resources and time towards their own reproductive success (Cant 2012). Allocare, i.e. care by individuals other than the parents, however, may also confer benefits to helpers through increased inclusive fitness when directed towards related individuals (Bales et al. 2000; Silk 2007; Hodge 2005; Riedman 1982), or by gaining valuable experience in offspring-rearing (Riedman 1982). Alloparents may also care if the costs of refusing to help are higher than those of helping (Ratnieks & Wenseleers 2008; Gaston 1978). Alloparental care is proposed to provide substantial benefits through higher offspring survival or through load-lightening effects on maternal reproductive costs that should increase female reproductive output (Crick 1992; Meade et al. 2010; Wisenden 1999). Although alloparents perform a diverse range of care behaviours, past studies investigating the costs and benefits of allocare do not discriminate between them, with some also considering care by males as a form of allocare (e.g. Isler & van Schaik 2012; Tecot et al. 2012; Burkart et al. 2009; Lewis & Pusey 1997). Conversely, we have previously shown that the identity of the carer matters, as male care and allocare (regardless of the specific behaviour) exhibit different patterns of associations with life history traits in mammals and, crucially, different male care behaviours are not equivalent in their relationship with fecundity (Chapter 3; West & Capellini 2016). Thus, understanding which specific care behaviours by non-parental helpers associate with female life history traits is a key piece of the puzzle if we are to understand the costs and benefits underlying the evolution of allocare, and more broadly, parental care. Here we address this question by explicitly considering the diversity of allocare behaviours and by investigating how allocare behaviours compare to male care behaviours in their associations with life history traits.

Additional carers provide resources that may ultimately reduce the energetic costs of reproduction for the mother, a ‘load-lightening effect’, and in turn increase female fecundity and reproductive success (Crick 1992). Specifically, females supported by alloparents could either reduce their own energetic investment into current offspring and divert the saved energy into recovering more quickly to breed sooner, or use the additional resources provided by the helpers to produce more offspring. Support for the prediction that allocare increases reproductive frequency is mostly found in birds and mammals (Riedman 1982; Mitani & Watts 1997; Ridley & Raihani 2008; Santos & Macedo 2011). Parents aided by helpers can rear two overlapping broods, with the first being cared for primarily by the helpers and the second by the parents, as in the pied babbler (*Turdoides bicolor*) (Ridley & Raihani 2008). Also, bird species with alloparents often produce larger broods (Brown 1987; Meade et al. 2010) and mammals with both male care and care by other helpers have larger litters (Isler & van Schaik 2012; West & Capellini 2016; Moehlman & Hofer 1997). A recent comparative study in mammals shows that polytocy (multiple offspring per birth) is an evolutionary prerequisite for cooperative breeding, a social system where non-breeding helpers assist in raising the young of dominant females (Lukas & Clutton-Brock 2012a). However, alloparental care occurs in many non-cooperatively breeding mammals with diverse social systems (Isler & van Schaik 2012), and in these species allocare may facilitate the evolution of larger litters through load-lightening. Importantly, distinct behaviours performed by the helpers may exhibit different associations with female fecundity, as it is the case for male care (Chapter 3; West & Capellini 2016), but it is still unclear which allocare behaviour, if any, associates with larger litters. As well as larger litters, care by alloparents may also allow females to produce more frequent litters. Like for male care (Chapter 3; West & Capellini 2016), females assisted by alloparents may increase their rate of reproduction by producing more or better quality milk and weaning the offspring faster, which in turn may allow them to breed again sooner (Isler & van Schaik 2012). Alternatively, allocare may allow females to reduce interbirth intervals by saving energy over the course of reproduction, recover more quickly and resume breeding faster, even without weaning the offspring earlier. The few studies that investigate load-lightening in wild mammals focus on the energetic benefits for the females. Thus, meerkat (*Suricata suricatta*) helpers allonurse and babysit the offspring, leading to a remarkable reduction in maternal daily energy expenditure during lactation (Scantlebury et al. 2002), while chimpanzee (*Pan troglodytes schweinfurthii*) allomothers carry the infants and help mothers reduce the costs of lactation as the infants suckle less frequently and maternal milk contributes less to their diet (Bădescu et al. 2016). Finally, female capped langurs (*Presbytis pileata*) with helpers carrying their offspring spend more time foraging (Stanford 1992). These studies show that alloparents may provide substantial energetic benefits to the mother, however, no study to date has tested whether this allows females to wean the offspring sooner and/or speed up reproduction by recovering more quickly postweaning.

Care by helpers should also benefit the offspring by enhancing their survival to independence, growth rates or size – as larger offspring typically enjoy greater survival (Hodge 2005; Emlen 1984; Woodroffe & Vincent 1994; Clutton-Brock 1991). Non-phylogenetic studies of allocare in primates and carnivores, where helpers either carry, provision, or allonurse the offspring, suggest that allocare may boost offspring growth rates (Mitani & Watts 1997; Oftedal & Gittleman 1989). The additional resources that alloparents provide may ultimately increase offspring weight (Sparkman et al. 2011; Woodroffe & Vincent 1994; Canestrari et al. 2011; Clutton-Brock et al. 2001; Hodge 2005), as in carrion crows (*Corvus corone*), where, despite reduced maternal investment in egg size, the presence of helpers increases offspring weight compared to offspring of broods without helpers (Canestrari et al. 2011). Field studies also find support for long-term beneficial effects of allocare for the young. Allocare in meerkats, which consists of primarily of provisioning and defence of the young (Clutton-Brock et al. 2001; Nowak 1999), associates with pups' higher daily weight gain and heavier pup size at independence, which in turn enhance survival (Clutton-Brock et al. 2001). Likewise, in banded mongooses (*Mungos mungo*) offspring that spend more time with helpers, receive more food, grow faster and enjoy higher survival than offspring which spend less time with helpers (Hodge 2005). Chapter 3 (West & Capellini 2016) also shows that carnivores, but not other mammals, with allocare produce heavier neonates and, since helpers typically provision offspring in this group (West & Capellini 2016; Nowak 1999), the benefits of allocare may be specifically linked to this behaviour. Finally, there is some evidence that allonursing may associate with large litters across mammals (Packer et al. 1992; MacLeod & Lukas 2014), although previous studies propose that this may only reflect the reduced costs of allonursing as litter size increases, rather than any energetic benefits to the females (Packer et al. 1992; MacLeod & Lukas 2014). Lactation is however extremely expensive (Speakman & McQueenie 1995; Clutton-Brock et al. 1989; Hanwell & Peaker 1977) and allonursing is unlikely to have evolved without some yet unidentified benefits to outweigh such costs. Rather than the mother, allonursing may thus benefit the offspring through the gain of extra nutrition that increases growth rates and weaning mass, but this has never been comprehensively tested at a large-scale.

Like male and female care, alloparental care consists of many diverse behaviours that are likely to have different costs to the carer and different benefits for both the carers and recipient(s) (Isler & van Schaik 2012). For example, both fathers and alloparents carry the offspring in anthropoid primates (Mitani & Watts 1997), while among canids all members of a pack provision the young (Mech 1974; Malcolm 1985). Despite the similarities in the behaviours performed, it remains unclear whether specific allocare behaviours exhibit similar associations with life history traits to those found across the range of male care behaviours (Chapter 3; West & Capellini 2016). Accounting for diversity in male care behaviours, for example, reveals that only mammals in which males either carry the offspring or provision reproducing females have shorter lactations and higher breeding frequency, and suggests that these behaviours have the greatest load-lightening effect on female reproduction (Chapter 3; West & Capellini 2016). Likewise, considering the diversity in allocare has the potential to inform our understanding of mechanisms such load lightening effects. Few studies consider the specific behaviour performed by helpers, the only exception being allonursing another female's offspring.

Using modern phylogenetic comparative methods, we test the hypothesis that allocare provides load-lightening effects and increases female fecundity, and/or is beneficial to the offspring and boosts growth rate or mass, but that the benefits may differ across specific behaviours. We consider five allocare behaviours: carrying, provisioning, nursing, huddling and grooming. In support of the load-lightening hypothesis we have previously found that the presence of alloparents in mammals associates with larger and more frequent litters (Chapter 3; West & Capellini 2016). Here, we build on these results and investigate which specific alloparental behaviours associate with these benefits. Thus, species with alloparents should exhibit a shorter lactation, more frequent breeding and/or larger litters; particularly in mammals where alloparents carrying, provision or nurse the offspring. Likewise, if allocare is beneficial to the offspring, species with allocare should have a faster growth rate and/or larger neonates and/or weanlings, particularly when offspring are carried, provisioned or nursed by alloparents.

## Method

### Data collection

We include in our study only species for which data on at least two life history traits are available. For these species, we collect data on specific alloparental care behaviours, here defined as care by additional helpers towards the offspring but excluding the male. The total sample size in this dataset is 537 mammals, including species with or without allocare, although not all life history traits are available for all species.

We update the dataset of life history traits in West & Capellini (2016) with data for an additional 8 species in Capellini et al (2015) and include the following variables; female adult body mass (g, n=468), lactation time (days, n=444), gestation time (days, n=466), weaning mass (g, n=262), neonatal mass (g, n=445), litter size (n=507), and litters per year (n=438). We calculate postnatal body mass increase (n=262) as the difference between weaning and neonatal body masses to better capture potential benefits of allocare during lactation.

We define alloparental care as any care behaviour by any individual other than the parents towards dependent offspring, or towards a reproducing female, as this may indirectly benefit the offspring (Chapter 3; West & Capellini 2016). We consider forms of allocare the following behaviours; provisioning the offspring or reproducing females although we are unable to differentiate between the two, carrying, nursing, grooming, or huddling with the offspring. Data on allocare are extracted from a variety of primary and secondary sources (Appendix 5: Supplementary methods). Altogether 92 species exhibit at least one allocare behaviour and 49 species more than one. Helpers provision the offspring or female in 34 species, carry the offspring in 33, allonurse in 68 species, allogroom the offspring in 30, and huddle with offspring in 11 species. We group huddling with grooming for the analyses because sample sizes drop below 10 for huddling when it is investigated with life history traits.

Because allocare may co-occur with the male care in several species, we also include those male care behaviours, that we previously found associate with a given life history trait, as an independent variable in relevant models. Male parental behaviours are taken from West & Capellini (2016) and include provisioning the female, and provisioning, carrying, grooming, and huddling with the offspring. We include social monogamy as a covariate in all models as monogamy, male care, and alloparental care may all be present in the same species due to the correlated evolution between these traits; social monogamy precedes the evolution of at least some male care behaviours (Lukas & Clutton-Brock 2013; Opie et al. 2013; Chapter 4), and is also an evolutionary precursor to cooperative breeding (Lukas & Clutton-Brock 2012b) and may associate with the evolution of alloparental care. We define social monogamy as a single male and female that breed together, share a home range or territory, and remain together for more than one breeding season. Alloparental care, male care, and monogamy are coded as binary variables, with 1 representing the presence of the trait and 0 its absence.

Finally, we control for variation in research effort among species in our dataset because the lack of data on an allocare behaviour in the literature for a species may either indicate that the behaviour is not present in a species or that a species is insufficiently studied for the behaviour to be reported in the literature. We quantify research effort as total citation count defined as the total number of references published on a species since 1950 as reported in Web of Science, using the species' scientific name or common name as search parameters (Date last accessed: 02/11/2015). All continuous data are log-transformed for the analyses to normalise their distribution.

### Statistical analysis

We use phylogenetic generalized least squares (PGLS) models to test the evolutionary associations between life history traits and allocare behaviours (Freckleton et al. 2002; Pagel 1999). We build PGLS models using the 'caper' package (Orme 2013) in the programme 'R' and all parameters in the models are estimated with maximum likelihood (Orme 2013). We incorporate a comprehensive mammalian phylogeny (Fritz & Purvis 2010) to account for species' shared ancestry and quantify the strength of the phylogenetic signal in a model's residuals with the parameter lambda (λ) (Freckleton et al. 2002; Revell 2010). λ varies between 0 and 1, where 0 indicates lack of phylogenetic signal, and 1 that species' similarity is directly proportional to the time of shared evolutionary history as expected under a Brownian motion model of evolution (Freckleton et al. 2002). We assess the association between a life history trait of interest, as dependent variable, and each of the allocare behaviours as independent variables, while incorporating allometric effects, other life history traits that covary with the one of interest (Bielby et al. 2007), research effort (as measured as citation count), social monogamy, and any specific male care behaviours that associates with the dependent variable (Chapter 3; West & Capellini 2016). These PGLS models are conceptually similar to ANCOVA models with parallel slopes, where we test for differences in intercepts between species with and without alloparental behaviours (Capellini et al. 2011). We employ a model simplification procedure, beginning with a 'full' model containing all relevant variables, and then reducing this model until a 'reduced' model containing only significant predictors remains (Crawley 2007). We assess model fit to the data by comparing models with and without the alloparental behaviour of interest using the likelihood ratio (LR) test for nested models (Quinn & Keough 2002) and AIC scores for comparisons of non-nested models. The LR test is calculated as twice the difference between the log-likelihoods of the two competing models. Models that fit the data better have higher log-likelihood scores and lower AIC scores (Quinn & Keough 2002). All statistical tests are two-tailed with a α-level of significance set at 0.05.

## Results

Individual alloparental behaviours associate differently with life history traits. Species with allocarrying produce more litters annually than species without, while accounting for allometry, the duration of lactation and gestation, and carrying and grooming by males (Table 1, Figure 1). No other alloparental behaviour is associated with reproductive frequency (Appendix 5: Supplementary tables and figures; Table S1, model 1). Carrying by helpers explains a further 2% of variance in breeding frequency compared to a model without it, and significantly increases the fit of the model to the data (Table 1 vs table S1, model 2: $LR_1=7.10$, $p=0.008$). Unlike for male care, higher breeding frequency in species with allocarrying is not the consequence of having a shorter lactation, since lactation time is unrelated to carrying by alloparents (Table S2, model 1). Lactation time, instead, is shorter in species in which alloparents either groom and/or huddle with the offspring, while accounting for allometry, gestation time, and carrying by males (Table 1, Figure 2). Allogrooming and huddling together explain a further 2% of variance in lactation time, relative to a model without these behaviours, and significantly improve the model fit to the data (Table 1 vs table S2, model 2: $LR_1=9.62$, $p=0.002$). This result is qualitatively similar when allogrooming alone is considered and species that huddle are classified as no-care (Table S2, models 3 & 4; Table 1 vs model 4 in Table S2: $\Delta AIC = 2.22$), suggesting that allogrooming has an association with lactation time, independent of huddling.

Gestation time is longer in species with allonursing, while accounting for allometry, lactation time, litter size, and research effort (Table 1, Figure 3), but no other allocare behaviour associates with gestation time (Table S3, model 1). Allonursing explains an additional 2% of variance in gestation time relative to a model without it, significantly improving the model fit (Table 1 vs table S2, model 2: $LR_1=6.94$, $p=0.008$).

Litters are larger in mammals with provisioning by helpers, while accounting for allometric effects, provisioning of females by the male, and citation count (Table 1, Figure 4).

No other alloparental behaviours show any significant association with litter size (Table S4, model 1). Alloprovisioning explains a further 2% of variance in litter size and significantly improves the fit of the model to the data relative to a model without it (Table 1 vs Table S4, model 2: $LR_1$=7.12, p=0.008).

Finally, we find no significant relationship between any of alloparental behaviours and mass at birth, mass at weaning, or mass gain from birth to weaning, while accounting for litter size, lactation time and gestation time where relevant (Table S5). The inclusion of allocare behaviours, relative to a model without, does not improve the model fit to the data for any of these traits (Table S5a, model 1 vs model 2: $LR_5$=4.38, p=0.496; table S5b, model 1 vs model 2: $LR_6$=9.52, p=0.146; table S5c, model 1 vs model 2: $LR_6$=9.58, p=0.144).

**Table 1: Best fitting models for life history traits and alloparental behaviours across all mammals.** For each independent variable in each model, we report the β-values with standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh) and AIC score. The total sample size for models with litters per year is 371 species, of which 25 have allocarrying, and 22 male grooming. The total sample size for models with lactation and gestation time as dependent variables is 390 species, of which 26 species have alloparents that either groom or huddle with the offspring, 56 species with allonursing, and 14 species carrying by the male. The total sample size for models with litter size is 450 species, of which 32 have alloprovisioning, and 13 provisioning reproducing females by the male.

| | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Dependent Variable** | **Independent Variables** | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **Litters per year** (n=371) | Female body mass | -0.1 | <0.1 | -2.9 | 0.004 | 0.89 | 0.23 | 159.55 | -307.11 |
| | Gestation time | -0.2 | 0.1 | -3.2 | 0.002 | | | | |
| | Lactation time | -0.2 | <0.1 | -3.8 | <0.001 | | | | |
| | Allocarrying | 0.1 | 0.1 | 2.7 | 0.008 | | | | |
| | Male care (grooming) | 0.1 | <0.1 | 2.2 | 0.030 | | | | |
| **Lactation time** (n=390) | Female body mass | 0.1 | 0.0 | 6.2 | <0.001 | 0.81 | 0.28 | 51.17 | -92.33 |
| | Gestation time | 0.4 | 0.1 | 4.3 | <0.001 | | | | |
| | Allogrooming & huddling | -0.1 | 0.1 | -3.1 | 0.002 | | | | |
| | Male care (carrying) | -0.2 | 0.1 | -2.6 | 0.009 | | | | |
| **Gestation time** (n=390) | Female body mass | 0.1 | <0.1 | 8.2 | <0.001 | 1.00 | 0.28 | 329.75 | -649.51 |
| | Lactation time | 0.1 | <0.1 | 2.5 | 0.012 | | | | |
| | Litter size | -0.2 | <0.1 | -4.7 | <0.001 | | | | |
| | Allonursing | <0.1 | <0.1 | 2.6 | 0.009 | | | | |
| **Litter size** (n=450) | Female body mass | -0.1 | <0.1 | -5.4 | <0.001 | 0.96 | 0.17 | 271.22 | -532.45 |
| | Alloprovisioning | 0.1 | <0.1 | 2.7 | 0.008 | | | | |
| | Male care (prov. females) | 0.2 | 0.1 | 4.3 | <0.001 | | | | |
| | Citation count | <0.1 | <0.1 | 5.7 | <0.001 | | | | |

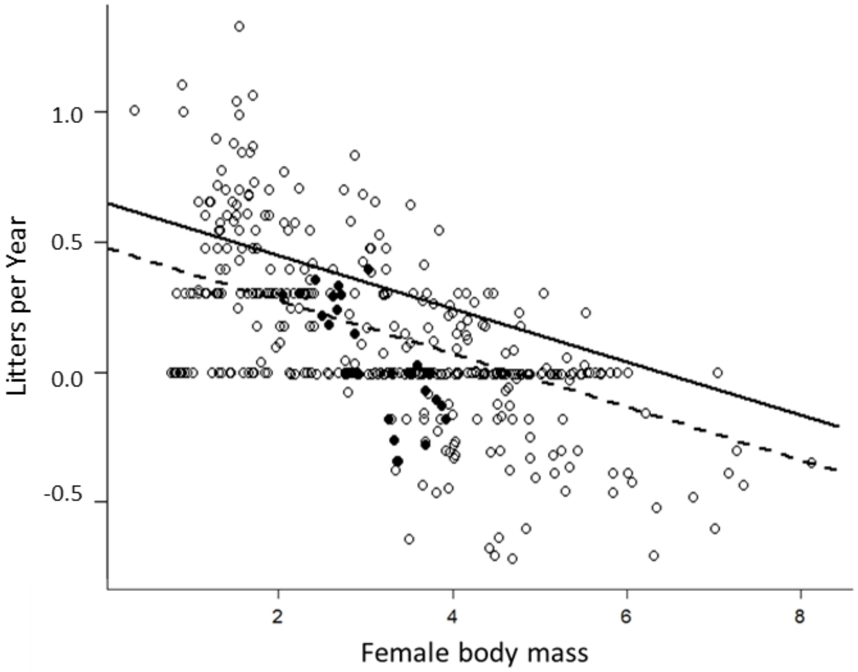


**Figure 1: Litters per year and allocarrying.** For a given body size, species with carrying by alloparents (filled circles, continuous line) have more litters per year than those without (open circles, dotted line).

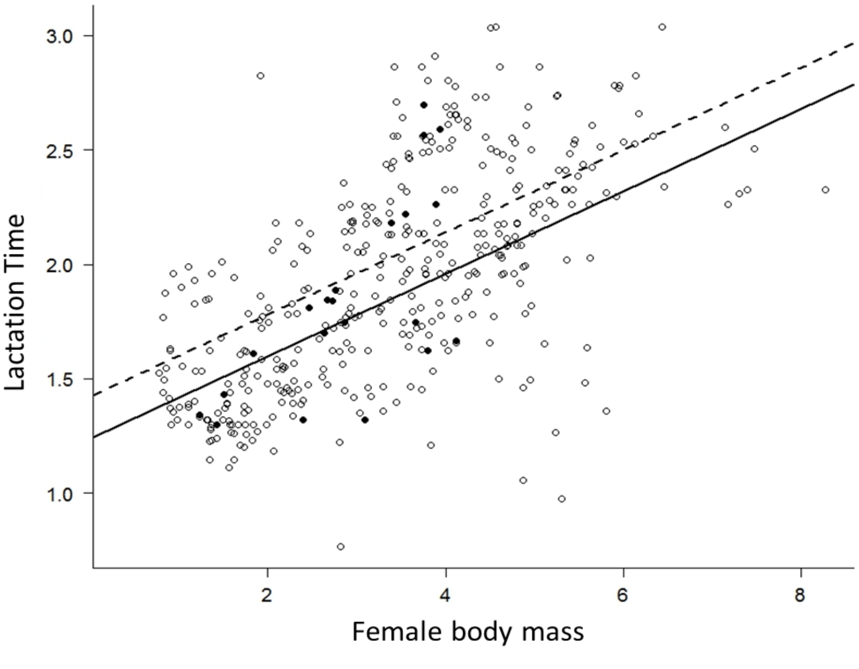


**Figure 2: Lactation time and allogrooming.** For a given body size, species with grooming by alloparents (filled circles, continuous line) have a shorter gestation than those without (open circles, dotted line).

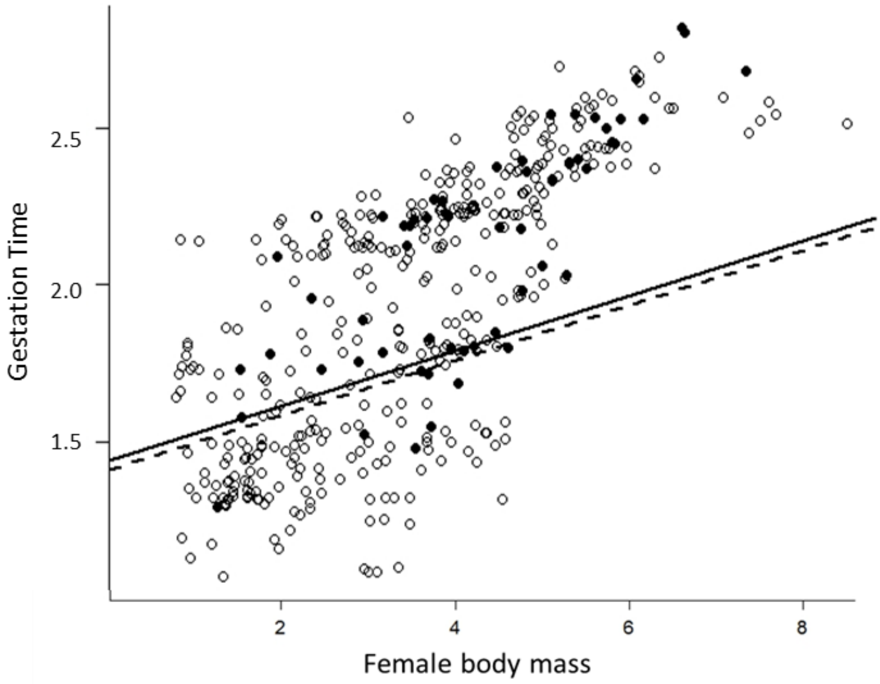


**Figure 3: Allonursing and gestation time.** For a given body size, species with allonursing (filled circles, continuous line) have a longer gestation than those without (open circles, dotted line).

