



Evolution of cooperative breeding in mammals : an interspecific approach focused on the evolution of constitutive traits

Valentine Federico

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Evolution of cooperative breeding in Mammals: An interspecific approach focused on the evolution of constitutive traits

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Résumé

Evolution de la reproduction coopérative chez les Mammifères : Une approche interspécifique centrée sur la coévolution des traits constitutifs

La reproduction coopérative est un système social dans lequel seuls les individus dominants ont accès à la reproduction et où les subordonnés, en grande majorité leurs descendants, apportent des soins aux jeunes. Son évolution peut être expliquée par des hypothèses non-exclusives incluant le gain indirect de valeur sélective, un coût élevé de dispersion dans des environnements difficiles, ou une compensation par des bénéfices liés à la taille du groupe. Afin d'éclaircir les mécanismes évolutifs de la reproduction coopérative, nous avons utilisé une approche interspécifique fondée sur la reconstitution phylogénétique de la coévolution des trois traits la constituant (retard de dispersion, suppression reproductive et alloparentalité) dans les ordres de Mammifères où elle est présente. Nous avons mis en évidence des chemins évolutifs différents chez les primates et les carnivores en termes de directionnalité et de stabilité des configurations intermédiaires. Nous avons également montré que les variables climatiques associées à la reproduction coopérative étaient associées à différents traits constitutifs, et donc à différentes étapes de son évolution. Cette thèse a ainsi souligné l'importance de considérer les systèmes sociaux complexes comme des combinaisons de leurs traits constitutifs plutôt que comme des ensembles indissociables. Cette approche est particulièrement pertinente pour les systèmes sociaux rares, car elle apporte aussi une réponse méthodologique aux problématiques rencontrées lors de leur étude. Elle a également montré que des systèmes sociaux apparemment similaires pouvaient être sous-tendus par des mécanismes évolutifs très différents d'un taxon à l'autre.

Mots-clés : mammifères, socialité, coopération, systèmes sociaux, reproduction coopérative, reproduction communale, approche interspécifique, coévolution, reconstruction phylogénétique, retard de dispersion, suppression reproductive, alloparentalité

Summary

Evolution of cooperative breeding in Mammals: An interspecific approach focused on the coevolution of constitutive traits

Cooperative breeding is a social system in which only dominant individuals access reproduction while subordinates, which are mostly their previous offspring, care for the young. The evolution of cooperative breeding may be explained by non-exclusive hypotheses including indirect fitness gains, high costs of dispersal in harsh environments, or compensation by group-size benefits. In order to shed light on the evolutionary mechanisms of cooperative breeding, we used an interspecific approach focused on the phylogenetic reconstruction of the coevolution of the three constitutive traits (delayed dispersal, reproductive suppression and alloparenting) in the mammalian orders where it occurs. We showed that evolutionary pathways to cooperative breeding in Primates and Carnivores were different in terms of directionality and stability of intermediate combinations. We also suggested climate variables displaying an association with cooperative breeding to be actually associated with different constitutive traits, and therefore different evolutionary steps. This thesis thus emphasized the importance of treating complex social systems as combinations of their constitutive traits rather than indivisible sets. This approach is especially relevant for rare social systems, as it also provides a methodological answer to rarity-related issues. It also stressed that highly similar social systems could actually be underlain by strikingly different evolutionary processes depending on taxa.

Keywords: mammals, sociality, cooperation, social systems, cooperative breeding, communal breeding, interspecific approach, coevolution, phylogenetic reconstruction, delayed dispersal, reproductive suppression, alloparenting

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Introduction

What is cooperative breeding?

Evolutionary implications of cooperation

Cooperation plays a key role in a number of biological processes at different levels of biological organization, including symbiosis, gene expression, interspecific mutualism, and intraspecific sociality (Boucher 1988; Bourke 2011; Kiers et al. 2011). Understanding the evolution of cooperation is crucial in explaining how single biological entities such as cells or individuals merge into collective ones such as multicellular organs or structured social groups, and how these complex structures are stabilized into new levels of organization (West et al. 2015). Individuals performing extreme cooperative behaviors, referred as altruistic behaviors, incur direct fitness costs, while individuals towards which these behaviors are directed gain direct benefits. Given that natural selection penalizes such costs, the emergence and maintenance of altruism represent an evolutionary paradox that attracted increasing attention in the recent years (Axelrod 2006; Lehmann and Keller 2006; Nowak 2006; Németh and Takács 2010; Heath and Stinchcombe 2014).

Defining cooperative breeding

In animal societies, individuals can cooperate in a variety of tasks, including foraging, hunting, resource or mate defense, but also raising young (Dugatkin, 1997). Cooperation towards young rearing, which we define as alloparenting, includes a variety of behaviors, such as allofeeding, infant carrying and monitoring, which all involve direct costs in terms of fitness components (Carlisle and Zahavi 1986; Snowdon 1996; Schradin and Anzenberger 2001). Societies involving these forms of cooperation in raising young are sorted into three social systems: Communal breeding, cooperative breeding and eusociality.

Communal breeding

Communal breeding encompasses social systems in which breeders pool their offspring and share care and feeding among them (Gittleman 1985). Communally breeding societies are mostly egalitarian, with low or no hierarchy among the individuals of the sex in charge of parental care (Table 1). Reproduction may be equally shared, such as in African lions (*Panthera leo*) in which females that pool their offspring consistently produce similar numbers of surviving offspring (Packer et al. 2001). In other cases, a small reproductive skew may be reported, but all adults present in the group typically reproduce, such as in banded mongooses (Gilchrist 2006a). Synchronous breeding is widely observed in communal breeders. A possible explanation for this may be that it reduces incentives to reduce the reproduction of other

group members (Hayes 2000; Packer et al. 2001; Gilchrist 2006a). Consequently, all individuals in communally breeding groups both provide and benefit from help in rearing young, which makes relationships between communal breeders highly symmetrical. Communal breeding typically arises in polygynous species (Lukas and Clutton-Brock 2012a). If one sex, typically males, does not provide parental care, it may display a higher reproductive skew than the caring sex. However, this skew remains lower than in cooperative and eusocial systems, with the most dominant male usually failing to monopolize reproduction in communal mammals (Lukas and Clutton-Brock 2012a).

Cooperative breeding

In contrast, cooperative breeding refers to social systems in which only dominant individuals breed and are assisted in caring for their offspring by non-breeding adults (Table 1). In most cases non-breeders forego dispersal and breeding, and remain within their natal group as helpers (Clutton-Brock 2016), although in some bird species they may have bred and lost their offspring (Hatchwell et al. 2002), or be unrelated to the breeders (Riehl 2013). Cooperative breeding is present in a wide range of taxa, including fishes (Taborsky 1994, 2009; Wong and Balshine 2011; Josi et al. 2019), birds (Hatchwell 2009), insects (Hughes et al. 2008) and mammals (Clutton-Brock 2016). In cooperative breeders, subordinates may inherit from a breeding position later in their life, either by dispersing or by taking a dominant position within their natal group (Table 1). This point separates cooperative breeding from eusociality.

Eusociality

Likewise, eusociality is defined by alloparenting behaviors, overlapping generations via delayed dispersal, and the division of social groups between breeders and non-breeders (Table 1). However, eusocial breeders usually form specialized behavioral groups via the division of labor into reproductive and non-reproductive groups, usually called castes. In eusocial systems, individuals of one caste usually lose permanently the ability to perform at least one behavior of another caste. In particular, eusocial non-breeders usually remain non-breeders through their lifetime and perform different tasks than breeders, whereas in cooperative breeders the dominance turnover allows a significant part of subordinates to reach dominance at some point (Table 1).

Due to their striking similarities, cooperative breeding and eusociality are widely considered to form a continuum rather than being distinct social systems, as their main difference lies in the distribution of lifetime reproductive success among group members (Sherman et al. 1995). Indeed, lifetime reproductive success is highly skewed in eusocial systems, whereas in cooperative breeders the distribution of reproductive success is balanced by the turnover of the dominant position (Sherman et al., 1995, Table 1).

Table 1 – Main characteristics of communal breeding, cooperative breeding and eusociality.

All three social systems involve alloparenting and generation overlap. Social hierarchy corresponds to the presence of dominant and subordinate individuals, and the extent of the privileges of dominants. It is variable within each social system, but it tends to be low in communal breeders (i.e no dominance hierarchy, or low extent of dominant privileges), very high in eusocial breeders (permanent castes involving a division of labor between subordinates and dominants), and intermediate in cooperative breeders. Instant reproductive skew corresponds to reproductive skew at a given time, and is noted as high in cooperative and eusocial breeders in which dominants produce the vast majority of the offspring at any breeding season, and low in communal breeders where most adults typically reproduce. Lifetime reproductive skew was marked as low when non-reproductive individuals at a given time were likely to access reproduction in their lifetime due to high breeding tenure turnover, and high in eusocial systems where most helpers remained non-reproductive in their lifetime.

		Cooperative		
		Communal breeding	breeding	Eusociality
Alloparenting		yes	yes	yes
Social hierarchy		low	high	high (castes)
Dominance turnover		NA	high	low
Mating system		promiscuity/polygyny	monogamy	monogamy/polyandry
Reproductive skew	Instant	low	high	high
	Lifetime	low	low	high
Generation overlap		yes	yes	yes
Examples	Mammals	Lions (<i>Panthera leo</i>)	Meerkats (<i>Suricata suricatta</i>)	Naked mole-rats (<i>Heterocephalus glaber</i>)
	Non-mammals		Seychelles warbler (<i>Acrocephalus sechellensis</i>)	Wasps (<i>Polistes versicolor</i>)

Evolutionary hypotheses for the evolution of cooperative breeding

Kinship and inclusive fitness

the direct fitness cost of reproductive suppression has led to the hypothesis that the evolution of cooperative breeding is driven by the indirect fitness benefits accrued through raising offspring that

are not its own (Vehrencamp 2000; Gilchrist 2007; Fewell et al. 2009). Accordingly, several evolutionary reconstructions have suggested family living to be a stepping stone to cooperative breeding. In birds, a recent phylogenetic comparative analysis showed that families first formed by prolonging parent–offspring associations, and that adult offspring then began helping at the nest (Griesser et al. 2017).

In addition to increasing the benefits gained by related offspring, the presence of helpers may increase the future survival and/or reproductive output of the breeders, which also results in indirect fitness gains for the helpers. Such benefits may be acquired by reducing the energetic costs of raising young for breeders. This process is called the load-lightening hypothesis (Crick 1992; Meade et al. 2010; Johnstone 2011)

However, kinship does not provide the sole explanation to the evolution of cooperative and communal breeding. As much as 30% of cooperatively breeding birds are estimated to nest in mixed-groups of relatives and non-relatives, and 15% nest primarily with non-relatives (Riehl 2013). Non-kin cooperation is far more frequent in obligate cooperative breeders, 77% of which nest in groups involving non-kin whereas only 38% of facultative cooperative breeders do (Riehl 2013). In non-kin cooperative and communal breeders, individuals do disperse and either join an unrelated pair or group where they may inherit a breeding position (i.e. *Ceryle rudis*, Reyer, 1984 ; *Psophia leucoptera*, Sherman, 1995) , or form a new communally breeding coalition with unrelated individuals (e.g. *Catharacta lonnbergi*, Young, 1998). Inversely, a wide range of species that live in kin groups do not display cooperative breeding.

The existence of non-kin cooperative breeders and non-cooperative family-living species show that, despite its major role, high kinship and the resulting indirect benefits are not a standalone explanation for the evolution of cooperative breeding. Thus, explaining the evolution of alloparenting is likely to involve a variety of direct fitness benefits for helpers, in the form of increased survival or future breeding opportunities.

Costs and benefits of dispersal strategies: Benefits of philopatry and costs of dispersal

The ecological constraints hypothesis argues that delayed dispersal occurs when environmental harshness lowers the expected fitness outcomes of dispersing to breed independently or become a floater while waiting for a breeding position, and that cooperative breeding subsequently occurs after the emergence of family groups via delayed dispersal (Emlen, 1994, 1982; Hatchwell, 2009; Koenig et al., 1992).

However, this hypothesis alone has been shown to have limited predictive power at the interspecific level. Indeed, current evidence indicates that numerous noncooperative species without delayed dispersal share the same harsh environment as cooperative breeders, and have just as few dispersal opportunities as them. Thus ecological constraints alone cannot explain the differences in the two dispersal patterns. As an alternative, a "benefits of philopatry" hypothesis, which proposes that nonbreeding helpers remain at home only when there is a net fitness benefit to doing so, was suggested. Under this hypothesis, territory quality may vary greatly, leading individuals to benefit from staying in their natal den if its quality is unusually high; or fitness may be highly reliant on group size due to the existence of cooperation. Theoretical models comparing variance in reproductive success among territories in cooperative and noncooperative species suggested that the territories of cooperative species varied more than those of noncooperative species in quality, and were thus consistent with the benefits-of-philopatry hypothesis (Stacey and Ligon 1991).

In a number of species documenting the fate of dispersers, delaying dispersal and reproduction has been effectively shown to increase direct fitness compared to attempting early dispersal and reproduction (i.e. *Leuconotopicus borealis*, Walters et al., 1992).

The proportion of individuals delaying dispersal and becoming helpers in their natal nest can be highly dependent on the costs of dispersal. For instance, in Azure-winged Magpies (*Caynopica cyanus*), the number of helpers was shown to increase in the years with harsher climate conditions entailing dispersal, and the presence of helpers significantly increased breeding success in helpers (Canário et al. 2004).

Group augmentation

Theoretical models showed that individuals can benefit from increasing the survival of unrelated juveniles when these advantages are substantially high (Kokko et al. 2001).

However, dispersal at sexual maturity widely coexists with delayed dispersal in some cooperative breeders, and non-kin cooperative breeders have been extensively described in birds, whereas delayed dispersal increasing group size would be expected under the group augmentation hypothesis. Therefore, while group augmentation may substantially enhance the direct benefits of helping in most cooperatively breeding species, it does not provide a satisfying explanation for the evolution of non-kin cooperative breeding. Furthermore, among polytocus taxa, to which cooperative breeding is restricted in mammals (Lukas and Clutton-Brock 2012b), allonursing is most common in species that form small groups (Packer et al. 1992). Finally, in some species, large groups split into smaller ones when they reach a limit group size, rather than more individuals becoming non-reproductive. These examples include Cape ground squirrels (*Xerus inaurus*) (Waterman 2002).

A disproven hypothesis: Social prestige

It has been hypothesized that helping could act as a signal of individual quality to potential mates, thus increasing the odds of accessing reproduction later (Bergmüller et al. 2007). However, empirical studies conducted on birds (Wright 1997; McDonald et al. 2008; Nomano et al. 2013) showed that the presence of other individuals had no effect on helping behaviors. Unexpectedly, marmosets have even been shown to share less food in the presence of other group members, thus providing further support against the social prestige hypothesis (Brügger et al. 2018).

What drives the evolution of cooperative breeding?

Life history traits

The links between cooperative breeding and life history have been extensively studied in birds and invertebrates, but due to contradictory results it remains unclear which life history traits enhance or inhibit the evolution of cooperative breeding. The proportion of cooperatively breeding species, as well as the extent of cooperative breeding behaviors, have indeed been suggested to be associated with low annual mortality in a study (Arnold and Owens 1998), whereas another conducted on Australian Corvidae suggested a possible marginal enhancement of cooperative breeding by high mortality (Poiani and Jermiin 1994), and another one did not show any association between cooperative breeding and survival (Yom-Tov et al. 1992). Models showed that life history traits required helpers to eventually inherit their parent's territories to have an effect on the evolution of cooperative breeding; and that their effects depended on whether density dependence acted on the survival of dispersers or on fecundity. In the former case high annual adult survival favored alloparenting due to higher direct benefits for helpers, whereas in the latter case it prevented the evolution of alloparenting (Pen and Weissing 2000). The inversion of the effects of the same life history trait according to other variables such as territory inheritance may partially explain the contradictory results between taxa.

In mammals, the literature regarding the relationship between cooperative breeding and life history is scarcer. Cooperative breeding has been shown to only evolve in polytocous taxa, and transitions to monotocous in cooperative breeders to result in the rapid loss of cooperative breeding (Lukas and Clutton-Brock 2012b). The authors explained the prerequisite of polytocous by the benefits of helpers being too low to offset the costs of breeding in monotocous species. Despite polytocous evolving before cooperative breeding, a retroaction increasing reproductive rate in cooperative breeders is likely, due to either reproductive suppression allowing for bigger litters (Moehlman and Hofer 1997) or reduction of birth intervals (Mitani and Watts 1997). Allonursing also occurs in

monotocous species, albeit at a lesser frequency, but in contrast to polytocous it is highly associated with milk theft by parasitic infants and continued nursing after the loss of the individual's own infant (Packer et al. 1992). In contrast, no association was found between cooperative breeding and a vast array of life history traits, including pace of life traits (age at first reproduction, longevity), demographic traits (annual survival), and reproductive traits (absolute and relative weight of offspring, weanlings and whole litters at birth) (Lukas and Clutton-Brock 2012b).

Mating system

Social systems (i.e. how groups are formed, how many individuals of each sex and age group are in them and how they are related with each other) and mating systems (i.e. how the matings are organized within these groups, e.g. monogamy, polygyny or polygynandry) are closely associated. Although pre-established cooperation can theoretically favor evolution towards monogamy (Peck and Feldman 1988), it has been suggested that the evolution of cooperative breeding in mammals is restricted to species that are already socially monogamous, most likely due to monogamy leading to high relatedness between group members (Lukas and Clutton-Brock 2012a). Social monogamy was similarly found to be required for the evolution of eusociality in insects (Hughes et al. 2008). In contrast, communal breeding has evolved among polygynous or promiscuous species (Lukas and Clutton-Brock, 2012b). In birds, cooperative behaviors have been shown to evolve in long-lived promiscuous species, in addition to monogamous ones (Downing et al. 2015).

However, cooperative breeding does not prevent further mating system for further evolving. Transitions from monogamy to polygyny or to polygynandry have been reported in cooperative breeders, and are thought to be key in evolutionary transitions to communal or independent breeding (Cornwallis et al. 2010). Furthermore, recent studies questioned the causality link between monogamy and cooperative breeding. Indeed, the ecologically driven covariance hypothesis suggests that the evolution of monogamy and cooperative breeding share an array of common causes thought to be involved in high dispersal costs, limited reproductive output and dominance systems (Dillard and Westneat 2016). These potential causes include scarce food resources, harsh environment (Emlen and Oring 1977; Barlow 1988), limited nest sites and predation pressure (Dillard and Westneat 2016; Groenewoud et al. 2016).

Environmental variables

Climate

A vast body of literature has already investigated the relationship between climate and cooperative breeding in birds. Stable food availability seems to be a pre-requisite for the evolution of cooperative

breeding (Ford et al. 1988). High mean temperature (Arnold and Owens 1999), high temperature predictability (Arnold and Owens 1999) and low precipitation predictability (Jetz and Rubenstein 2011) have also been associated to cooperative breeding in birds. Habitat also seems to play a role, as savanna has specifically been linked to the evolution of cooperative breeding (Rubenstein and Lovette 2007). However, in birds, the existing literature has also provided inconsistent results regarding which environments favored cooperative breeding. Cooperative breeding has indeed been suggested to be favored by both harsh environments (Soucy and Danforth 2002; Avilés 2007; Gonzalez 2013) and stable environments (Rubenstein and Lovette 2007, Jetz and Rubenstein 2011).

Few studies have specifically investigated the relationship between climate and cooperative breeding in Mammals. However, Lukas and Clutton-Brock showed a strong association between low annual rainfall and cooperative breeding, with cooperative breeders being located in drier areas than non-cooperative monogamous species (Lukas and Clutton-Brock 2017).

Interactions with other species

In addition to select for group-living, high predation risk has also been shown to be a driver of the evolution of complex social structures. A study conducted on the cooperatively breeding cichlid *Neolamprologus pulcher* showed that high predation and shelter limitation led to highly socially structured groups involving few small and many large members, which was explained by the benefits of cooperative defense (Groenewoud et al. 2016). Such predation risks are thought to be especially increased during dispersal due to the unfamiliarity with the distribution of refuges, thus leading to high mortality rates in some species such as dwarf mongooses, in which 50% of males and 78% of females do not survive dispersal (Lucas et al. 1994; Creel and Waser 1997). Therefore, high predation risks can be a strong incentive for delaying or cancelling dispersal due to increased dispersal costs (Tanaka et al. 2016), which may further enhance the evolution of cooperative breeding due to high kinship.