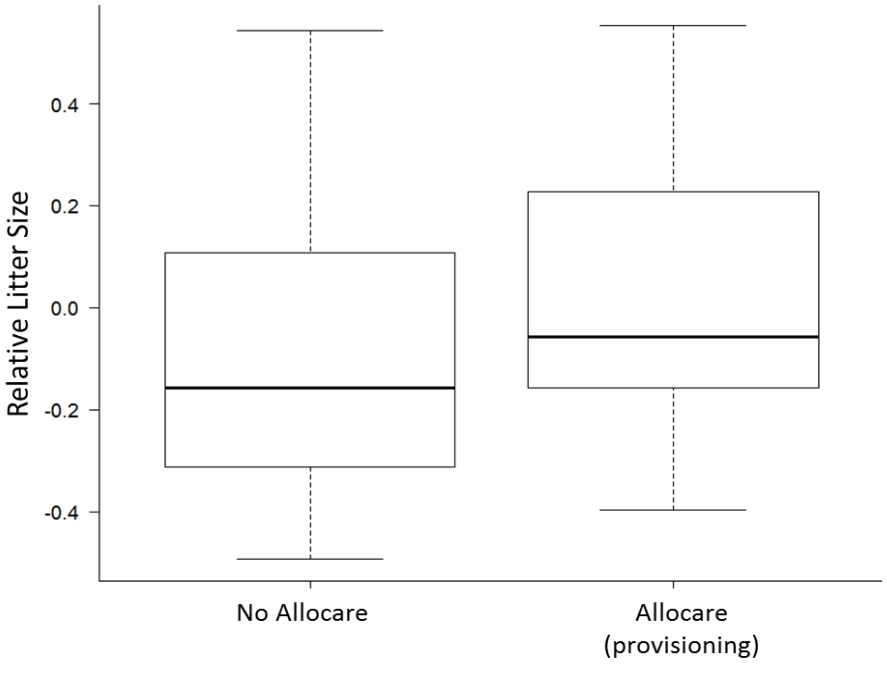


**Figure 4: Alloprovisioning and litter size.** For a given body size, species with provisioning by alloparents have larger litters than those without.

## Discussion

The importance of the specific behaviours expressed by carers has been largely unrecognised in studies on the evolution of parental care. This chapter and chapter 3 (West & Capellini 2016) demonstrate that individual behaviours, as well as the same behaviours performed by either the male or by alloparents, may have remarkably different associations with female life history traits, suggesting that the underpinning mechanisms, costs and benefits to the carer depend on the identity of the carer and the behaviour performed. In line with the predictions of the load-lightening hypothesis (Crick 1992), species where helpers carry the offspring have more frequent litters but, unlike those with male care, do not have a shorter lactation. Thus, allocarrying may allow females to regain body condition faster post-weaning, rather than reducing the energetic costs during lactation as carrying by the male (Chapter 3; West & Capellini 2016). Furthermore, species in which alloparents provision the offspring have larger litters than species without. However, allonursing, grooming and huddling by helpers do not conform the load-lightening hypothesis and the selective pressures that have promoted their evolution remains unclear.

Allocare enables females to produce larger litters, as in both birds and mammals (Brown 1987; Meade et al. 2010; West & Capellini 2016), through load-lighthening (Crick 1992). Here we show that larger litter sizes are found in species with provisioning by helpers, as well as provisioning by males (West & Capellini 2016; Stockley & Hobson 2016), suggesting that provisioning has the same benefits regardless of which individual is providing the resources. Provisioning is energetically costly (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012), and searching for additional food may increase risks of predation or injury (Harfenist & Ydenberg 1995). Additional provisioning by helpers or the father may help to reduce these costs for the mother while also providing extra resources that may allow females to meet the higher energetic demands of larger litters. At present, however, there is insufficient information to separate provisioning by helpers of only the offspring from provisioning both mothers and offspring. Because direct offspring provisioning can only occur post-weaning, we cannot identify yet whether the benefits of provisioning are indirect by supporting the mother during gestation and lactation, or are direct by supporting the offspring once they begin feeding on solid food, or are a combination of both. Few studies measure how much food helpers provide, but those that do show that alloparents contribute substantially to the offspring's diet (Hodge 2005; Brotherton et al. 2001), with as much food as parents bring to their own offspring in meerkats (Brotherton et al. 2001). Post-weaning provisioning may be essential for offspring growth and survival to independence, as the energetic costs of offspring growth may be higher during this period than during weaning. In several species including meerkats, mongooses, and many canid species helpers continue to provision offspring heavily post-weaning (Hodge 2005; Brotherton et al. 2001; Moehlman 1979; Sparkman et al. 2011; Mech 1974; Walton & Joly 2003), but no studies have investigated the potential benefits of postweaning provisioning at a large scale.

Provisioning of both offspring and females by males precedes the evolution of large litters (Stockley & Hobson 2016), in support of the hypothesis that it allows females to raise more offspring than they could raise alone. No study to date has tested the order of evolution between alloprovisioning and litter size, although (Lukas & Clutton-Brock 2012a) propose that the evolution of cooperative breeding, a social system that involves substantial alloparental help, follows the evolution of large litters. This may suggest that selection favours the evolution of allocare behaviours in species with larger litters, as these may require more resources than parents can provide alone. However, allocare is found in species with diverse social systems, and in these non-cooperative species, the directionality of the relationship between provisioning and litter size may differ, with alloprovisioning facilitating the evolution of larger litters through load-lightening. Regardless of the order in which these litter size and alloprovisioning evolve however, we show that litters size and provisioning by helpers (this study), as well as provisioning by the male (Chapter 3; West & Capellini 2016), are evolutionarily associated, and that the energetic contribution of provisioning towards female fecundity are the same regardless of the identity of the carer.

Allocare is proposed to have a load-lightening effect on maternal reproductive costs and ultimately enhance female fitness (Crick 1992). If females are assisted in offspring care by helpers, they may produce more frequent litters; either by weaning the current offspring more quickly (Chapter 3; West & Capellini 2016), or by regaining condition faster post-weaning to breed again sooner (Stanford 1992). Here we find that females of species with allocarrying produce more litters per year but that this is not determined by a reduction in either lactation or gestation time. These results thus suggest that allocarrying is likely to increase reproductive frequency by allowing females to speed up post-weaning recovery. Carrying is not only energetically costly (Sánchez et al. 1999; Tardif 1994), but it can also compromise the carer's foraging ability and survival (Schradin & Anzenberger 2001; Sánchez et al. 1999; Tardif 1994). For example, leaping ability in callitrichid primates decreases proportionally with the weight of the offspring being carried (Schradin & Anzenberger 2001). By carrying the offspring, helpers may allow the mother to invest more time foraging for herself (Mitani & Watts 1997), especially if carrying continues post-weaning when offspring are likely to be extremely heavy (Bales et al. 2000). Interestingly, the same behaviour performed by males associates with shorter lactation and has a load-lightening effect on female reproductive investment during the most expensive period of reproduction (Chapter 3; West & Capellini 2016). Thus, the same behaviour appears to influence female reproduction at different times through potentially different mechanisms; male carrying is more likely to enable females to invest the saved energy into greater milk quality or quantity, while carrying by helpers is more likely to facilitate post-weaning recovery. Ultimately, however, both increase female reproductive frequency and fitness, which in turn benefits both the males and alloparents that are older offspring or other related individuals.

Altogether, results for allocarrying and alloprovisioning are consistent with the hypothesis that these behaviours reduce females' reproductive costs and increase maternal fitness (Crick 1992). However, other allocare behaviours do not appear to conform the load-lightening hypothesis and the selective pressure that promoted their evolution remains elusive. Allonursing is associated with a longer gestation but is unrelated to neonate or weaning mass, lactation time, frequency of breeding, and litter size. Previous studies conclude that allonursing may evolve simply because the costs to the mother are low (MacLeod & Lukas 2014; Packer et al. 1992; MacLeod et al. 2015), yet given the high costs of lactation (Hanwell & Peaker 1977; Clutton-Brock et al. 2009) it seems unlikely that this behaviour has no associated benefits. One possibility is that by receiving milk from multiple females offspring may gain a wider range of immune compounds and increase their immunocompetence (Roulin & Heeb 1999), a hypothesis that has yet to be tested. Moreover, at present allonursing includes all cases where offspring gain milk from other females beyond their mothers, but there is substantial interspecific variation about how this happens. For example, while lionesses share nursing of their offspring (Pusey & Packer 1994b), in pinnipends allonursing appears to be misdirected parental care by females unable to discriminate their own pups (Maniscalco et al. 2007), and in several artiodactyls allonursing appears to be the results of milk theft (Murphey et al. 1995; Packer et al. 1992). Thus it is unlikely that the benefits and costs of allonursing are the same across such a diverse range of conditions. Allogrooming and huddling associate with shorter lactation but no other life history trait. Grooming and huddling have substantial energetic costs in some species (Fietz & Dausmann 2003; Campbell et al. 2009; Kenkel et al. 2014; Saltzman et al. 2015) and if performed by helpers they may reduce these costs for the mother. However, our results do not suggest any specific benefits for female reproductive output or offspring growth. These behaviours may thus provide benefits not studied here, such as improved thermoregulation of neonates or reduced parasite load, and thus improve offspring survival. At present however, data are not sufficient to test these hypotheses and why allogrooming and huddling associates with shorter lactation remains unclear.

Finally, mammals with care by helpers are predicted to have larger or faster growing offspring (Hodge 2005; Emlen 1984). We find no indication that any specific behaviour is associated with an increase in offspring neonate or weaning mass, after controlling for the relevant duration of maternal investment. We previously found that carnivores with care by helpers have significantly larger neonates than those without allocare (Chapter 3; West & Capellini 2016), but this does not appear to be linked to a specific allocare behaviour.

To conclude, by investigating specific care behaviours and considering the identity of the carer, we reveal a far more complex patterns of associations between allocare, male care, and life history traits, which provides important insight into the potential underlying mechanisms driving the evolution of parental care and its implications for female reproduction. While both male care and care by helpers associate with increased female fecundity, this may be achieved through different mechanisms at different stages of female reproduction, depending on the behaviour considered. Carrying by helpers associates directly with more frequent breeding, suggesting that females might recover body condition for the next breeding attempt more quickly post-weaning (Stanford 1992). Conversely, carrying by the male is more likely to reduce female energetic costs during lactation (Chapter 3; West & Capellini 2016), and only indirectly lead to increase breeding frequency. Provisioning is associated with larger litters when performed by either the male or the alloparents. However, the sequence of evolutionary events leading to the presence of alloprovisioning, male provisioning, and increased fecundity, remains unclear and may differ in relation to the identity of the carer. Altogether, these results therefore highlight the importance of considering the identity of allomaternal carers and the specific behaviours performed when investigating costs and benefits of parental behaviours.

# CHAPTER 7: THESIS CONCLUSIONS

This project investigates the evolution of biparental care in mammals and reveals a complex evolutionary feedback between parental behaviours, mating systems, paternity and life histories. Theoretical models suggest that the evolution of male care depends on high certainty of paternity (Trivers 1972; Queller 1997). However, I find that in mammals certainty of paternity is more strongly associated with the presence of social monogamy than male care, and monogamous species show reduced investment in traits for sperm competition (Chapter 2). Species with male care exhibit greater female fecundity and faster offspring growth rates (Chapter 3; West & Capellini 2016), in support of the hypothesis that males provide an energetic contribution towards female reproduction (‘load-lightening’ Crick 1992). However, male care behaviours are not equivalent; rather, the benefits to females vary across behaviours, as only carrying and provisioning females – but not grooming and huddling - associate with greater maternal reproductive output (Chapter 3; West & Capellini 2016). By considering the diversity in male care I demonstrate that only those male care behaviours related to ‘high fecundity benefits’ (carrying and provisioning) clearly follow the evolution of social monogamy (Chapter 4). I suggest that high-benefit behaviours can only evolve when males already gain high certainty of paternity (Chapter 2) through the presence of social monogamy and, once evolved, these behaviours in turn enhance female fecundity (Stockley & Hobson 2016) through load lightening (Chapter 3; West & Capellini 2016), helping males to further offset the costs of lost mating opportunities. Conversely, the evolutionary relationship between ‘low-benefit’ male care behaviours (grooming and huddling), as measured by female fecundity, and mating system is more dynamic as these care behaviours may both precede and follow the evolution of social monogamy (Chapter 4). Altogether these results indicate that there is a complex positive feedback between mating system, paternity, male care and female productivity (Figure 1). In chapter 5, I demonstrate that there is no evidence in support of the hypothesis that male care evolves to protect the offspring against high infanticide risk in mammals (Paul et al. 2000; Opie et al. 2013). Finally, parents are not the only individuals to care for the offspring, and older siblings and unrelated group members may help (‘alloparents’) (Wisenden 1999; Lukas & Clutton-Brock 2012a; Brown 1987; Riedman 1982; Mitani & Watts 1997; Ridley & Raihani 2008; Santos & Macedo 2011). Chapter 6 reveals that, like male care, some allocare behaviours (carrying and provisioning) but not others (grooming and huddling) associate with higher female fecundity through increased breeding frequency, consistent with a load-lightening mechanism (Crick 1992). Thus, the relationship between life history and parental care depends on the behaviour performed, the time of female reproduction at which it is performed, and the identity of the carer, with males having a greater impact during gestation and lactation, and alloparents post-weaning.

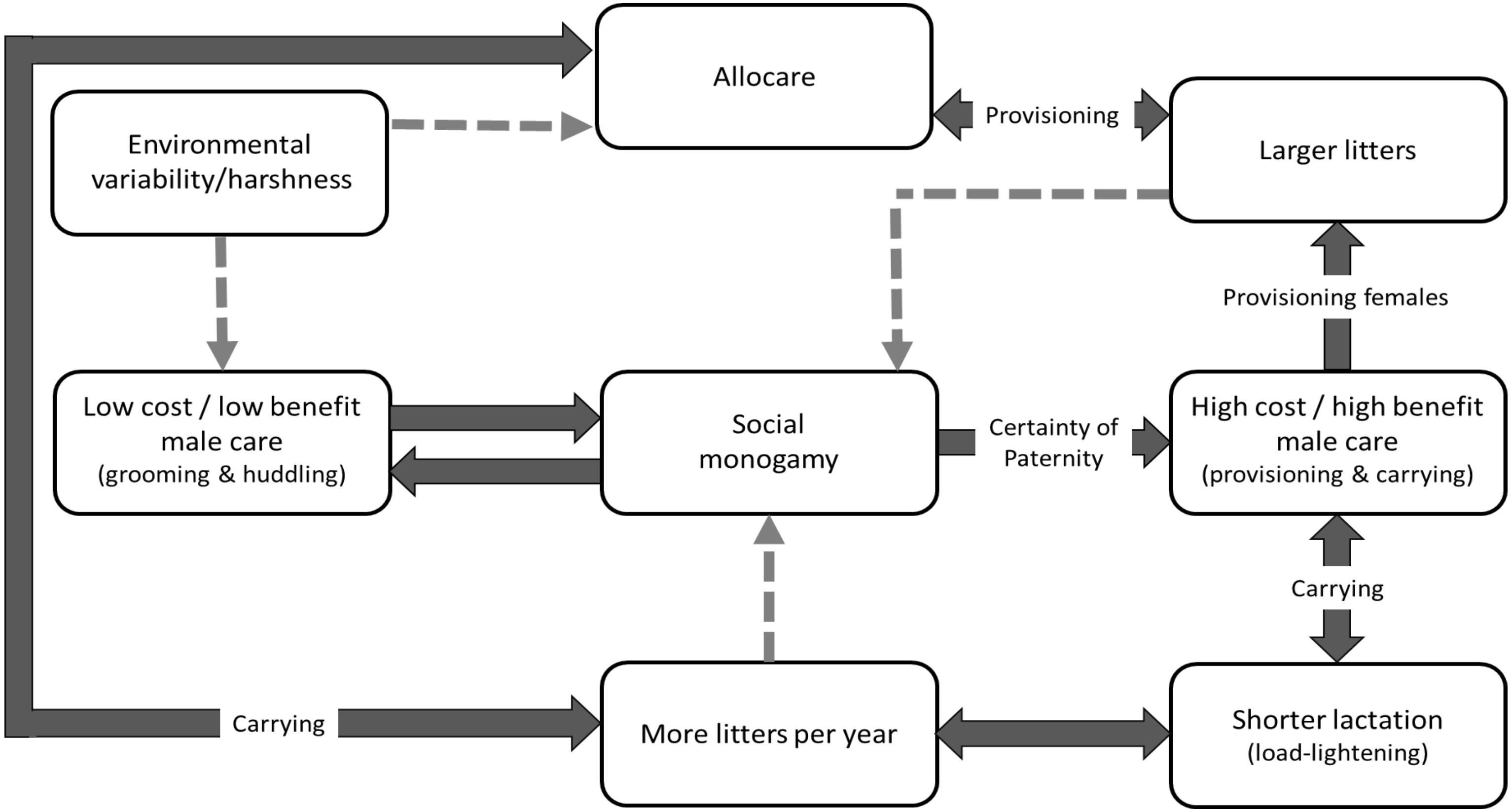


**Figure 1: Theoretical framework on the evolutionary feedback between male care, mating system, paternity and life history traits in mammals.** Behaviours that have low benefits for female fecundity may both precede and follow the evolution of social monogamy, which in turn leads to a higher certainty of paternity and promotes the evolution of more costly male care behaviours. High-cost, high-reward care behaviours increase female fecundity, either through the production of larger litters or a reduction in lactation time, which in turn leads to increased frequency of breeding. Greater female fecundity should then feed back into social monogamy, helping males to outweigh the opportunity costs of this mating system. Alloparental care also associates with life histories but through different mechanisms. I also propose that environmental harshness may be a driver in the evolution of both allocare and care behaviours which have low fecundity benefits, but which may have important survival benefits. The dark arrows represent the pathways tested here, with single headed arrows representing associations where directionality is known while dual headed arrows represent associations where directionality remains to be investigated. The dashed arrows indicate paths I propose which are yet to be investigated.

Certainty of paternity is often considered a key driver for the evolution of male care (Alonzo & Klug 2012; Trivers 1972; Queller 1997). Given the potentially high costs of caring, males should only invest heavily in rearing offspring that they have sired (Trivers 1972), thus species in which males care should have a higher certainty of paternity than those without (Kokko & Jennions 2012). This in turn should reduce the intensity of selection for investment in traits for sperm competition (Chapter 2). While I find that mammals with male care have greater levels of paternity than species without, so do socially monogamous mammals. However, only socially monogamous males exhibit a reduction in sperm competition related traits. Altogether, this suggests that higher paternity in species with male care is indirectly gained through social monogamy (Figure 1), which in mammals also leads to a lower intensity of sperm competition (Chapter 2). In other taxa with biparental care, such as birds however, social monogamy is not as strongly linked to paternity as in mammals due to frequent extra-pair mating (Griffith et al. 2008). In these systems, therefore, the interplay between male care, mating system, and paternity may differ; while high genetic paternity may still promote the evolution of male care (Møller & Cuervo 2000), a causal link between social monogamy and biparental care is less likely. Surprisingly, no comparative study to date has investigated the association between biparental care, mating system and paternity at a large scale in birds, despite the wealth of data for this group. To establish the generality of principles regarding how paternity and mating system relate to the evolution of biparental care, future studies should focus on investigating the directionality of the evolutionary pathway between paternity and care, and test whether certainty of paternity is an evolutionary precursor to care by males in other taxa.

While in mammals males can only care for the offspring within a biparental context, in many other taxa males may be the sole carer of the offspring (Mank et al. 2005; Balshine 2012). High certainty of paternity is thus expected to be an important pre-requisite for the evolution of uniparental care by males (Trivers 1972). The prevalence of uniparental male care in externally fertilizing species may indicate that males can achieve a higher certainty of paternity in these species (Gross & Shine 1981; Mank et al. 2005), as females should have fewer opportunities to influence fertilization (Trivers 1972; Clutton-Brock 1991; Blumer 1979; Evans & Rosengrave 2013, but see: Alonzo et al. 2016). Accordingly, males of some externally fertilizing species achieve high levels of genetic monogamy (e.g. DeWoody et al. 2000) and may be better able to estimate their likely paternity level for a clutch. However, cuckoldry and brood parasitism may also occur in externally fertilizing species (Clutton-Brock 1991; Alonzo & Warner 2000; Ota & Kohda 2015). We currently lack large-scale studies to comprehensively investigate whether males in externally fertilizing species achieve a higher certainty of paternity than those of internally fertilizing ones. Uniparental care by males may also be a strategy by which males can increase access to mates and in turn paternity and mating success (Kvarnemo 2005; Clutton-Brock 1991; Woodruff 1977). In frogs and insects, for example, males guard the fertilized eggs, despite this not always increasing offspring survival (Tallamy 2000; Woodruff 1977). If females mate preferentially with guarding males, however, selection should favour male egg guarding as a strategy to obtain copulations (Tallamy 2000; Kvarnemo 2005). As with biparental care, therefore, we may expect an evolutionary feedback between male care and paternity in male uniparental systems.

The majority of research on the evolution of male care has focused on the costs and benefits of parental care for the male, particularly with regard to certainty of paternity (Alonzo 2010; Queller 1997; Møller & Birkhead 1993; Gross & Sargent 1985). However, the energy, time and resources that males invest should also benefit females and offspring. Consistent with the hypothesis that males contribute to the energetic costs of female reproduction (Crick 1992), chapter 3 reveals that, by helping, males increase female fecundity and thus in turn their own fitness. This should be particularly important in monogamous species, which more frequently exhibit male care (Lukas & Clutton-Brock 2013; Opie et al. 2013), since by remaining with one female and helping to raise the offspring, monogamous males lose out on additional mating opportunities (Maynard Smith 1977). Biparental care in some insects, birds, and cichlid fishes may also evolve when additional mating opportunities are limited (Gilbert & Manica

2015; Remeš et al. 2015; Gonzalez-Voyer et al. 2008). Thus, the potential influence of male care on the cost/benefit trade-offs underpinning the evolution of mating system should be considered in future studies, since achieving a greater reproductive output via increased female fecundity can be a crucial way by which males can reduce the costs of a solitary or monogamous lifestyle. Specifically, if male care in non-mammalian species primarily evolves when males are unlikely to gain multiple partners due to a solitary lifestyle, care by males may lead to similar fecundity benefits to outweigh the costs of lost matings as those found in mammals. Whether this applies to uniparental systems though is unclear. Previous research in fish and frogs shows that the presence of parental care is associated with larger egg size (Summers et al. 2006; Kolm & Ahnesjö 2005; Sargent et al. 1987). Yet these studies do not consider the sex of the carer or the specific behaviour performed, making it difficult to evaluate exactly how parental care mediates the evolution of life history traits and the trade-offs between them. Specifically, egg size is often traded off against egg number (Charnov & Ernest 2006; Smith & Fretwell 1974; Closs et al. 2013; Walker et al. 2008; Warne & Charnov 2008). Thus, the evolution of uniparental care may not be linked to load-lightening and increased female fecundity as in biparental mammals (Chapter 3; West & Capellini 2016), but may instead indicate a greater investment in offspring size to promote survival, which in turn may move the species' life history strategy towards the slow end of the life history continuum ('safe-harbour' hypothesis: Shine 1978; Sargent et al. 1987). To fully understand how parental care fits within and possibly alters species' life history strategies in biparental and uniparental systems, further comparative studies are needed to determine what benefits uniparental care has for the offspring and females, and whether these benefits differ depending on the sex of the carer.

In addition to providing energetic benefits for females, male care can also benefit the offspring, increasing offspring size or growth rates either pre or post-natally, either through direct provisioning or indirectly by supporting the mother. In egg-laying species, females supported by males are often able to produce larger eggs and subsequently hatchlings which enjoy greater survival to adulthood (Shine 1978; Clutton-Brock 1991; Kolm & Ahnesjö 2005; Gross & Sargent 1985). Likewise in mammals the presence of male care may allow females to produce larger neonates (Woodroffe & Vincent 1994), although I find no support for this hypothesis. Alternatively care can be directed towards the offspring themselves; males may directly provision the young for example (Royle et al. 2006; Lyon et al. 1987; Muldal et al. 1986). I find that the presence of male care in mammals enables offspring to grow at a faster rate from birth to weaning. A faster growth rate enhances offspring survival in both mammal and non-mammal species (Wright & Brown 2002; Côté & Festa-Bianchet 2001; Eggert et al. 1998). For example in birds, such as snow buntings (*Plectrophenax nivalis*) and zebra finches (*Taeniopigia guttata*), offspring growth and fledging success are substantially improved by the presence of two provisioning parents (Royle et al. 2006; Lyon et al. 1987; Muldal et al. 1986). Few studies thus far have explicitly measured the direct energetic benefits male care may have for the offspring however. A limited number of studies in mammals and birds quantify the amount of food that the male brings to the offspring (Garrott et al. 1984; Hodge 2005), but these studies can only quantify the benefits of care during life-stages when offspring are feeding (post-weaning in mammals and post-hatching in brids), and whether there are other energetic benefits for the offspring as a result of male care is currently little studied. Future studies in mammals, for example, could investigate the energetic benefits of male care by quantifying how milk quantity, composition, and energetic content change when males assist the female in offspring care as compared when absent. If care by males has a load lightening effect on females during lactation (Chapter 3; West & Capellini 2016), females supported by caring males should produce higher quality milk in greater quantities. Future empirical studies should also focus on the longer-term benefits of male care on the offspring such as whether faster growth or a larger size improves offspring survival to independence and the offspring's reproductive success.

Male care is diverse across mammals in the specific behaviour expressed. This research demonstrates that such diversity matters and that not all behaviours have the same potential benefits. Carrying and provisioning behaviours, generally thought to be more energetically costly (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012), appear to have a load-lightening effect on females and associate with increased female fecundity and faster offspring growth (Chapter 3; West & Capellini 2016). Conversely, grooming and huddling with the offspring, often considered to be less costly (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012 but see: Campbell et al. 2009; Fietz & Dausmann 2003; Kenkel et al. 2014; Saltzman et al. 2015), are unrelated to life history traits (Chapter 3; West & Capellini 2016). Thus, while the relative costs of these behaviours remain unknown, my results demonstrate that they do not have the same benefits, which may help to explain the differences in their evolutionary relationship with social monogamy. Carrying and provisioning behaviours consistently evolve after social monogamy, while huddling and grooming can both precede and follow it (Chapter 4). Therefore, given that social monogamy is associated with a higher certainty of paternity in mammals (Chapter 2; Soulsbury 2010), altogether these results suggest that selection should favour the evolution of costly care behaviours, such as carrying and provisioning, only when the male has a greater certainty of paternity (Trivers 1972) (Figure 1). In other groups, the relationship between paternity and social mating system is weaker and parental care may not be evolutionarily dependent on social monogamy, but the evolution of high-cost male care may still require a high certainty of paternity. For example, of a suite of care behaviours (provisioning, nest building, and incubation) in birds only provisioning is associated with higher certainty of paternity (Møller & Cuervo 2000). Thus, I expect that only provisioning, but not nest building or incubation, would have a load lightening effect on female reproductive costs and enhance maternal reproductive output.

Grooming and huddling behaviours on the other hand appear to have no benefits in terms of maternal fecundity (Chapter 3; West & Capellini 2016), and are possibly less expensive than carrying and provisioning (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012 but see: Campbell et al. 2009; Fietz & Dausmann 2003; Kenkel et al. 2014; Saltzman et al. 2015). If the costs of these care behaviours are lower than those of carrying and provisioning but grooming and huddling still improve offspring survival (Gubernick & Teferi 2000; Wright 2006; Wynne-Edwards & Lisk 1989), selection may promote their evolution even in species with high levels of female promiscuity and despite risk of caring for unrelated offspring (Griffin et al. 2013). There is a remarkable paucity of data on the relative costs of specific care behaviours. Few studies have experimentally measured weight changes over time, as an indication of energetic costs, in fathers that care compared with males housed with non-reproducing females and without offspring (Campbell et al. 2009; Fietz & Dausmann 2003; Kenkel et al. 2014; Saltzman et al. 2015). These studies suggest high costs to care behaviours such as grooming and huddling as males performing these behaviours show a significant reduction in weight. However these studies are limited to a laboratory setting. While it is possible to monitor weight changes in the wild (e.g. Clutton-Brock et al. 2001), the energetic costs of specific activities can also be measured in the field with heart-rate monitoring that, in conjunction with behavioural observations, can provide a more accurate estimate of energy expenditure for different behaviours (Butler et al. 2004). More recently, the development of novel triaxal accelerometers (Ropert-Coudert & Wilson 2005; Wilson et al. 2006) has opened up unique opportunities to quantify energy costs for very specific behaviours in wild animals, and have successfully measured the energetic expenditure of hunting in cheetahs (*Acinonyx jubatus*)(Wilson et al. 2013), deep diving in shags (*Phalacrocorax aristotelis*) (Sakamoto et al. 2009), swimming in bonefish (*Albula vulpes*) (Murchie et al. 2011), and foraging in sea lions (*Eumetopias jubatus*) (Fahlman et al. 2008). Thus, accelerometers could help quantifying the energetic costs of diverse care behaviours, such as carrying the offspring and huddling, and provide reliable and comparable data of their relative costs. Once data become available on costs of different care behaviours for a large number of taxa, we can more fully evaluate to what extent costs help explain the evolutionary origin and maintenance of parental care by males.

Chapter 4 shows that grooming and huddling can both follow and precede the evolution of monogamy (Figure 1), while provisioning and carrying follow monogamy most likely because higher certainty of paternity is needed to compensate for their high costs (Figure 1). The potential drivers for the evolution of huddling and grooming behaviours are currently unclear, but one hypothesis is that these care behaviours enhance offspring survival in harsh or variable environments. Although numerous studies in a range of species show that the presence of male care increases offspring survival (Townsend et al. 1984; Wolf et al. 1988; Markman et al. 1996; Gubernick et al. 1993; Gubernick & Teferi 2000; Wright 2006; Wynne-Edwards & Lisk 1989), few focus on the specific behaviour performed by the male (Gubernick & Teferi 2000; Wright 2006; Wynne-Edwards & Lisk 1989) or the impact of environmental conditions on offspring survival (Wynne-Edwards & Lisk 1989). However, some studies do indicate that the survival benefits of parental care in harsh environments may act as evolutionary drivers for certain care behaviours (Santos et al. 2016; Lukas & Clutton-brock 2017). A recent study in insects, for example, finds that higher predation risk in hot, humid environments may promote the evolution of parental care, in the form of offspring guarding, by either sex, as this behaviour can increase offspring survival (Santos et al. 2016), while cooperative breeding and alloparental care are more likely in species occupying arid environments (Lukas & Clutton-brock 2017). One still untested possibility, therefore, is that environmental factors select for additional care by males, initially as lower costs behaviours that increase offspring survival and this can in turn trigger a cascade of evolutionary events, promoting the evolution of social monogamy and increased paternity, followed by costly care and lastly greater female fecundity (Figure 1).

By analysing behaviours separately, I have uncovered a complexity in the correlated evolution between male parental care and monogamy that would have otherwise remained masked. There is therefore great potential in considering the full diversity and complexity of phenotypes when investigating their evolutionary causes and consequences. Parity mode, for example, is much more diverse than the simple oviparity vs viviparity distinction often assumed. Cartilaginous fish species exhibit a wide range of reproductive strategies, from simple egg-laying to highly complex placental viviparity or in-utero cannibalism (Dulvy &

Reynolds 1997). While viviparity is another means by which females provide extra resources and protection to their developing offspring, the diverse forms of viviparity may require different levels of maternal investment (Wourms & Lombardi 1992; Dulvy & Reynolds 1997; Meiri et al. 2012). Considering the specific parity type may not only reveal different life history trade-offs across modes of reproduction but also clarify the evolutionary origin and history of more complex placental structures. Crucially, by explicitly considering the diversity of phenotypes, future studies could identify evolutionary feedbacks in complex systems, including in the context of evolutionary arms races between the sexes (Brennan et al. 2007; Hosken & Stockley 2004; Arnqvist & Rowe 2002), parent-offspring conflict or male-male competition (Stockley & Parker 2002; Bro-Jørgensen 2007; Emlen 2008; Hill 1991).

Recent work reveals that biparental care and social monogamy are evolutionarily correlated in mammals (Lukas & Clutton-Brock 2013; Opie et al. 2013), but it remains unclear what role, if any, infanticide plays in this relationship. Infanticide risk is proposed to promote the evolution of male care, as caring males may deter or defend against infanticidal conspecifics (Paul et al. 2000). Moreover, Opie et al. (2013) propose that infanticide in primates facilitates the evolution of social monogamy and in turn male care, but these results remain contentious (Opie et al. 2014; Lukas & Clutton-Brock 2014). Finally, both male care and a shorter lactation may be adaptive responses to reduce neonatal mortality due to infanticide (Opie et al. 2013; van Schaik 2000). In chapter 5 I find that, while male care and infanticide by males are evolutionarily associated, they are almost entirely mutually exclusive, implying that infanticide does not drive the evolution of male care in mammals. There are however exceptions to this general principle; in several rodent species for example, males are aggressive towards unfamiliar offspring but care for their own young (Elwood 1985; Elwood 1977; Gibber et al. 1984; Makin & Porter 1984). Why and how these species are exceptions from the general pattern remains unclear, and understanding how infanticide relates to male care in these species may prove an inviting venue for further study. In other taxa the evolutionary relationship between infanticide and care by males may differ from the patterns we observe in mammals. In numerous other groups, such as amphibians, birds, and fish, males can exhibit both caring and infanticidal behaviours. In some taxa, infanticide by males appears to be a means to ensure the paternity of the offspring that the male subsequently cares for (Chen et al. 2008; Robertson & Stutchbury 1988; Whittingham et al. 1993; Ringler et al. 2017). In tree swallows (*Tachycineta bicolor*) for example, males are territorial, and when they take over nesting sites from other males they kill any offspring from the previous male, but provision their own offspring when certain of their paternity (Robertson & Stutchbury 1988; Whittingham et al. 1993). Likewise, male frogs (*Allobates femoralis*) ensure paternity by cannibalizing all eggs in their territory prior to mating, but provide extensive care for any subsequent eggs laid in their territory (Ringler et al. 2017). In other groups however, cannibalistic infanticide appears to be a response to environmental conditions; males of some fish species that typically exhibit offspring care may cannibalize their own eggs if food supplies are scarce (Kvarnemo et al. 1998; Rohwer 1978). Similarly, male gerbils (*Meriones unguiculatus*) show a significant increase in their rates of infanticide and cannibalism in response to food deprivation (Elwood & Ostermeyer 1984). In these cases the switch between care and infanticide may represent a trade-off between current and future investment if, by consuming the current offspring, a male can ensure his own survival. Thus, infanticide in territorial species may represent an adaptation to achieve high levels of paternity and to ensure that care is directed towards the offspring of the caring male, while cannibalism may be driven by changing environmental conditions. The general pattern of evolution between male care and infanticide in these groups however, remains unclear. Further studies on the correlated evolution between male care and infanticide in other taxa are needed to determine not only whether species where males switch between infanticide and care are common coevolving adaptations or, as in mammals, they are exceptions to the rule, but also how infanticide relates to other factors such as paternity or environmental variability.

Alloparental helpers may also contribute to caring for the offspring in a wide range of species, from insects and fish, to mammals and birds (Wisenden 1999; Lukas & Clutton-Brock

2012a; Brown 1987; Riedman 1982; Queller et al. 2000; Cant 2012). These individuals help either when they are closely related to the offspring and gain inclusive fitness benefits (Isler & van Schaik 2009; Mitani & Watts 1997; Woxvold & Magrath 2005; Queller et al. 2000) or when the costs of not helping are high (Ratnieks & Wenseleers 2008). Chapter 6 finds support for the load-lightening hypothesis of alloparental care (Crick 1992) but, as with male care, only some specific behaviours benefit females. Specifically carrying and provisioning by helpers associate with increased maternal fecundity through the production of larger and more frequent litters. While the benefits of allocare and care by males may at first appear similar, I identify substantial differences in the specific timing of maternal reproduction they may influence. While care by males appears to increase female breeding frequency by enabling females to wean the offspring earlier (Chapter 3; West & Capellini 2016), alloparental care appears to allow females to speed up post-weaning recovery and to breed again sooner (Chapter 6). Why similar behaviours have different evolutionary outcomes is currently unclear however, and the specific timing of behaviours performed by both males and helpers need to be investigated in order to help understand these differences. Males and helpers may differ in their degree of relatedness to the offspring. While helpers can be full-siblings, and therefore equally related to the young as the parents are (assuming all young are equally related), half-siblings, cousins or even unrelated individuals may provide offspring care (Cant 2012; Wisenden 1999; Dunn et al. 1995; Queller et al. 2000). Several studies identify relatedness as an important factor in an individual’s decision to care (Kokko et al. 2001; Reyer 1986; Komdeur 1994), but whether differences in relatedness alter the relationship between allocare and life-histories is uncertain. Because alloparents may be less closely related to the offspring than the parents (Cant 2012; Queller et al. 2000; Dunn et al. 1995), the costs of care are likely to differ and be potentially higher for helpers than the parents. Furthermore, in some species, such as the western bluebird (*Sialia mexicana*), parents reduce their own levels of offspring care in response to the presence of helpers, implying that helpers incur higher costs during offspring care than parents do (Dickinson et al. 1996). As for male care, however, data on the energetic costs of different allocare behaviours are scarce, making direct comparisons of behavioural costs difficult, it may be, for example, that helpers invest less in energetically costly behaviours than parents do.

As with male parental care, the evolution of care by helpers may also be favoured in harsh environments if these behaviours help to increase offspring survival. Numerous studies find a close association between drier or more variable environments and social systems where alloparenting is prevalent, such as cooperative breeding (Jetz & Rubenstein 2011; Rubenstein & Lovette 2007; Lukas & Clutton-brock 2017). This association has been suggested to indicate either a need for help in such environments, or a prohibitively high cost of reproducing individually (Emlen 1984; Covas et al. 2008; Rubenstein 2011). However, the directionality of this association remains uncertain; while the survival benefits of allocare may drive the evolution of helping behaviours in harsh environments, it is also possible that the presence of helpers may instead allow species to move into more challenging environments. A similar question has recently been investigated in birds and, contrary to prevailing views, the evolution of cooperative breeding systems is found to precede the colonization of harsh environments (Cornwallis et al. 2017). Further comparative studies are needed to investigate not only whether this pattern applies in other taxa, but also whether this relationship is specific to cooperative breeding or is determined by alloparental care that is present in some cooperative species (Figure 1). Furthermore, future studies need to identify whether male care and care by helpers evolved in a correlated fashion and the possible order of evolution between them. Both male care and care by helpers associate with larger litters, but while male provisioning promotes the evolution of larger litters (Stockley & Hobson 2016), the order of evolution for allocare and litter size is unknown. Large litters may be a prerequisite for the evolution of cooperative breeding systems where parents rely on alloparental help (Lukas & Clutton-Brock 2012a), suggesting that the directionality of the relationship between male care, life histories, and allocare may differ depending on carer identity, with biparental care preceding or facilitating the evolution of cooperative care systems (Figure 1).

In conclusion, this project provides compelling evidence for a complex evolutionary interplay between parental care, other behavioural traits and life history characteristics. Future studies should consider the costs and benefits of care for each sex in the context of how these may relate to both the recipient(s) and the other parent. Here I identify that one of the key drivers for the evolution of care by males is the presence of a social monogamy and its associated high certainty of paternity. Some male care behaviours also have a load-lightening effect on female reproductive costs and allow for an increase in female fecundity, which in turn helps males to balance the costs of monogamy (Figure 1). Social monogamy and male care follow a two-step process of evolution, with the evolution of care behaviours with low fecundity benefits preceding the evolution of a social monogamy and higher paternity levels, which in turn facilitates the evolution of care behaviours that associate with increased female fecundity (Figure 1). The results of this work have broader implications for other taxa, from uniparental species to complex traits such as viviparity. Future studies should quantify the specific energetic costs and benefits of individual care behaviours, to identify the direction of the evolutionary relationships between male care, allocare, and life histories, and investigate how the results presented here might apply to uniparental systems. Thus, future studies in mammals and other systems need to take a more holistic approach to the evolution of parental care and how it relates to other traits, such as life history evolution, mating systems, paternity assurance, and other reproductive behaviours.

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# APPENDICES

# Appendix 1: Supplementary Information for Chapter 2

## Supplementary methods

We collected data on sperm competition related traits from a variety of available primary and secondary sources (Anderson et al. 2005; Gage & Freckleton 2003; Gage 1998; Lemaître et al. 2009; Lüpold 2013; Iossa et al. 2008; Gomendio et al. 2011; Kenagy & Trombulak 1986; Breed & Taylor 2000; Cummins & Woodall 1985; Tourmente et al. 2011; Tourmente et al. 2013; Anderson & Dixson 2009) (see also main text, Methods, Data collection). Following Soulsbury (2010), data on testes mass are included in our dataset if taken during the breeding season from healthy adult males, and unambiguously referred to as the combined wet mass of both testes, excluding the epididimus. To control for allometry, data on male body mass are taken from same sources of testes mass data when available. Where body mass data are not available in the source of the testes mass data, the average male body mass for the species is taken from other available sources (Jones et al. 2009; Silva & Downing 1995).

We follow Gomendio et al.‘s (2011) protocol to ensure comparability of data collected for sperm measurements across species. Specifically, total sperm length measurements are included in our dataset if taken from the tip of the head to end of the flagella; head length is measured from tip of sperm head to the base of the flagella; and sperm head width is taken as the widest point of the sperm head. Mid-piece volume is calculated as a cylindrical volume (π*(width/2)2*length), following Anderson et al. (2005) and Gage (1998), using the width and length of mid-pieces from sperm of healthy adult males. We include estimate of sperm velocity if measured as the average distance that the sperms travel in a straight line per second at 37°C, as specified in Tourmente et al. (2011; 2013). Following previous studies (Iossa et al. 2008; Soulsbury 2010), we include data on numbers of sperm per ejaculate if measured as the average number of motile sperm per ejaculate. We ensure that all sperm measures are taken from sperm of healthy adult males at the peak of the reproductive season (Iossa et al. 2008; Soulsbury 2010).

Data on multiple paternity are extracted from available datasets and the primary literature (Soulsbury 2010; Avise & Liu 2011; Maher & Duron 2010; Ratkiewicz & Borkowska 2000; Borkowska et al. 2009; King & Winstanley 2014; Bergeron et al. 2011). We check all data on multiple paternity taken from secondary sources against the primary source to ensure that they conformed to our definition and protocols for data comparability (see main text, Methods, Data collection). Where more than one value is available for a species, we calculate the mean value for multiple paternity. Since species with larger litters also appear to have higher levels of multiple paternity, data on litter size are taken from comprehensive datasets of life history traits (Jones et al. 2009; West & Capellini 2016).

**Supplementary results**

The relationships between male care and all the morphological sperm traits are non-significant (Tables S3-8) and the inclusion of male care to these models does not improve model fit relative to a model without male care (total sperm length: Table S3, model 1 vs model 2, $LR_1$=1.70, p=0.192; flagellum length: Table S4, model 1 vs model 2, $LR_1$=0.66, p=0.417; mid-piece volume: Table S5, model 1 vs model 2, $LR_1$=2.68, p=0.102; head length: Table S6, model 1 vs model 2, $LR_1$=0.30, p=0.584). For head width (Table S7), body mass is non-significant so no likelihood ratio test can be conducted. The inclusion of male care in models with sperm count does not improve the fit of the model compared to a model without (Table S8, model 1 vs model 2, $LR_1$=1.04, p=0.308).

There is no significant association between social monogamy and total sperm length, sperm head length, sperm width, and sperm numbers (Tables S3 & 6-8). The inclusion of social monogamy to these models does not improve the fit of the model to the data (total sperm length: Table S3, model 1 vs model 3, $LR_1$=2.8, p=0.094; head length: Table S6, model 1 vs model 3, $LR_1$=0.12, p=0.729; sperm count: Table S8, model 1 vs model 3, $LR_1$=1.36, p=0.244). Again, for head width (Table S7) body mass is non-significant so no likelihood ratio test can be conducted.

While smaller bodied species have longer sperm than larger species (Table S3; see also (Gomendio et al. 2011; Lüpold & Fitzpatrick 2015), the relationship between total sperm length and body mass is not different in species with and without male care (Table S3, model 7), or social monogamy (Table S3, model 8), nor does including this interaction improve the fit of the model relative to models without interactions (Table S3, model 2 vs model 7: $LR_1$=0.02, p=0.888; model 3 vs model 8: $LR_1$=0.84, p=0.359). Shorter flagellum length with social monogamy is not restricted to small bodied species, as the interaction term between monogamy and body mass is non-significant in this model (Table S4, model 5), and does not improve the model fit (Table S4, model 3 vs model 5; $LR_1$=0.68, p=0.410). Similar results are found for male care and flagellum length (Table S4, model 2 vs model 4; $LR_1$=0.04, p=0.842) while mid-piece volume does not associate with male body mass (Table S5, model 4). Among large species, sperm number is considered a more important determinant for success in sperm competition than sperm size (Gomendio et al. 2011; Lüpold & Fitzpatrick 2015). However, we find no significant interaction between male body mass and either male care or social monogamy in models considering their relationship with sperm count, and including an interaction term does not improve model fit (Table S8, model 2 vs model 5: LR1=0.30, p=0.584; model 3 vs model 6: LR1=0.28, p=0.597).