Demography

The evolution of life history, ecology and demography are extensively linked due to the latter being led by the processes of birth and death (Metcalf and Pavard 2007; Pelletier et al. 2007, 2009; Rees and Ellner 2016). Furthermore, demography is involved in multiple parameters that impact cooperative breeding such as group size, group structure, mating system and reproductive suppression. Therefore, we expect demography to influence whether a branch evolves toward cooperative breeding. Despite this, few studies have actually investigated the role of demographic parameters. In birds, adult sex ratio (ASR) variation greatly influence breeding systems because the rarer sex has more potential partners than the most common sex (Székely et al. 2014), but no similar studies have been conducted in Mammals yet. This can be explain by the fact that mammalian ASR are widely thought to be difficult

to estimate due to high intraspecific variation and detection bias stemming from certain estimation methods. However, our recent evaluation of the repeatability of ASR estimates suggests them to be actually reliable at the species level, which may facilitate further studies investigating the relationship between demography and cooperation (See Appendix: The estimation of mammalian sex ratios: a critical reappraisal). In addition to possible roles in breeding systems, demography has been suggested to be linked to the social evolution of a number of mammalian species. For instance, in the cooperatively breeding banded mongoose (*Mungos mungo*), the small group size, high relatedness and population viscosity have been suggested to be linked to the cooperative breeding features of the species (reproductive suppression in both sexes, alloparenting in the form of babysitting) (Cant et al. 2013). Uneven sex ratios may have a strong impact on reproductive strategies, and lead to reproductive suppression in the more frequent sex.

The three constitutive traits of cooperative breeding

Delayed dispersal

Despite being a key mechanism in increasing kinship among group members, delayed dispersal does not always result in highly related groups. In several bird species, extremely high rates of adult mortality and turnover (*i.e* *Parus niger*, Tarboton, 1981) and extra-group copulations (*i.e* *Malurus spp.*, Dunn et al., 1995) have been shown to decrease relatedness to negligible levels despite the presence of delayed dispersal. However, to our knowledge such no case has been reported in mammals in the current literature.

Reproductive suppression

While some species display total reproductive suppression, in others subordinates may sire a minority of juveniles, either within their own group or due to extra-pair reproduction. For instance, [total suppression]. Inversely, in African wild dogs (*Lycaon pictus*), a study showed that subordinate beta females bred in a short majority of years (54.5%), and reproduction was split between the three top-ranking males with a majority of pups being produced by the alpha male (56.0%), and the rest being split between the two following males (32.0 and 12.0%, respectively) (Spiering et al. 2010). Social reproductive suppression may be caused by a wide range of mechanisms, which are reviewed below.

Mate guarding

Eviction

Rather than or in addition to preventing subordinate mating, some dominants evict breeding subordinates from the group. For instance, dominant female banded mongooses (*Mungos mungo*)

respond to the costs of subordinate reproduction by evicting breeding subordinates from the group (Cant et al. 2010). Similar behaviors are observed in meerkats (*Suricata suricatta*) (Stephens et al. 2004), in which the eviction of pregnant subordinates typically results in their pregnancy being unsuccessful (Clutton-Brock et al. 2008). Recently pregnant subordinate females are then likely to allolactate the pups of dominant females (MacLeod et al. 2013).

In some cases, breeders may allow for a window of reproductive share in subordinates, and evict only subordinates that overreach their allowed reproductive share (Reeve 2000). For instance, observations conducted on American crows suggest that male breeders have the ability to forcibly evict subordinates, but only do so over a specific level of reproduction (Townsend et al. 2009).

Infanticide

Infanticide of subordinate offspring by dominants has been reported in some cooperatively breeding species, such as common marmosets (*Callithrix jacchus* Digby, 1995), banded mongooses (Gilchrist 2006b). In other species such as meerkats (*Suricata suricatta*), infanticide is performed by both pregnant dominants and subordinates, and the greater reproductive success of dominants mostly relies on their ability to prevent pregnancy in subordinates (Young and Clutton-Brock 2006). Infanticide is not exclusive to cooperative breeding and is also vastly performed by unrelated males joining a female group as the new male breeder (McLean 1983; Macdonald et al. 1987; Coulon et al. 1995), and resident males that have not mated with the mother (Soltis et al. 2000).

Lack of subordinate partners

In some species, the lack of suitable partners for subordinates vastly contributes to their reproductive suppression. Indeed, due to the costs of inbreeding (Charlesworth and Willis 2009), inbreeding avoidance is vastly observed in animals (Pusey and Wolf 1996a), including cooperatively breeding ones. For instance, naked mole-rats (*Heterocephalus glaber*) have been shown to preferentially mate with non-relatives when offered the choice (Ciszek 2000). Additionally, most cooperatively breeding species live in family groups in which dominants and subordinates are highly related, such as species where subordinates are mostly previous offspring of dominants (Koenig and Haydock 2004). Therefore, in such species, subordinates may avoid reproducing due to the lack of unrelated partners. For instance, in both eusocial Damaraland mole rats (*Cryptomys damarensis*) and cooperatively breeding meerkats (*Suricata suricatta*), previously reproductively suppressed subordinate females became sexually active when given access to unrelated males (Cooney and Bennett 2000; O’Riain et al. 2000).

Physiological suppression

In some species, physiological mechanisms underlying reproductive suppression have been identified in males, females or both. For instance, in cooperatively breeding common marmosets (*Callithrix*

jacchus), either all or all but one subordinate females were shown to fail to ovulate due to low luteinizing hormone – releasing hormone (LHRH) secretion (Abbott 1984). Their subsequently low levels of luteinizing hormone (LH) were further suggested to be maintained by scent contact with dominant females (Barrett et al. 1990). Similarly, subordinate dwarf mongooses (*Helogale parvula*) females have low baseline and peak oestrogen levels, and low mating rates (Creel et al. 1992). Rodent examples include the Damaraland mole-rat (*Cryptomys damarensis*), which subordinate females are anovulatory and display low levels of oestrogen and creatinine, whereas the reproductive suppression of subordinate males is exclusively behavioral (Bennett 1994). The physiological reproductive suppression of female Damaraland mole-rats seems to be mediated by the lack of unrelated males rather than the presence of dominant females, thus suggesting it to be primarily an inbreeding avoidance mechanism (Clarke et al. 2001). Physiological and behavioral mechanisms of reproductive suppression are, however, not mutually exclusive. A number of cooperatively breeding species, including meerkats and dwarf mongooses, rely on both (Creel et al. 1992). For instance, in meerkats, subordinates display lower levels of luteinizing hormone (LH) than dominants, but do breed when presented with unrelated males, albeit at a lower rate than dominants, thus suggesting that their reproductive suppression rely both on both low levels of hormones involved in reproduction and lack of reproductive opportunities (O’Riain et al. 2000).

Alloparenting

Food provisioning

The sharing of food with juveniles by adults other than their parents have been documented in several species. For instance, meerkats have been documented to bring caught prey to pups (Clutton-Brock et al. 2001a).

Occasional occurrences of subordinates feeding the pregnant female have been reported in some species such as *Lycaon pictus* (Courchamp and Macdonald 2001). Although this behavior is highly likely to increase the fitness outcome of pups, it is not directly performed towards them, and may be a part of preferential food sharing towards dominants in general, and not specifically pregnant ones. Therefore, we do not include this behavior in our definition of alloparenting.

Allonursing

Allonursing occurs when female suckle juveniles that are not their own. This occurs both in cooperative breeders, in which female helpers nurse young born to the dominant female (Moehlman and Hofer 1997; Creel and Creel 2002), and in communal breeders in which females nurse each other’s young (Hayes 2000; Devillard et al. 2003). In cooperative breeders, physiological mechanisms leading to lactation in subordinates include pseudopregnancy (Creel and Creel 1991) and the loss of a litter, due

to either eviction during pregnancy (Clutton-Brock et al. 2008; MacLeod et al. 2013) or infanticide after parturition (Young and Clutton-Brock 2006).

Mammalian allonursing may also provide immunological benefits via the transmission of immunological compounds (Roulin and Heeb 1999; Becker et al. 2007).

Allonursing is different from milk theft, in which mothers preferentially suckle their own offspring but juveniles manage to obtain milk from unrelated females (Gloneková et al. 2016; Paul and Bhadra 2017). Milk theft is widely thought to result from misdirected care, given that it occurs mostly in species displaying poor kin recognition [ref] and in inexperienced females (Maniscalco et al. 2007). It can also occur despite good kin recognition if females are unable to repel non-offspring, which mostly occurs in large groups (Packer et al. 1992; Manning et al. 1995). In species that display milk theft, non-offspring juveniles can be aggressively rejected by females when identified as such (Maniscalco et al. 2007).

Vigilance

Cooperative and communal breeders may engage in sentinel behavior and other forms of vigilance, which can be especially beneficial to juveniles when predation risk is high. Sentinel behavior has indeed been reported in a number of cooperative and communal breeders, including meerkats (*Suricata suricatta*), dwarf mongooses (*Helogale parvula*) and vervet monkeys (*Cercopithecus aethiops*) (Bednekoff 2015). Sentinel behavior is associated with dry habitats (Rasa 1987; Wright et al. 2001; Sorato et al. 2012). In meerkats (*Suricata suricatta*), both female and male subordinates were more likely to perform sentinel behavior when pups joined the groups on foraging trips, and females performed more bipedal vigilance, thus suggesting that these behaviors were at least partly directed toward protecting pups (Santema and Clutton-Brock 2013).

This form of alloparenting is likely to be costly due to lost foraging time (Bednekoff 2001). Meerkats lose weight when babysitting pups (Clutton-Brock et al. 1999). Within individuals, the propensity to engage in sentinel behaviors is positively correlated to body mass in both birds and mammals (Wright et al. 2001; Clutton-Brock et al. 2002).

The relationship between vigilance and dominance varies between cooperatively breeding species. In dwarf mongooses, the highest rates of sentinel behavior are displayed by subordinate males (Rasa 1987), but in meerkats dominant males perform this behavior the most (Clutton-Brock et al. 1999). Therefore, even in hierarchic societies involving subordinate helpers, this behavior is not always associated with helpers and can be widely performed by dominants.

Alloparenting

Non-parental carrying of offspring has been documented in a number of primates, including silky Sifakas (*Propithecus candidus*, Thalmann et al., 2007)), tufted capuchins (*Sapajus paella*, Back et al., 2019).

Thermoregulation

Active thermoregulation of related pups by non-breeding adults during hibernation has been reported in several hibernating rodent species such as alpine marmots (Arnold 1993) and golden marmots (Blumstein and Arnold 1998), which increases pup overwinter survival and thus provides indirect benefits to subordinates in some, but not all species (Arnold 1993; Blumstein et al. 2004). There is no general consensus regarding whether thermoregulation of juveniles by non-breeding adults should be included in the definition of alloparenting. Some authors choose to include it, and thus classify Alpine marmots as cooperative breeders due to the thermoregulation benefits of subordinates on pups (Allainé and Theuriau 2004), despite the lack of other forms of alloparenting such as vigilance specifically directed toward pups (Cino n.d.). Others authors exclude it based on the relative lack of evidence that thermoregulation is costly to the individuals performing it (Lukas and Clutton-Brock 2012a). Nevertheless, the thermoregulatory needs of juveniles have been repeatedly brought as a possible strong explanation for the presence of non-breeding individuals at the nest. Furthermore, subordinate alpine marmots display higher mass loss during winter when infants are present, which suggests that their thermoregulation role is energetically costly (Walter 1990). Thus, we consider thermoregulation towards juveniles to be an alloparenting behavior, which costs may be low compared to those of allonursing, and thus include it in the behavioral repertoire of cooperative breeders.

The coevolution of constitutive traits of complex social systems

Rationale behind a coevolution focused-approach

Complex social systems are defined by the association of several traits. For instance, cooperative breeding is characterized by the association of delayed dispersal, reproductive suppression and alloparenting. This statement also applies to other social systems. Despite the existence of different definitions of eusociality, all authors defined it as the association of several traits. For instance, Crespi and Yanega defined it as the combination of the presence of irreversibly behaviorally distinct castes, helping by individuals of the less reproductive caste, and behavioral totipotency of either the more reproductive caste or no caste at all (Crespi and Yanega 1995). Most definitions of eusociality include generational overlap, alloparenting, and reproductive division of labor (Wilson and Hölldobler 2005).

More generally, complex processes characterized by the association of several features are widespread in biology. For instance, ecosystems are characterized by both a community of living organisms, and the abiotic components of their environments (O'Neill et al. 1986). Medical conditions are associated with specific combinations of symptoms and signs. Studying the interaction between the features that define a process is key to shedding light on its understanding.

However, so far, most of the scientific literature regarding the evolution of social systems has considered social system as traits rather than combinations of traits. For instance, in their study regarding the coevolution of cooperative breeding and monogamy in Mammals, Lukas and Clutton-Brock (2012b) used a binary classification of species, as either cooperative or non-cooperative and either monogamous or non-monogamous, and performed a two-trait phylogenetic reconstruction of ancestral states which suggested that monogamy always evolved before cooperative breeding. Although this result implied that monogamy always evolved before all three defining traits of cooperative breeding were present and allowed for the species to be defined as a cooperative breeder, this did not involve that monogamy evolved before every single defining trait, and thus that monogamy preceded the beginning of the evolutionary route to cooperative breeding. This issue can be raised in a number of evolutionary studies of social systems such as cooperative breeding (Langen 2000; Hatchwell 2009; Downing et al. 2015).

Treating complex social systems as combinations of several potentially co-evolving traits rather than single traits is especially important when their defining traits exist separately outside of the social system. In the case of cooperative breeding, all three defining traits, which are delayed dispersal, reproductive suppression and alloparenting, exist in species that are not cooperative breeders. Delayed dispersal occurs in a large number of social but non-cooperative species (Ekman et al. 2004) ; and occasionally even in non-social species. Reproductive suppression is also common outside cooperative breeding (Wasser and Barash 1983; Beehner and Lu 2013). Finally, alloparenting is also a defining trait of communal breeders and eusocial species (Gittleman 1985; Sherman et al. 1995). The separate existence of the three defining traits outside of cooperative breeding raises two major consequences:

- A complex social system may evolve from intermediate configurations that display some, but not all of its defining traits. For instance, it can be hypothesized that cooperative breeding, which displays delayed dispersal, reproductive suppression and alloparenting, may have evolved from communal breeding, which lacks reproductive suppression but is otherwise very similar to cooperative breeding. Communal breeding may itself have evolved from a social system that shares some of its traits, such as a gregarious system with delayed dispersal.

Therefore, it is possible that social systems have gradually evolved along evolutionary routes in which their defining traits sequentially evolved, with possible coevolution between them, in which case studying the coevolution between traits is key to deciphering these routes understanding the evolutionary relationships between complex social systems.

- Although life history and ecological parameters that correlate with cooperative breeding are already vastly identified, we lack information regarding which defining traits of cooperative breeding have specifically been favored by each variable. For instance, low rainfall has been identified as a key factor in the evolution of cooperative breeding in Mammals, but whether it enhanced the evolution of delayed dispersal, reproductive suppression, alloparenting or a combination of these traits remains unknown. In birds, long incubation and its associated geographic correlates (temperate and tropical regions) are observed in all family-living birds, and not specifically cooperative breeders (although the latter are included in the former) (Drobniak et al. 2015). Two variables may correlate with two different traits and, therefore, be involved at different points of the route to cooperative breeding. Therefore, it is crucial to study relationships between key parameters involved in the evolution of cooperative breeding and each of the three defining traits in order to reconstruct the evolutionary route to cooperative breeding.

The three defining traits of cooperative breeding are widely thought to coevolve, mostly due to the strong links between kinship and cooperation, and between group composition and mating system. Therefore, it is very likely that the evolution of one of the three traits has strong implications for the evolution of the others, and may be the start of an evolutionary route to cooperative breeding. However, the directionality of this coevolution between traits is crucial to understand how cooperative breeding evolved. For instance, if reproductive suppression is strongly favored by alloparenting, it makes the evolution of cooperative breeding from communal breeding likely. More generally, if a trait A strongly enhances the evolution of a trait B but there are no evolutionary mechanisms for B favoring A as well, it is extremely likely that A will evolve before B in the evolutionary route to cooperative breeding. Furthermore, negative impacts between traits, *i.e* a trait making the evolution of another trait less likely or enhancing evolutionary reversions of these traits, should be examined as well. In the next paragraph, we will thus review the existing hypotheses regarding the existence and directionality of the coevolution between each pair of traits involved in cooperative breeding.

Hypotheses on the coevolution of the constitutive traits of cooperative breeding

Delayed dispersal and alloparenting

How does delayed dispersal affect alloparenting?

Delayed dispersal is often assumed to be a prerequisite of alloparenting. Indeed, delayed dispersal is a key mechanism in the formation of family groups, with high within-group kinship (Emlen 1994). These higher levels of relatedness increase indirect fitness benefits of cooperative behaviors, including alloparenting, which has indeed been shown to be strongly positively associated to relatedness in mammals, even when correcting for group size (Briga et al. 2012). This is especially true when relatedness is highly variable within groups, which makes indiscriminate cooperation costly and enhances kin discrimination (Cornwallis et al. 2009). Therefore, coevolution between delayed dispersal and alloparenting is expected to be strong, and its directionality to be either from delayed dispersal to alloparenting, or bidirectional.

However, competition between kin may appear with delayed dispersal, thus limiting cooperative benefits and lessening the incentive to display altruistic behavior toward kin, including alloparenting (Platt and Bever 2009). Furthermore, in cooperative breeders where helpers pay to stay by performing alloparenting behaviors, increased kinship may actually decrease alloparental care. This has been observed in cichlids, in which unrelated subordinates have been shown to provide more alloparental care than related ones, and only unrelated helpers increased alloparenting behaviors after simulating punishment from dominants (Zöttl et al. 2013).

How does alloparenting affect delayed dispersal?

Although delayed dispersal is often thought of as a prerequisite for the evolution of alloparenting, more recent studies have highlighted that pre-existing cooperation can also enhance delayed dispersal. In birds, cooperative breeding appears to lengthen offspring dependence due to a reduction of both parental cost and incentives for offspring to become independent (Langen 2000). A theoretical model of coevolution between sociality and dispersal also shows that dispersal levels become less important after cooperation becomes frequent (Purcell et al. 2012). Indeed, the presence of cooperation in a group can increase the benefits of philopatry by increasing fitness outcomes of staying in the group rather than dispersing, and waiting for a breeding tenure within the group rather than reproducing sooner but without benefiting from the presence of the helpers. Therefore, an enhancement of delayed dispersal by pre-existing alloparenting cannot be ruled out.

To my knowledge, there is no evolutionary rationale behind alloparenting enhancing early dispersal, which would involve alloparenting decreasing either dispersal costs or benefits of philopatry. Therefore, a negative evolutionary effect of alloparenting on delayed dispersal is highly unlikely.

Reproductive suppression and alloparenting

How does reproductive suppression affect alloparenting?

Reproductive suppression may highly enhance the evolution of alloparenting under the best-of-a-bad-job hypothesis. Indeed, it may be the only strategy to increase fitness in reproductively suppressed individuals that do not disperse. However, the best-of-a-bad-job hypothesis involves pre-existing dispersal stemming from other causes, such as high dispersal costs or benefits of philopatry. Otherwise, individuals would disperse rather than remaining in the group and making the best of a bad job. Therefore, this positive impact of reproductive suppression on alloparenting is conditioned to pre-existing delayed dispersal.

It is to note that, rather than having a causal link, reproductive suppression and alloparenting might both simultaneously stem from delayed dispersal. Indeed, under the pay-to-stay hypothesis, both reproductive suppression and alloparenting may be forms of sacrifices from subordinates in order to avoid eviction. Under that hypothesis, both reproductive suppression and alloparenting are consequences of the co-existence of a dominance hierarchy and high benefits of delayed dispersal. However, given that there is little empirical support for the pay-to-stay hypothesis in cooperative breeders (Zöttl et al. 2013), it is unlikely that this process highly affects the apparent link between reproductive suppression and alloparenting.

How does alloparenting affect reproductive suppression?

The extent of indirect fitness gained from alloparenting may have implications for the evolution of reproductive suppression. First, if these benefits are high enough for individuals to remain in their natal group without being prevented from dispersing, dominants have no interest in yielding any reproductive concessions to subordinates (Clutton-Brock 2016). Therefore, when alloparenting highly benefits the offspring and relatedness is high, it may enhance the further evolution of reproductive suppression. Furthermore, when the turnover of breeding tenure is fast enough for any individual remaining in their natal group to have a high probability of accessing reproduction in their lifetime, alloparenting may increase the future reproductive outcome of subordinates, and thus reduce the costs of postponing reproduction. Thus, alloparenting is likely to enhance reproductive suppression, but the extent of its impact depends on dominance turnover and alloparenting benefits. Therefore, we

expect this effect to be highly variable between taxa, due to the wide range of alloparenting behaviors, benefits, and dominance turnovers.

Delayed dispersal and reproductive suppression

How does delayed dispersal affect reproductive suppression?

The impact of delayed dispersal on reproductive suppression mostly relies on the subsequent increase in group size. Indeed, group size can be constrained by a number of factors, including predation (Waterman 2002) or a limitation in food resources [refs]. In such cases, delayed dispersal may lead a group to reach its maximal size, which thus no longer allows all mature individuals to reproduce due to survival outcomes of juveniles being lower. This may provide an explanation to why, for instance, the probability for dominant female meerkats to evict pregnant subordinates increases with group size (Clutton-Brock et al. 2008). Large group size may also increase stress in subordinates, and thus lead to the physiological suppression of their reproduction. Furthermore, a large group size may incur more competition for mates, which results in reproductive suppression in some individuals of the group (Stockley and Bro-Jørgensen 2011).

However, the high group relatedness resulting from delayed dispersal may reduce the incentive for dominants to suppress reproduction in subordinates, due to the indirect benefits they may get from subordinate reproduction (Johnstone and Cant 1999). Therefore, delayed dispersal may not enhance reproductive suppression as much as other group augmentation mechanisms do.

How does reproductive suppression affect delayed dispersal?

To my knowledge, the current literature has not provided any rationale for previously existing reproductive suppression to have any effect on the further evolution of delayed dispersal.

From mutual enhancement of constitutive traits to the stability of cooperative breeding

If the constitutive traits of cooperative breeding indeed enhance and stabilize each other, cooperative breeding is likely to be more stable than intermediate configurations involving some, but not of all, of the three traits of interest. Indeed, the three traits may prevent each other from being lost, and intermediate configurations may tend to evolve towards cooperative breeding due to the existing traits enhancing the further evolution of the remaining ones. Empirical observations are mostly consistent with this hypothesis, with losses of cooperative breeding being unlikely (Lukas and Clutton-Brock 2012a). It should be noted that, based on this reasoning, cooperative breeding may be more

stable than communal breeding if alloparenting indeed enhances and/or stabilizes reproductive suppression, which depends on the frequency of dominance turnovers and the extent of alloparenting benefits.

Unusual examples of losses over recent timescales have been observed in birds. The bird genus *Aphelocoma* displays bidirectional evolutionary changes involving at least one gain and one loss, the latter most likely taking place either once after the divergence of Florida scrub-jays or twice in *Aphelocoma woodhouseii* and the ancestor of *A. californica* and *A. insularis* (Berg et al. 2012, p. 201).

The three taxa of interest

Carnivores

Carnivores display a substantial diversity in social and mating systems. Communal and cooperative breeding, although uncommon, are widely distributed among families and there are a few occurrences of closely related species displaying markedly different social organizations. For instance, group-living, female-philopatric, independently nesting ring-tailed coatis (*Nasua nasua*) (Hirsch 2007) are phylogenetically close to communally breeding white-tailed coatis (*Nasua narica*) (Gompper 1995). The most recent common ancestor of Carnivores is likely to be solitary, and most species in this order live solitarily outside mother-offspring association and temporary feeding groups (Bekoff et al., 1984; Gittleman, 1989). A phylogenetic reconstruction of carnivore social organizations suggested that the ancestor of Carnivora may be socially flexible (Dalerum 2007), but given that the methodology classified species as flexible based on a single instance of an additional social organization, its results may be interpreted with caution. Despite the majority of carnivores being solitary, several exhibit long-term social units, which allows for the emergence of complex social systems such as communal and cooperative breeding. The diet of carnivores, and more specifically the benefits of cooperative hunting in species that feed on large prey, is thought to be a key factor in the evolution of carnivore sociality.

In carnivores, females are usually the philopatric sex (Greenwood 1980; Johnson 1986; McNutt 1996). Exceptions include domestic cats (*Felis catus*), in which only females disperse (Devillard et al. 2003), and African wild dogs (*Lycaon pictus*), in which males delay dispersal longer than females, although they disperse further when they do (McNutt 1996). In many group-living carnivores, both sexes are philopatric (*i.e.* banded mongooses *Mungos mungo* (Cant et al. 2001), Ethiopian wolves *Canis simensis* (Sillero-Zubiri et al. 1996)), which further increases relatedness between group members. Alloparenting behaviors in cooperatively and communally breeding carnivores are also mostly performed by females (Macdonald and Moehlman 1982; Moehlman and Hofer 1997).

Primates

Primate species widely vary in their social organizations, ranging from solitary lorises (*Perodicticus sp.*, to pair-living owl monkeys (*Aotus azarai*) (Fernandez-Duque 2016), uni-male and multi-male groups, with a large proportion of species living in mixed-sex groups (Kappeler and Schaik 2002; Sussman et al. 2005; Dunbar 2013a). The order also includes socially flexible species such as the mostly solitary, but occasionally family-living slow loris (*Nycticebus cougang*) (Wiens and Zitzmann 2003), or gorillas (*Gorilla gorilla*) which may live in one-male or multi-male groups (Doran and McNeilage 1998). Recent ancestral node reconstructions suggest that the most recent common ancestor of primates is solitary, and that pair-living and single-male harem systems evolved from larger multi-male, multi-female groups (Shultz et al. 2011).

In contrast to carnivores, delayed dispersal and reproductive suppression are widespread among primates, including in non-cooperative breeders. Depending on species, delayed dispersal can be present in both sexes (Pereira et al. 1988a), females only (Bennett and Sebastian 1988), males only (Symington 1987), or absent (Fuentes 2000). Reproductive suppression is widespread among males, mostly in the form of harems in which subordinate males are excluded from both social groups and reproduction (i.e. *Cercopithecus solatus*, (Charpentier et al. 2008), *Macaca cyclopis*, (Wu and Lin 1992)), but also in species where subordinates males remain in the group. For instance, in multi-male groups of stumptailed macaques (*Macaca arctoides*), alpha males achieve reproductive monopoly despite the presence of other males in the group (Bauers and Hearn 1994). Female reproductive suppression also occurs in a wide range of species.

Despite the various occurrences of delayed dispersal and reproductive suppression in primates, cooperative breeding is mostly restricted to the Cebidae family (Lukas and Clutton-Brock 2012b). A few isolated species display complex forms of communal breeding. In black-and-white ruffed lemurs (*Varecia variegata*), adult offspring of both sexes can delay dispersal (Pereira et al. 1988a), all females reproduce whereas subordinates males are excluded from reproduction (Foerg 1982) and both sexes participate in alloparenting behaviors including infant guarding (Pereira et al. 1988a; Baden et al. 2013). The participation of both sexes in alloparenting behaviors, in contrast to carnivores in which only females were involved, blurs the distinction between cooperative and communal breeding in primates.

Rodents

Rodents display a wide range of breeding strategies, thoroughly described in the existing literature (Hayes 2000). Rodents also include the only known example of mammalian eusociality: Naked mole-rats (*Heterocephalus glaber*) live in highly related subterranean colonies in which sterile males and

females cooperatively rear the litters produced by a single reproductive female (Jarvis 1981; Faulkes et al. 1990; Reeve et al. 1990).

Alloparenting behaviors in cooperative and communal rodents mostly consist in allonursing, defense and thermoregulation. Juvenile rodents are strongly dependent on older individuals for thermoregulatory ability (Hill 1992), and thus benefit from the additional heat provided by supplementary adults.

Hypotheses used to explain the occurrence of communal nursing in rodents include a wide range of adaptive functions such as increasing pup growth and survival (König 1994), getting rid of excess milk or maintaining social relationships within the herd. However, other arguments suggest that it may be a non-adaptive by-product of communal nesting instead. Indeed, the cost of lactation has been shown to be exceptionally high in some rodents (Rogowitz 1996), and may exceed the aforementioned benefits of allonursing. In such conditions, allonursing may stem from the inability of mothers to discriminate their offspring, which has been reported in a variety of species including house mice (Manning et al. 1995), or from milk parasitism.

Empirical studies showed that some rodents were indeed able to nurse discriminately. Degus (*Octodon degus*) mothers have been shown to nurse their own offspring preferentially over that of an unrelated female, but not that of a sister (Jesseau et al. 2009).

Occurrences of alloparenting in other taxa

Besides carnivores, primates and rodents, isolated occurrences of cooperative and communal breeding have been occasionally reported in other taxa.

For instance, African elephant females have been reported to direct movements of juveniles during family displacements, and to frequently allonurse calves other than their own (Sikes 1971). Such behaviors are especially frequent in young nulliparous females, which thus play the role of non-reproductive helpers, compared to parous females (Dublin 1983; Lee 1987). The long generation time of African elephants, which leads to generation overlap, has been thought to play a role in the evolution of alloparenting in elephants, just like in other cooperatively breeding taxa (Dublin 1983).

However, these occurrences are isolated and occur in taxa lacking other evolutionary transitions toward cooperative breeding. Therefore, no interspecific study of the evolution of cooperative breeding can be conducted on these taxa. Thus, the following manuscript focuses on carnivores, primates and rodents.

Interest of studying taxa separately

So far, most research conducted at the interspecific level on the evolution of cooperative breeding (Lukas and Clutton-Brock 2012*b*, 2012*a*, 2017) and its constitutive traits (Raihani and Clutton-Brock 2010; Clutton-Brock and Lukas 2012) in Mammals have studied all taxa simultaneously. This approach has several advantages. First, it allows for a greater number of species, which can be crucial to statistical robustness, especially when studying rare social systems such as communal and cooperative breeding. Second, despite the differences in the patterns of reproductive suppression and the nature of alloparenting behaviors, cooperative breeding systems remain strikingly similar between all three taxa. It is therefore reasonable to hypothesize that some evolutionary patterns underlying the evolution of cooperative breeding may be shared by all the taxa where it exists. These studies have indeed highlighted general patterns, such as the association between monogamy and cooperative breeding (Lukas and Clutton-Brock 2012*a*). However, each taxon displays specific patterns that may impact the coevolutionary relationships between the constitutive traits of cooperative breeding (Table 2). For instance, a number of carnivores rely on cooperative hunting due to their diet (Fanshawe and Fitzgibbon 1993; MacNulty et al. 2014), which greatly increases the benefits of group living (Packer and Rutten 1988; Courchamp and Macdonald 2001), and may thus enhance the evolution of reproductive suppression and alloparenting in group-living species due to the bigger incentive to remain in groups despite the costs. Additionally, the varying nature of alloparenting behaviors between taxa (*i.e* mostly allofeeding in carnivores, allocarrying in primates, and thermoregulation in rodents, Table 2) may not provide the same extent of alloparenting costs and benefits. This may strongly impact the evolution of reproductive suppression. For instance, the benefits of some behaviors such as allocarrying may not be high enough on their own for non-breeding individuals to have interest in remaining in their natal group without being prevented from dispersing, which may mean that breeders would have interest in yielding them reproductive concessions (Clutton-Brock 2016). Therefore, the enhancement of reproductive suppression by alloparenting may be greater in taxa where alloparenting behaviors are the most beneficial. Therefore, studying taxa separately may shed a new light on the evolution of cooperative breeding by highlighting different coevolutionary relationships between constitutive traits according to mammalian taxa, just like differences were found between mammals and birds (Greenwood 1980; Riedman 1982; Raihani and Clutton-Brock 2010).

Although a number of studies with an interspecific approach were conducted specifically on carnivores (Bekoff et al. 1984; Creel and Creel 1991; Smith et al. 2012), primates (Rutberg 1983; Hemelrijk and Luteijn 1998; Silk 2005; Beehner and Lu 2013) and rodents (Hayes 2000; Solomon 2003), they did not always use similar methodologies. Therefore, using their results to compare the

evolutionary patterns of cooperative breeding between the three taxa may raise a number of issues. We thus aim at providing comparable results regarding the coevolution of the constitutive traits of cooperative breeding in carnivores, primates and rodents.

Table 2 – Characteristics of the three main taxa displaying cooperative breeding

Only the main alloparental care behavior of the taxon is reported, but some species may display other alloparenting behaviors. Delayed dispersal is displayed as permanent when species that delay dispersal mostly remain philopatric in their lifetime, and temporary when they typically delay dispersal for a season but do disperse at some point. Aggression refers to dominants actively preventing subordinates to mate by aggressing them during their attempts at mating. Physiological reproductive suppression refers to physiological indicators involved in reproduction, such as hormonal levels, being altered in subordinates in a way that may impair reproduction. Intermediate configurations stand for species that display at least one of the three constitutive traits of cooperative breeding (delayed dispersal, reproductive suppression and alloparenting), but are neither cooperative nor communal breeders.

		Carnivores	Primates	Rodents
Alloparental care (Clutton-Brock 2016)		feeding	carrying	feeding + thermoregulation
Typical helper sex		female	both	variable
Delayed dispersal		permanent	permanent	temporary
Reproductive suppression	Aggression	yes	yes (Beehner and Lu 2013)	yes
	Infanticide	yes	Yes (Digby and Saltzman 2009)	yes
	Eviction	yes	rare in females (Henry 2011)	no
	Physiological	yes	Yes (Beehner and Lu 2013)	yes
Intermediate configurations		Rare (Bekoff et al. 1984)	Frequent (Dunbar 2013b)	Frequent (Gromov 2007)
Ancestral social system		Solitary (Bekoff et al. 1984; Gittleman 1989)	Solitary (Shultz et al. 2011)	unknown

Objectives

1/ First, we aim at investigating the coevolutionary relationships between delayed dispersal, reproductive suppression and alloparenting in order to reconstruct evolutionary pathways to communal and cooperative breeding in the Mammalian taxa where it occurs. These taxa will be studied separately in order to highlight possible differences in the evolutionary patterns. We ultimately aim at determining the order in which constitutive traits of communal and cooperative breeding evolved, and whether they enhance and/or stabilize each other.

2/ Second, we aim at providing a reappraisal of climate as an evolutionary driver of cooperative breeding in Mammals in the light of the reconstructed evolutionary routes. Indeed, each climate variable that displays an association to cooperative breeding may play a role in one or more steps of the identified pathways to cooperative breeding. We thus aim at disentangling the specific relationships between climate variables associated with cooperative breeding, such as annual precipitation or precipitation predictability, and our traits of interest.

Material and methods

Analysis of correlated evolution of discrete traits

The choice of a discrete, binary framework

The constitutive traits of cooperative breeding are not binary. For instance, the definition of delayed dispersal as offspring remained on their natal territories after sexual maturity includes permanent philopatry as well as non-permanent delay, i.e. when individuals do disperse but do so after they reach sexual maturity. In some species, some but not all individuals delay dispersal, and delayed dispersal can be quantified as the proportion of individuals that do not disperse at sexual maturity (Ekman et al. 2001b; Dickinson and McGowan 2005; Peer and Taborsky 2007). Similarly, species can display varying levels of reproductive skew and extra-group reproduction, thus making reproductive suppression a quantitative variable (Keller and Reeve 1994; Cant and English 2006). However, to our knowledge, there are very few species where quantitative data are available for all traits, which makes a quantitative multi-trait analysis impossible to perform. Furthermore, based on the current literature, the classification of species as displaying or not each trait leaves little room to uncertainty, even though the traits can be displayed at varying extents. Therefore, we chose to use a discrete, binary framework, in which traits are encoded as present or absent for each species.

Comparison between our binary trait framework and the definition of social systems

Combinations of social traits provide substantial information regarding the social systems of species, which refer to the patterns in the composition and structure of groups (i.e. number of individuals of each sex and life stage, hierarchy and relatedness between individuals). However, social systems cannot be defined according to the presence or absence of our characteristic traits alone, and it is not possible to link all combinations back to the classification of social systems. The only exceptions are the combination of delayed dispersal and alloparenting and reproductive suppression in addition to

the former combination, which respectively stand for communal breeding and cooperative breeding or eusociality,. Studying the coevolution of these traits provides insight on the evolution of the two social systems that are actually defined by them. Classifying social systems is indeed a difficult task. Depending on the focus, several classifications have been proposed (Crook et al., 1976; Dunbar, 2013; Shultz et al., 2011; Wilson, 1971). To our knowledge, no consensus about how social systems should be classified has been reached so far. For instance, Crook and colleagues (1976) classified species into twelve sociotypes according to the rearing tactic, the mating tactic, and the grouping tactic. Cooperative breeders are spread among three of these sociotypes (IVa, IVb, IVc) and separated according to whether the groups are refuge-based or not, whether several family groups can merge or not, and how tight relationships between mates are (Table 3). As cooperation is not included in the definition of social systems, one of these sociotypes (IVb) also includes non-cooperative breeders. Shultz and colleagues (2011), on the other hand, divided social systems in primates according to group composition only. In this system, cooperative breeders are included in multimale-multifemale groups along with plural breeders. It is even more difficult to classify other combinations among our three traits of interest into social systems. For instance, the lack of all three traits may be found in solitary, pair-living or gregarious species according to Shultz et al. (2011) and is compatible with seven of the Crook's sociotypes. Similarly, if we refer to social systems defined by Wilson (1971), where cooperation is included in the definition of social systems and the definitions of quasi-sociality and semi-sociality match those for communal and cooperative breeding, respectively, most combinations of the three traits are compatible with several social systems. This provides a further example of the difficulty for social categorizations to accurately depict the social interactions observed in species, in addition to the issues raised by a top-down approach based on removing the distinctive features of complex social systems such as eusociality (Legendre and Grandcolas, 2018).

Table 3 - Classification of Mammalian Social Systems according to Crook et al. (1976)

Sociotype	Rearing strategy	Mating strategy	Grouping and dispersion strategy	Examples
	System variables: 1. Male's presence in rearing group. 2. Duration of male's presence. 3. Duration of mother-infant (M-I) bond.	System variables: 1. Number of female consorts per male. 2. Duration of male-female bond.	System variables: 1. Group size. 2. Group stability. 3. Refuge utilization. 4. Range exclusivity.	
Ia	Male absent from rearing group.	Promiscuous matings.	Single M-I unit, males and juveniles also range individually. Refuge (cache or nest-based) system, exclusive ranges.	Tree squirrels. Gophers.
Ib	Same as Ia. Longer M-I bond.	Same as Ia.	Similar to Ia except that ranges are not exclusive.	Bush-babies.
Ic	Same as Ia. M-I bond persists past weaning.	Promiscuous matings, brief copulatory meetings. Males may enter female herds or females may visit mating territory of male.	M-I units join together in large herds. Males may form separate herds or remain solitary. No refuges. M-I herds free-ranging. Solitary males may have exclusive ranges.	Elephants. Kob.
IIa	Males present with rearing group, but only in loose association, not bonded.	Promiscuous; brief copulatory meetings within-in groups.	M-I units, males, and independent juveniles remain together in groups. Non-exclusive ranges.	Some bats. Badgers.
IIb	Same as IIa.	Same as IIa.	Same as IIa, except non-refuge based, free-ranging	Bison, Wildebeest.
IIIa	Male present in rearing group.	Harem; several females per male, membership varies through the season. Some male-female bonds may be re-established in successive years but not necessarily so.	Individual harem groups during breeding season, may gather into colonies—break up after breeding season. Refuge based. Non-exclusive foraging range.	Seals.
IIIb	Same as IIIa.	Same as IIIa	Exclusive rearing and breeding sites; units grouped into colonies, each unit with an exclusive foraging range. May be maintained outside breeding season.	Rabbits, Prairie dogs
IVa	Male remains with rearing (M-I) group, usually for more than one season. M-I bond lasts from 1 to several seasons.	Mated pairs.	Refuge-based groups may include offspring from successive seasons. Ranges may be exclusive or non-exclusive.	Beavers.
IVb	Same as IVa.	Same as IVa.	Same as IVa except non-refuge based.	Marmosets, Gibbon, Titi.
IVc	Same as IVa.	Same as IVa but looser relations between mates.	Several 'family' groups may join together, otherwise, same as IVa, and IVb.	Wolves, hunting dogs Hyaenas.
IVd	Same as IVa.	Harem groups of long duration.	'Excess' males may form independent groups or maybe integrated within rearing-mating groups. 'Herding' of basic harem groups may occur. May or may not be refuge-based. May or may not maintain exclusive ranges.	Horse, Vicuña, Patas monkey, Blue monkey, Gelada baboon Hamadryas baboon.
IVe	Same as IVa.	Multimale groups with several females of long duration.	Same as IVd except all males are integrated male-female groups; no 'excess' males. Herding of basic units not known to occur.	Papio baboons, other than hamadryas, Vervet monkeys, macaques.