## Supplementary tables

**Table S1: PGLS models for multiple paternity with male care and social monogamy while accounting for litter size.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for these models is 70 species, of which 15 have male care and 15 are socially monogamous. Sample sizes are too small (<8) to include either individual male care behaviours or high/low groups in the models. Models are numbered for ease of presentation.

| **Multiple Paternity** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **P** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Male care | -13.5 | 5.6 | -2.4 | 0.018 | 0.25 | 0.09 | -284.52 | 575.05 |
| | Litter size | 1.4 | 7.7 | 0.2 | 0.859 | | | | |
| **2** | Social Monogamy | -13.1 | 5.4 | -2.4 | 0.017 | 0.31 | 0.09 | -284.35 | 574.70 |
| | Litter size | 0.7 | 7.7 | 0.1 | 0.931 | | | | |
| **3** | Male Care | -7.5 | 7.7 | -1.0 | 0.333 | 0.28 | 0.10 | -283.86 | 575.72 |
| | Social Monogamy | -8.3 | 7.3 | -1.1 | 0.264 | | | | |
| | Litter size | 1.0 | 7.7 | 0.1 | 0.898 | | | | |

**Table S2: PGLS models for testes mass with individual male care behaviours.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for these models is 263 species, of which 36 have male care (11 carrying, 16 provisioning, of which 8 provision reproducing females, 17 grooming, and 15 huddling), and 40 are socially monogamous. The sample size for models with litter size is 217 species, of which 34 have male care while 37 are socially monogamous. Models are numbered for ease of presentation.

| **Testes Mass** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Male body mass | 0.7 | <0.1 | 17.7 | <0.001 | 0.87 | 0.55 | -115.03 | 236.07 |
| | Male Care | -0.1 | 0.1 | -1.0 | 0.324 | | | | |
| **2** | Male body mass | 0.7 | <0.1 | 17.5 | <0.001 | 0.88 | 0.55 | -114.15 | 242.30 |
| | Carrying | 0.1 | 0.1 | 0.8 | 0.445 | | | | |
| | Provisioning females | <0.1 | 0.2 | 0.1 | 0.897 | | | | |
| | Provisioning offspring | -0.1 | 0.2 | -0.4 | 0.668 | | | | |
| | Grooming | -0.1 | 0.1 | -0.7 | 0.473 | | | | |
| | Huddling | -0.1 | 0.2 | -0.5 | 0.618 | | | | |
| **3** | Male body mass | 0.7 | <0.1 | 17.6 | <0.001 | 0.86 | 0.56 | -112.34 | 240.68 |
| | Carrying | 0.1 | 0.1 | 0.9 | 0.360 | | | | |
| | Provisioning females | 0.1 | 0.2 | 0.3 | 0.787 | | | | |
| | Provisioning offspring | <0.1 | 0.2 | 0.1 | 0.899 | | | | |
| | Grooming | -0.1 | 0.1 | -0.4 | 0.692 | | | | |
| | Huddling | -<0.1 | 0.2 | -0.1 | 0.906 | | | | |
| | Social Monogamy | -0.2 | 0.1 | -1.9 | 0.059 | | | | |
| **4** | Male body mass | 0.6 | <0.1 | 17.7 | <0.001 | 0.82 | 0.61 | -90.49 | 188.97 |
| | Litter size | <0.1 | 0.1 | 0.3 | 0.767 | | | | |
| | Male Care | -0.1 | 0.1 | -1.0 | 0.301 | | | | |
| **5** | Male body mass | 0.6 | <0.1 | 17.6 | <0.001 | 0.84 | 0.60 | -89.61 | 195.23 |
| | Litter size | <0.1 | 0.1 | 0.3 | 0.776 | | | | |
| | Carrying | -<0.1 | 0.3 | -<0.1 | 0.983 | | | | |
| | Provisioning females | -0.2 | 0.4 | -0.4 | 0.663 | | | | |
| | Provisioning offspring | -0.1 | 0.2 | -0.4 | 0.706 | | | | |
| | Grooming | -0.2 | 0.1 | -1.6 | 0.119 | | | | |
| | Huddling | 0.1 | 0.3 | 0.4 | 0.677 | | | | |
| **6** | Male body mass | 0.6 | <0.1 | 17.7 | <0.001 | 0.81 | 0.62 | -88.46 | 186.92 |
| | Litter size | <0.1 | 0.1 | 0.2 | 0.837 | | | | |
| | Male Care | <0.1 | 0.1 | 0.1 | 0.943 | | | | |
| | Social Monogamy | -0.2 | 0.1 | -1.0 | 0.046 | | | | |
| **7** | Male body mass | 0.6 | <0.1 | 17.6 | <0.001 | 0.82 | 0.62 | -87.37 | 192.74 |
| | Litter size | <0.1 | 0.1 | 0.2 | 0.857 | | | | |
| | Carrying | -<0.1 | 0.3 | -<0.1 | 0.980 | | | | |
| | Provisioning females | -0.2 | 0.4 | -0.4 | 0.661 | | | | |
| | Provisioning offspring | <0.1 | 0.2 | 0.2 | 0.829 | | | | |
| | Grooming | -0.1 | 0.1 | -0.7 | 0.460 | | | | |
| | Huddling | 0.2 | 0.3 | 0.6 | 0.563 | | | | |
| | Social monogamy | -0.2 | 0.1 | -2.1 | 0.037 | | | | |
| **8** | Male body mass | 0.7 | <0.1 | 17.8 | <0.001 | 0.86 | 0.56 | -113.06 | 232.13 |
| | Social Monogamy | -0.2 | 0.1 | -2.2 | 0.027 | | | | |
| **9** | Male body mass | 0.6 | <0.1 | 17.8 | <0.001 | 0.81 | 0.62 | -88.46 | 184.92 |
| | Litter size | <0.1 | 0.1 | 0.2 | 0.832 | | | | |
| | Social Monogamy | -0.2 | 0.1 | -2.3 | 0.024 | | | | |

**Table S3: PGLS models for total sperm length with male care and social monogamy.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for all these models is 204 species, of which 22 have male care (10 species either carry the offspring or provision the female, 10 species provision the offspring, 11 groom, and 10 huddle with offspring), and 24 are socially monogamous.

| **Total Sperm Length** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Male body mass | -<0.1 | <0.1 | -3.1 | 0.002 | 0.82 | 0.05 | 149.16 | -294.32 |
| **2** | Male body mass | -<0.1 | <0.1 | -3.3 | 0.001 | 0.81 | 0.05 | 150.01 | -294.01 |
| | Male care | -<0.1 | <0.1 | -1.3 | 0.197 | | | | |
| **3** | Male body mass | -<0.1 | <0.1 | -3.3 | 0.001 | 0.80 | 0.06 | 150.56 | -295.13 |
| | Social monogamy | -0.1 | <0.1 | -1.7 | 0.093 | | | | |
| **4** | Male body mass | -<0.1 | <0.1 | -3.3 | 0.001 | 0.80 | 0.06 | 150.63 | -293.26 |
| | Male care | -<0.1 | <0.1 | -0.4 | 0.716 | | | | |
| | Social monogamy | -<0.1 | <0.1 | -1.1 | 0.263 | | | | |
| **5** | Male body mass | -<0.1 | <0.1 | -3.3 | 0.001 | 0.82 | 0.07 | 151.65 | -291.29 |
| | Carrying & prov. Females | -0.1 | 0.1 | -1.7 | 0.099 | | | | |
| | Provisioning offspring | <0.1 | 0.1 | 0.2 | 0.840 | | | | |
| | Grooming | -0.1 | 0.1 | -0.8 | 0.435 | | | | |
| | Huddling | <0.1 | 0.1 | 0.5 | 0.628 | | | | |
| **6** | Male body mass | -<0.1 | <0.1 | -3.4 | <0.001 | 0.80 | 0.08 | 152.14 | -290.28 |
| | Carrying & prov. Females | -0.1 | 0.1 | -1.4 | 0.159 | | | | |
| | Provisioning offspring | <0.1 | 0.1 | 0.6 | 0.584 | | | | |
| | Grooming | -0.1 | 0.1 | -0.9 | 0.365 | | | | |
| | Huddling | 0.1 | 0.1 | 0.8 | 0.422 | | | | |
| | Social Monogamy | -<0.1 | <0.1 | -1.0 | 0.316 | | | | |
| **7** | Male body mass | -<0.1 | <0.1 | -3.2 | 0.002 | 0.82 | 0.05 | 150.02 | -292.04 |
| | Male care | -<0.1 | 0.1 | -0.4 | 0.690 | | | | |
| | (Male body mass: Male care) | -<0.1 | <0.1 | -0.2 | 0.880 | | | | |
| **8** | Male body mass | -<0.1 | <0.1 | -3.2 | 0.002 | 0.80 | 0.07 | 150.98 | -293.96 |
| | Social monogamy | <0.1 | 0.1 | 0.2 | 0.863 | | | | |
| | (Male body mass: Social monogamy) | -<0.1 | <0.1 | -0.9 | 0.368 | | | | |
| **9** | Male body mass | -<0.1 | <0.1 | -3.3 | 0.001 | 0.80 | 0.07 | 151.55 | -291.10 |
| | Male care | -0.1 | 0.1 | -1.1 | 0.291 | | | | |
| | Social monogamy | 0.1 | 0.1 | 0.8 | 0.427 | | | | |
| | (Male body mass: Male care) | 0.1 | 0.1 | 1.0 | 0.345 | | | | |
| | (Male body mass: Social monogamy) | -0.1 | <0.1 | -1.3 | 0.182 | | | | |

**Table S4: PGLS models for flagellum length with male care and social monogamy.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for these models is 158 species, of which 17 have male care, and 20 are socially monogamous. Sample sizes are too small (<8) to include individual male care behaviours in the models.

| Flagellum Length | | Variable statistics | | | | Model statistics | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Male body mass | -<0.1 | <0.1 | -2.7 | 0.008 | 0.65 | 0.29 | 129.38 | -252.76 |
| | Sperm head length | 0.6 | 0.1 | 7.2 | <0.001 | | | | |
| **2** | Male body mass | -<0.1 | <0.1 | -2.8 | 0.006 | 0.65 | 0.30 | 129.71 | -251.43 |
| | Sperm head length | 0.6 | 0.1 | 7.1 | <0.001 | | | | |
| | Male care | -<0.1 | <0.1 | -0.8 | 0.421 | | | | |
| **3** | Male body mass | -<0.1 | <0.1 | -3.0 | 0.004 | 0.64 | 0.32 | 132.22 | -256.43 |
| | Sperm head length | 0.6 | 0.1 | 7.1 | <0.001 | | | | |
| | Social monogamy | -0.1 | <0.1 | -2.4 | 0.019 | | | | |
| **4** | Male body mass | -<0.1 | <0.1 | -2.7 | 0.007 | 0.65 | 0.30 | 129.73 | -249.47 |
| | Sperm head length | 0.6 | 0.1 | 7.1 | <0.001 | | | | |
| | Male care | -<0.1 | 0.1 | -0.1 | 0.896 | | | | |
| | Male body mass: Male care | -<0.1 | <0.1 | -0.2 | 0.838 | | | | |
| **5** | Male body mass | -<0.1 | <0.1 | -2.8 | 0.006 | 0.66 | 0.32 | 132.56 | -255.12 |
| | Sperm head length | 0.6 | 0.1 | 7.0 | <0.001 | | | | |
| | Social monogamy | -<0.1 | 0.1 | -0.1 | 0.913 | | | | |
| | Male body mass: Social monogamy | -<0.1 | <0.1 | -0.8 | 0.408 | | | | |
| **6** | Male body mass | -<0.1 | <0.1 | -2.8 | 0.006 | 0.64 | 0.33 | 133.32 | -252.63 |
| | Sperm head length | 0.6 | 0.1 | 7.1 | <0.001 | | | | |
| | Male care | -0.1 | 0.1 | -0.8 | 0.439 | | | | |
| | Social monogamy | <0.1 | 0.1 | 0.3 | 0.780 | | | | |
| | Male body mass: Male care | 0.1 | <0.1 | 1.1 | 0.283 | | | | |
| | Male body mass: Social monogamy | -<0.1 | <0.1 | -1.3 | 0.202 | | | | |

**Table S5: PGLS models for mid-piece volume with sperm length and male body mass.** We report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for the model with male body mass is 77 species while the sample size for the model without is 78 species. Sample sizes are too small (<8) to test individual male care behaviours against mid-piece volume.

| **Mid-piece Volume** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Total sperm length | 0.7 | 0.3 | 2.3 | 0.027 | 0.65 | 0.06 | -7.27 | 18.55 |
| **2** | Total sperm length | 0.6 | 0.3 | 2.1 | 0.043 | 0.67 | 0.09 | -5.93 | 17.85 |
| | Male Care | -0.2 | 0.1 | -1.6 | 0.107 | | | | |
| **3** | Total sperm length | 0.4 | 0.3 | 1.5 | 0.133 | 0.75 | 0.14 | -3.58 | 13.15 |
| | Social monogamy | -0.3 | 0.1 | -2.8 | 0.006 | | | | |
| **4** | Male body mass | -0.1 | <0.1 | -1.7 | 0.091 | 0.55 | 0.12 | -5.89 | 17.79 |
| | Total sperm length | 0.1 | 0.3 | 2.0 | 0.046 | | | | |

**Table S6: PGLS models for sperm head length with male care and social monogamy.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for these models is 160 species, of which 17 have male care, and 20 are socially monogamous. Sample sizes are too small (<8) to include individual male care behaviours in the models.

| **Sperm Head Length** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Flagellum length | 0.4 | 0.1 | 7.2 | <0.001 | 0.73 | 0.25 | 160.91 | -317.81 |
| **2** | Flagellum length | 0.4 | 0.1 | 7.2 | <0.001 | 0.73 | 0.25 | 161.06 | -316.13 |
| | Male Care | <0.1 | <0.1 | -0.6 | 0.578 | | | | |
| **3** | Flagellum length | 0.4 | 0.1 | 7.2 | <0.001 | 0.74 | 0.25 | 160.97 | -315.95 |
| | Social Monogamy | -<0.1 | <0.1 | 0.4 | 0.720 | | | | |
| **4** | Flagellum length | 0.4 | 0.1 | 7.2 | <0.001 | 0.73 | 0.25 | 161.38 | -314.76 |
| | Male care | -<0.1 | <0.1 | -0.9 | 0.373 | | | | |
| | Social Monogamy | <0.1 | <0.1 | 0.8 | 0.432 | | | | |

**Table S7: PGLS models for sperm head width with male care and social monogamy.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for these models is 106 species, of which 12 have male care, and 12 are socially monogamous. Sample sizes are too small (<8) to include individual male care behaviours in the models.

| **Sperm Head Width** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Male Care | <0.1 | 0.1 | 0.3 | 0.755 | 0.80 | <0.01 | 63.41 | -122.81 |
| **2** | Social Monogamy | 0.1 | <0.1 | 1.5 | 0.125 | 0.82 | 0.02 | 64.54 | -125.08 |
| **3** | Social Monogamy | 0.1 | 0.1 | 1.9 | 0.062 | 0.84 | 0.03 | 65.10 | -124.19 |
| | Male care | -0.1 | 0.1 | -1.1 | 0.289 | | | | |

**Table S8: PGLS models for sperm count with male care and social monogamy.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$, the model log-likelihood (Lh), and the AIC scores. The total sample size for these models is 55 species, of which 8 have male care, and 10 are socially monogamous. Sample sizes are too small (<8) to include individual male care behaviours in the models.

| **Sperm Count** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **AIC** |
| **1** | Male body mass | 0.4 | 0.2 | 2.8 | 0.007 | 0.82 | 0.13 | -58.04 | 120.08 |
| **2** | Male body mass | 0.4 | 0.2 | 2.5 | 0.016 | 0.83 | 0.15 | -57.52 | 121.03 |
| | Male care | -0.4 | 0.4 | -1.0 | 0.320 | | | | |
| **3** | Male body mass | 0.4 | 0.2 | 2.5 | 0.018 | 0.83 | 0.15 | -57.36 | 120.73 |
| | Social Monogamy | -0.4 | 0.3 | -1.1 | 0.260 | | | | |
| **4** | Male body mass | 0.4 | 0.2 | 2.4 | 0.020 | 0.83 | 0.15 | -57.35 | 122.71 |
| | Male Care | -0.1 | 0.6 | -0.2 | 0.885 | | | | |
| | Social Monogamy | -0.3 | 0.5 | -0.6 | 0.583 | | | | |
| **5** | Male body mass | 0.3 | 0.2 | 2.4 | 0.022 | 0.83 | 0.15 | -57.37 | 122.74 |
| | Male care | -0.9 | 1.0 | -0.9 | 0.398 | | | | |
| | Male body mass: Male care | 0.2 | 0.4 | 0.5 | 0.601 | | | | |
| **6** | Male body mass | 0.4 | 0.2 | 2.3 | 0.024 | 0.82 | 0.15 | -57.22 | 122.45 |
| | Social monogamy | -0.8 | 1.0 | -0.8 | 0.405 | | | | |
| | Male body mass: Social monogamy | 0.2 | 0.3 | -0.5 | 0.612 | | | | |

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## Appendix 2: Supplementary Information for Chapter 3

### Supplementary methods

We collected life history data from a range of available databases (Jones et al. 2009; Capellini et al. 2011; Silva & Downing 1995; Bielby et al. 2007; Barton & Capellini 2011; Ernest 2003; Carey & Judge 2002; Tacutu et al. 2013) (see also chapter 3 main text, Methods, Data collection). Data on male care were collected from a variety of primary and secondary sources (Walton & Joly 2003; Audet et al. 2002; Gompper & Vanak 2006; Egoscue 1979; Wolovich 2006; Wolovich 2008; Rotundo et al. 2005; Nowak 1999; Mason & Mendoza 1993; Lukas & Clutton-Brock 2013; Dettling 2002; Santos & Martins 2000; Wakenshaw 1999; Yamamoto et al. 1996; Nunes et al. 2000; Townsend 2001; Oftedal & Gittleman 1989; Malcolm 1985; Sharpe & Rosell 2003; Fietz & Dausmann 2003; Tardif et al. 1984; Elwood 1975; Hartung & Dewsbury 1979; McGuire & Henyey 2003; Fauske et al. 1997; Oliveras & Novak 1986; Woodroffe & Vincent 1994; Drygala et al. 2008; Ebensperger & Ramírez-Otarola 2010; McCarty & Southwick 1977; Pauw 2000; Dewsbury 1985; Runcie 2000; Lappan 2009; Roemer & Smith 2001; Garrott 1984), for species with life history data (see chapter 3 main text, Methods, Data collection, for data collection, data comparability protocols and sample sizes). Data for care by helpers were also extracted from a range of secondary literature sources (Lukas & Clutton-Brock 2012; Isler & van Schaik 2012; Snowdon 1996; Silk 2007; Nowak 1999) and where possible checked against the original primary source.

We define male care as any of the following behaviours, performed by an adult male towards neonates or dependent offspring; provisioning, carrying, grooming, and huddling (see main text). We consider a form of male care behaviour the provisioning of a pregnant or lactating female by the male (see chapter 3 main text). We include cases where offspring are either unweaned or weaned, provided the offspring are still heavily dependent on the parents for survival. For example, wolves (*Canis lupus*) provision the pups for at least a few months post-weaning (Mech 1974); likewise in tamarinds and marmosets, helpers, including males, carry the offspring for a few more weeks post-weaning (Bales et al. 2000, Nowak 1999).

Previous studies classify as male care only provisioning or carrying the offspring, as these behaviours are believed to be more costly than huddling and grooming (Lukas & Clutton-Brock 2013; Isler & van Schaik 2012). Male cotton-top tamarinds (*Saguinus oedipus*) that carry their offspring lose up to 11% of body weight between birth and weaning (Sánchez et al. 1999), while males of other primate species have reduced foraging efficiency and face greater risk of predation when carrying the offspring (Altmann & Samuels 1992; Wright 1990; Schradin & Anzenberger 2001). Although less well studied, the costs of huddling and grooming, however, appear to be substantial in the few species where they have been quantified. For example, male prairie voles (*Microtus ochrogaster*) and dwarf lemurs (*Cheirogaleus medius*) that huddle with their offspring exhibit a significant reduction in body mass (Campbell et al. 2009; Fietz & Dausmann 2003). Importantly, the loss of body mass in males over the course of reproduction are more likely to be due to care behaviours, including grooming and huddling with the offspring, than the cohabitation with pregnant females (Saltzman et al. 2015). Among primates, grooming is associated with reduced foraging time and increased exposure to parasites (Nunn & Altizer 2006; Moore 2002). Thus, we include grooming and huddling in our definition of male care along with carrying and provisioning.

**Supplementary notes**

In Supplementary Tables 1-7 we report further details on full models for the life history traits significantly associated with male care and individual male care behaviours, and all models for the life history traits that are unrelated to male care. For each independent variable in each model we report β estimates with standard errors (S.E.), t-statistics and p-values (under ‘Variable statistics’), and for each model we report the estimated lambda value (λ), R2, model log likelihood (Lh) and the non-phylogenetic variance inflation factors (VIF, see Supplementary

Methods, Statistical analysis) under ‘Model statistics’. The models in each table are numbered for ease of presentation, and follow the order of presentation of results in the main text.

For each life history trait tested as a response variable, we include those life history traits known to associate with it (Bielby et al. 2007) as independent variables. Thus, because life history traits in mammals covary along two independent axis, a ‘timing’ axis of reproductive events and an ‘output’ axis capturing mostly diversity in litter size and its trade-off with neonatal body mass, we do not include litter size as a predictor in models of variables aligning along the timing axis. Including litter size in models for lactation time and litters per year confirms that this variable is not significantly associated with these variables, and its inclusions does not alter the results (Supplementary Table 7).

In Supplementary tables 8-13 we report the results of both full and reduced models in each of the three major orders - primates, carnivores and rodents - where male care behaviours are most common and so sample sizes sufficient for the analyses (i.e. the number of species with male care behaviour is equal or greater than 10). In these analyses we test individual behaviours but not male care based on all behaviours together, as diversity in male care behaviour is lower within orders than across all mammals. We test care by helpers only in models for carnivores and primates because less than 10 rodent species exhibit care by other helpers. All other independent variables – other life history traits, mating system, and citation count – are retained in all the analyses within orders. Sample sizes are however too low for within order analyses for the following life history traits, used as dependent variables, as less than 10 species with male care behaviours are retained: maximum longevity (all orders) and body mass gain from birth to weaning (primates and carnivores).

Analyses within orders show that lactation time is significantly shorter and females produce significantly more litters per year in primates where males carry the offspring (Supplementary Tables 8 & 10). In carnivores, species in which males provision the female have significantly shorter lactation and larger litters (Supplementary Tables 8 & 11). In rodents we find no significant association between any life history traits and either grooming or huddling (Supplementary Tables 8-13).

Finally, in Supplementary Table 14 we report the results of phylogenetic t-tests (Organ et al. 2007) between citation count and male care, social monogamy, and care by helpers. We find no significant association between citation count and male care, indicating that species with and without male care do not differ in research effort. However, citation counts is higher in species with care by helpers and lower in socially monogamous species, suggesting that research effort is greater for species exhibiting care by helpers and polygynous mating system.

We conclude that our results are robust and not influenced by the correlated evolution of history traits (Bielby et al. 2007), small levels of multicollinearity between predictors; differences in research effort among species; and confounding variables such as monogamy and care by helpers.