The Bayesian method

The Bayesian approach to probability, formalized by Bayes in the eighteenth century, relies on a prior hypothesis on the probability of an event, which is readjusted based on new information in order to obtain a posterior probability. It is widely known as the Bayes formula, which states:

$$P(B|A) = \frac{P(A|B)P(B)}{P(A)}$$

The posterior probability of the event B given the new information A equals the probability of A given B ($P(A|B)$) multiplied by the probability of B and divided by the probability of A (Link and Barker 2009).

The application of Bayesian methods to the reconstruction of evolutionary pathways provides several advantages:

- First, it allows for the estimation of the posterior probability distribution of values rather than just calculating the maximum-likelihood estimates of parameters such as transition rates as done in maximum likelihood models (e.g. Pagel, 1999). Therefore, it provides useful information regarding the uncertainty of parameter estimates. For instance, the stronger the signal in the data, the closer around the maximum-likelihood estimate posterior distributions should be distributed.
- Second, it is compatible with the incorporation of phylogenetic uncertainty in the form of a collection of trees used as hypotheses about the phylogenetic relationships between species, which has been shown to reduce the error rates in the estimates of model parameters (de Villemereuil et al. 2012). Such trees can be obtained as a posterior sample from a Bayesian method of phylogenetic inference based on the genetic data of species of interest (Arnold et al. 2010).

The Bayesian method for investigating the coevolution of a pair of discrete binary traits was described by Pagel and Meade (2006), and is encoded in the computer package BayesTraits (Meade and Pagel 2017). This method requires a set of current species, their phylogeny and the state of two traits for

each species. It then seeks the continuous-time Markov models that best describe the joint evolution of the pair of traits on a phylogeny. It visits both independent and correlated models of evolution in proportion to their posterior probabilities, which produces an estimation of the support for the correlated model.

Assessing convergence and assessing for model fitting.

Markov chain Monte Carlo (MCM) procedures in Bayesian frameworks sample parameter rates according to their posterior probability. At each step, parameter values are slightly randomly modified, and the likelihood of the data (i.e the distribution of social traits in species) given the current parameter values (i.e transition rates) is then calculated. The parameter values are then accepted or rejected depending on the changes in likelihood compared to the previous set of parameters. These steps are repeated until the areas of parameter search are narrowed to a space that provide higher likelihoods, which means that *convergence* has been reached and the parameter space explored by the chain is the posterior distribution. Therefore, estimating whether convergence has been reached or not at a point in the chain is key to determining the possible values of parameters. Here, accordingly with the recommendations of Currie and Meade ([2014](#)), we considered a chain to have converged when the distribution of harmonic mean log-likelihoods was approximately normal and the likelihood traces did not show jumps across runs. This allowed us to make sure that likelihoods are no longer climbing from low-likelihood areas and that the chain has indeed reached a stable parameter area that provides reasonably good fits for the data.

Rate parameters and directionality

In addition to estimating whether there is significant support for the correlated model of evolution, Pagel and Meade's method estimates the posterior distributions of the transition rate parameters of the model of trait evolution. This provides information about the directionality of evolution, which is crucial to our analyses. For instance, if the transition rate for the evolution of one trait A in the absence

of the other trait B is zero in the vast majority of post-convergence iterations, B is highly likely to be a prerequisite for the evolution of A.

Controlling reconstructions for phylogenetic robustness

Accounting for phylogenetic uncertainty

Regardless of the method used for phylogenetic reconstructions, all constructed trees involve uncertainty regarding topology and branch lengths. Indeed, the construction of phylogenetic trees from nucleotide sequences involves several prerequisites, including sequence alignment, substitution modeling. The subsequent reconstruction of trees can then be performed according to different possible methods, including distance methods (Saitou and Nei 1987), maximum likelihood (Zwickl 2006), maximum parsimony (Swofford and Berlocher 1987) and Bayesian approaches (Huelsenbeck and Ronquist 2005). The relative efficiency of these methods can vary depending on various conditions, including the substitution rate and its variability (Tateno et al. 1994; Kolaczkowski and Thornton 2004). Each of the steps between nucleotide sequences and reconstructed trees involves uncertainty, which ultimately results in possible alternative topologies and branch lengths. This uncertainty of the phylogenetic relationships among taxa translates into uncertainty in the evolution of traits according to their distribution among current taxa. This is especially true in rare traits, where the number of evolutionary transitions is low. Thus, ensuring that the evolutionary reconstructions are robust to phylogenetic uncertainty is a key issue.

In order to take phylogenetic uncertainty into account, we ran BayesTraits models over a sample of 100 generated by the 10kTrees project (Arnold et al. 2010) rather than a consensus tree. The trees were sampled from a Bayesian tree inference in proportion to their posterior probabilities using Markov chain Monte Carlo (MCMC).

Accounting for the strength of phylogenetic signals

Estimating phylogenetic signal for traits of interest is crucial to performing transition rate analyses. Indeed, if phylogenetic signal is limited, there is little ability to test for coevolutionary relationships. Given that BayesTrait does not take this caveat into account, we needed to perform separate tests in order to disentangle coevolution from correlation that does not depend on phylogeny. We thus estimated the phylogenetic signal for each trait and each tree by calculating the phylogenetic signal as Pagel's λ (Pagel 1999), using the function *phylosig* from the Phytools package (Revell 2012). This allowed us to make sure that phylogenetic signals were high enough to test for coevolutionary relationships.

In addition to this, we also investigated whether the observed coevolutionary patterns resulted from coevolution or correlation between traits. In order to do so, for both carnivores and primates, we randomized combinations of traits according to the phylogeny in 100 simulated datasets. We then performed the BayesTraits reconstructions, as well as CorDISC reconstructions which allow for the reconstruction of evolutionary pathways in a three-trait binary framework (Beaulieu et al. 2016), on these datasets. We calculated the transition coefficients and investigated whether coevolution was still detected between all pairs of traits in all randomized datasets ($BF > 2$), and whether the order in which traits evolved and the stabilizing effects of traits remained consistent with the ones we detected in our results. In this case, a part of the detected coevolution could be attributed to a strong correlation between traits. We also ran simulations where traits, rather than combinations of traits, were independently randomized between species.

Assessment of the reliability of phylogenetic reconstructions performed on multiple traits

Available methods for reconstructing phylogenetic coevolution between more than two discrete traits

Although Bayesian phylogenetic reconstructions of coevolving traits have been performed in a number of previous publications (Robertson et al. 2011), those studies were usually limited to pairs of traits. Indeed, BayesTrait does not perform correlated models of evolution on more than two traits. Research involving more than two traits thus used analyzed pairs of traits separately and inferred the conclusion from the results obtained on these pairs of traits (Leys and Hogendoorn 2008; Furness et al. 2019). For instance, to analyze the directionality of the coevolution of sperm size, sperm speed and sperm competition, all of which were encoded as binary traits, a study used BayesTraits separately on each pair of traits, and subsequently concluded that sperm competition increased first, then sperm speed, and lastly sperm size (Fitzpatrick et al. 2009, Figure 1).

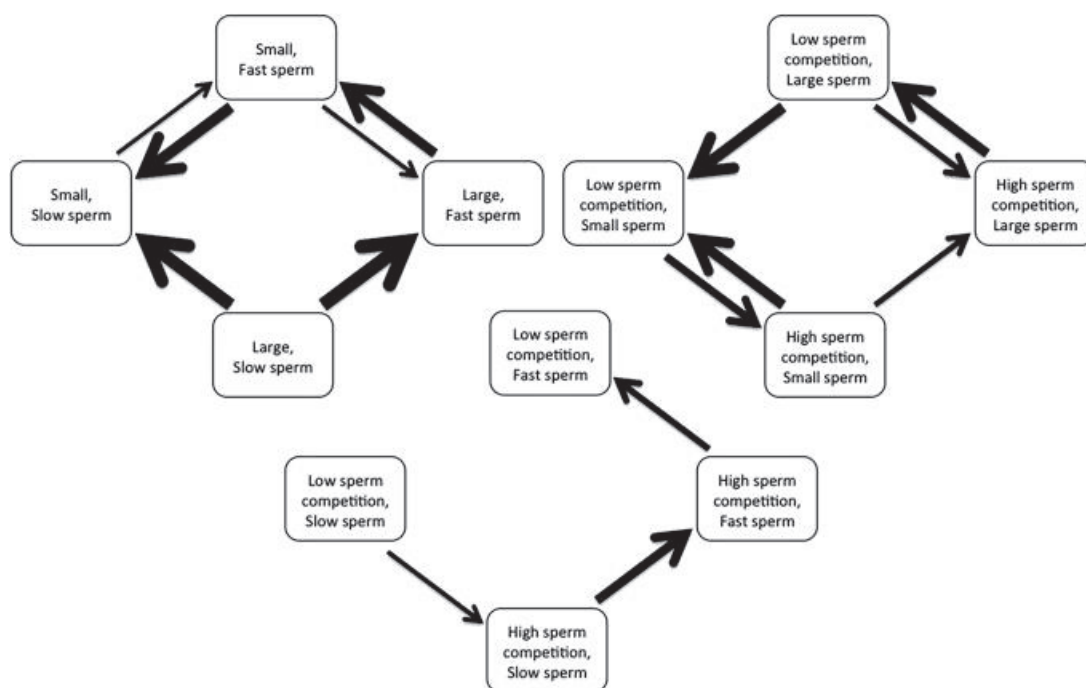


Figure 1. Flow diagrams showing the inferred rates of change from three analyses of sperm competition and sperm characteristics in cichlid fish

Ancestral state reconstructions indicate that the common ancestor of 29 species of these fish had slow, small sperm and experienced low levels of sperm competition. Sperm gets faster before getting larger (top left), and both sperm size (top right) and sperm speed (bottom middle) increase after sperm competition increases. Figure from Currie and Meade (2014).

However, this method does not account for the possibility that a trait may have evolved in response to the evolution of the two others. A satisfying solution was provided by the corDISC function of the package corHMM in R (Beaulieu et al. 2016), which fits models of correlated evolution among three binary traits. However, this function cannot fit more than three traits. Therefore, when a fourth trait such as monogamy was included, we resorted to running separate analyses for pairs or triads of traits.

Can combinations be coded as a single trait?

The lack of methods including more than three discrete traits raises a number of limitations in our studies, such as the impossibility to take into account all the interactions between traits. This issue could theoretically be solved by coding combinations of traits as a single multistate trait, which was attempted in preliminary unpublished analyses. We coded all combinations as different states of a single trait to analyze the transitions between combinations with the multistate module from BayesTraits. In order to test whether transitions could be simultaneous or not, we tested both an unrestricted model in which transitions were possible between any combinations of traits, including those involving multiple traits transitioning simultaneously, and a restricted model in which only transitions involving a single change of trait were allowed (Figure 2). Unfortunately, these models severely lacked power and did not allow us to differentiate between different scenarios. Such a lack of power can be explained by the high number of states of the combination trait. Indeed, there are 16 theoretical possible combinations of four binary traits. For carnivores, 7 of them are effectively present in the dataset, with 3 more being possibly present depending on the state of traits for which no data are available (i.e. *Urocyon cinereoargenteus* may correspond either to delayed dispersal + monogamy, or to monogamy alone). A dataset of 163 species does not allow for a robust analysis of a trait that displays at least 7 states. This was even worse for the primate dataset, which includes less species

(122) and more trait combinations (12). Furthermore, some of the combinations are rare (i.e delayed dispersal + reproductive suppression + monogamy, which has only one occurrence in carnivores), which further lowers robustness. By contrast, analyses that consider each trait separately do not encounter this issue, because each trait displays sufficient frequency to allow for a robust analysis.

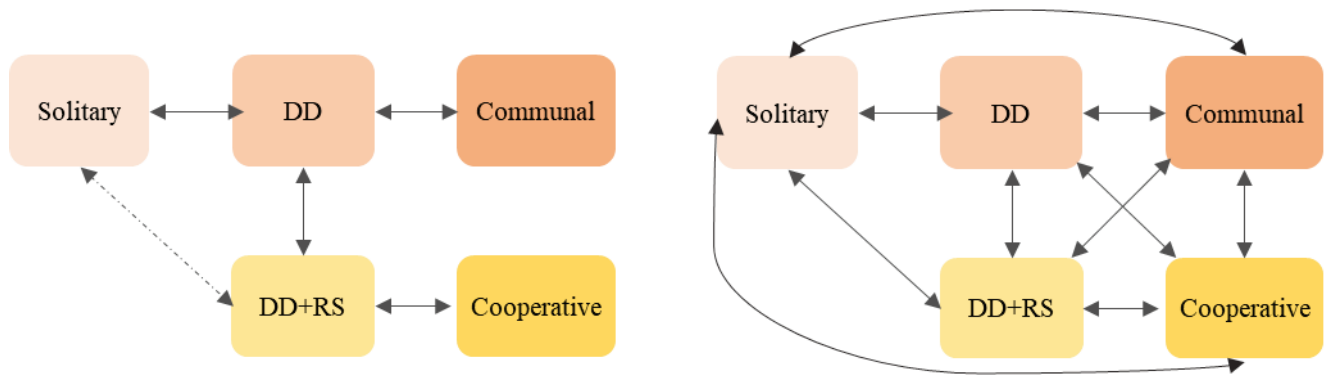


Figure 2 - Restricted and unrestricted single trait, multistate model

DD and RS stand for delayed dispersal and reproductive suppression, respectively.

Assessing for robustness when reconstructing the coevolution of rare traits

How rare are the constitutive traits of cooperative breeding?

Delayed dispersal is the most frequent constitutive traits of cooperative breeding, with a frequency ranging from 21% in carnivore females to 48% in primate males. Reproductive suppression and alloparenting are rarer (reproductive suppression: 10% of carnivore females, 17% of primate females and 11% of primate males; alloparenting: 12% of carnivore females, 10% of primate females and 12% of primate males).

Potential issues raised by rare traits

Rare traits tend to display a low number of evolutionary transitions, which makes it difficult to quantify their phylogenetic signature and evolutionary patterns adequately. This issue is further exacerbated when combinations of traits are examined. For instance, three binary traits can be displayed in 8 combinations of traits. If all of these traits are rare, each combination is likely to be rare as well, which

makes it difficult to tell apart coevolutionary relationships and assess how the existing trait combination affects the further evolution of each trait. Furthermore, low trait frequency may increase the probability of type I errors in coevolutionary analyses, i.e favoring the dependent model over the independent one due to the over-interpretation of a low number of simultaneous trait transitions.

In some cases, although traits are not rare themselves, some trait combinations evolved in very few occurrences along the phylogenetic trees. For instance, although the frequency of alloparenting is similar in carnivores (12%) and in primates (10% for females and 12% for males), the extremely low number of evolutionary transitions to alloparenting in primates (2) makes it impossible to actually draw conclusions regarding the interactions between alloparenting and other traits such as delayed dispersal and reproductive suppression in primates, hence the exclusion of alloparenting from the primate analysis (see Chapter 2).

Interest of approaches focusing on the coevolution of constitutive traits

It should be noted that working on the constitutive traits of complex social systems such as cooperative breeding allows us, to an extent, to avoid the issues raised by extreme trait rarity. Indeed, while less than one percent of Mammalian species are cooperative breeders, all three constitutive traits of cooperative breeding are more frequent. Therefore, assessing separately the association of a parameter of interest with each constitutive trait of a complex social system may lead to more robust results than its association with the social system, in addition to provide further information regarding its possible involvement in the evolutionary route to the social system. However, it is possible for parameters to display a strong association with a social system without being closely associated to each of its components, especially if the latter are all separately involved in other social systems. Therefore, we recommend that all associations, including the one with the whole social system, are explored when assessing for the role of a parameter in the evolution of a complex social system.

Our solution: Assessing robustness on simulations with similar trait frequencies

In order to check whether the observed coevolutionary effects are robust despite trait rarity, we generated simulated data with the same proportion of the different states but with pre-determined coevolutionary relationships.

Assessing for type I error

In order to check that the detected coevolutionary relationships among our traits did not result from a type I error stemming from the rarity of our traits, we simulated 1,000 phenotypic datasets with no coevolutionary relationships among the three traits of interest using the function `rTraitDisc` from the APE package (Paradis, 2012; Paradis et al., 2004). We simulated the evolution of each trait independently over the consensus tree, and set the equilibrium trait frequencies to those of our empirical dataset. In these trees we subsequently tested for a coevolution among all three possible pairs of traits according to the procedure used for the empirical dataset. We used the Pagel coevolution test, and calculated the Bayes Factor (BF) between the independent and dependent model. We expected no support for coevolution to occur in these simulations because the evolution of each trait was simulated independently. In 99% of simulated datasets, there was indeed no detectable support for coevolution, while the signal for coevolution was dramatically stronger in our empirical datasets (Figure 3). Only 14 of 1000 datasets returned a Bayes Factor superior to 3 in favor of the dependent model. Therefore, our model does not falsely detect coevolution among traits that evolved independently, even when these traits are rare. These results are likely to be different in rarer traits (i.e frequency <5%), or with similar trait frequencies but a smaller dataset. Therefore, building large datasets may compensate for low trait frequencies by increasing the number and/or detected robustness of the evolutionary transitions taken into account by the model. This is encouraging for further studies focusing on the evolution of rare traits.

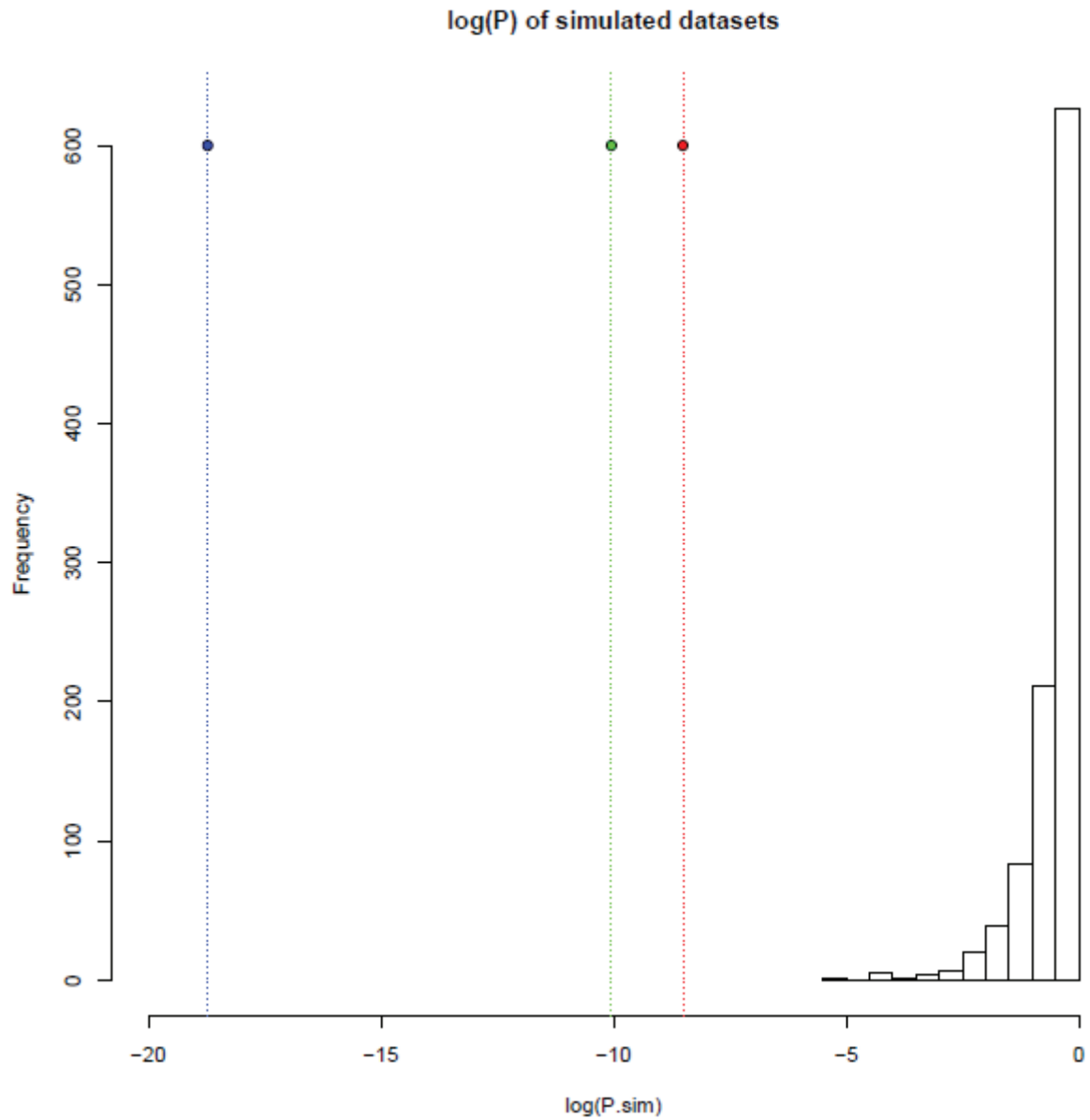


Figure 3 - P-values of the Pagel coevolution test for pairs of traits in carnivores

The histogram displays the distribution of the p-values obtained from the 1,000 simulated datasets with trait frequencies identical to our carnivore dataset. 12 simulated datasets produce a P-value just under 0.05. P-values for our empirical carnivore dataset are shown in blue (Delayed dispersal x Alloparenting, $p=7.4 \times 10^{-9}$), green (Reproductive suppression x Alloparenting, $P=7.4 \times 10^{-5}$) and red (Delayed dispersal x Reproductive suppression, $P=2.0 \times 10^{-4}$).

Assessing for the robustness of coevolutionary effects identified in the data

To assess the robustness of our model in deciphering the existence of directional coevolutionary relationships among traits as those presented in our results, we first simulated data using the transition

matrix reconstructed from the observed data. Indeed, obtaining alternate datasets that reflected the evolutionary patterns observed in our data allowed us to investigate whether these patterns were still detected when conducting our analyses on a greater number of datasets. We simulated datasets using a discrete Markov model of coevolution implemented into the function `rTraitMult` from the `APE` package (Paradis, 2014), which allowed us to provide our transition matrix as the transition rates used by the simulation. Then, in order to check whether our model was able to capture the directional evolution observed in our results, we conducted ancestral reconstructions on these new simulated datasets using `corDISC`, according to the same procedure used on the observed data. This resulted in new matrices indicating the reconstructed transition rate for each evolutionary step (e.g. delayed dispersal → delayed dispersal + reproductive suppression). We then calculated the overall transition rate for each evolutionary *pathway* by multiplying the estimated transition rate for each *step*, and recorded the preferred evolutionary pathway as the one with the highest overall transition rate. We also classified the reconstruction as unidirectional when a single pathway to cooperative breeding was identified (100% of the transition rates led to a single pathway), as quasi-unidirectional when several pathways to cooperative breeding were possible but 80% of the transition rates led to a given pathway, and as multidirectional otherwise. We finally checked whether the directionality and preferred evolutionary pathway were consistent with the effects observed in our data. In carnivores, we found that 73% of the reconstructions that used the transition matrix from the observed data were unidirectional and 23% were quasi-unidirectional, whereas only 4% of reconstructions were multidirectional, which suggested that unidirectional pathways detected in empirical datasets were caused by an actual coevolutionary relationship rather than mere positive correlations between traits (Figure 4).

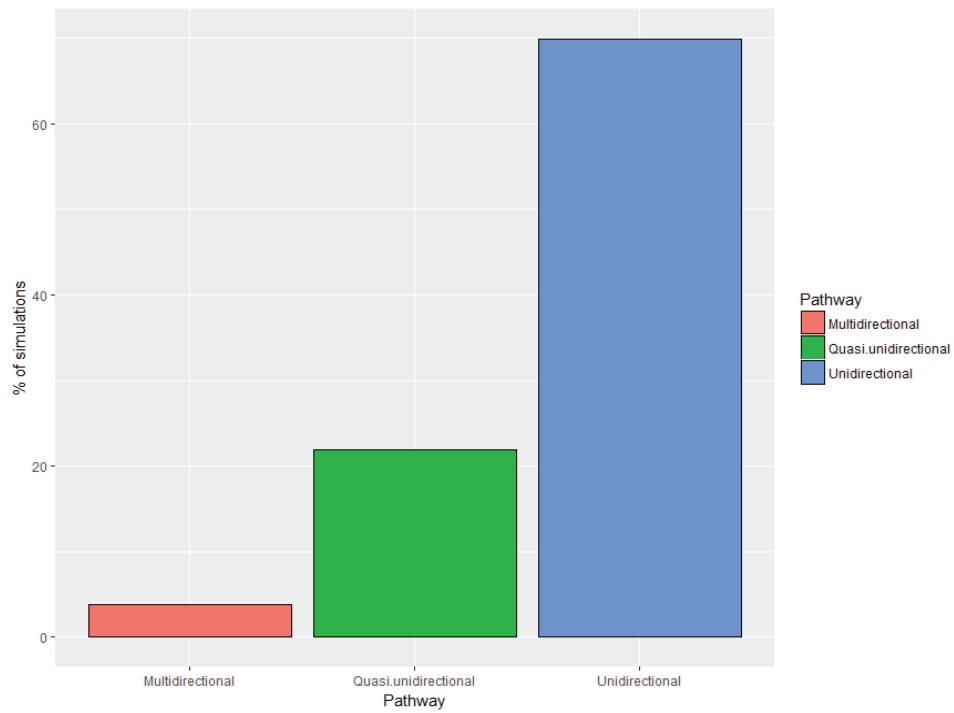


Figure 4 - Percentage of multidirectional, quasi-unidirectional and unidirectional reconstructions obtained from carnivore data simulated using the reconstructed transition matrix from the observed data

Multidirectional, quasi-unidirectional and unidirectional reconstructions are displayed in red, green and blue, respectively.

Chapter 1 – Evolutionary pathways to cooperative and communal breeding in Carnivores

Abstract

In animal societies, individuals can cooperate in a variety of tasks, including rearing young. Such cooperation is observed in complex social systems, including communal and cooperative breeding. In mammals, both these social systems are characterized by delayed dispersal and alloparenting, whereas only cooperative breeding involves reproductive suppression. While the evolution of communal breeding has been linked to direct fitness benefits of alloparenting, the direct fitness cost of reproductive suppression has led to the hypothesis that the evolution of cooperative breeding is driven by indirect fitness benefits accrued through raising the offspring of related individuals. To decipher between the evolutionary scenarios leading to communal and cooperative breeding in carnivores, we investigated the coevolution among delayed dispersal, reproductive suppression, and alloparenting. We reconstructed ancestral states and transition rates between these traits. We found that cooperative breeding and communal breeding evolved along separate pathways, with delayed dispersal as the first step for both of them. The three traits coevolved, enhancing and stabilizing each other, which resulted in cooperative social systems being stable as opposed to intermediate configurations. These findings promote the key role of coevolution among traits to stabilize cooperative social systems, and highlight the specificities of evolutionary patterns of sociality in carnivores.

Introduction

Cooperation plays a key role in a number of biological processes at different levels of biological organization, including symbiosis, gene expression, mutualism, and sociality (Boucher 1988; Bourke 2011; Kiers et al. 2011). Understanding the evolution of cooperation is crucial in explaining how single biological entities such as cells or individuals merge into collective ones such as multicellular organs or structured social groups, and how these complex structures are stabilized into new levels of organization (West et al., 2015). In animal societies, individuals can cooperate in a variety of tasks, including foraging, hunting, resource or mate defense but also raising young (Dugatkin 1997). Cooperation towards rearing young includes a variety of alloparenting behaviors such as allofeeding, infant carrying, and infant monitoring, that all involve fitness costs (Carlisle and Zahavi 1986; Snowdon 1996; Schradin and Anzenberger 2001; Clutton-Brock et al. 2004). Such cooperation is observed, along with three main cooperative social systems: communal breeding, cooperative breeding, and eusociality (Koenig and Dickinson 2004; Wilson and Hölldobler 2005; Cockburn 2006; Lukas and Clutton-Brock 2012b). Communal breeding encompasses social systems in which breeders pool their offspring and share care and feeding among them (Clutton-Brock 2016), which provides various short-term benefits such as securing food resources, protection against predators and thermoregulation for the young (Lewis and Pusey 1997). Cooperative breeding refers to social systems in which only dominant individuals breed and are assisted in caring for their offspring by non-breeding individuals. In most cases non-breeders forego dispersal and breeding, and remain within their natal group as helpers (Clutton-Brock, 2016), although in some bird species they may have bred and lost their offspring (Hatchwell et al. 2002), or be unrelated to the breeders (Riehl 2013). Although both communal and cooperative breeding involve delayed dispersal and alloparenting, cooperative breeding further involves reproductive suppression leading to the presence of non-breeding helpers (Figure 5). Given that alloparenting is only observed in communal breeding, cooperative breeding and eusociality, it is likely that delayed dispersal and reproductive suppression are crucial to the development of alloparental care (Riehl 2013; Griesser et al. 2017). To understand the evolution of

cooperative social systems, we need to uncover the evolutionary routes to communal and cooperative breeding from solitary ancestors and, thus, to decipher the coevolution between their constitutive traits (i.e. delayed dispersal, reproductive suppression and alloparenting) is key. In most cooperative social systems, individuals engaging in alloparenting behaviors are sexually mature individuals that did not disperse due to strong ecological constraints, benefits of philopatry or both (Emlen 1982, 1994; Sheehan et al. 2015), which results in unusually high levels of kinship within social units. Delayed dispersal thus increases the indirect fitness benefits of alloparenting behaviors, and is thus often assumed to be a prerequisite of the evolution of alloparenting (Emlen 1982; Hatchwell et al. 2002; Cornwallis et al. 2009; Briga et al. 2012), although recent studies have highlighted the possibility of pre-existing cooperation that lengthens offspring dependence (Langen 2000) and decreases dispersal propensity (Purcell et al. 2012) (Figure 5). The extent of these indirect fitness benefits gained from delaying dispersal may have implications for the evolution of reproductive suppression. Indeed, when remaining in the natal group increases indirect fitness, dominants do not benefit from yielding reproductive concessions to subordinates, which do not need to be prevented from dispersing, thus leading to the evolution of cooperative breeding (Clutton-Brock, 2016, Figure 5). By contrast, the direct fitness benefits of delayed dispersal may favor egalitarian forms of cooperation, such as communal breeding. Therefore, while the evolution of cooperation towards rearing young can be explained by an increase in the individual's own fitness (direct benefits) and/or the fitness of its relatives (indirect benefits), the relative extent of these benefits to the costs may determine the favored pathway (Creel and Creel 1991). While communal breeding has been hypothesized to evolve mostly due to the direct fitness benefits of group living, the direct fitness cost of reproductive suppression has led to the hypothesis that the evolution of cooperative breeding is driven by the indirect fitness benefits accrued through raising offspring that are not its own (Vehrencamp 2000; Gilchrist 2007; Fewell et al. 2009). Although previous work has generally assumed that a strong relationship between reproductive suppression and alloparenting, especially under the best-of-a-bad-job hypothesis that suggests alloparenting to be the only strategy to increase fitness in reproductively suppressed individuals

(Canário et al., 2004; Hatchwell, 2009; Shen et al., 2017, Figure 5), the order in which these two traits evolved in cooperatively breeding lineages has not yet been assessed.

Previous research hints toward a close association between social and mating system. Although pre-established cooperation can theoretically favor evolution towards monogamy (Peck and Feldman 1988), it has been suggested that the evolution of cooperative breeding in mammals is restricted to species with a pre-established socially monogamous mating system leading to high relatedness between group members, whereas communal breeding has evolved in polygynous or promiscuous species (Lukas and Clutton-Brock 2012a). Social monogamy was also found to be required for the evolution of sociality in lineages of eusocial insects (Hughes et al. 2008). In birds, cooperative behaviors have been shown to evolve in long-lived promiscuous species in addition to monogamous ones (Downing et al. 2015). Indeed, social monogamy has been suggested to increase relatedness between group members, which is thought to favor cooperative behaviors due to indirect benefits, including alloparenting. Nonetheless, cooperative breeding does not prevent further evolution of the mating system. Transitions from monogamy to polygyny or to polygynandry occur in cooperative breeders, and play a major role in evolutionary transitions to communal or independent breeding (Cornwallis et al. 2010). However, both the occurrence and the role of the transition towards monogamy in the pathway from independent to cooperative breeding remain unclear. So far, the existence and directionality of coevolution between social monogamy and traits related to cooperative breeding such as delayed dispersal and reproductive suppression have not been investigated.

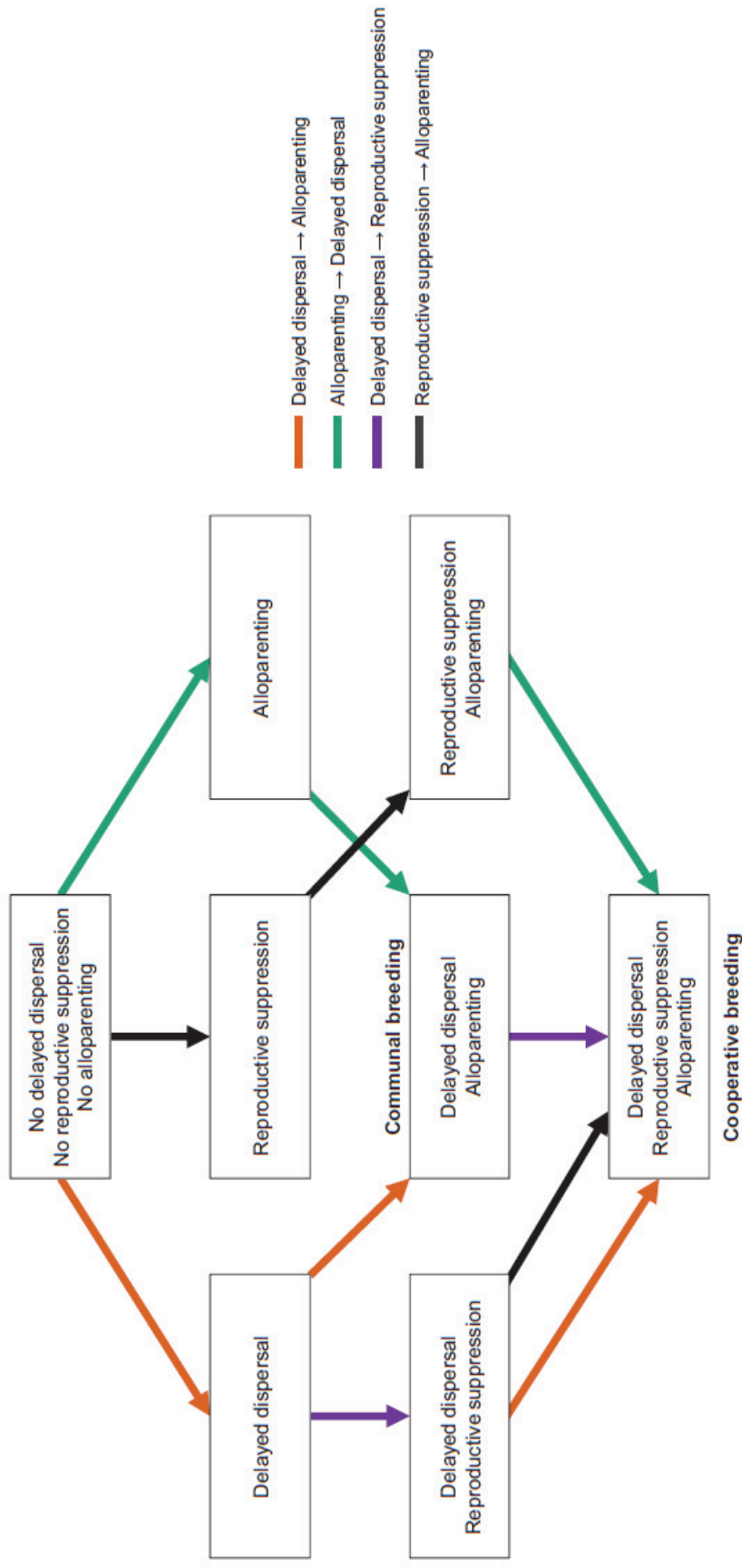


Figure 5: Hypotheses for the evolution of traits related to cooperative breeding. Orange arrows represent transitions supporting delayed dispersal as a prerequisite for the evolution of alloparenting; these transitions include the evolution of delayed dispersal in the absence of other traits and the evolution of alloparenting from configurations where delayed dispersal is present. Green arrows represent transitions supporting delayed dispersal as favored by preexisting cooperation; they include the evolution of alloparenting in the absence of other traits and the evolution of delayed dispersal from configurations where alloparenting is present. Purple arrows represent transitions supporting the evolution of reproductive suppression to be enhanced by delayed dispersal due to the emergence of indirect benefits. Black arrows represent transitions supporting the evolution of alloparenting to be subsequent to reproductive suppression because it is the only strategy to increase fitness in reproductively suppressed individuals. All transitions have been assessed by assuming the absence of three-way interactions among traits.

The mammalian order of Carnivora displays a substantial diversity in social organization, including social and mating systems, with communal and cooperative breeding, although uncommon, being widely distributed among families and with closely related species displaying markedly different social organizations as for instance the group-living, female-philopatric but independently nesting ring-tailed coatis (*Nasua nasua*) (Hirsch 2007) and the communally breeding white-tailed coatis (*Nasua narica*) (Gompper 1995). The most recent common ancestor of Carnivores is likely to be solitary, and most species in this order live solitarily outside mother-offspring association and temporary feeding groups (Bekoff et al., 1984; Gittleman, 1989; but see Dalerum, 2007) . However, several species exhibit long-term social units that include more than two adults, which allows for the emergence of complex social systems such as communal and cooperative breeding. Therefore, the pattern of distribution of social systems and traits related to cooperate towards breeding makes the Carnivora a group of particular interest for the study of the evolutionary routes to communal and cooperative breeding.

We aim at understanding the evolutionary routes toward cooperative and communal breeding in Carnivores through addressing the evolution of delayed dispersal, reproductive suppression, alloparental care and monogamy. We expect delayed dispersal to be the first step in the route from solitary ancestors to both communal and cooperative breeders and to facilitate the subsequent evolution towards alloparenting and reproductive suppression. We further expect that communal and cooperative breeding have evolved along two separate evolutionary pathways with reproductive suppression preceding the evolution of alloparenting in cooperative breeding species. To test these expectations, we first assess the existence, directionality and potential coevolution among these traits by using reconstructions of transition rates. We then perform phylogenetic reconstructions of ancestral states to identify the most likely evolutionary routes from solitary to communal and cooperative breeding. Finally, we explore the association between social system and mating system by assessing the occurrence of monogamy in the evolution from independent to cooperatively breeding systems.

Material and methods

Assessing the occurrence of delayed dispersal, reproductive suppression, alloparental care and monogamy in Carnivora species

We looked for published information on delayed dispersal, reproductive suppression and alloparental care in Carnivora and built a database including 163 species (Table 4). We used the database compiled by Lukas and Clutton-Brock (2012a) as a starting point, and then reduced the number of species based on the availability of data about delayed dispersal (DD), reproductive suppression (RS), cooperation towards rearing offspring other than its own (A), and social mating systems in the species-specific literature. In carnivores displaying delayed and sex-biased dispersal, females are usually the philopatric sex (Greenwood 1980; Johnson 1986; McNutt 1996). Moreover, alloparenting behaviors in carnivores are mostly performed by females (Macdonald and Moehlman 1982; Moehlman and Hofer 1997). Therefore, we restricted our analysis to females. For each species, we assessed whether females remain in their natal social unit beyond sexual maturity, whether reproductive suppression of females is reported in the majority of social units regardless of the proportion of non-breeding females, whether alloparenting behavior occurs, and whether the species is socially monogamous (hereafter monogamous). We coded these traits as binary states (*i.e.* 0 and 1 standing for the absence and presence of the trait of interest, respectively). We considered delayed dispersal to occur when female offspring remained in their natal social unit after they were sexually mature, in accordance with Ekman *et al.* (2004). This definition includes females' permanent philopatry as well as delayed dispersal *stricto sensu* (*i.e.* when females do disperse but do so after they reach sexual maturity). Reproductive suppression was considered to occur when either a reproductive skew involving the monopolization of reproduction by dominant individuals and a presence of non-reproductive individuals in a social unit were observed, or when reproductive suppression mechanisms such as successful monopolization of mating, physiological suppression of reproductive functions, exclusion of pregnant females from their social unit, or infanticide were reported. We assumed that an occurrence of reproductive skew in the literature involved the existence of such mechanisms, even if they were not explicitly reported. We

restricted our definition of alloparenting to behaviors that benefit non-offspring juveniles and are known to be costly in terms of energetic expenditure and survival, such as allofeeding (MacLeod et al. 2015), infant carrying (Sánchez et al. 1999) and infant guarding (Clutton-Brock et al. 1998). It is noteworthy that reproductive suppression and alloparenting cannot occur in solitary species. Thus, any species described as solitary in the primary literature was considered to lack those traits. We classified a species as monogamous when breeding groups included a single breeding adult of each sex, according to Clutton-Brock *et al.* (2012). A species was therefore considered as a communal breeder when displaying delayed dispersal and alloparenting without reproductive suppression, and as a cooperative breeder when all traits were present.