## Supplementary tables

**Supplementary Table 1. PGLS full models for the duration of lactation for male care (model 1) and individual care behaviour (model 2).** Reduced models for lactation time with male care and individual care behaviours in Table 1, main text. The sample size for these models is 390 species, of which 47 have male care, with 14 carrying, 24 provisioning, of which 12 also provision reproducing females, 18 huddling, and 23 grooming. 80 species in these models exhibit care by other helpers, while 55 are socially monogamous. Models are numbered for ease of presentation.

| **Lactation time** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **VIF** |
| **1 (Full)** | Female body mass | 0.13 | 0.02 | 6.0 | <0.001 | 0.82 | 0.26 | 46.75 | 2.4 |
| | Gestation time | 0.38 | 0.09 | 4.3 | <0.001 | | | | 2.3 |
| | Male care | -0.11 | 0.05 | -2.3 | 0.023 | | | | 1.9 |
| | Care by helpers | -0.04 | 0.03 | -1.4 | 0.171 | | | | 1.3 |
| | Social monogamy | 0.01 | 0.04 | 0.3 | 0.786 | | | | 1.9 |
| | Citation Count | 0.01 | 0.02 | 0.6 | 0.565 | | | | 1.2 |
| **2 (Full)** | Female body mass | 0.13 | 0.02 | 6.0 | <0.001 | 0.82 | 0.27 | 49.49 | 2.5 |
| | Gestation time | 0.37 | 0.09 | 4.1 | <0.001 | | | | 2.4 |
| | Carrying | -0.16 | 0.07 | -2.3 | 0.025 | | | | 1.4 |
| | Provisioning females | -0.19 | 0.12 | -1.6 | 0.114 | | | | 2.2 |
| | Provisioning offspring | -0.06 | 0.08 | -0.8 | 0.426 | | | | 2.7 |
| | Grooming | -0.04 | 0.06 | -0.6 | 0.586 | | | | 2.5 |
| | Huddling | 0.01 | 0.07 | 0.2 | 0.849 | | | | 2.4 |
| | Care by helpers | -0.03 | 0.03 | -1.1 | 0.278 | | | | 1.3 |
| | Social monogamy | 0.01 | 0.04 | 0.3 | 0.769 | | | | 1.9 |
| | Citation count | 0.01 | 0.02 | 0.4 | 0.701 | | | | 1.2 |

**Supplementary Table 2. PGLS full and reduced models for the duration of gestation.** The reduced model is the same for both full models 1 and 3. The sample size for these models is 390 species, of which 47 have male care, with 14 carrying, 24 provisioning, of which 12 also provision reproducing females, 18 huddling, and 23 grooming. 80 species in these models exhibit care by other helpers, while 55 are socially monogamous. Models are numbered for ease of presentation.

| **Gestation time** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **VIF** |
| **1 (Full)** | Female body mass | 0.10 | 0.01 | 8.8 | <0.001 | 1.00 | 0.24 | 321.42 | 1.8 |
| | Lactation time | 0.07 | 0.02 | 3.1 | 0.002 | | | | 1.7 |
| | Male care | 0.02 | 0.03 | 0.6 | 0.559 | | | | 2.0 |
| | Care by helpers | 0.03 | 0.01 | 2.4 | 0.017 | | | | 1.2 |
| | Social monogamy | 0.01 | 0.02 | 0.4 | 0.701 | | | | 1.9 |
| | Citation count | -0.01 | 0.01 | -2.0 | 0.044 | | | | 1.2 |
| **2 (Reduced)** | Female body mass | 0.10 | 0.01 | 8.8 | <0.001 | 1.00 | 0.24 | 321.04 | |
| | Lactation time | 0.07 | 0.02 | 3.1 | 0.002 | | | | |
| | Care by helpers | 0.03 | 0.01 | 2.5 | 0.014 | | | | |
| | Citation count | -0.01 | 0.01 | -2.1 | 0.040 | | | | |
| **3 (Full)** | Female body mass | 0.10 | 0.01 | 8.7 | <0.001 | 1.00 | 0.24 | 321.53 | 1.9 |
| | Lactation time | 0.07 | 0.02 | 3.0 | 0.003 | | | | 1.8 |
| | Carrying | 0.01 | 0.03 | 0.2 | 0.872 | | | | 1.4 |
| | Provisioning females | -0.01 | 0.04 | -0.3 | 0.793 | | | | 2.2 |
| | Provisioning offspring | 0.02 | 0.04 | 0.7 | 0.519 | | | | 2.7 |
| | Grooming | -0.01 | 0.03 | -0.3 | 0.772 | | | | 2.5 |
| | Huddling | 0.01 | 0.03 | 0.2 | 0.810 | | | | 2.4 |
| | Care by helpers | 0.03 | 0.01 | 2.3 | 0.021 | | | | 1.3 |
| | Social monogamy | 0.01 | 0.02 | 0.4 | 0.659 | | | | 1.9 |
| | Citation count | -0.01 | 0.01 | -2.0 | 0.046 | | | | 1.2 |

**Supplementary Table 3. PGLS full models for the number of litters per year for male care (model 1) and individual care behaviours (models 2 & 3).** Reduced models for this variable with male care and individual care behaviours in Table 1, main text. Full models 1 and 2 include the duration of maternal investment; full model 3 excludes it (see main text). The sample size is 370 species. In these models, 46 species exhibit male care, with 14 carrying, 23 provisioning, of which 12 also provision reproducing females, 18 huddling, and 22 grooming; 77 species exhibit care by helpers, while 48 are socially monogamous. Models are numbered for ease of presentation.

| **Litters per year** | | **Variable statistics** | | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **VIF** |
| **1 (full)** | Female body mass | -0.05 | 0.02 | -2.7 | 0.007 | 0.90 | 0.23 | 159.54 | 2.7 |
| | Lactation time | -0.15 | 0.04 | -3.9 | <0.001 | | | | 2.3 |
| | Gestation time | -0.24 | 0.07 | -3.4 | 0.001 | | | | 1.8 |
| | Male care | 0.06 | 0.04 | 1.6 | 0.120 | | | | 2.3 |
| | Care by helpers | 0.06 | 0.02 | 2.4 | 0.015 | | | | 1.3 |
| | Social monogamy | 0.03 | 0.03 | 0.8 | 0.455 | | | | 2.2 |
| | Citation count | -0.01 | 0.01 | -0.4 | 0.698 | | | | 1.2 |
| **2 (full)** | Female body mass | -0.05 | 0.02 | -2.6 | 0.009 | 0.90 | 0.23 | 161.43 | 3.0 |
| | Lactation time | -0.15 | 0.04 | -3.8 | <0.001 | | | | 2.5 |
| | Gestation time | -0.24 | 0.07 | -3.4 | 0.001 | | | | 1.8 |
| | Carrying | 0.08 | 0.05 | 1.4 | 0.153 | | | | 1.5 |
| | Provisioning females | -0.04 | 0.11 | -0.3 | 0.741 | | | | 2.2 |
| | Provisioning offspring | -0.01 | 0.06 | -0.1 | 0.925 | | | | 2.7 |
| | Grooming | 0.09 | 0.05 | 2.0 | 0.047 | | | | 2.6 |
| | Huddling | -0.07 | 0.06 | -1.3 | 0.196 | | | | 2.6 |
| | Care by helpers | 0.06 | 0.02 | 2.5 | 0.015 | | | | 1.4 |
| | Social monogamy | 0.04 | 0.03 | 1.1 | 0.278 | | | | 2.1 |
| | Citation count | -0.00 | 0.01 | -0.2 | 0.880 | | | | 1.2 |
| **3 (full)** | Female body mass | -0.01 | 0.02 | -6.7 | <0.001 | 0.92 | 0.15 | 145.80 | 1.2 |
| | Carrying | 0.09 | 0.05 | 1.7 | 0.092 | | | | 1.4 |
| | Provisioning females | 0.03 | 0.11 | 0.3 | 0.775 | | | | 2.2 |
| | Provisioning offspring | -0.00 | 0.06 | -0.0 | 0.965 | | | | 2.7 |
| | Grooming | 0.10 | 0.05 | 2.0 | 0.047 | | | | 2.5 |
| | Huddling | -0.08 | 0.06 | -1.3 | 0.186 | | | | 2.4 |
| | Care by helpers | 0.05 | 0.02 | 2.1 | 0.035 | | | | 1.3 |
| | Social monogamy | 0.04 | 0.04 | 1.0 | 0.310 | | | | 1.9 |
| | Citation count | 0.00 | 0.01 | 0.4 | 0.721 | | | | 1.2 |

**Supplementary Table 4. PGLS full and reduced models for litter size for male care (model 1) and individual care behaviours (model 3).** Reduced model 2 results from model simplification of full model 1; the reduced model of full model 3 with individual care behaviours is presented in Table 1, main text. The sample size for these models is 448 species. In these models, 53 species have male care, with 19 carrying, 26 provisioning, 13 of which also provision reproducing females, 18 huddling, and 25 grooming; 85 species exhibit care by helpers, while 62 are socially monogamous. Models are numbered for ease of presentation.

| **Litter size** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **VIF** |
| **1** | Female body mass | -0.07 | 0.01 | -5.6 | <0.001 | 0.94 | 0.12 | 254.65 | 1.1 |
| **(full)** | Male care | 0.04 | 0.03 | 1.4 | 0.178 | | | | 2.0 |
| | Care by helpers | 0.01 | 0.02 | 0.6 | 0.562 | | | | 1.2 |
| | Social monogamy | -0.03 | 0.03 | -1.1 | 0.288 | | | | 2.0 |
| | Citation count | 0.05 | 0.01 | 5.7 | <0.001 | | | | 1.2 |
| **2** | Female body mass | -0.07 | 0.01 | -5.7 | <0.001 | 0.94 | 0.12 | 253.45 | |
| **(reduced)** | Citation count | 0.05 | 0.01 | 6.3 | <0.001 | | | | |
| **3** | Female body mass | -0.07 | 0.01 | -5.5 | <0.001 | 0.95 | 0.17 | 267.67 | 1.2 |
| **(full)** | Carrying | 0.03 | 0.04 | 0.7 | 0.490 | | | | 1.5 |
| | Provisioning females | 0.25 | 0.05 | 4.7 | <0.001 | | | | 2.0 |
| | Provisioning offspring | 0.04 | 0.04 | 0.8 | 0.420 | | | | 2.4 |
| | Grooming | -0.03 | 0.03 | -1.0 | 0.314 | | | | 2.2 |
| | Huddling | 0.00 | 0.04 | 0.1 | 0.923 | | | | 1.9 |
| | Care by helpers | -0.00 | 0.02 | -0.1 | 0.904 | | | | 1.3 |
| | Social monogamy | -0.03 | 0.03 | -1.2 | 0.218 | | | | 2.1 |
| | Citation count | 0.05 | 0.01 | 5.8 | <0.001 | | | | 1.2 |

**Supplementary Table 5. PGLS full and reduced models for (a) neonatal body mass and (b) body mass increase from birth to weaning for male care and individual male care behaviours.** The reduced model 2 is the same for both full models 1 and 3 in both (a) and (b). The sample size in (a) is 394 species while in (b) is 232 species. In the models for neonatal mass (a), 48 species exhibit male care, with 14 carrying, 24 provisioning, 12 of which also provision reproducing females, 17 huddling, and 23 grooming; 79 species exhibit care by helpers, while 51 are socially monogamous. In the models for postnatal mass gain (b), 25 species exhibit male care, with 13 huddling, and 16 grooming; sample sizes for carrying and provisioning are too small (<10) to be used in these analyses. 49 species in (b) exhibit care by helpers, while 22 are socially monogamous. Models are numbered for ease of presentation.

| **(a) Neonatal body mass** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **VIF** |
| **1<br>(full)** | Female body mass | 0.61 | 0.02 | 28.3 | <0.001 | 0.97 | 0.81 | 79.27 | 2.4 |
| | Gestation time | 0.70 | 0.10 | 7.3 | <0.001 | | | | 3.3 |
| | Litter size | -0.40 | 0.07 | -5.4 | <0.001 | | | | 2.1 |
| | Male care | 0.02 | 0.05 | 0.4 | 0.668 | | | | 2.1 |
| | Care by helpers | 0.05 | 0.03 | 1.7 | 0.083 | | | | 1.3 |
| | Social monogamy | -0.09 | 0.04 | -2.3 | 0.024 | | | | 2.0 |
| | Citation count | -0.00 | 0.01 | 0.1 | 0.959 | | | | 1.3 |
| **2<br>(reduced)** | Female body mass | 0.61 | 0.02 | 29.4 | <0.001 | 0.97 | 0.81 | 77.58 | |
| | Gestation time | 0.72 | 0.09 | 7.6 | <0.001 | | | | |
| | Litter size | -0.38 | 0.07 | -5.3 | <0.001 | | | | |
| | Social monogamy | -0.07 | 0.04 | -2.1 | 0.037 | | | | |
| **3<br>(full)** | Female body mass | 0.61 | 0.02 | 28.1 | <0.001 | 0.97 | 0.81 | 80.02 | 2.6 |
| | Gestation time | 0.70 | 0.10 | 7.4 | <0.001 | | | | 3.3 |
| | Litter size | -0.40 | 0.08 | -5.2 | <0.001 | | | | 2.3 |
| | Carrying | -0.05 | 0.07 | -0.7 | 0.491 | | | | 1.4 |
| | Provisioning females | 0.06 | 0.09 | 0.7 | 0.500 | | | | 2.2 |
| | Provisioning offspring | -0.04 | 0.07 | -0.5 | 0.591 | | | | 2.6 |
| | Grooming | 0.01 | 0.05 | 0.3 | 0.797 | | | | 2.3 |
| | Huddling | 0.03 | 0.06 | 0.4 | 0.662 | | | | 2.2 |
| | Care by helpers | 0.04 | 0.03 | 1.4 | 0.150 | | | | 1.4 |
| | Social monogamy | -0.08 | 0.04 | -2.2 | 0.032 | | | | 2.0 |
| | Citation count | 0.00 | 0.01 | 0.0 | 0.983 | | | | 1.3 |

| (b) Body mass increase | | Variable statistics | | | | Model statistics | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **VIF** |
| **1**<br>**(full)** | Female body mass | 0.83 | 0.02 | 41.6 | <0.001 | 0.30 | 0.94 | 10.19 | 1.9 |
| | Lactation time | 0.19 | 0.06 | 3.2 | 0.002 | | | | 1.9 |
| | Litter size | -0.27 | 0.08 | -3.2 | 0.002 | | | | 1.8 |
| | Male care | 0.01 | 0.07 | 0.1 | 0.935 | | | | 1.8 |
| | Care by helpers | -0.01 | 0.05 | -0.2 | 0.878 | | | | 1.3 |
| | Social monogamy | -0.07 | 0.07 | -1.0 | 0.306 | | | | 1.7 |
| | Citation count | 0.02 | 0.02 | 0.9 | 0.378 | | | | 1.3 |
| **2**<br>**(reduced)** | Female body mass | 0.84 | 0.02 | 43.9 | <0.001 | 0.28 | 0.94 | 9.00 | |
| | Lactation time | 0.19 | 0.06 | 3.3 | 0.001 | | | | |
| | Litter size | -0.24 | 0.08 | -3.1 | 0.003 | | | | |
| **3**<br>**(full)** | Female body mass | 0.83 | 0.02 | 41.1 | <0.001 | 0.30 | 0.94 | 10.57 | 1.9 |
| | Lactation time | 0.17 | 0.06 | 3.2 | 0.002 | | | | 1.9 |
| | Litter size | -0.27 | 0.08 | -3.2 | 0.002 | | | | 1.8 |
| | Grooming | 0.02 | 0.09 | 0.2 | 0.845 | | | | 2.4 |
| | Huddling | -0.07 | 0.10 | -0.7 | 0.459 | | | | 2.3 |
| | Care by helpers | -0.01 | 0.05 | 0.2 | 0.880 | | | | 1.3 |
| | Social monogamy | -0.05 | 0.07 | -0.9 | 0.348 | | | | 1.2 |
| | Citation count | 0.02 | 0.02 | 1.0 | 0.328 | | | | 1.2 |

**Supplementary Table 6. PGLS full and reduced models for maximum lifespan for male care and individual male care behaviours.** The reduced model is the same for both full models 1 and 3. The sample size for these models is 332 species, of which 42 have male care, with 13 carrying, 22 provisioning, of which 11 also provision reproducing females, 17 huddling, and 20 grooming; 77 species in these models exhibit care by other helpers, while 45 are socially monogamous. Models are numbered for ease of presentation.

| **Maximum Lifespan** | | **Variable statistics** | | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** | **VIF** |
| **1**<br>**(full)** | Lactation time | 0.12 | 0.04 | 2.8 | 0.005 | 0.86 | 0.26 | 123.49 | 2.13 |
| | Gestation time | 0.35 | 0.07 | 4.8 | <0.001 | | | | 2.01 |
| | Litters per Year | -0.13 | 0.06 | -2.3 | 0.021 | | | | 2.43 |
| | Male care | -0.02 | 0.04 | -0.5 | 0.599 | | | | 2.12 |
| | Care by helpers | 0.00 | 0.03 | 0.2 | 0.865 | | | | 1.25 |
| | Social monogamy | 0.04 | 0.04 | 1.1 | 0.272 | | | | 2.05 |
| | Citation count | 0.06 | 0.01 | 4.6 | <0.001 | | | | 1.11 |
| **2**<br>**(reduced)** | Lactation time | 0.12 | 0.04 | 2.9 | 0.005 | 0.86 | 0.26 | 122.84 | 2.03 |
| | Gestation time | 0.35 | 0.07 | 4.9 | <0.001 | | | | 1.93 |
| | Litters per year | -0.13 | 0.06 | -2.3 | 0.024 | | | | 2.41 |
| | Citation count | 0.06 | 0.01 | 4.8 | <0.001 | | | | 1.02 |
| **3**<br>**(full)** | Lactation time | 0.12 | 0.04 | 2.7 | 0.008 | 0.87 | 0.26 | 125.77 | 2.14 |
| | Gestation time | 0.34 | 0.07 | 4.7 | <0.001 | | | | 2.06 |
| | Litters per Year | -0.13 | 0.06 | -2.2 | 0.029 | | | | 2.53 |
| | Carrying | -0.11 | 0.06 | -1.7 | 0.085 | | | | 1.50 |
| | Provisioning females | -0.03 | 0.11 | -0.3 | 0.772 | | | | 2.15 |
| | Provisioning offspring | 0.03 | 0.06 | 0.5 | 0.597 | | | | 2.72 |
| | Grooming | 0.05 | 0.06 | 0.8 | 0.409 | | | | 2.69 |
| | Huddling | -0.04 | 0.06 | -0.7 | 0.493 | | | | 2.58 |
| | Care by helpers | 0.00 | 0.03 | 0.0 | 0.996 | | | | 1.31 |
| | Social monogamy | 0.05 | 0.04 | 1.3 | 0.211 | | | | 2.08 |
| | Citation count | 0.06 | 0.01 | 4.7 | <0.001 | | | | 1.11 |

**Supplementary Table 7. PGLS full and reduced models for lacation (a) and litters per year (b), including litter size as an additional predictor, for male care and the individual care behaviours.** In both (a) and (b) reduced model 2 results from model simplification of full model 1, and reduced model 4 results from the simlification of full model 3. In (b) reduced model 6 results from the simplification of full model 5. Note that the sample sizes of these models are slightly smaller than in Table 1 and Supplementary tables 1 and 3 as there are no data on litter size for 2 species. The sample size in (a) is 389 species. In these models, 46 species have male care, with 14 carrying, 23 provisioning, 11 of which also provision reproducing females, 18 huddling, and 23 grooming. 79 species in these models exhibit care by helpers, while 49 are socially monogamous. In (b) the total sample size is 368, of which 45 species have male care, with 14 carrying, 22 provisioning, 11 of which also provision reproducing females, 18 huddling, and 22 grooming; 76 species in these models exhibit care by helpers, while 47 are socially monogamous. Models are numbered for ease of presentation.

| **(a) Lactation time** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1 (full)** | Female body mass | 0.12 | 0.02 | 5.8 | <0.001 | 0.81 | 0.27 | 46.76 |
| | Gestation time | 0.34 | 0.09 | 3.6 | <0.001 | | | |
| | Litter size | -0.10 | 0.08 | -1.2 | 0.222 | | | |
| | Male care | -0.11 | 0.05 | -2.2 | 0.032 | | | |
| | Care by helpers | -0.04 | 0.03 | -1.4 | 0.179 | | | |
| | Social Monogamy | 0.01 | 0.04 | 0.2 | 0.866 | | | |
| | Citation count | 0.02 | 0.02 | 0.9 | 0.369 | | | |
| **2 (reduced)** | Female body mass | 0.13 | 0.02 | 6.2 | <0.001 | 0.81 | 0.26 | 44.97 |
| | Gestation time | 0.37 | 0.09 | 4.2 | <0.001 | | | |
| | Male care | -0.11 | 0.05 | -2.5 | 0.013 | | | |
| **3 (full)** | Female body mass | 0.13 | 0.02 | 5.9 | <0.001 | 0.82 | 0.28 | 49.13 |
| | Gestation time | 0.34 | 0.09 | 3.6 | <0.001 | | | |
| | Litter size | -0.07 | 0.08 | -0.9 | 0.398 | | | |
| | Carrying | -0.16 | 0.07 | -2.2 | 0.029 | | | |
| | Provisioning females | -0.17 | 0.12 | -1.4 | 0.155 | | | |
| | Provisioning offspring | -0.05 | 0.08 | -0.7 | 0.494 | | | |
| | Grooming | -0.03 | 0.06 | -0.5 | 0.592 | | | |
| | Huddling | 0.01 | 0.07 | 0.2 | 0.874 | | | |
| | Care by helpers | -0.04 | 0.03 | -1.1 | 0.265 | | | |
| | Social Monogamy | 0.01 | 0.04 | 0.2 | 0.826 | | | |
| | Citation count | 0.01 | 0.02 | 0.7 | 0.519 | | | |
| **4 (reduced)** | Female body mass | 0.13 | 0.02 | 6.2 | <0.001 | 0.82 | 0.27 | 47.43 |
| | Gestation time | 0.36 | 0.09 | 4.1 | <0.001 | | | |
| | Carrying | -0.17 | 0.07 | -2.6 | 0.010 | | | |
| | Provisioning females | -0.22 | 0.11 | -2.0 | 0.051 | | | |

| **(b) Litters per Year** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | -0.05 | 0.02 | -2.7 | 0.007 | 0.89 | 0.23 | 158.49 |
| | Lactation time | -0.15 | 0.04 | -3.9 | <0.001 | | | |
| | Gestation time | -0.24 | 0.08 | -3.3 | 0.001 | | | |
| | Litter size | -0.01 | 0.06 | -0.2 | 0.858 | | | |
| | Male care | 0.06 | 0.04 | 1.6 | 0.115 | | | |
| | Care by helpers | 0.06 | 0.02 | 2.5 | 0.014 | | | |
| | Social Monogamy | 0.03 | 0.03 | 0.7 | 0.473 | | | |
| | Citation count | -0.01 | 0.01 | -0.4 | 0.668 | | | |
| **2<br>(reduced)** | Female body mass | -0.05 | 0.02 | -3.0 | 0.003 | 0.90 | 0.23 | 158.03 |
| | Lactation time | -0.15 | 0.04 | -3.9 | <0.001 | | | |
| | Gestation time | -0.23 | 0.07 | -3.3 | 0.001 | | | |
| | Male care | 0.07 | 0.03 | 2.2 | 0.033 | | | |
| | Care by helpers | 0.06 | 0.02 | 2.5 | 0.012 | | | |
| **3<br>(full)** | Female body mass | -0.05 | 0.02 | -2.6 | 0.001 | 0.90 | 0.23 | 160.29 |
| | Lactation time | -0.15 | 0.04 | -3.8 | <0.001 | | | |
| | Gestation time | -0.24 | 0.08 | -3.3 | 0.001 | | | |
| | Litter size | -0.00 | 0.07 | -0.0 | 0.967 | | | |
| | Carrying | 0.08 | 0.05 | 1.4 | 0.157 | | | |
| | Provisioning females | -0.03 | 0.11 | -0.3 | 0.773 | | | |
| | Provisioning offspring | -0.01 | 0.06 | -0.1 | 0.933 | | | |
| | Grooming | 0.09 | 0.05 | 2.0 | 0.050 | | | |
| | Huddling | -0.07 | 0.06 | -1.3 | 0.204 | | | |
| | Care by helpers | 0.06 | 0.02 | 2.5 | 0.014 | | | |
| | Social Monogamy | 0.04 | 0.03 | 1.1 | 0.285 | | | |
| | Citation count | -0.00 | 0.01 | -0.2 | 0.830 | | | |
| **4<br>(reduced)** | Female body mass | -0.05 | 0.02 | -2.9 | 0.004 | 0.90 | 0.22 | 157.97 |
| | Lactation time | -0.15 | 0.04 | -4.1 | <0.001 | | | |
| | Gestation time | -0.23 | 0.07 | -3.3 | 0.001 | | | |
| | Grooming | 0.07 | 0.04 | 2.2 | 0.035 | | | |
| | Care by helpers | 0.05 | 0.02 | 2.5 | 0.013 | | | |
| **5<br>(full)** | Female body mass | -0.10 | 0.02 | -6.3 | <0.001 | 0.90 | 0.15 | 135.65 |
| | Litter size | 0.05 | 0.07 | 0.8 | 0.421 | | | |
| | Carrying | 0.11 | 0.06 | 1.9 | 0.066 | | | |
| | Provisioning females | 0.00 | 0.10 | 0.0 | 0.985 | | | |
| | Provisioning offspring | -0.02 | 0.06 | -0.4 | 0.704 | | | |
| | Grooming | 0.09 | 0.05 | 1.9 | 0.059 | | | |
| | Huddling | -0.10 | 0.06 | -1.6 | 0.104 | | | |
| | Care by helpers | 0.05 | 0.03 | 2.1 | 0.036 | | | |
| | Social Monogamy | 0.04 | 0.04 | 1.0 | 0.308 | | | |
| | Citation count | -0.00 | 0.01 | -0.2 | 0.808 | | | |
| **6<br>(reduced)** | Female body mass | -0.11 | 0.01 | -7.2 | <0.001 | 0.90 | 0.14 | 132.79 |
| | Carrying | 0.11 | 0.05 | 2.2 | 0.032 | | | |
| | Care by helpers | 0.06 | 0.02 | 2.4 | 0.017 | | | |