Phylogenetic reconstruction

For phylogenetic reconstruction and to account for phylogenetic uncertainty, we used a consensus tree generated from a set of 100 chronograms generated by the 10kTrees project and pruned to the species of interest (Arnold et al. 2010). For each trait, we calculated the phylogenetic signal as Pagel's λ (Pagel 1999) using *phylosig* from the *Phytools* package (Revell 2012).

Coevolution and directionality in the evolution of traits related to communal and cooperative breeding

To understand the evolutionary transitions from solitary toward communal and cooperative breeding, we had to determine whether delayed dispersal, reproductive suppression and alloparenting either evolved independently or coevolved. In the latter case, the directionality of the coevolution – in other words, which trait was likely to have occurred first and led to the occurrence of the other - also had to be assessed.

We first performed coevolution analyses on pairs of traits using the DISCRETE method of BayesTraits (Meade and Pagel 2017). For each pair of traits, we tested both dependent models assuming coevolution and independent models in which a trait does not affect the evolution of the other. In agreement with previous work on the evolution of social systems in carnivores, we assumed the most recent common ancestor of carnivores to be solitary and thus to lack all three traits of interest (Bekoff

et al., 1984; Gittleman, 1989). We used a reversible-jump Markov chain Monte Carlo (RJ-MCMC). We ran the chain for 1,000,000 iterations after a burn-in of 10,000 iterations, and sampled the chain at intervals of 1,000 iterations. We used gamma-distributed priors for transition rates (Currie and Meade, 2014). To reduce the uncertainty of choosing priors, we used uniform hyperpriors to draw values for the mean and variance of the gamma parameters. To assess the consistency of our results, we ran every model 5 times and verified the convergence of the chain, consistency of transition rates, and alpha and beta parameters of the gamma function. We checked the convergence of the chain by assessing that the distribution of harmonic mean log-likelihoods was approximately normal and that the likelihood traces did not show jumps across runs. Bayes Factor (BF) between the independent and dependent models was used to evaluate whether two traits coevolved. We estimated log-likelihoods of each model using a stepping stone sampler with 100 stones per 10,000 iterations (Xie et al. 2010), and calculated the Bayes Factor as twice the difference between the log-likelihoods of the two models, according to Meade and Pagel (2017). We then characterized transitions between states. Transitions between states (Z scores) that were frequently assigned to zero (approximating independent models of trait evolution) were considered to be unlikely, whereas those only rarely assigned to zero (i.e. approximating dependent models of trait evolution) were considered to be highly likely evolutionary transitions. We further determined the mean \pm SE transition parameter (q value), which indicates the instantaneous probability of each transition between states. To check for the consistency of our results against phylogenetic uncertainty, we further performed coevolution analyses using the whole set of 100 chronograms and verified that the results remained unchanged.

Second, to account for the possibility that a trait may have evolved in response to the evolution of the two others, we fitted a model of correlated evolution among all three binary traits using the corDISC function of the package 'corHMM' in R (Beaulieu et al. 2016). As previously, the most recent common ancestor was assumed to be solitary and lacking all three traits of interest. We used an all rates different model (ARD) to estimate the transition rates (q') from one of the eight theoretically possible combinations of the three traits' states to another and to estimate the probability of the

ancestral combination for each internal node with a marginal method (Holder and Lewis 2003). Like previously, the model was run 5 times to check the consistency of the results. We also counted the transitions between states in the reconstructed phylogenetic tree by assessing consecutive nodes where the most probable state was different. We considered nodes, and thus transitions involving them, as uncertain when the ratio of the two most probable states at a node was less than 2. Both the number of multiple transitions, corresponding to multiple traits changing within the same internal branch, and single trait transitions, were assessed.

Finally, due to the rarity of the occurrence of the three constitutive traits of cooperative breeding and the subsequently low number of transitions, we assessed the robustness of our results. To make sure that our model did not falsely detect coevolution patterns, we fitted our model to simulated data where traits evolved independently and for which equilibrium frequencies closely matched those observed in our dataset. To assess whether our model accurately captured the coevolution patterns existing in the data, we simulated datasets using the transition rates estimated from fitting our model to the empirical data. We then fitted our model to these simulated datasets and assessed whether the existence and directionality of coevolution was accurately captured (see Online Appendix A for further information regarding the simulations).

Association between monogamy and traits related to communal and cooperative breeding

Finally, to investigate the coevolution between reproductive cooperation and mating system, we fitted models of correlated evolution between monogamy (M) and traits related to communal and cooperative breeding. First, in order to assess the existence and directionality of coevolution between monogamy and traits related to communal and cooperative breeding, we performed three coevolution analyses, using the DISCRETE method of BayesTraits as previously, on pairs of traits. Each pair included monogamy and one of the three previously investigated traits (i.e delayed dispersal, reproductive

suppression and alloparenting). We assumed that the most recent common ancestor of carnivores was solitary and non-monogamous (Bekoff et al. 1984; Gittleman 1989). The same analysis was performed on monogamy with either cooperative or communal breeding, the two latter traits being assessed from the dataset according to the presence of the defining traits of both social systems. Second, to account for possible dependence between monogamy and each pair of traits defining cooperatively breeding species, we fitted models of correlated evolution between three traits using corDISC. In each model, we thus included monogamy in addition to two of the three traits present in cooperative social systems (delayed dispersal, reproductive suppression and alloparenting). Like previously, we used ARD models and reconstructed internal nodes with a marginal method.

Results

Distribution of communal and cooperative breeding and their related traits

Among the 163 species used in our study, 124 were classified as solitary (76%), 13 as cooperative breeders (8%), 6 as communal breeders (4%), and the remaining 20 species were neither solitary, nor cooperative or communal (12%) (Table 4). In 34 species, individuals delayed dispersal, in 16 species reproductive skew occurred (including 12 species with identified reproductive suppression mechanisms), 19 species displayed alloparenting behaviors, and 27 species were monogamous (Table 4).

Evolutionary origins of cooperative and communal breeding

Ancient independent transitions from solitary breeding to communal breeding were revealed in Procyonidae and Hyaenidae by ancestral node reconstructions, as well as two recent transitions among Felidae, leading to a sparse distribution of communally breeding species, such as lions (*Panthera leo*), surrounded by closely related species breeding solitarily (Figure 6). Independent transitions toward cooperative breeding were established at the root of the *Canis* genus and among Herpestidae species (Figure 6). Despite their apparent similarities, communal and cooperative breeding occurred independently and only one transition between these two systems was observed in Herpestidae, where a transition from cooperative to communal breeding is likely to have taken place in a recent

ancestor of the banded mongoose (*Mungos mungo*) (Figure 6). There were between 11 and 14 clearly identified single trait transitions, and between 1 and 5 multiple-trait transitions occurring on the same branch of the tree (Figure 10).

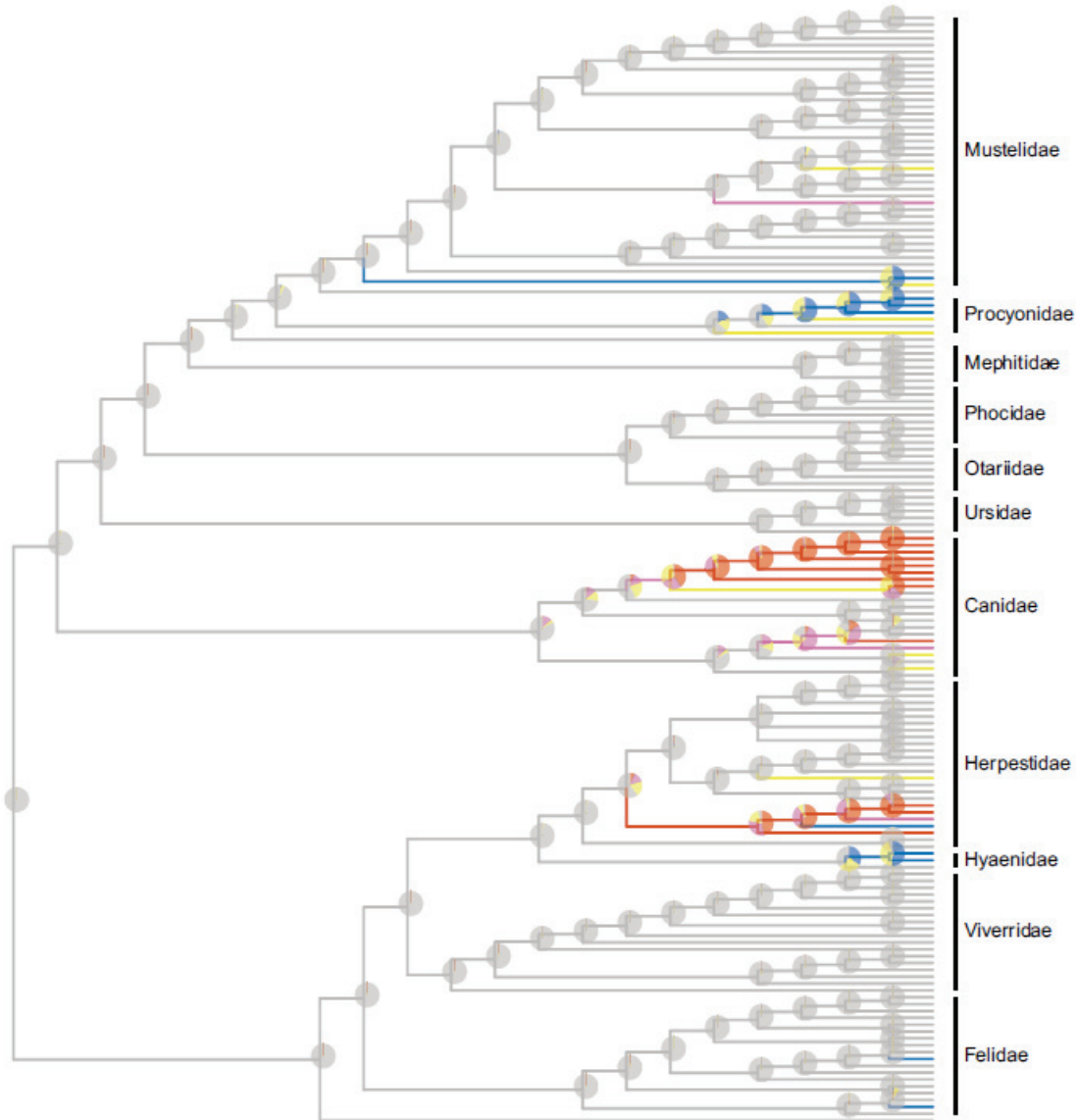


Figure 6 - Carnivore phylogeny showing ancestral state reconstructions for delayed dispersal, reproductive suppression, and alloparenting under the all-rates different correlated model of evolution. Combinations of traits are presented in the following order: delayed dispersal, reproductive suppression, and alloparenting. Branches are colored according to the most probable combination of states. The combination 0,0,0 is displayed as gray; 1,0,0 as yellow; 1,1,0 as pink; 1,0,1 as blue; 0,1,1 as pink; and 1,1,1 as orange. Thus, communal and cooperative breeding appear in blue and orange, respectively. Other combinations are absent in the reconstruction. Pies represent the probability distribution of the combinations of traits at each node. The tree topology is the consensus tree obtained from the 10kTrees project posterior distribution. Branch lengths are drawn proportional to time.

Coevolution of traits related to cooperative breeding

For all traits, phylogenetic signal estimates were high and statistically different from zero (range: 0.69-1.00, all $P < 0.05$, see Table 5). A coevolution between delayed dispersal, reproductive suppression and alloparenting was supported by a stronger statistical support for the dependent models than for the independent ones (delayed dispersal - reproductive suppression: marginal likelihood = -76.25 vs. -87.53, BF = 22.50; delayed dispersal - alloparenting: marginal likelihood = -73.59 vs. -98.88, BF = 50.43; reproductive suppression - alloparenting: marginal likelihood = -74.59 vs. -99.04, BF = 80.97, Figure 7a). It is noteworthy that the presence of coevolution between all traits still occurs when combinations are randomized, thus suggesting that the detected coevolution results from a strong correlation between them (Figure 11).

Transition coefficients indicated that, although reproductive suppression could be the first trait to occur, delayed dispersal typically occurred before reproductive suppression ($Z_{\rightarrow DD} = 0.00 < Z_{\rightarrow RS} = 0.84$ and $q_{\rightarrow DD} = 1.24 > q_{\rightarrow RS} = 0.03$, Figure 7a; $q'_{000 \rightarrow 100} = 2.6 > q'_{000 \rightarrow 010} = 0.6$, Figure 7b). Furthermore, the extremely high transition coefficients from reproductive suppression alone to the ancestral state ($q'_{RS \rightarrow 0} = 100$) and to the subsequent evolution of delayed dispersal ($q'_{RS \rightarrow RS, DD} = 100$) make it unlikely that this state was maintained long enough to show up in the tree. Alloparenting never occurred in species without delayed dispersal ($Z_{S \rightarrow DD} = 0.00 < Z_{S \rightarrow A} = 1.00$; $q_{S \rightarrow DD} = 2.85 > q_{S \rightarrow A} = 0.00$, Figure 7a; $q'_{0 \rightarrow A} = 0.00$, Figure 3b) but could occur in species with or without reproductive suppression as long as delayed dispersal was present. In the pathway towards communal breeding, alloparenting consistently evolved following delayed dispersal ($q_{DD \rightarrow DD, A} = 38.25$) but reproductive suppression never occurred (Figure 3b). Similarly, in the pathway towards cooperative breeding, alloparenting always evolved last but two routes existed. The main route implied a primary transition to delayed dispersal followed by reproductive suppression while the reverse occurred in the alternative route (Figure 7b). Thus, if one transition from cooperative breeding to communal breeding occurred, no transition from communal breeding to cooperative breeding showed up ($q_{DD, A \rightarrow DD, RS, A} = 0$, Figure 7b).

Transition rates towards a second trait when one was already present were higher than those from the solitary state to this same trait, and this whether the trait already present was delayed dispersal ($q'_{DD \rightarrow DD,RS} = 19.9 > q'_{0 \rightarrow RS}$; $q'_{DD \rightarrow DD,A} = 76.6 > q'_{0 \rightarrow A} = 0$, Figure 7b) or reproductive suppression ($q'_{RS \rightarrow DD,RS} = 100 > q'_{0 \rightarrow DD} = 4.6$, Figure 7b). The joint presence of delayed dispersal and reproductive suppression further enhanced the emergence of alloparenting ($q'_{DD,RS \rightarrow DD,RS,A} = 48.4 > q'_{DD \rightarrow DD,A} = 36.6$, Figure 7b). Delayed dispersal and reproductive suppression loss were also unlikely when the other traits were present, showing that the three traits not only facilitated the occurrence of one another but also mutually stabilized each other (Figure 7b). Delayed dispersal was stabilized by alloparenting ($q'_{DD \rightarrow 0} = 8.4 > q'_{DD,A \rightarrow A} = 3.1$, Figure 7b) and by the joint presence of reproductive suppression and alloparenting ($q'_{DD,RS,A \rightarrow RS,A} = 0.00$, Figure 7b). Reproductive suppression was stabilized by delayed dispersal ($q'_{RS \rightarrow 0} = 100 > q'_{DD,RS \rightarrow DD} = 40.1$, Figure 7b), and by the joint presence of delayed dispersal and alloparenting ($q'_{DD,RS,A \rightarrow DD,A} = 4.1 < q'_{DD,RS \rightarrow DD} = 40.1$, Figure 7b). Alloparenting was also stabilized by reproductive suppression ($q'_{DD,RS,A \rightarrow DD,RS} = 6.7 < q'_{DD,A \rightarrow DD} = 33.4$, Figure 7b). These stabilizing effects do not show up when trait combination are randomized, which suggesting indicates a strong phylogenetic signal and a coevolution independent on correlation between traits.

Finally, being solitary was highly stable, as indicated by the lower transition rates to other states from this state ($q_{00 \rightarrow 01} < q_{01 \rightarrow 00}$ and $q_{00 \rightarrow 10} < q_{10 \rightarrow 00}$ for all three pair of traits, Figure 7a; $q'_{0 \rightarrow DD} = 2.6 < q'_{DD \rightarrow 0} = 8.4$; $q'_{0 \rightarrow RS} = 0.6 < q'_{RS \rightarrow 0} = 100$; $q_{0 \rightarrow A} = 0$, Figure 7b). Communal and cooperative breeding states were stable as well ($q'_{DD \rightarrow DD,A} = 36.6 > q'_{DD,A \rightarrow DD} = 33.4$; $q'_{A \rightarrow DD,A} = 98.2 > q'_{DD,A \rightarrow A} = 3.1$; $q'_{DD,RS \rightarrow DD,RS,A} = 48.4 > q'_{DD,RS,A \rightarrow DD,RS} = 6.7$, Figure 7b). In contrast, delayed dispersal, reproductive suppression and alloparenting were unstable until combined (Figure 7b). The instability of intermediate configurations resulted in fast transitions to communal and cooperative breeding, with intermediate configurations unlikely to have persisted over more than three successive nodes, such as in Canidae (Figure 6).

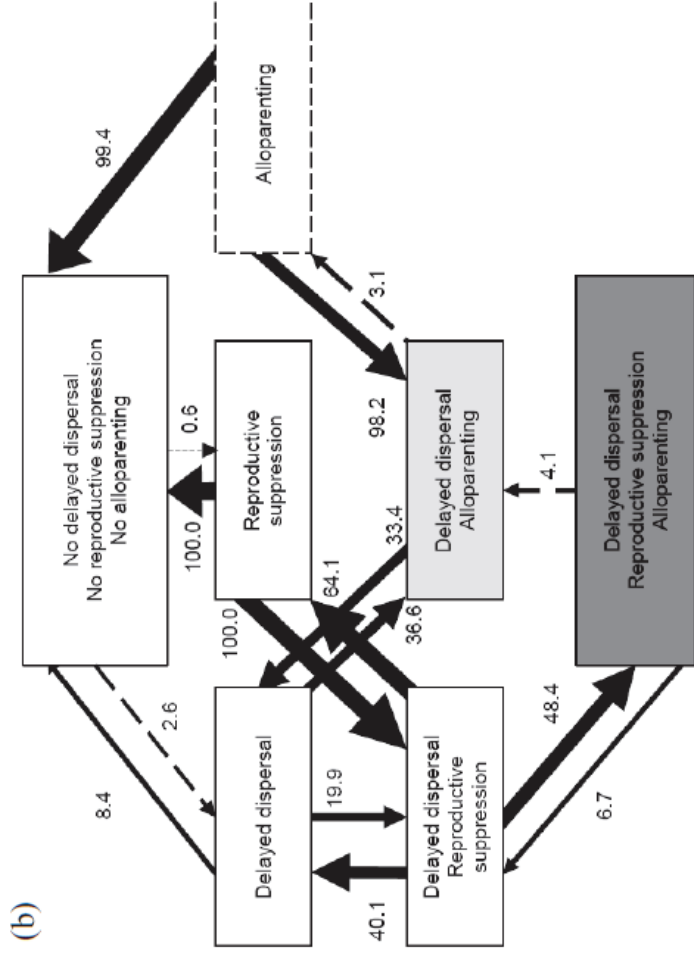
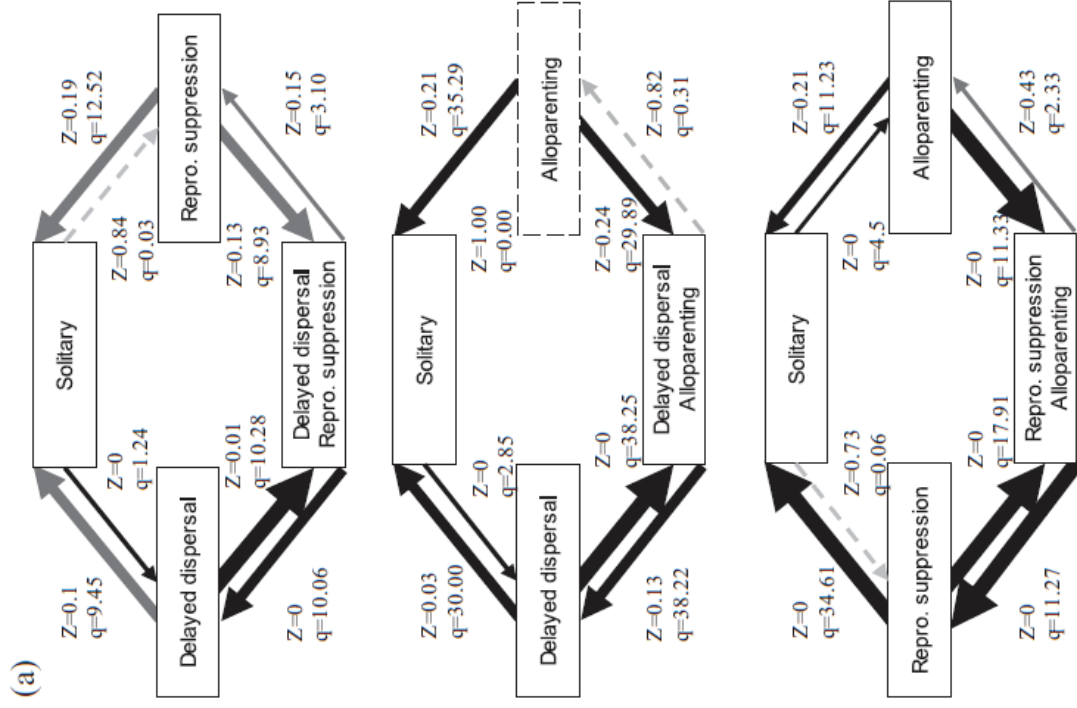