**Supplementary Table 8. PGLS models for the duration of lactation in primates (a), carnivores (b) and rodents (c).** In (a) the sample size is 70 primate species, of which 11 exhibit male care, with 10 carrying; 35 species in these models exhibit care by other helpers, while 16 are socially monogamous. Sample sizes for provisioning, huddling, and grooming are too small (<10) to be used in these analyses. In (b) the sample size is 80 carnivore species, of which 17 have male care, all of which provision the offspring and 12 also provision the female. Sample sizes for carrying, huddling, and grooming are too small (<10) to be used in these analyses. 22 species in these models exhibit care by other helpers, while 18 are socially monogamous. In (c) the sample size is 90 rodent species, of which 18 have male care, 14 of which groom the offspring and 12 huddle with them; 16 species are socially monogamous. Sample sizes for carrying and provisioning are too small (<10) to be used in these analyses, as are the sample sizes for care by other helpers. Models are numbered for ease of presentation. The reduced models for primates (a) and carnivores (b) are in Table 2 (main text).

| **(a) Primates** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | 0.21 | 0.07 | 3.1 | 0.003 | 0.00 | 0.68 | 11.40 |
| | Gestation time | 1.24 | 0.34 | 3.7 | 0.001 | | | |
| | Carrying | -0.27 | 0.11 | -2.4 | 0.018 | | | |
| | Care by helpers | -0.07 | 0.06 | -1.2 | 0.227 | | | |
| | Social monogamy | 0.07 | 0.09 | 0.8 | 0.416 | | | |
| | Citation count | 0.03 | 0.04 | 0.7 | 0.487 | | | |

| **(b) Carnivores** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | 0.16 | 0.07 | 2.4 | 0.020 | 0.84 | 0.18 | 5.32 |
| | Gestation time | -0.09 | 0.20 | -0.4 | 0.660 | | | |
| | Provisioning females | -0.29 | 0.14 | -2.1 | 0.039 | | | |
| | Provisioning offspring | -0.23 | 0.19 | -1.2 | 0.233 | | | |
| | Care by helpers | 0.07 | 0.07 | 0.9 | 0.358 | | | |
| | Social monogamy | 0.08 | 0.16 | 0.5 | 0.613 | | | |
| | Citation count | -0.01 | 0.04 | -0.3 | 0.762 | | | |

| **(c) Rodents** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | 0.09 | 0.04 | 2.3 | 0.022 | 0.88 | 0.21 | 35.83 |
| | Gestation time | 0.22 | 0.19 | 1.2 | 0.239 | | | |
| | Grooming | -0.01 | 0.07 | -0.1 | 0.928 | | | |
| | Huddling | -0.03 | 0.07 | -0.4 | 0.725 | | | |
| | Social monogamy | 0.10 | 0.05 | 2.1 | 0.041 | | | |
| | Citation count | -0.00 | 0.02 | -0.1 | 0.940 | | | |
| **2<br>(reduced)** | Female body mass | 0.12 | 0.03 | 3.7 | <0.001 | 0.88 | 0.20 | 34.91 |
| | Social monogamy | 0.09 | 0.04 | 2.1 | 0.030 | | | |

**Supplementary Table 9. PGLS full and reduced models for the duration of gestation in primates (a), carnivores (b) and rodents (c).** In (a) the sample size is 70 primate species, of which 11 exhibit male care, with 10 carrying offspring; 35 species exhibit care by other helpers, while 16 are socially monogamous. Sample sizes for provisioning, huddling, and grooming are too small (<10) to be used in these analyses. In (b) the sample size is 80 species, of which 17 have male care, all of which provision the offspring and 12 also provision the female. Sample sizes for carrying, huddling, and grooming are too small (<10) to be used in these analyses. 22 species in (b) exhibit care by other helpers, while 18 are socially monogamous. In (c) the sample size is 90 species, of which 18 have male care, 14 of which groom the offspring and 12 huddle with them. Sample sizes for carrying and provisioning are too small (<10) to be used in these analyses, as are sample sizes for care by other helpers. In (c) 16 species are socially monogamous. Models are numbered for ease of presentation.

| **(a) Primates** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | 0.07 | 0.02 | 3.7 | 0.001 | 1.00 | 0.34 | 118.06 |
| | Lactation time | 0.02 | 0.02 | 1.1 | 0.270 | | | |
| | Carrying | -0.02 | 0.03 | -0.6 | 0.552 | | | |
| | Care by helpers | -0.02 | 0.01 | -1.8 | 0.076 | | | |
| | Social monogamy | -0.01 | 0.02 | -0.3 | 0.803 | | | |
| | Citation count | 0.01 | 0.01 | 0.8 | 0.404 | | | |
| **2<br>(reduced)** | Female body mass | 0.09 | 0.02 | 5.0 | <0.001 | 1.00 | 0.27 | 114.63 |

| **(b) Carnivores** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | 0.14 | 0.04 | 3.8 | <0.001 | 1.00 | 0.27 | 53.83 |
| | Lactation time | -0.02 | 0.06 | -0.4 | 0.730 | | | |
| | Provisioning females | -0.04 | 0.06 | -0.7 | 0.504 | | | |
| | Provisioning offspring | -0.06 | 0.13 | -0.5 | 0.639 | | | |
| | Care by helpers | 0.06 | 0.03 | 1.8 | 0.073 | | | |
| | Social monogamy | 0.02 | 0.10 | 0.3 | 0.813 | | | |
| | Citation count | -0.01 | 0.02 | -0.8 | 0.423 | | | |
| **2<br>(reduced)** | Female body mass | 0.14 | 0.03 | 4.8 | <0.001 | 1.00 | 0.23 | 51.58 |

| **(c) Rodents** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | 0.09 | 0.02 | 4.7 | <0.001 | 1.00 | 0.32 | 94.02 |
| | Lactation time | 0.07 | 0.05 | 1.4 | 0.172 | | | |
| | Grooming | 0.01 | 0.03 | 0.3 | 0.744 | | | |
| | Huddling | 0.01 | 0.03 | 0.4 | 0.666 | | | |
| | Social monogamy | 0.02 | 0.02 | 0.8 | 0.420 | | | |
| | Citation count | -0.02 | 0.01 | -1.3 | 0.188 | | | |
| **2<br>(reduced)** | Female body mass | 0.10 | 0.02 | 5.4 | <0.001 | 1.00 | 0.25 | 90.00 |

**Supplementary Table 10. PGLS models for the number of litters per year in primates (a), carnivores (b) and rodents (c).** In (a) models 1 and 2 include the duration of maternal investment, models 3 and its reduced model in Table 2 (main text) exclude it (see main text). The sample size for these models is 63 primate species, of which 11 have male care, with 10 carrying offspring; 33 species exhibit care by other helpers, while 12 are socially monogamous. Sample sizes for provisioning, huddling, and grooming are too small (<10) to be used in these analyses. In (b) the sample size is 78 carnivore species, of which 16 exhibit male care, all of which provision the offspring and 12 also provision the female. Sample sizes for carrying, huddling, and grooming are too small (<10) to be used in these analyses. In (b) 22 species exhibit care by other helpers, while 17 are socially monogamous. In (c) the sample size is 84 rodent species, of which 18 have male care, 14 of which groom the offspring and 12 huddle with them. Sample sizes for carrying and provisioning are too small (<10) to be used in these analyses, as are sample sizes for care by other helpers. In (c) 14 species are socially monogamous. Models are numbered for ease of presentation.

| **(a) Primates** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1 (full)** | Female body mass | -0.19 | 0.06 | -3.0 | 0.005 | 0.93 | 0.55 | 42.31 |
| | Lactation time | -0.20 | 0.07 | -3.2 | 0.003 | | | |
| | Gestation time | 0.34 | 0.36 | 1.0 | 0.337 | | | |
| | Carrying | 0.12 | 0.09 | 1.4 | 0.178 | | | |
| | Care by helpers | 0.11 | 0.04 | 2.7 | 0.010 | | | |
| | Social monogamy | -0.01 | 0.07 | -0.1 | 0.941 | | | |
| | Citation count | -0.01 | 0.02 | -0.6 | 0.571 | | | |
| **2 (reduced)** | Female body mass | -0.18 | 0.05 | -3.6 | 0.001 | 0.93 | 0.52 | 40.25 |
| | Lactation time | -0.22 | 0.06 | -3.7 | 0.001 | | | |
| | Care by helpers | 0.08 | 0.03 | 2.3 | 0.024 | | | |
| **3 (full)** | Female body mass | -0.22 | 0.05 | -4.0 | <0.001 | 0.86 | 0.49 | 37.31 |
| | Carrying | 0.20 | 0.09 | 2.3 | 0.027 | | | |
| | Care by helpers | 0.12 | 0.04 | 2.9 | 0.005 | | | |
| | Social monogamy | -0.03 | 0.07 | -0.4 | 0.670 | | | |
| | Citation count | -0.01 | 0.03 | -0.3 | 0.755 | | | |

| **(b) Carnivores** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1 (full)** | Female body mass | -0.02 | 0.03 | -0.4 | 0.664 | 0.17 | 0.33 | 50.69 |
| | Lactation time | -0.15 | 0.06 | -2.6 | 0.013 | | | |
| | Gestation time | -0.20 | 0.10 | -2.0 | 0.047 | | | |
| | Provisioning females | 0.02 | 0.10 | 0.2 | 0.830 | | | |
| | Provisioning offspring | 0.14 | 0.10 | 1.4 | 0.159 | | | |
| | Care by helpers | 0.05 | 0.05 | 1.2 | 0.251 | | | |
| | Social monogamy | -0.19 | 0.09 | -2.3 | 0.028 | | | |
| | Citation count | -0.04 | 0.03 | -1.4 | 0.181 | | | |
| **2 (reduced)** | Lactation time | -0.16 | 0.06 | -2.8 | 0.006 | 0.22 | 0.24 | 46.44 |
| | Gestation time | -0.24 | 0.07 | -3.3 | 0.001 | | | |

| **(c) Rodents** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1** | Female body mass | -0.06 | 0.05 | -1.2 | 0.244 | 1.00 | 0.06 | 25.63 |
| **(full)** | Lactation time | 0.01 | 0.13 | 0.1 | 0.912 | | | |
| | Gestation time | -0.15 | 0.26 | -0.6 | 0.571 | | | |
| | Grooming | 0.07 | 0.07 | 1.0 | 0.315 | | | |
| | Huddling | -0.09 | 0.07 | -1.3 | 0.216 | | | |
| | Social monogamy | 0.05 | 0.05 | 1.0 | 0.312 | | | |
| | Citation count | 0.01 | 0.03 | 0.2 | 0.852 | | | |
| **2 (reduced)** | Female body mass | -0.06 | 0.04 | -1.6 | 0.125 | 1.00 | 0.03 | 24.16 |

**Supplementary Table 11. PGLS models for litter size in primates (a), carnivores (b) and rodents (c).** In (a) the sample size is 84 primate species, of which 16 species have male care, with 15 carrying offspring. Sample sizes for provisioning, huddling, and grooming are too small (<10) to be used in these analyses. 40 species in (a) exhibit care by helpers, while 21 are socially monogamous. In (b) the sample size is 82 carnivore species, of which 18 have male care, all of which provision the offspring and 12 also provision the female. Sample sizes for carrying, huddling, and grooming are too small (<10) to be used in these analyses. 22 species in (b) exhibit care by other helpers, while 18 are socially monogamous. In (c) the sample size is 113 rodent species; 18 species have male care, 14 of which groom the offspring and 12 huddle with them. Sample sizes for carrying and provisioning are too small (<10) to be used in these analyses, as are sample sizes for care by other helpers. In (c) 17 species are socially monogamous. The reduced model for carnivores (b) is presented in Table 2 (main text). Models are numbered for ease of presentation.

| **(a) Primates** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **$\beta$** | **S.E.** | **t** | **p** | **$\lambda$** | **$R^2$** | **Lh** |
| **1** | Female body mass | -0.02 | 0.03 | -0.7 | 0.505 | 1.00 | 0.07 | 103.82 |
| **(full)** | Carrying | 0.01 | 0.04 | 0.2 | 0.847 | | | |
| | Care by helpers | 0.01 | 0.02 | 0.4 | 0.727 | | | |
| | Social monogamy | 0.05 | 0.03 | 1.7 | 0.102 | | | |
| | Citation count | 0.01 | 0.01 | 0.7 | 0.459 | | | |
| **2** | Female body mass | -0.03 | 0.03 | -1.2 | 0.217 | 1.00 | 0.02 | 101.41 |
| **(reduced)** | | | | | | | | |

| **(b) Carnivores** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **$\beta$** | **S.E.** | **t** | **p** | **$\lambda$** | **$R^2$** | **Lh** |
| **1** | Female body mass | -0.10 | 0.04 | -2.8 | 0.007 | 0.77 | 0.34 | 45.90 |
| **(full)** | Provisioning females | 0.32 | 0.08 | 3.9 | <0.001 | | | |
| | Provisioning offspring | 0.14 | 0.11 | 1.3 | 0.193 | | | |
| | Care by helpers | -0.01 | 0.04 | -0.3 | 0.756 | | | |
| | Social monogamy | -0.03 | 0.08 | -0.4 | 0.698 | | | |
| | Citation count | 0.08 | 0.03 | 3.1 | 0.003 | | | |

| **(c) Rodents** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **$\beta$** | **S.E.** | **t** | **p** | **$\lambda$** | **$R^2$** | **Lh** |
| **1** | Female body mass | -0.05 | 0.03 | -1.7 | 0.088 | 0.86 | 0.31 | 52.25 |
| **(full)** | Grooming | -0.05 | 0.07 | -0.8 | 0.444 | | | |
| | Huddling | 0.01 | 0.07 | 0.2 | 0.881 | | | |
| | Social monogamy | -0.09 | 0.04 | -2.2 | 0.032 | | | |
| | Citation count | 0.11 | 0.02 | 6.3 | <0.001 | | | |
| **2** | Social monogamy | -0.10 | 0.04 | -2.5 | 0.014 | 0.94 | 0.20 | 53.55 |
| **(reduced)** | Citation count | 0.09 | 0.02 | 5.0 | <0.001 | | | |

**Supplementary Table 12. PGLS full and reduced models for neonatal body mass in primates (a), carnivores (b) and rodents (c).** In (a) the sample size is 71 primate species, 12 species exhibit male care, with 11 carrying. Sample sizes for provisioning, huddling, and grooming are too small (<10) to be used in these analyses. In (a) 36 primate species exhibit care by helpers, while 15 are socially monogamous. In (b) the sample size is 78 carnivore species, 17 species exhibit male care, all of which provision the offspring while 12 also provision the female. Sample sizes for provisioning, huddling, and grooming are too small (<10) to be used in these analyses. In (b) 20 species exhibit care by helpers, while 16 are socially monogamous. In (c) the sample size is 90 rodent species, of which 18 species exhibit male care, 14 of which groom the offspring while 12 huddle with the offspring. Sample sizes for care by helpers in rodents are too small (<10) to be used in the analyses. In (c) 15 species are socially monogamous. Models are numbered for ease of presentation.

| **(a) Primates** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1** | Female body mass | 0.66 | 0.04 | 15.1 | <0.001 | 0.90 | 0.89 | 65.07 |
| **(full)** | Gestation time | 0.03 | 0.25 | -0.1 | 0.922 | | | |
| | Litter size | -0.53 | 0.15 | -3.5 | 0.001 | | | |
| | Carrying | -0.11 | 0.06 | -1.9 | 0.067 | | | |
| | Care by helpers | 0.01 | 0.03 | 0.2 | 0.817 | | | |
| | Social monogamy | 0.05 | 0.05 | 1.0 | 0.344 | | | |
| | Citation count | 0.03 | 0.02 | 1.7 | 0.094 | | | |
| **2** | Female body mass | 0.67 | 0.03 | 19.3 | <0.001 | 0.88 | 0.88 | 62.97 |
| **(reduced)** | Litter size | -0.53 | 0.14 | -3.8 | <0.001 | | | |
| | Citation count | 0.03 | 0.02 | 2.1 | 0.037 | | | |

| **(b) Carnivores** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1** | Female body mass | 0.57 | 0.07 | 8.7 | <0.001 | 1.00 | 0.76 | 11.42 |
| **(full)** | Gestation time | 0.30 | 0.21 | 1.4 | 0.159 | | | |
| | Litter size | -0.62 | 0.16 | -3.8 | <0.001 | | | |
| | Provisioning females | 0.03 | 0.11 | 0.3 | 0.800 | | | |
| | Provisioning offspring | -0.10 | 0.25 | -0.4 | 0.685 | | | |
| | Care by helpers | 0.12 | 0.06 | 2.0 | 0.047 | | | |
| | Social monogamy | -0.07 | 0.11 | -0.7 | 0.506 | | | |
| | Citation count | 0.08 | 0.03 | 2.4 | 0.020 | | | |
| **2** | Female body mass | 0.62 | 0.06 | 10.7 | <0.001 | 0.98 | 0.76 | 10.06 |
| **(reduced)** | Litter size | -0.72 | 0.15 | -4.9 | <0.001 | | | |
| | Care by helpers | 0.14 | 0.05 | 2.5 | 0.014 | | | |
| | Citation count | 0.08 | 0.04 | 2.2 | 0.034 | | | |

| **(c) Rodents** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1**<br>**(full)** | Female body mass | 0.63 | 0.03 | 19.6 | <0.001 | 0.99 | 0.89 | 57.42 |
| | Gestation time | 0.64 | 0.17 | 3.8 | <0.001 | | | |
| | Litter size | -0.29 | 0.09 | -3.2 | 0.002 | | | |
| | Grooming | 0.09 | 0.05 | 1.8 | 0.071 | | | |
| | Huddling | -0.04 | 0.05 | -0.8 | 0.436 | | | |
| | Social monogamy | -0.12 | 0.04 | -3.3 | 0.001 | | | |
| | Citation count | -0.05 | 0.02 | -2.3 | 0.027 | | | |
| **2**<br>**(reduced)** | Female body mass | 0.62 | 0.03 | 19.2 | <0.001 | 0.98 | 0.89 | 55.47 |
| | Gestation time | 0.65 | 0.17 | 3.9 | <0.001 | | | |
| | Litter size | -0.30 | 0.09 | -3.4 | 0.001 | | | |
| | Social monogamy | -0.11 | 0.03 | -3.2 | 0.002 | | | |
| | Citation count | -0.04 | 0.02 | -2.0 | 0.047 | | | |

**Supplementary Table 13. PGLS full and reduced models for postnatal body mass gain from birth to weaning in rodents.** The sample size for these models is 62 species; 15 species exhibit male care, 12 of which groom the offspring while 10 huddle with the offspring; 10 species are socially monogamous. Sample sizes for provisioning, carrying and care by helpers are too small (<10) to be used in this analysis. Models are numbered for ease of presentation.

| **Body mass increase** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1<br>(full)** | Female body mass | 0.77 | 0.05 | 14.0 | <0.001 | 0.40 | 0.84 | 11.36 |
| | Lactation time | 0.21 | 0.18 | 1.2 | 0.241 | | | |
| | Litter size | 0.07 | 0.17 | 0.4 | 0.702 | | | |
| | Grooming | 0.12 | 0.11 | 1.1 | 0.267 | | | |
| | Huddling | -0.17 | 0.11 | -1.4 | 0.176 | | | |
| | Social monogamy | -0.07 | 0.08 | -0.9 | 0.376 | | | |
| | Citation count | -0.05 | 0.04 | -1.2 | 0.221 | | | |
| **2<br>(reduced)** | Female body mass | 0.80 | 0.05 | 17.1 | <0.001 | 0.30 | 0.83 | 8.04 |

**Supplementary Table 14. PGLS models for male care, social monogamy, and care by helpers, against citation count.** For each independent variable in each model we report the parameter estimate (β) with standard error (SE), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$ and the model log-likelihood (Lh). The sample size for these models is 529 species, of which 65 have male care, 92 species exhibit care by other helpers, while 78 are socially monogamous.

| **Citation count** | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|
| **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **Male care** | 0.03 | 0.14 | 0.2 | 0.831 | 0.52 | 0.00 | -607.40 |
| **Care by helpers** | 0.70 | 0.09 | 7.5 | <0.001 | 0.59 | 0.10 | -580.90 |
| **Social monogamy** | -0.28 | 0.12 | -2.4 | 0.016 | 0.50 | 0.01 | -604.50 |

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## Appendix 3: Supplementary Information for Chapter 4

### Supplementary results

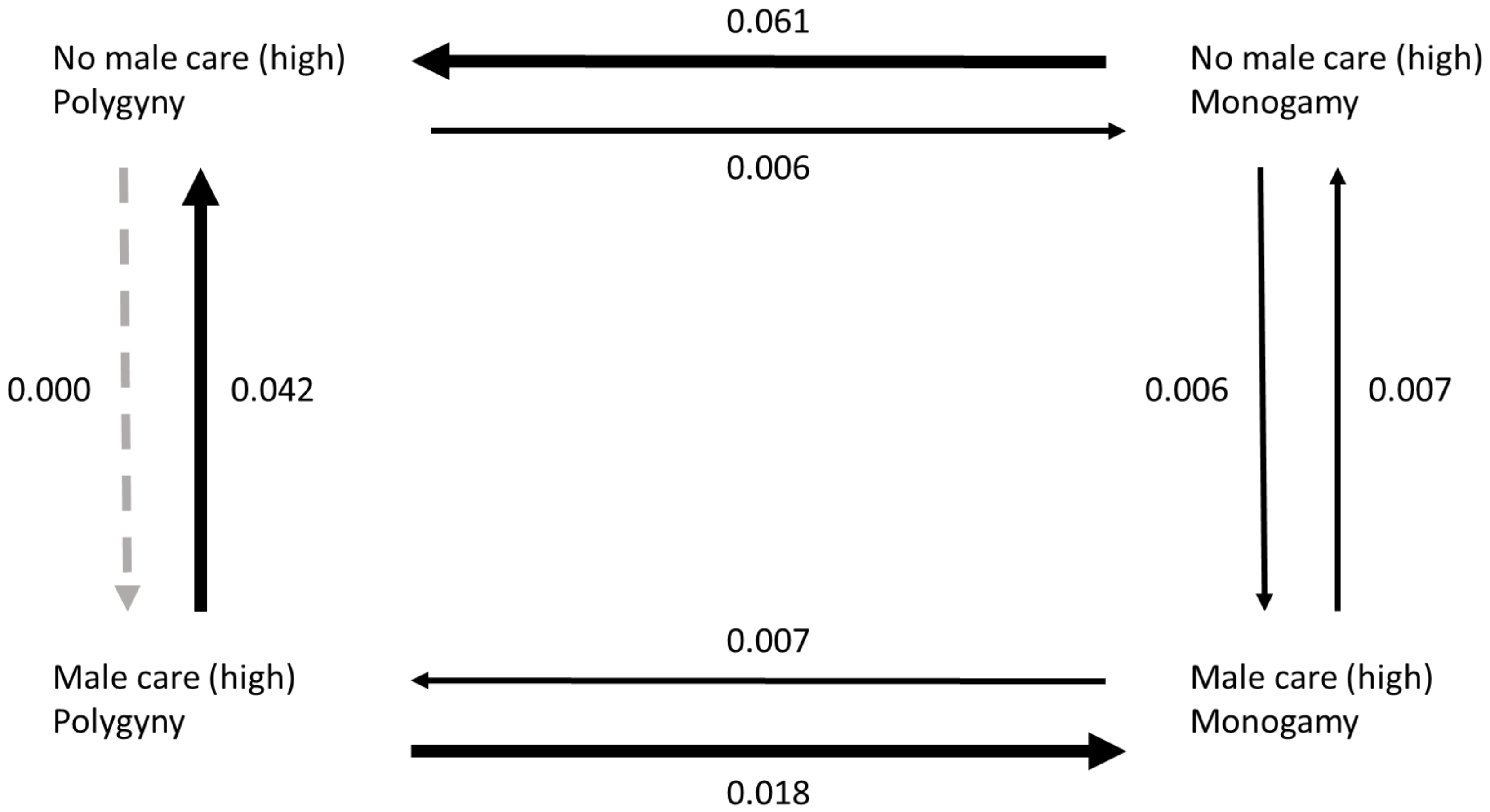
As when the male care behaviours are considered individually we find support for correlated evolution between social monogamy and all care behaviours when they are clustered as high cost/benefit (carrying and provisioning), or low cost/benefit (grooming and huddling). In all cases the dependent model of evolution provides a better fit to the data than the independent model (high: BF=37.54; low: BF=26.70).

When considered together, high-benefit behaviours follow the evolution of social monogamy (Figure S1). From the absence of both care and monogamy, monogamy is more likely to evolve in the absence of male care ($q_{12}$=0.006), while care does not evolve in the absence of a monogamous mating system ($q_{13}$=0.000). Once social monogamy has evolved, it can either be lost, back to the absence of both states ($q_{21}$=0.061), or male care evolves ($q_{24}$=0.006). Male care with polygyny is an unstable state, which arises though the loss of monogamy ($q_{43}$=0.007), and is either rapidly lost back to an absence of both care and monogamy ($q_{31}$=0.042), or monogamy is quickly regained ($q_{34}$=0.018).

Low benefit behaviours on the other hand, show a more dynamic pattern (Figure S2). From a state of polygyny and the absence of care either low-benefit male care or social monogamy can evolve, although the transition rate for the initial evolution of care is slightly higher ($q_{13}$=0.008, $q_{12}$=0.004). Low benefit male care in the absence of monogamy is less stable than social monogamy in the absence of care, and is lost at a higher rate ($q_{31}$=0.125, $q_{21}$=0.004). However, the evolution of monogamy in the presence of care and the evolution of care in the presence of monogamy occur at similar rates ($q_{34}$=0.095, $q_{24}$=0.117), and either behaviour can be lost similarly rapidly ($q_{43}$=0.122, $q_{42}$=0.118).

## Supplementary figures

**a)**



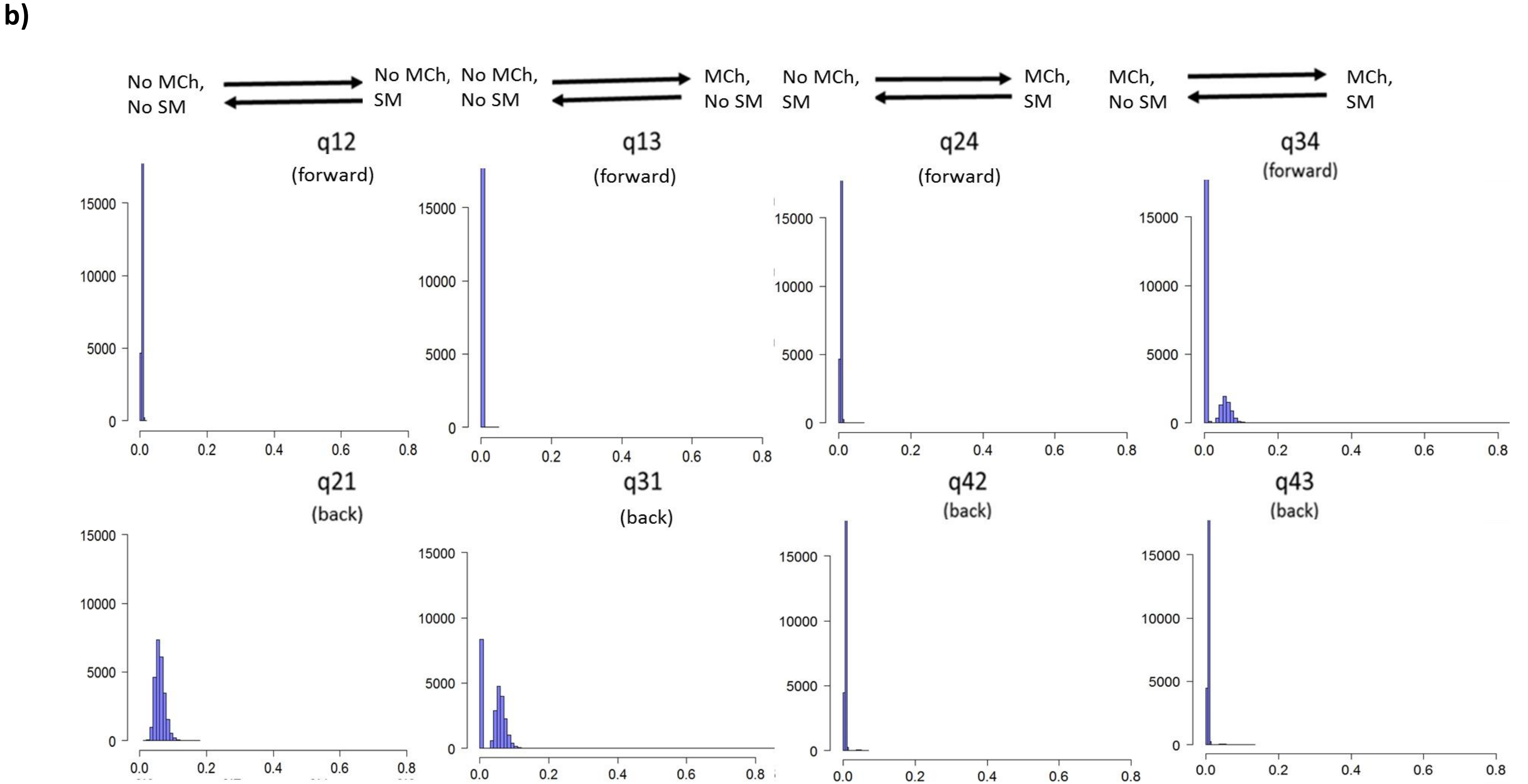
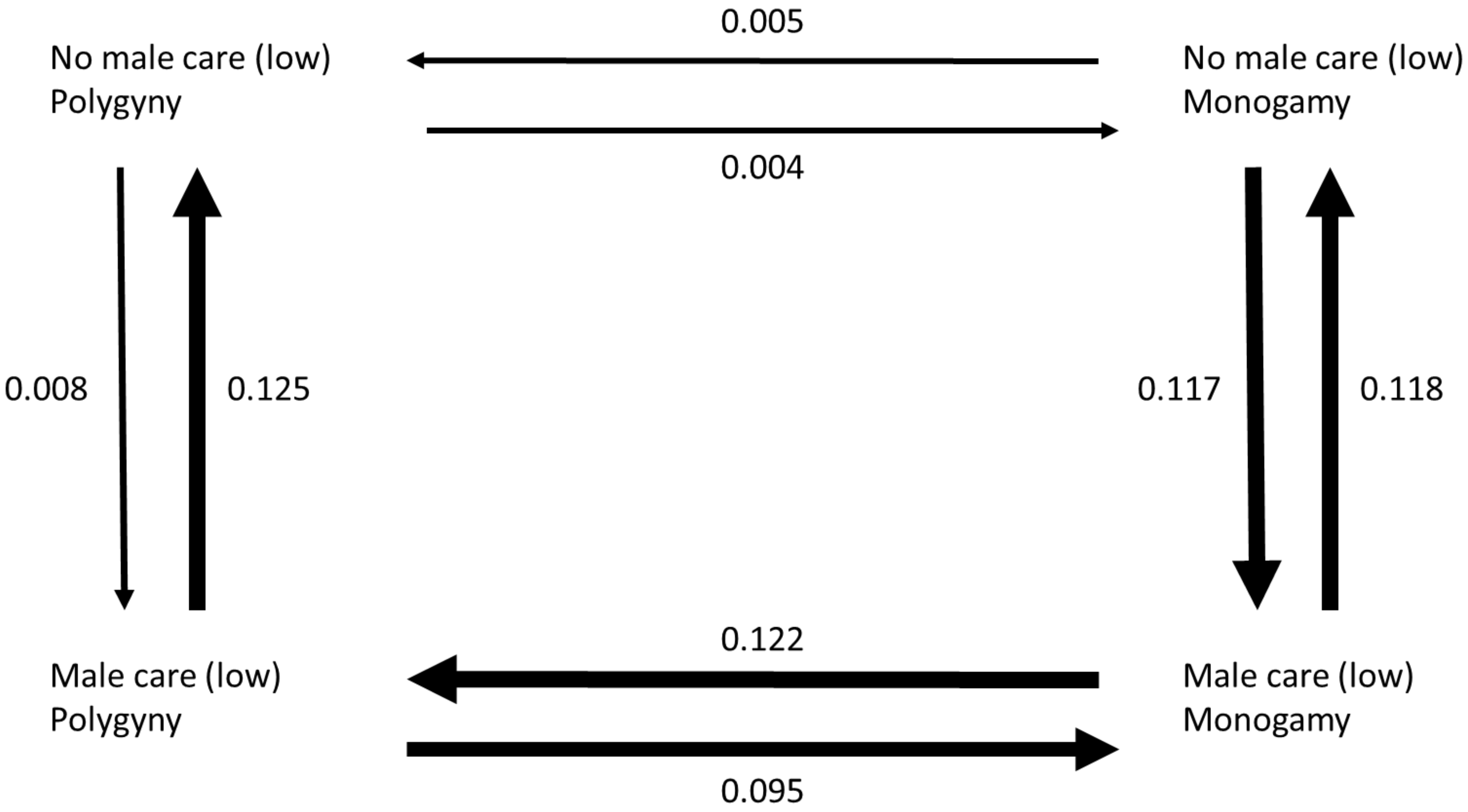


**Figure S1: The dependent model of evolution between high cost/benefit male care (carrying and provisioning) (MCh) and social monogamy (SM) (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions. Greyed out transitions never occur within the model. The arrow labels represent the mean rate for each transition taken from the posterior distribution.

**a)**


0.005
No male care (low)
Polygyny
No male care (low)
Monogamy
0.004
0.008
0.125
0.117
0.118
0.122
Male care (low)
Polygyny
Male care (low)
Monogamy
0.095

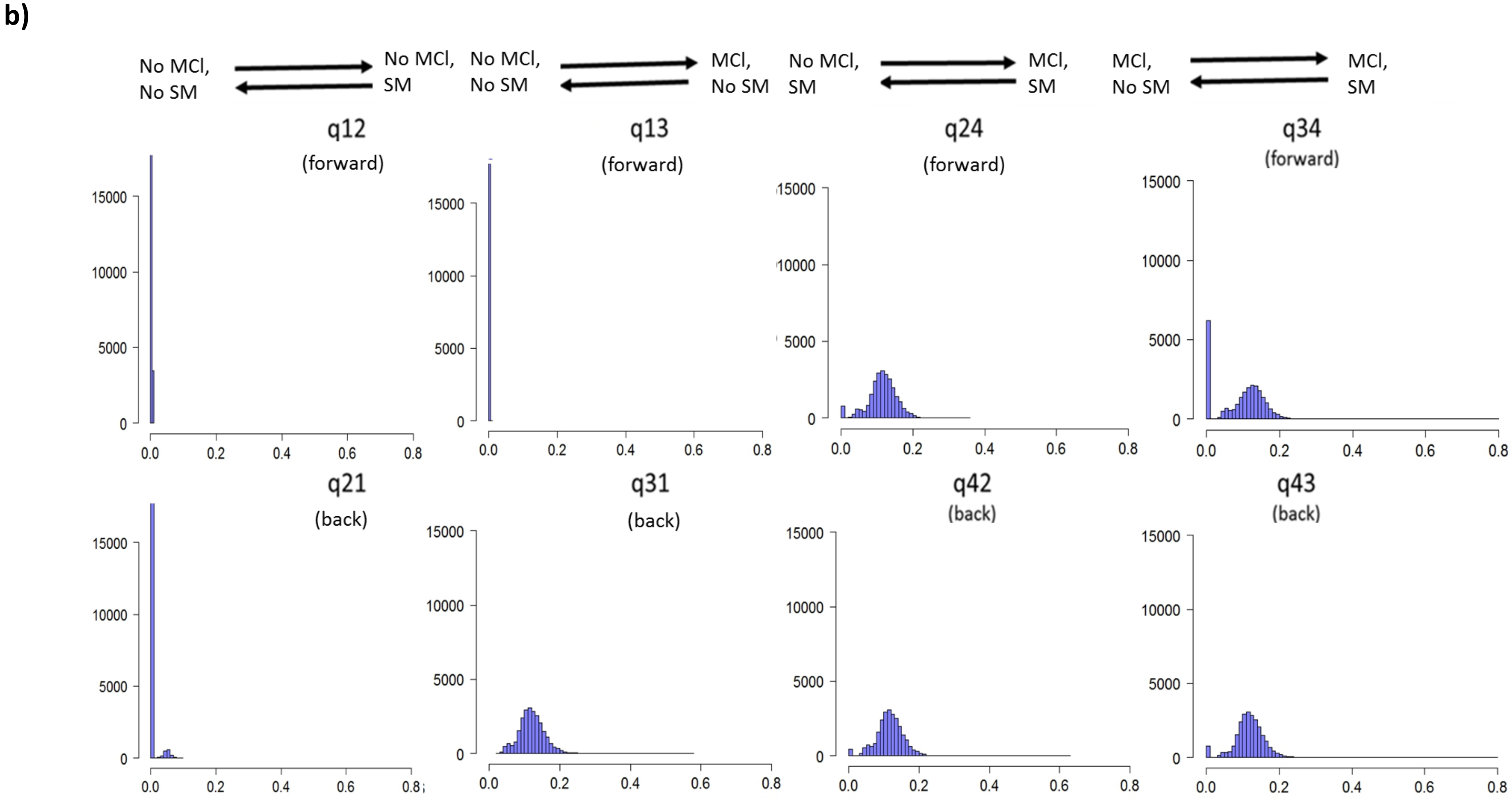


**Figure S2: The dependent model of evolution between low cost/benefit male care (grooming and huddling) (MCl) and social monogamy (SM) (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions. Greyed out transitions never occur within the model. The arrow labels represent the mean rate for each transition taken from the posterior distribution.

## Appendix 4: Supplementary Information for Chapter 5

### Supplementary results

When testing our hypotheses including all male care behaviours (grooming, huddling and provisioning offspring as well as carrying offspring and provisioning females) our results remain quantitavely similar. As predicted by the male energetic contribution hypothesis there is a significant interaction between gestation time and male care (all) (Table S1). Thus while lactation increases with gestation in species without male care, it is unrelated to gestation in species with biparental care. A full model with male care (all) and the interaction between male care (all) and gestation explains an additional 6% of variance compared to a model without male care ($LR_2$=33.5, p=<0.001).

Like male care (high), male care (all) is evolutionarily correlated with infanticide as the dependent model of evolution fits the data substantially better than the independent model of evolution (BF=13.4). Specifically, the dependent model of evolution (Figure S1) estimates that the ancestral combination of character states in mammals is most likely to have been either no male care with no infanticide (41%) or infanticide without male care (26%), while estimates for other combinations are lower (male care without infanticide, 17%; male care and infanticide, 17%). From a state of no male care and no infanticide (0,0), infanticide evolves more readily than male care (transition rate mean: $q_{12}$=0.013, $q_{13}$<0.001). Male care in the absence of infanticide (1,0) and infanticide without male care (0,1) revert back to the absence of both behaviours more quickly or as quickly as they are gained (transition rate mean $q_{31}$=0.012; $q_{21}$=0.014). Gaining male care in infanticidal species and gaining infanticide in species with male care occur at a moderate rate (transition rate mean $q_{24}$=0.013; $q_{34}$=0.014). Furthermore, the presence of both infanticide and male care (1,1) appears to be an unstable condition as it is very rapidly lost either back to a state of infanticide without male care (mean $q_{42}$=0.050), or to a state with male care only (mean $q_{43}$=0.198). The evolution of the combination infanticide with male care (1,1) therefore occurs at a much lower rate than the transitions away from this state. Overall these results indicate that male care and infanticide are evolutionarily associated but that the coexistence of these two behaviours in the same species is extremely rare, and represents an unusual and evolutionary unstable condition.

When we restrict the analysis to only primates, the presence of infanticide is not associated with the duration of lactation (Table S2, model 1). The relationship between male care (all) and lactation time is the same in primates as it is in all mammals, species with male care have a significantly shorter lactation but among primates, we find no significant interaction between male care and gestation time (Table S2, model 2). This may be due to the smaller sample size used in these analyses, or it may be indicative of an underlying difference between primates and mammals as a whole (as proposed by Opie et al. 2014). Regardless, even among primates we find no evidence that infanticide drives the reduction in lactation time associated with male care (Table S2, models 3&4).

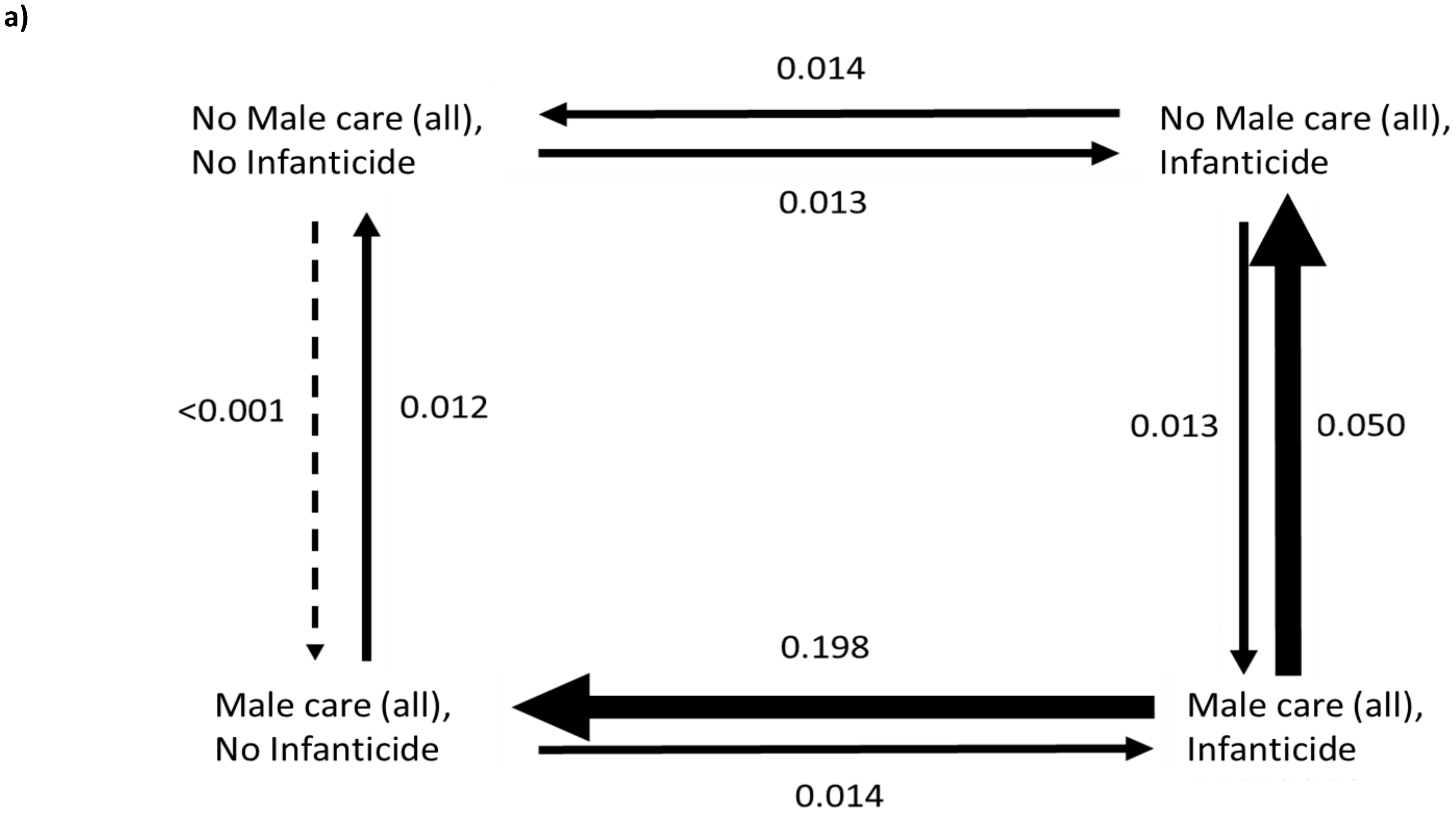
## Supplementary tables and figures

**Table S1: Best fitting PGLS model for the duration of lactation with male care (all) across all mammals.** For each independent variable in each model, we report the β-values, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$ and the model log-likelihood (Lh). The total sample size for models with male care is 413 species, of which n have male care.