Figure 7: a) Evolutionary pathways for the most likely phylogenetic reconstructions under each dependent model of evolution of two traits following the Discrete method, with (from top to bottom) delayed dispersal and reproductive suppression; delayed dispersal and alloparenting; reproductive suppression and alloparenting. All the models were run using the same method and can thus be compared. The q values represent the mean of postconvergence transition rates, while Z-values correspond to the proportion of iterations assigned to zero, depicting the probability that a transition has not occurred. The thickness and darkness of the arrows were scaled to reflect the q and Z-values, respectively, with thicker arrows representing higher q values and darker arrows representing higher Z-values. The lowest q values are represented by dashed arrows. Transitions with Z-values higher than 0.9 are not represented because they are highly unlikely to occur. **b) Pathways under the correlated model of evolution among all three traits, with q0 values corresponding to the mean of the postconvergence transition rate and thicker arrows representing higher transition rates. Due to the extremely low ratio between transitions to alloparenting alone and transitions from alloparenting alone, this combination is extremely unlikely to actually occur and is thus represented in a dashed box. Given that they were based on two different methods, transition coefficients from panels a and b cannot be compared.**

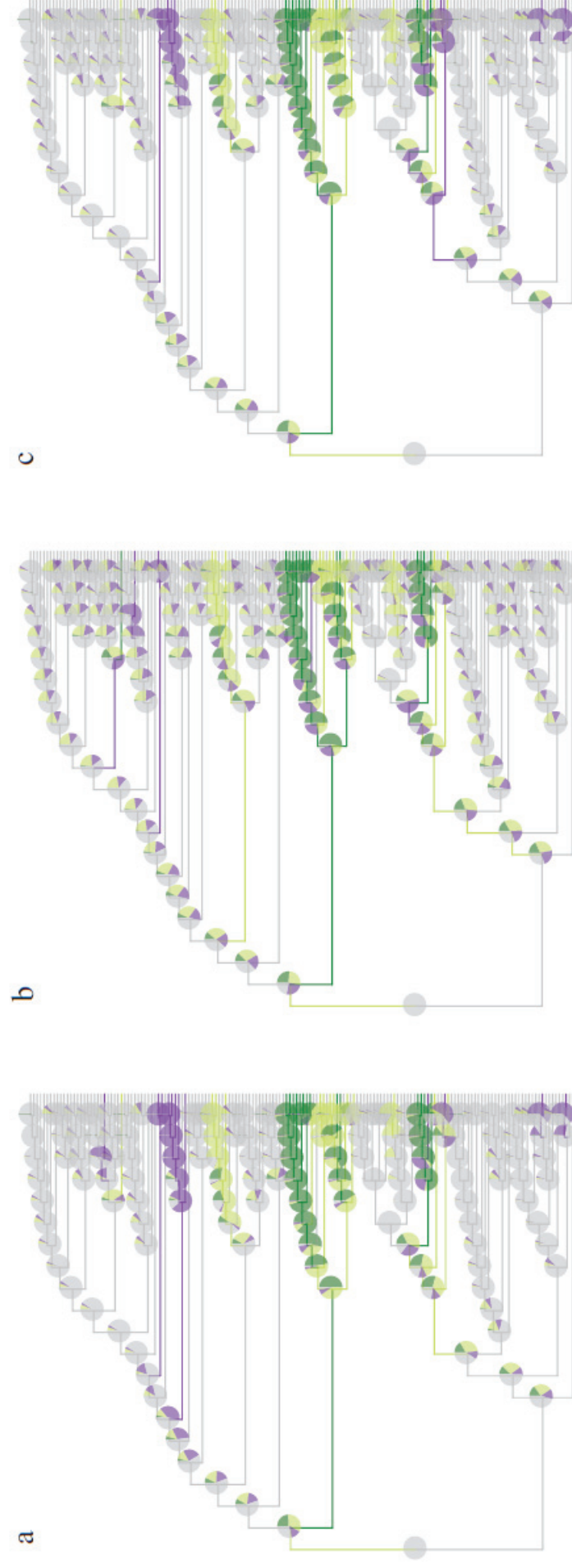


Figure 8: Carnivore phylogenies showing ancestral state reconstructions for monogamy and delayed dispersal (a), monogamy and reproductive suppression (b), and monogamy and alloparenting (c) under discrete Bayesian reconstruction. The ancestral non monogamous state lacking the trait of interest is displayed as light gray; monogamy alone as light green; delayed dispersal, reproductive suppression, or alloparenting alone as purple; and the combination of each of these traits and monogamy as dark green. Branches are colored according to the most probable combination of states. Pies represent the probability distribution of the combinations of traits at each node. The tree topology is the consensus tree obtained from the 10kTrees project posterior distribution. Branch lengths are drawn proportional to time.

Association between monogamy and traits related to communal and cooperative breeding

The timing of the evolution of monogamy relative to the three traits related to cooperative breeding varied according to branches. Monogamy preceded the occurrence of all three traits in Canidae but evolved after delayed dispersal in Herpestidae. A coevolution between monogamy and the three traits characterizing cooperative breeding was statistically supported (monogamy - delayed dispersal: dependent marginal likelihood = -107.19 vs. independent marginal likelihood = -109.02, BF = 3.66; monogamy – reproductive suppression: -83.35 vs. -112.81, BF = 56.93; monogamy - alloparenting: -104.70 vs. -107.63, BF = 3.87, Figure 3).

Monogamy could precede the evolution of any of the traits linked to cooperative breeding (monogamy vs. delayed dispersal: $Z_{0 \rightarrow M} = 0.01$; monogamy vs. reproductive suppression: $Z_{0 \rightarrow M} = 0.00$; monogamy vs. alloparenting: $Z_{0 \rightarrow M} = 0.02$, Figure 8a), and any of these traits could precede the evolution of monogamy (monogamy vs. delayed dispersal: $Z_{0 \rightarrow DD} = 0.00$; monogamy vs. reproductive suppression: $Z_{0 \rightarrow RS} = 0.01$; monogamy vs. alloparenting: $Z_{0 \rightarrow A} = 0.00$, Figure 8a). Furthermore, once a given trait has evolved, any other one could occur (Figure 8a). Nevertheless, monogamy was more likely to evolve first, as indicated by lower Z-values and higher q-values from the monogamous intermediate state compared to the monogamous one (delayed dispersal: $Z_{DD \rightarrow DD,M} = 0.27$, $Z_{M \rightarrow DD,M} = 0.04$; $q_{DD \rightarrow DD,M} = 0.02$, $q_{M \rightarrow DD,M} = 0.03$; reproductive suppression: $Z_{RS \rightarrow RS,M} = 0.11$, $Z_{M \rightarrow RS,M} = 0.05$, $q_{RS \rightarrow RS,M} = q_{M \rightarrow RS,M} = 0.08$; alloparenting: $Z_{A \rightarrow A,M} = 0.15$, $Z_{M \rightarrow A,M} = 0.01$, $q_{A \rightarrow A,M} = 0.04$, $q_{M \rightarrow A,M} = 0.05$, Figure 8a). It is noteworthy that the directionality of the coevolution between monogamy and reproductive suppression is uncertain in most branches, due to monogamy alone and reproductive suppression having equal or near-equal probabilities to occur in the ancestral nodes. When monogamy coexisted with another trait, the latter was more likely to be lost than monogamy, indicating that delayed dispersal, reproductive suppression and alloparenting had a strong stabilizing effect on monogamy, whereas the reverse effect was weaker (Delayed dispersal: $Z_{DD,M \rightarrow M} = 0.06 < Z_{DD,M \rightarrow DD} = 0.34$, $q_{DD,M \rightarrow M} = 0.05 > q_{DD,M \rightarrow DD} = 0.01$; Reproductive suppression: $Z_{RS,M \rightarrow M} = 0.01 < Z_{RS,M \rightarrow RS} = 0.64$,

$q_{RS,M \rightarrow M} = 0.08 > q_{RS,M \rightarrow RS} = 0.002$; Alloparenting: $Z_{A,M \rightarrow M} = 0.01 < Z_{A,M \rightarrow A} = 0.36$, $q_{A,M \rightarrow M} = 0.06 > q_{A,M \rightarrow A} = 0.01$, Figure 8a).

Robustness of coevolution analyses

We found that 96% of ancestral reconstructions conducted on datasets simulated using the transition rates from our results provided a vast support for our pathway to cooperative breeding (delayed dispersal, then reproductive suppression, and finally alloparenting). Therefore, our model accurately captures the directionality of coevolutionary relationships. Furthermore, only 1.2% of coevolution analyses conducted on simulated datasets where traits evolved independently displayed a signal for coevolution of pair of traits (Pagel coevolution test $P < 0.05$), which strongly suggests that our model is highly unlikely to falsely detect coevolution among traits that evolved independently and that observed coevolution does not result from type I error. For more information on these reconstructions, see Appendix for this chapter.

Discussion

Our findings indicate that delaying dispersal has been a prerequisite to alloparenting, and thus the first step in both pathways to cooperative breeding and communal breeding, in Carnivores. In such species, the evolution towards cooperative or communal breeding follows separate routes and communal breeding is not a step in the evolutionary route towards cooperative breeding. Another important finding was that delayed dispersal and reproductive suppression facilitated and stabilized each other's evolution. Alloparenting further stabilizes initially unstable delayed dispersal and reproductive suppression, and thus plays a key role in the stability of social structure in Carnivores. The mutual facilitation and stabilization of the constitutive traits of cooperative breeding leads this social system to be highly stable, contrary to intermediate combinations lacking cooperation. Monogamy shows association with traits related to cooperative breeding, but the directionality of the coevolution between monogamy and these traits is variable according to branches. Although delayed dispersal,

reproductive suppression and alloparenting stabilize monogamy, our study provides no support for the reverse effect.

Our study was limited by the fact that we performed pairwise analyses of the ancestral reconstructions because it was not possible to analyze all four traits simultaneously. Although there are currently no tools for ancestral reconstructions of four binary traits, this could have been done in theory by encoding all possible combinations of the four traits as states of a single multistate variable. However, this would have led to 16 theoretical possible combinations of four binary traits, with only 7 of them effectively present in the dataset and 3 more potentially present depending on the state of traits for which no data are available. Our dataset including 163 species does not allow for a robust analysis of a trait that displays at least 7 states. Furthermore, some of the combinations occurred only rarely, such as the combination involving delayed dispersal, reproductive suppression and monogamy, which only occurred once. This would have further lowered the power of a four-trait analysis. By contrast, separate trait-based analyses do not face this problem because each trait is frequent enough to allow for a robust analysis.

Our findings confirm that the formation of groups by delayed dispersal was the first key step in the evolution of cooperation. This is consistent with previous theoretical and empirical findings highlighting the crucial role of delayed dispersal that leads to higher kinship and increased group size, both prerequisites for the evolution of cooperation (Ekman et al., 2001; Emlen, 1994). Delayed dispersal is expected to result from the balance between benefits of philopatry and dispersal costs. In carnivores, such costs are high given that dispersers are especially likely to incur fatal attacks from residents (Fritts and Mech 1981; Packer and Pusey 1982; Messier 1985; Boydston et al. 2001). The stronger evidence for such directionality in Canidae than in Herpestidae may be explained by high benefits of philopatry stemming from their diet. Indeed, they mostly feed on large prey such as ungulates. Solitary hunting success is low and the number of individuals involved in the hunting increases hunting success, prey mass and the probability of multiple kills (Fanshawe and Fitzgibbon

1993; Creel and Creel 1995; MacNulty et al. 2014). Such high benefits of cooperative hunting leads to high benefits of group living, especially in species taking multiple prey (Packer and Rutan 1988; Courchamp and Macdonald 2001). However, the present work focus on carnivores, in which delayed dispersal and reproductive suppression are mostly observed in group-living species. In taxa in which delayed dispersal is not crucial to the transition to group-living, such as birds, the coevolution between delayed dispersal and alloparenting or reproductive suppression may not be as strong (Riehl, 2013). Further research focusing on other taxa with different group formation processes should therefore be carried out in order to investigate possible differences in the patterns of coevolution between constitutive traits of cooperative breeding.

Once species delay dispersal, two separate pathways can respectively lead to cooperative or communal breeding. Communal breeding is not a step in the pathway to cooperative breeding, where reproductive suppression clearly evolves before alloparenting. This challenges the widespread view of a systematic association between reproductive suppression and alloparenting, but is consistent with the hypothesis that reproductive suppression evolves in environments that cannot sustain the offspring of multiple individuals. This results in the presence of non-breeding individuals, for which providing alloparental care while waiting for a mating opportunity may be the best strategy. In further agreement with this hypothesis, extremely low transition rates between cooperative breeding and communal breeding are observed, with a sole transition from cooperative breeding towards communal breeding in a recent ancestor of *Mungos mungo*. Thus, the transition to communal breeding observed in *Mungos mungo* might be due to a release of environmental pressures, allowing for a greater reproductive share.

The drastic changes in social structure and mating system involved in transitions between communal and cooperative breeders may provide another explanation for their rarity. Indeed, in addition to cooperative breeding involving reproductive suppression, it is also characterized by monogamy and strong social hierarchy, as contrasted with communal breeding. It is therefore likely

that different arrays of traits and conditions are determinant for the evolution of a species toward either of the two systems. Traits that have been shown to enhance hierarchical social structure and reproductive competition, such as dominant sex typically showing more skew (Engh et al. 2002), strong ecological constraints impacting future mating prospects (Hager 2009), or biased sex ratios (Székely et al. 2014), may lead them toward cooperative breeding rather than communal breeding. Further work will therefore be required to understand the impact of life history and environmental conditions on the evolution of communal and cooperative breeding.

Unlike solitary, communal and cooperative breeding, intermediate configurations are rare and unstable. This pattern results from the strong mutual enhancement of traits involved in cooperative breeding. It is probable that the facilitation of alloparenting and reproductive suppression is strongly favored by especially high relatedness between group members. Indeed, high kinship increases fitness benefits accrued to helpers through parental care; and the lack of unrelated potential partners plays a key role in reproductive suppression in several carnivore species (Greenwood 1980; Packer and Pusey 1987). One can suppose that the spread of delayed dispersal to both sexes in most group-living carnivore species results in high kinship, compared to species where delayed dispersal is limited to one sex. This may explain why primate species where females are philopatric but do not display reproductive suppression or cooperation are fairly common, in contrast to carnivores (Sterck et al. 1997; Kappeler and Schaik 2002). Indeed, in these species, strong sex-biased dispersal leads to the widespread presence of unrelated individuals in the group, and thus to more mating opportunities.

The intermediate configurations where non-breeding individuals are present but do not cooperate in rearing young are extremely rare in carnivores, in contrast to rodents and primates. A possible explanation may be that offspring get especially high benefits from helpers in carnivores due to the type of help provided. Indeed, cooperatively breeding carnivores typically provide the young with food (Rood 1978; Moehlman and Hofer 1997; Mech et al. 1999; Clutton-Brock et al. 2001b). Inversely, alloparental care seldom takes the form of allofeeding in other mammalian taxa, but mostly

of allocarrying and guarding in cooperatively breeding primates (Tardif et al. 1992; Silk 2005; Hall 2016) and of thermoregulating the offspring in rodents (Hayes 2000; Wolff and Sherman 2008). Such differences in alloparental care may be explained by the difficulty to obtain food in Carnivores. In contrast to allocarrying and thermoregulating, the benefits of allofeeding may always be sufficient for it to evolve once related non-breeding adults are present in the group.

One unanticipated finding was that the evolution of monogamy did not always precede all traits related to cooperative breeding, contrasting the widespread view that the evolution of cooperative breeding in mammals is restricted to monogamous species and that monogamy is derived exclusively from solitary social systems (Lukas and Clutton-Brock 2012a, 2013). All three traits, including alloparenting, have evolved in both monogamous and non-monogamous species. However, results obtained when applying Lukas and Clutton-Brock's protocol on our set of species, with cooperative breeding treated as a trait rather than a combination of three traits, are consistent with their conclusions (Figure 9). This suggests that our unexpected result does not result from a specificity of carnivores. It is instead caused by the fact that we consider cooperative breeding as a combination of traits, contrary to previous research. Indeed, this methodology allows us to detect that although monogamy is never the last trait to evolve, it is not automatically the first either, and therefore does not always precede the onset of evolution towards cooperative breeding. It can thus be suggested that, rather than being a preliminary condition for the evolution of cooperative breeding, monogamy is a step in the pathway to cooperative breeding, along with the other involved traits. A possible explanation may lie in the ecologically driven covariance hypothesis, where the evolution of monogamy and cooperative breeding share an array of common causes thought to be involved in high dispersal costs, limited reproductive output and dominance systems (Dillard and Westneat, 2016). Such causes may include reliance on scarce food resources, environmental harshness (Emlen and Oring 1977; Barlow 1988), limited nest sites and predation pressure (Dillard and Westneat 2016; Groenewoud et al. 2016). This corroborates the increasing number of studies highlighting the

importance of a holistic approach to studying the correlated evolution of cooperation and mating systems (Kramer and Russell 2014; Dillard and Westneat 2016).

Acknowledgements

We thank Nicolas Lartillot for his guidance in conducting Bayesian analyses. We also thank Emmanuel Paradis for his helpful insights regarding the evaluation of the robustness of detected coevolutionary relationships.

Appendix

Assessment of the Robustness of the Detected Coevolutionary Relationships

Methods

Assessment of the Robustness of Coevolutionary Patterns in Simulated Data Sets

First, in order to assess the robustness of our model in deciphering the existence of directional coevolutionary relationships among traits as those presented in our results, we simulated data with transition rates from the matrix reconstructed from the observed data (Figure 7). We simulated data sets using a discrete Markov model of coevolution implemented into the function `rTraitMult` in the `ape` package (Paradis 2014). In order to check whether our model was able to capture the directional evolution observed in our results, we then conducted ancestral reconstructions on these simulated data sets using `corDISC`, according to the same procedure used on the observed data (Figure 7). We then calculated the transition rate for each evolutionary pathway by multiplying the estimated transition rate for each step and recorded the preferred evolutionary pathway. We classified the reconstruction as unidirectional when a single pathway to cooperative breeding was identified (100% of the transition rates led to a single pathway), as quasi-unidirectional when several pathways to cooperative breeding were possible but 80% of the transition rates led to a given pathway, and as multidirectional otherwise.

Second, in order to check that the detected coevolution among our traits did not result from a type I error stemming from the rarity of our traits, we simulated 1,000 phenotypic data sets with no coevolutionary relationships among the three traits of interest using the function `rTraitDisc` in the `ape` package (Paradis et al. 2004; Paradis 2012). We simulated the evolution of each trait independently over the consensus tree and set the equilibrium trait frequencies to those of our empirical dataset. In these trees, we subsequently tested for a coevolution among all three possible pairs of traits according to the procedure used for the empirical data set. We used the Pagel coevolution test and calculated the Bayes factor (BF) between the independent and dependent models. We expected no support for coevolution to occur in these models because the evolution of each trait was simulated independently.

Results

We found that 73% of the reconstructions that used the transition matrix from the observed data were unidirectional and 23% were quasi-unidirectional, whereas only 4% of reconstructions were multidirectional (Figure 3). Moreover, the pathway to cooperative breeding we reported (i.e., delayed dispersal, then reproductive suppression, and finally alloparenting) was satisfactorily captured by the model. It was indeed the preferred evolutionary pathway in all simulations but one. Therefore, our model accurately assessed the directionality of simulated data. In 99% of simulated data sets with independent evolution, there was indeed no detectable support for coevolution, while the signal for coevolution was dramatically stronger in our empirical data set (Figure 4). Only 14 of 1,000 data sets returned a BF greater than three in favor of the dependent model. Therefore, our model does not falsely detect coevolution among traits that evolved independently, even when these traits are rare.