| **Lactation time** | | **Variable statistics** | | | | **Model statistics** | |
|---|---|---|---|---|---|---|---|
| **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| Female body mass | 0.13 | 0.02 | 6.6 | <0.001 | 0.82 | 0.27 | 57.31 |
| Gestation time | 0.36 | 0.09 | 4.2 | <0.001 | | | |
| Male care (all) | 0.45 | 0.21 | 2.1 | 0.036 | | | |
| Gestation:Male care (all) | -0.33 | 0.12 | -2.8 | 0.006 | | | |

**Table S2: Best fitting PGLS models for the duration of lactation with infanticide in primates.** For each independent variable in each model, we report the β-value, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, $R^2$ and the model log-likelihood (Lh). The total sample size for models including male care is 72 species, of which 11 species exhibit male care (all). The sample size for models including infanticide is 56 species, of which 35 exhibit male infanticide. Models are numbered for ease of presentation.

| **Lactation time** | | **Variable statistics** | | | | **Model statistics** | | |
|---|---|---|---|---|---|---|---|---|
| **Model** | **Independent Variable** | **β** | **S.E.** | **t** | **p** | **λ** | **$R^2$** | **Lh** |
| **1** | Female body mass | 0.23 | 0.06 | 3.8 | <0.001 | 0.00 | 0.67 | 10.78 |
| | Gestation time | 1.20 | 0.32 | 3.8 | <0.001 | | | |
| | Male care (all) | -0.23 | 0.08 | -3.0 | 0.004 | | | |
| **2** | Female body mass | 0.22 | 0.06 | 3.7 | 0.001 | 0.00 | 0.67 | 10.89 |
| | Gestation time | 1.19 | 0.32 | 3.7 | <0.001 | | | |
| | Male Care | -1.18 | 2.11 | -0.6 | 0.578 | | | |
| | Gestation:Male Care (all) | 0.44 | 0.97 | 0.5 | 0.653 | | | |
| **3** | Female Body mass | 0.32 | 0.09 | 3.5 | 0.001 | 0.00 | 0.60 | 2.17 |
| | Gestation time | 0.99 | 0.43 | 2.3 | 0.025 | | | |
| | Infanticide | -0.04 | 0.08 | -0.5 | 0.643 | | | |
| **4** | Female body mass | 0.33 | 0.09 | 3.5 | 0.001 | 0.00 | 0.61 | 2.35 |
| | Gestation time | 0.85 | 0.49 | 1.7 | 0.089 | | | |
| | Infanticide | -0.84 | 1.39 | -0.6 | 0.550 | | | |
| | Gestation:Infanticide | 0.36 | 0.62 | 0.6 | 0.570 | | | |


a)
0.014
No Male care (all),
No Infanticide
No Male care (all),
Infanticide
0.013
<0.001
0.012
0.013
0.050
0.198
Male care (all),
No Infanticide
Male care (all),
Infanticide
0.014

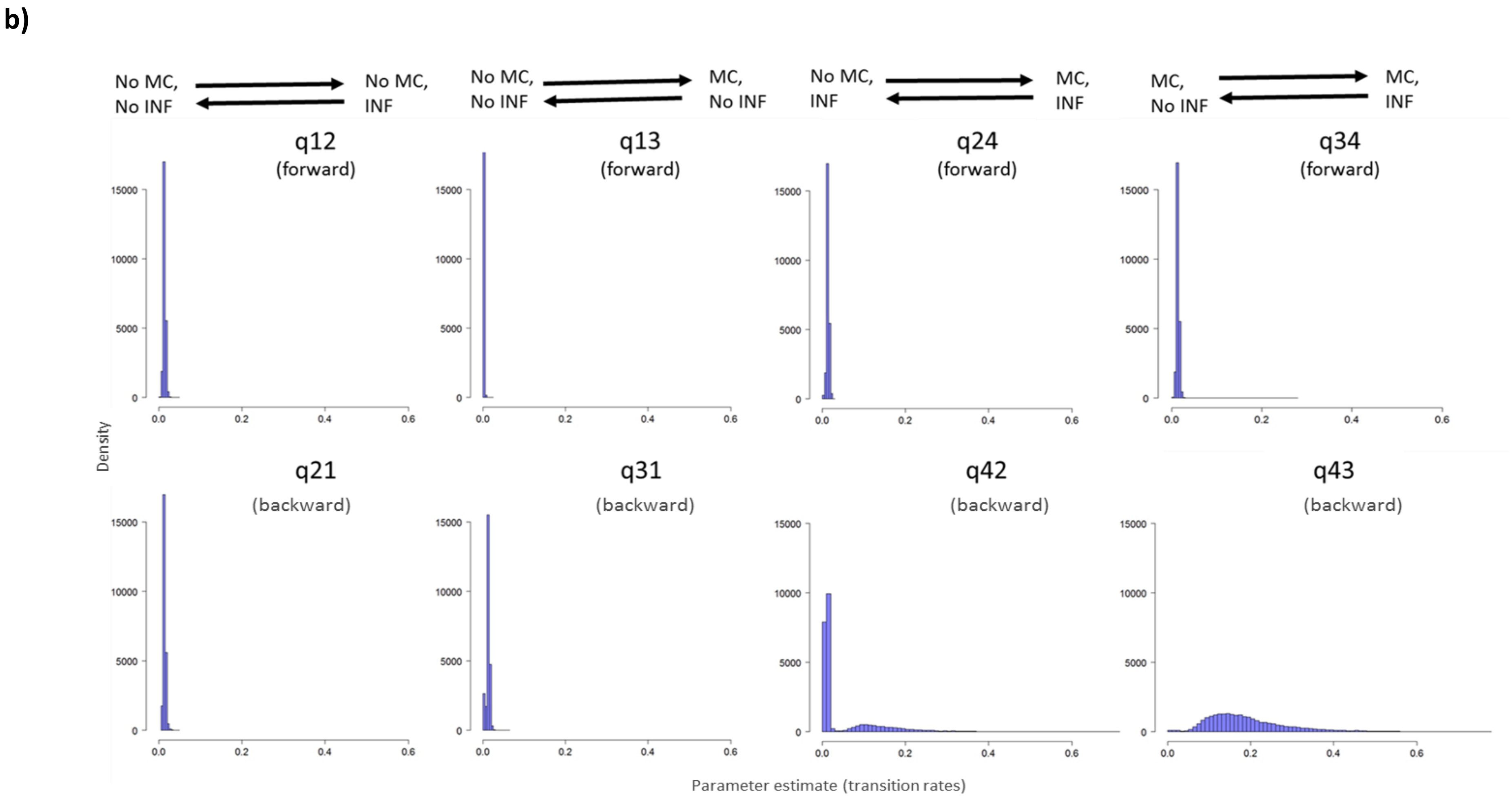


**Figure S1: The dependent model of evolution between male care (all) and infanticide (a), and the posterior distributions for all rates within the model (b).** Arrow thickness corresponds to the relative rates of transitions within the model, with thicker arrows indicating faster transitions, and dashed arrows representing unlikely transitions. The arrow labels represent the mean rate for each transition taken from the posterior distribution of the dependent model of evolution. MC=male care (all), INF=infanticide.

## Appendix 5: Supplementary Information for Chapter 6

### Supplementary methods

We collected data on the specific alloparental care behaviours performed by helpers from a variety of available primary and secondary sources (Kinzey et al. 1977; Watts & Holekamp 2007; Nettelbeck 1999; Bales et al. 2000; Packer et al. 1992; MacLeod & Lukas 2014; Pusey & Packer 1994; Isler & van Schaik 2012; Borries et al. 2010; Goodall 1986; Baden et al. 2013; Tecot et al. 2012; Nowak 1999; Walton & Joly 2003; Gompper & Vanak 2006; Mason & Mendoza 1993; Clutton-Brock et al. 2001; Mitani & Watts 1997; Woodroffe & Macdonald 2000; Moehlman 1979; Lukas & Clutton-Brock 2012; Hodge 2005; Sparkman et al. 2011; Kruchenkova et al. 2009; Snowdon 1996; Silk 2007), for species with life history data (see also main text, Methods, Data collection). As in chapter 3, we define care by helpers as care towards neonates or older dependent offspring by any individuals other than the presumed parents of the offspring. We consider allonursing, carrying, grooming, huddling with and provisioning the offspring, to be forms of care by helpers. As with male care, we do not include offspring defence, babysitting, or teaching under our definition of alloparental care, as these behaviours are difficult to reliably quantify in a comparative way (Chapter 3; West & Capellini 2016).

### Supplementary notes

In Supplementary Tables 1-5 we report the full models for the life history traits significantly associated with individual allocare behaviours, and all models for the life history traits that are unrelated to alloparental care. Models 3 and 4 in table S1 test the associations between allocare behaviours and litters per year, without including the durations of lactation and gestation and confirm that the association between allocarrying and breeding frequency is a side effect of a possible association between these behaviour and lactation time.

## Supplementary tables and figures

**Table S1: Litters per year and alloparental behaviours across all mammals.** For each independent variable in each model, we report the β-values, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, R2 and the model log-likelihood (Lh). Best fitting models are presented in Table 1 in the main text. The total sample size for models including lactation and gestation is 371 species, of which 72 species have allocare (25 carrying, 28 provisioning, 54 allonursing, 24 grooming or huddling), 46 have male care (14 carrying, 22 grooming), and 48 are socially monogamous. Models are numbered for ease of presentation.

| **Litters per Year (n=371)** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | Independent variable | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **1** | Female body mass | -0.1 | -<0.1 | -2.7 | 0.006 | 0.90 | 0.24 | 162.43 | -300.86 |
| (full) | Lactation time | -0.1 | <0.1 | -3.5 | 0.001 | | | | |
| | Gestation time | -0.2 | 0.1 | -3.3 | 0.001 | | | | |
| | Allocarrying | -<0.1 | <0.1 | -0.7 | 0.469 | | | | |
| | Alloprovisioning | 0.1 | 0.1 | 2.5 | 0.012 | | | | |
| | Allonursing | <0.1 | <0.1 | 1.3 | 0.184 | | | | |
| | Allogrooming & huddling | <0.1 | <0.1 | 0.1 | 0.961 | | | | |
| | Male care (carrying) | 0.1 | 0.1 | 1.2 | 0.244 | | | | |
| | Male care (grooming) | 0.1 | <0.1 | 1.4 | 0.177 | | | | |
| | Social monogamy | 0.1 | <0.1 | 1.4 | 0.157 | | | | |
| | Citation count | -<0.1 | <0.1 | -<0.1 | 0.965 | | | | |
| **2** | Female body mass | -0.1 | <0.1 | -2.7 | 0.007 | 0.89 | 0.21 | 156.00 | -301.98 |
| (no allocare) | Lactation time | -0.2 | <0.1 | -4.2 | <0.001 | | | | |
| | Gestation time | -0.2 | 0.1 | -3.1 | 0.002 | | | | |
| | Male care (grooming) | 0.1 | <0.1 | 2.2 | 0.027 | | | | |
| **3** | Female body mass | -0.1 | <0.1 | -6.7 | <0.001 | 0.92 | 0.16 | 147.66 | -275.32 |
| (full) | Alloprovisioning | -<0.1 | 0.1 | -0.5 | 0.616 | | | | |
| | Allocarrying | 0.1 | 0.1 | 2.7 | 0.008 | | | | |
| | Allonursing | <0.1 | <0.1 | 1.1 | 0.290 | | | | |
| | Allogrooming & huddling | <0.1 | <0.1 | 0.4 | 0.658 | | | | |
| | Male care (carrying) | 0.1 | 0.1 | 1.4 | 0.152 | | | | |
| | Male care (grooming) | 0.1 | <0.1 | 1.3 | 0.187 | | | | |
| | Social monogamy | <0.1 | <0.1 | 1.3 | 0.204 | | | | |
| | Citation count | <0.1 | <0.1 | 0.3 | 0.762 | | | | |
| **4** | Female body mass | -0.1 | <0.1 | -6.9 | <0.001 | 0.92 | 0.15 | 144.36 | -280.72 |
| (reduced) | Allocarrying | 0.1 | 0.1 | 3.1 | 0.002 | | | | |
| | Male care (carrying) | 0.1 | 0.1 | 2.1 | 0.038 | | | | |

**Table S2: Lactation time and alloparental behaviours across all mammals.** For each independent variable in each model, we report the β-values, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, R2 and the model log-likelihood (Lh). The total sample size for all models is 390 species, of which 74 species have allocare (26 carrying, 28 provisioning, 56 allonursing, and 26 either grooming or huddling), 47 have male care (14 carrying, 12 provisioning females), and 55 are socially monogamous. In models 3, 4 and 5 huddling by alloparents is classified as no care and the sample size for grooming alone is 21. Models are numbered for ease of presentation.

| **Lactation time (n=390)** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | Independent variable | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **1** | Female body mass | 0.1 | 0.0 | 5.9 | <0.001 | 0.83 | 0.29 | 54.94 | -87.88 |
| (full) | Gestation time | 0.4 | 0.1 | 4.1 | <0.001 | | | | |
| | Allocarrying | -0.1 | 0.1 | -1.9 | 0.059 | | | | |
| | Alloprovisioning | 0.0 | 0.1 | 0.3 | 0.804 | | | | |
| | Allonursing | 0.0 | 0.0 | 0.1 | 0.955 | | | | |
| | Allogrooming & huddling | -0.1 | 0.1 | -2.1 | 0.034 | | | | |
| | Male care (carrying) | -0.2 | 0.1 | -2.5 | 0.015 | | | | |
| | Male care (prov. females) | -0.2 | 0.1 | -1.9 | 0.053 | | | | |
| | Social monogamy | 0.0 | 0.0 | 0.1 | 0.922 | | | | |
| | Citation count | 0.0 | 0.0 | 0.4 | 0.695 | | | | |
| **2** | Female body mass | 0.1 | 0.0 | 6.2 | <0.001 | 0.81 | 0.26 | 46.36 | -84.73 |
| (no allocare) | Gestation time | 0.4 | 0.1 | 4.2 | <0.001 | | | | |
| | Male care (carrying) | -0.2 | 0.1 | -2.7 | 0.007 | | | | |
| **3** | Female body mass | 0.1 | <0.1 | 5.9 | <0.001 | 0.81 | 0.29 | 55.63 | -89.25 |
| (full) | Gestation time | 0.4 | 0.1 | 4.2 | <0.001 | | | | |
| | Allocarrying | -0.1 | 0.1 | -1.6 | 0.107 | | | | |
| | Alloprovisioning | <0.1 | 0.1 | 0.3 | 0.755 | | | | |
| | Allonursing | -<0.1 | <0.1 | -0.1 | 0.939 | | | | |
| | Allogrooming | -0.1 | 0.1 | -2.4 | 0.016 | | | | |
| | Male care (carrying) | -0.2 | 0.1 | -2.4 | 0.020 | | | | |
| | Male care (prov. females) | -0.2 | 0.1 | -2.0 | 0.053 | | | | |
| | Social monogamy | <0.1 | <0.1 | <0.1 | 0.967 | | | | |
| | Citation count | <0.1 | <0.1 | 0.4 | 0.675 | | | | |
| **4** | Female body mass | 0.1 | <0.1 | 6.2 | <0.001 | 0.82 | 0.29 | 52.27 | -94.55 |
| (reduced) | Gestation time | 0.4 | 0.1 | 4.4 | <0.001 | | | | |
| | Allogrooming | -0.2 | 0.1 | -3.4 | 0.001 | | | | |
| | Male care (carrying) | -0.2 | 0.1 | -2.5 | 0.014 | | | | |

**Table S3: Gestation time and alloparental behaviours across all mammals.** For each independent variable in each model, we report the β-values, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, R2 and the model log-likelihood (Lh). The total sample size for all models is 390 species, of which 74 species have allocare (26 carrying, 28 provisioning, 56 allonursing, and 26 either grooming or huddling), and 55 are socially monogamous. Models are numbered for ease of presentation.

| **Gestation time (n=390)** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | Independent variable | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **1**<br>(full) | Female body mass | 0.1 | <0.1 | 8.3 | <0.001 | 1.00 | 0.28 | 331.64 | -643.28 |
| | Lactation time | 0.1 | <0.1 | 2.6 | 0.011 | | | | |
| | Litter size | -0.2 | <0.1 | -4.5 | <0.001 | | | | |
| | Allocarrying | -<0.1 | <0.1 | -0.9 | 0.388 | | | | |
| | Alloprovisioning | <0.1 | <0.1 | 0.7 | 0.494 | | | | |
| | Allonursing | <0.1 | <0.1 | 2.5 | 0.013 | | | | |
| | Allogrooming & huddling | <0.1 | <0.1 | 0.6 | 0.559 | | | | |
| | Social monogamy | <0.1 | <0.1 | 0.2 | 0.834 | | | | |
| | Citation count | -<0.1 | <0.1 | -1.4 | 0.164 | | | | |
| **2**<br>(no allocare) | Female body mass | 0.1 | <0.1 | 8.8 | <0.001 | 1.00 | 0.26 | 326.28 | -644.57 |
| | Lactation time | 0.1 | <0.1 | 2.3 | 0.021 | | | | |
| | Litter size | -0.2 | <0.1 | -4.4 | <0.001 | | | | |

**Table S4: Litter size and alloparental behaviours across all mammals.** For each independent variable in each model, we report the β-values, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, R2 and the model log-likelihood (Lh). The total sample size for all models is 450 species, of which 79 species have allocare (30 carrying, 32 provisioning, 58 allonursing, and 28 either grooming or huddling), 53 have male care (13 provisioning females), and 62 are socially monogamous. Models are numbered for ease of presentation.

| **Litter size (n=450)** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | Independent variable | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **1**<br>(full) | Female body mass | -0.1 | <0.1 | -5.3 | <0.001 | 0.96 | 0.17 | 273.41 | -528.83 |
| | Allocarrying | -<0.1 | <0.1 | -0.7 | 0.505 | | | | |
| | Alloprovisioning | 0.1 | <0.1 | 3.1 | 0.002 | | | | |
| | Allonursing | -<0.1 | <0.1 | -0.8 | 0.407 | | | | |
| | Allogrooming & huddling | <0.1 | <0.1 | 0.4 | 0.705 | | | | |
| | Male care (prov. females) | 0.2 | 0.1 | 4.4 | <0.001 | | | | |
| | Social monogamy | -<0.1 | <0.1 | -1.8 | 0.069 | | | | |
| | Citation count | 0.1 | <0.1 | 5.7 | <0.001 | | | | |
| **2**<br>(no allocare) | Female body mass | -0.1 | <0.1 | -5.4 | <0.001 | 0.95 | 0.15 | 267.66 | -527.32 |
| | Male care (prov. females) | 0.2 | 0.1 | 5.1 | <0.001 | | | | |
| | Citation count | 0.1 | <0.1 | 6.0 | <0.001 | | | | |

**Table S5: Neonate mass (a), weaning mass (b), and body mass increase from birth to weaning (c), and alloparental behaviours across all mammals.** For each independent variable in each model, we report the β-values, standard error (S.E.), t-statistics and p-value, and for each model the estimated ML λ value, R2 and the model log-likelihood (Lh). The total sample size for neonate mass models is 394 species, of which 73 species have allocare (27 carrying, 26 provisioning, 54 allonursing, and 26 either grooming or huddling), and 51 are socially monogamous. The total sample size for weaning mass and mass increase models is 232 species, of which 44 species have allocare (18 carrying, 13 provisioning, 30 allonursing, and 16 either grooming or huddling), and 22 are socially monogamous. Models are numbered for ease of presentation.

| **a) Neonate mass (n=394)** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | Independent variable | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **1** | Female body mass | 0.6 | <0.1 | 28.2 | <0.001 | 0.97 | 0.81 | 80.53 | -141.05 |
| (full) | Gestation time | 0.7 | 0.1 | 7.3 | <0.001 | | | | |
| | Litter size | -0.4 | 0.1 | -5.5 | <0.001 | | | | |
| | Allocarrying | -<0.1 | 0.1 | -0.5 | 0.650 | | | | |
| | Alloprovisioning | <0.1 | 0.1 | 0.6 | 0.572 | | | | |
| | Allonursing | 0.1 | <0.1 | 1.6 | 0.106 | | | | |
| | Allogrooming & huddling | -<0.1 | <0.1 | -0.5 | 0.648 | | | | |
| | Social monogamy | -0.1 | <0.1 | -2.1 | 0.037 | | | | |
| | Citation count | <0.1 | <0.1 | 0.2 | 0.834 | | | | |
| **2** | Female body mass | 0.6 | <0.1 | 29.5 | <0.001 | 0.97 | 0.81 | 78.34 | -146.68 |
| (reduced) | Gestation time | 0.7 | 0.1 | 7.5 | <0.001 | | | | |
| | Litter size | -0.4 | 0.1 | -5.3 | <0.001 | | | | |
| | Social monogamy | -0.1 | <0.1 | -2.1 | 0.037 | | | | |

| **b) Weaning mass (n=232)** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | Independent variable | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **1** | Female body mass | 0.8 | <0.1 | 46.7 | <0.001 | 0.30 | 0.95 | 39.57 | -59.15 |
| (full) | Lactation time | 0.1 | 0.1 | 1.8 | 0.068 | | | | |
| | Litter size | -0.4 | 0.1 | -5.4 | <0.001 | | | | |
| | Allocarrying | -0.1 | 0.1 | -1.3 | 0.211 | | | | |
| | Alloprovisioning | 0.2 | 0.1 | 1.7 | 0.087 | | | | |
| | Allonursing | 0.1 | <0.1 | 1.1 | 0.270 | | | | |
| | Allogrooming & huddling | -0.1 | 0.1 | -0.9 | 0.359 | | | | |
| | Social monogamy | -0.1 | 0.1 | -1.6 | 0.115 | | | | |
| | Citation count | <0.1 | <0.1 | 1.0 | 0.312 | | | | |
| **2** | Female body mass | 0.8 | <0.1 | 48.0 | <0.001 | 0.32 | 0.95 | 34.81 | -61.62 |
| (reduced) | Lactation time | 0.1 | 0.1 | 2.3 | 0.021 | | | | |
| | Litter size | -0.4 | 0.1 | -5.1 | <0.001 | | | | |

| **c) Body mass increase (n=232)** | | **Variable statistics** | | | | **Model statistics** | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | Independent variable | β | S.E. | t | p | λ | $R^2$ | Lh | AIC |
| **1** | Female body mass | 0.8 | <0.1 | 43.1 | <0.001 | 0.25 | 0.95 | 13.79 | -7.59 |
| (full) | Lactation time | 0.2 | 0.1 | 2.8 | 0.005 | | | | |
| | Litter size | -0.3 | 0.1 | -3.5 | 0.001 | | | | |
| | Allocarrying | -0.1 | 0.1 | -1.4 | 0.172 | | | | |
| | Alloprovisioning | 0.2 | 0.1 | 1.6 | 0.108 | | | | |
| | Allonursing | 0.1 | 0.1 | 1.1 | 0.285 | | | | |
| | Allogrooming & huddling | -0.1 | 0.1 | -1.3 | 0.212 | | | | |
| | Social monogamy | -0.1 | 0.1 | -1.4 | 0.157 | | | | |
| | Citation count | <0.1 | <0.1 | 0.8 | 0.408 | | | | |
| **2** | Female body mass | 0.8 | <0.1 | 43.9 | <0.001 | 0.28 | 0.94 | 9.00 | -10.00 |
| (reduced) | Lactation time | 0.2 | 0.1 | 3.3 | 0.001 | | | | |
| | Litter size | -0.2 | 0.1 | -3.1 | 0.003 | | | | |

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## Appendix 6: Male care and Life History traits in mammals

West, H.E.R. & Capellini, I. (2016) Male care and life history traits in mammals. *Nature communications*, 7, e11854.