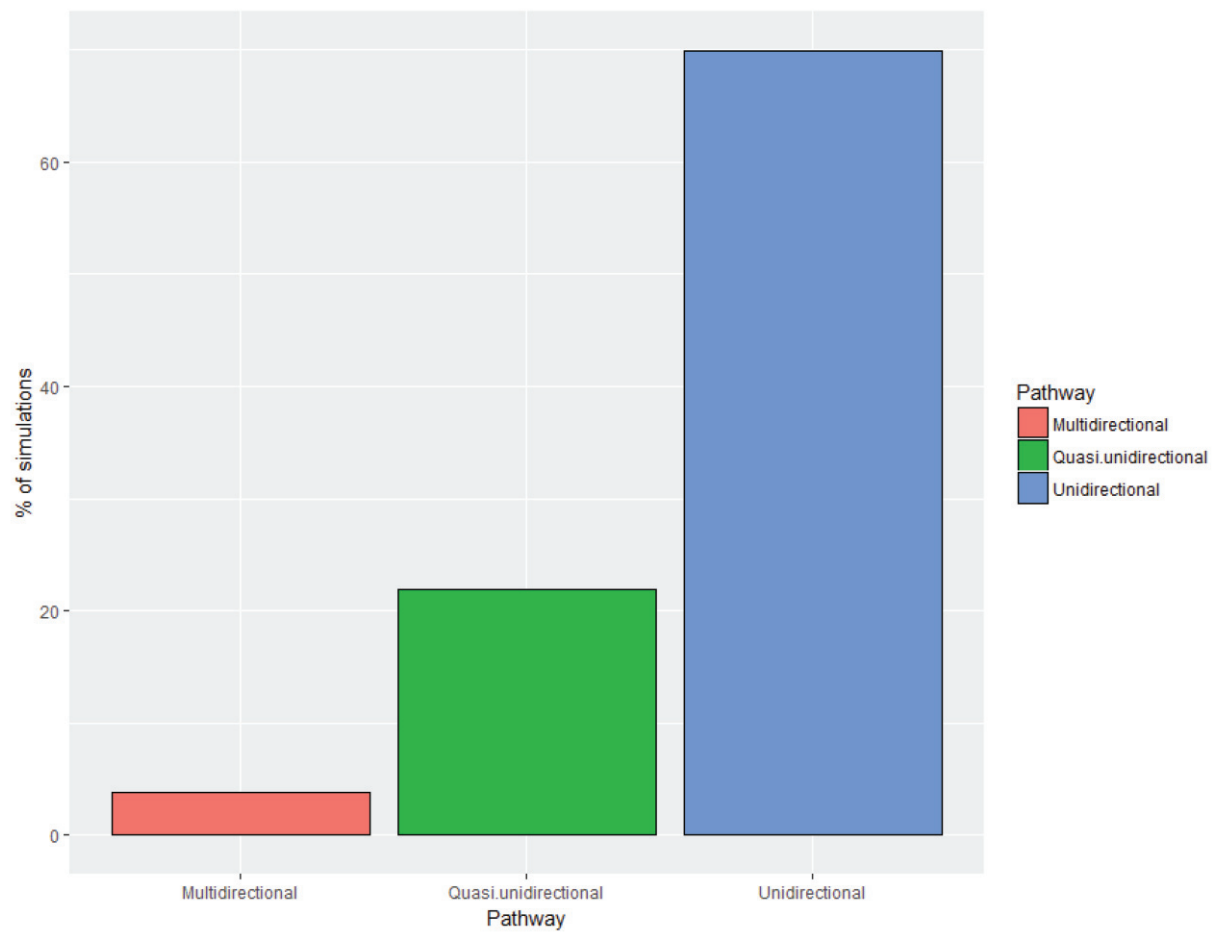


Figure 3 (cf Material and Methods): Percentage of multidirectional, quasi-unidirectional, and unidirectional reconstructions obtained from data simulated using the transition matrix reconstructed from the observed data.

Multidirectional, quasi-unidirectional, and unidirectional reconstructions are displayed in red, green, and blue, respectively.

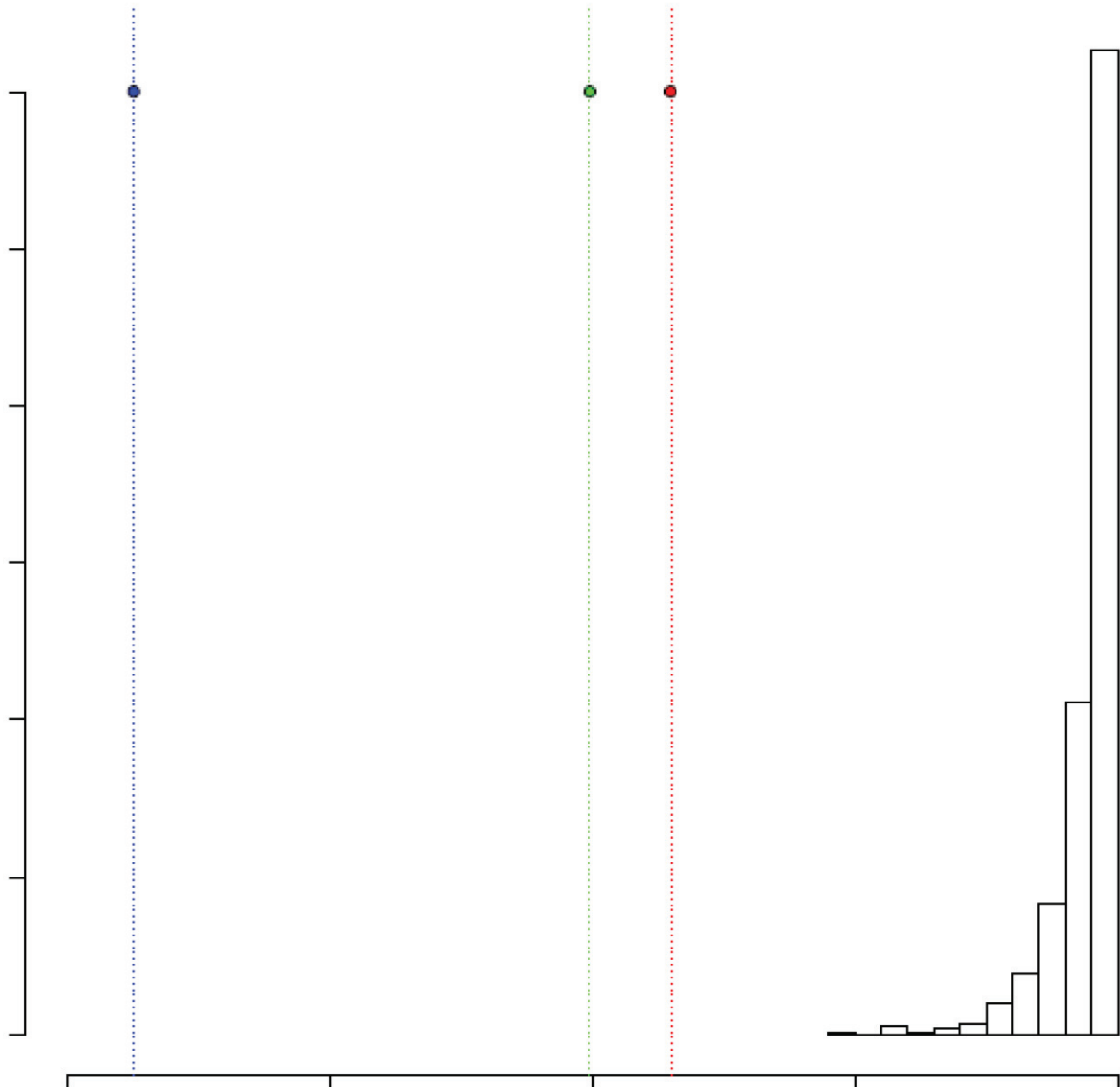


Figure 4 (cf Material and Methods): Histogram of P values of the Pagel coevolution test for pairs of traits obtained from the 1,000 simulated data sets.

Twelve simulated data sets produce a P value just under .05. For the empirical data set, P values are shown in blue (delayed dispersal x alloparenting, $P = 7.4 \times 10^{-9}$), green (reproductive suppression x alloparenting, $p = 7.4 \times 10^{-5}$), and red (delayed dispersal x reproductive suppression, $P = 2.0 \times 10^{-4}$).

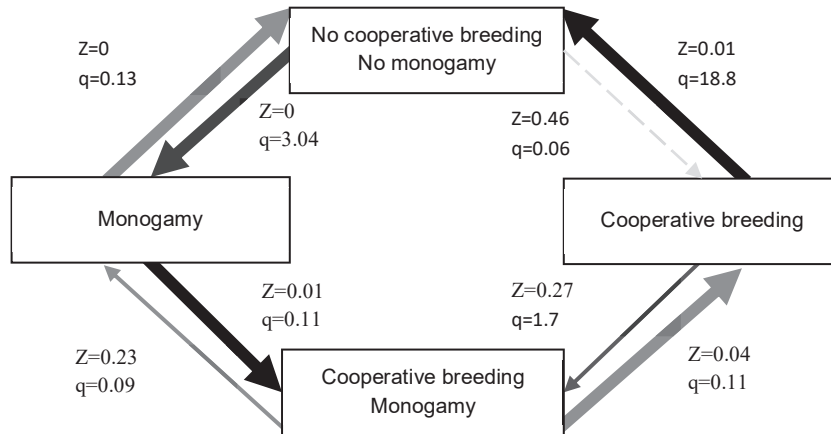


Figure 9 - Transition rates for the most likely phylogenetic reconstruction in a dependent, sequential evolution model between monogamy and cooperative breeding.

Transition rates for the most likely phylogenetic reconstruction in a dependent, sequential evolution model between monogamy and cooperative breeding. Cooperative breeding was here treated as a trait rather than a combination of traits. We used the Discrete method of BayesTraits. Here, q values represent the mean of postconvergence transition rates, and Z -values correspond to the proportion of iterations assigned to zero, depicting the probability that a transition has not occurred. The thickness and darkness of the arrows were scaled to reflect the q and Z -values, respectively, with thicker arrows representing higher q values and darker arrows representing higher Z -values. Transitions with Z -values higher than 0.9 are not represented because they are highly unlikely to occur.

		Final state							
		-,-,-	DD,-,-	-,RS,-	-, -,A	DD,RS	DD,-,A	-,RS,A	DD,RS
Initial state	-,-,-		6(9)	0	0	1(2)	0(2)	0	0
	DD,-,-	0		0	0	1(2)	2	0	0 (1)
	-,RS,-								
	-, -,A								
	DD,RS,-	0	1	0	0		0	0	1
	DD,-,A	0	1	0	0	0		0	0
	-,RS,A								
	DD,RS,A	0	0	0	0	0	1	0	

Figure 10 - Transitions displayed in the carnivore phylogenetic tree.

We counted the number of transitions between states in our reconstructed phylogenetic tree. We marked transitions as uncertain when the ratio of the two most probable states at a node was less than two. The number of certain transitions and the sum of certain and uncertain transitions are displayed outside and inside parentheses, respectively. Multiple transitions, corresponding to multiple traits changing within the same internal branch, and single-trait transitions are displayed in pink and blue, respectively.

		Stabilized trait		
		DD	RS	A
Stabilizing trait	DD		0	0
	RS	75		7
	A	72	4	
	DD+RS			30
	DD+A		33	
	RS+A	100		
	DD+RS+A			

Figure 11 - Proportions of stabilizing effects in randomized analyses

To investigate whether the observed coevolutionary patterns resulted from coevolution or correlation between traits, we randomized the combinations of traits of our data set according to the phylogeny in 100 simulated data sets. For each simulation, species were randomly reassigned a combination of traits, while respecting the total number of occurrences for each combination. Here, DD, RS, and A stand for delayed dispersal, reproductive suppression, and alloparenting, respectively. A trait or combination A is considered to have a stabilizing effect on a trait B when the coefficient of the transition corresponding to the loss of the trait B is smaller when the trait A is present. For each combination, the percentage of occurrences of randomized data that showed a stabilizing effect is displayed. Combinations where the empirical results show a stabilizing effect or not are displayed in blue and yellow, respectively. In addition to the results described in the table below, coevolution was detected between all pairs of traits in all randomized data sets (Bayesfactor > 2), and delayed dispersal was always detected as the first trait to evolve. However, in contrast to our results, transitions from communal breeding to cooperative breeding were detected and assigned with the highest transition coefficient in 96 out of 100 randomizations.

Table 4 - Data used in phylogenetic reconstructions

Species	DD	RS	AP	M	Reference
<i>Mustela lutreola</i>	0	0	0	0	Michaux et al., 2005; Youngman, 1990
<i>Mustela nigripes</i>	0	0	0	0	Hillman, 1968; Hillman and Clark, 1980
<i>Mustela putorius</i>	0	0	0	0	Blandford, 1987; Lodé, 2001, 2008
<i>Mustela erminea</i>	0	0	0	0	Erlinge, 1977; Erlinge, 1977; King, 1983
<i>Mustela frenata</i>	0	0	0	0	Sheffield and Thomas, 1997
<i>Mustela nivalis</i>	0	0	0	0	Sheffield and King, 1994
<i>Martes americana</i>	0	-	0	0	Clark et al., 1987; Hunter and Caro, 2008
<i>Martes zibellina</i>	0	0	0	0	Monakhov, 2011
<i>Martes martes</i>	0	0	0	0	Newman et al., 2011
<i>Martes foina</i>	0	0	0	0	Newman et al., 2011
<i>Martes flavigula</i>	0	0	0	0	Newman et al., 2011
<i>Martes pennanti</i>	0	0	0	0	Hunter and Caro, 2008; Powell, 1981
<i>Gulo gulo</i>	0	0	0	0	Pasitschniak-Arts and Larivière, 1995; Vangen et al., 2001
<i>Eira barbara</i>	0	0	0	0	Presley, 2000
<i>Galictis cuja</i>	0	0	0	0	Hunter and Caro, 2008; Yensen and Tarifa, 2003a
<i>Galictis vittata</i>	0	0	0	0	Yensen and Tarifa, 2003b
<i>Ictonyx striatus</i>	0	0	0	0	Larivière, 2002a
<i>Vormela peregusna</i>	0	0	0	0	Gorsuch and Larivière, 2005
<i>Poecilogale albinucha</i>	0	0	0	0	Larivière, 2001a
<i>Mellivora capensis</i>	0	0	0	0	Vanderhaar and Hwang, 2003
<i>Meles meles</i>	1	1	1	0	Newman et al., 2011; Woodroffe, 1993; Woodroffe et al., 1995; Woodroffe and Macdonald, 2000

<i>Lontra felina</i>	0	0	0	0	Larivière, 1998; Medina-Vogel et al., 2007
<i>Lontra provocax</i>	0	0	0	0	Hunter and Caro, 2008; Larivière, 1999a
<i>Lontra longicaudis</i>	0	0	0	0	Kruuk, 2006; Larivière, 1999b
<i>Lontra canadensis</i>	1	0	-	0	Kruuk, 2006; Larivière and Walton, 1998
<i>Lutra lutra</i>	0	0	0	0	Kruuk, 2006
<i>Aonyx capensis</i>	0	0	0	0	Kruuk, 2006; Larivière, 2001b
<i>Pteronura brasiliensis</i>	1	1	0	1	Carter and Rosas, 1997; Kruuk, 2006
<i>Enhydra lutris</i>	0	0	0	0	Estes, 1980; Garshelis et al., 1984; Kruuk, 2006
<i>Mephitis macroura</i>	0	0	0	0	Hwang and Larivière, 2001
<i>Mephitis mephitis</i>	0	0	0	0	Powell, 1979; Sandell, 1989; Wade-Smith and Verts, 1982
<i>Spilogale putorius</i>	-	0	0	0	Kinlaw, 1995; Lukas and Clutton-Brock, 2012
<i>Taxidea taxus</i>	0	0	0	0	Lindzey, 1994; Long, 1973
<i>Procyon lotor</i>	-	0	0	0	Fritzell, 1978; Gehr and Fritzell, 1998; Lotze and Anderson, 1979
<i>Nasua narica</i>	1	0	1	0	Gompper, 1995, 1996; Gompper et al., 1997; Russell, 1983
<i>Nasua nasua</i>	1	0	0	0	Gompper and Decker, 1998; Hirsch, 2007; Hirsch and Maldonado, 2011
<i>Potos flavus</i>	1	0	0	0	Kays and Gittleman, 1995, 2001
<i>Ailurus fulgens</i>	0	0	0	0	Roberts and Gittleman, 1984
<i>Odobenus rosmarus</i>	0	0	0	0	Fay, 1982, 1985
<i>Arctocephalus australis</i>	0	0	-	0	Cappozzo, 2002; Franco-Trecu et al., 2010, p.; PAVÉS and SCHLATTER, 2008; Stirling, 1983
<i>Arctocephalus forsteri</i>	0	0	0	0	Stirling, 1971, 1983
<i>Arctocephalus townsendi</i>	0	0	0	0	Belcher and Lee Jr, 2002
<i>Arctocephalus gazella</i>	-	0	-	0	Gemmell, 2003; Hoffman and Amos, 2005; Hoffman and Forcada, 2012
<i>Callorhinus ursinus</i>	0	0	0	0	Bartholomew and Hoel, 1953; Insley et al., 2003
<i>Halichoerus grypus</i>	0	0	0	1	Boness et al., 1995; Boness and James, 1979; McCann, 1982; Pomeroy et al., 1994

<i>Cystophora cristata</i>	0	0	0	1	Perrin et al., 2009; Stirling, 1983
<i>Erignathus barbatus</i>	0	0	0	0	Perrin et al., 2009; Stirling, 1983
<i>Hydrurga leptonyx</i>	0	0	0	0	Gjertz et al., 2000; Perrin et al., 2009; Stirling, 1983
<i>Mirounga leonina</i>	0	0	0	0	Laws, 1956; McCann et al., 1989; Perrin et al., 2009
<i>Ursus arctos</i>	0	0	0	0	Gittleman, 1984; Pasitschniak-Arts, 1993
<i>Ursus maritimus</i>	0	0	0	0	Gittleman, 1984; Ramsay and Stirling, 1986; Stirling, 2009
<i>Ursus thibetanus</i>	0	0	0	0	Gilbert, 1999; Gittleman, 1984
<i>Melursus ursinus</i>	0	0	0	0	Gittleman, 1984, 1994; Laurie and Seidensticker, 1977
<i>Ursus americanus</i>	0	0	0	0	Gilbert, 1999; Gittleman, 1984; Larivière, 2001c
<i>Ailuropoda melanoleuca</i>	0	0	0	0	Gittleman, 1984
<i>Canis lupus</i>	1	1	1	1	Derix et al., 1993; Harrington et al., 1983; Mech et al., 1999; Moehlman, 1986; Moehlman and Hofer, 1997
<i>Canis rufus</i>	1	1	1	1	Sparkman et al., 2010, 2011, 2012
<i>Canis latrans</i>	1	1	1	1	Messier and Barrette, 1982; Moehlman and Hofer, 1997
<i>Canis simensis</i>	1	1	1	1	Moehlman and Hofer, 1997, 1997; Sillero-Zubiri et al., 1996; Sillero-Zubiri and Gottelli, 1994
<i>Canis adustus</i>	-	0	-	0	Kingdon, 1971; Loveridge and Macdonald, 2001; Rautenbach and Nel, 1978; Sillero-Zubiri and Macdonald, 2004
<i>Canis aureus</i>	1	1	1	1	Bekoff et al., 1984; Macdonald, 1979; Moehlman and Hofer, 1997; Sillero-Zubiri and Macdonald, 2004
<i>Canis mesomelas</i>	1	1	1	1	Ferguson et al., 1983; Loveridge and Macdonald, 2001; Moehlman, 1979; Sillero-Zubiri and Macdonald, 2004
<i>Chrysocyon brachyurus</i>	0	0	0	0	Dietz, 1984a, 1984b, 1985; Kleiman, 1972
<i>Cuon alpinus</i>	1	1	1	1	Cohen, 1978; Johnsingh, 1982; Macdonald and Moehlman, 1982; Moehlman and Hofer, 1997; Sillero-Zubiri and Macdonald, 2004
<i>Lycaon pictus</i>	1	1	1	1	Courchamp and Macdonald, 2001; de Villiers et al., 2003; Frame et al., 1979; Gorman et al., 1997; Malcolm and Marten, 1982; McNUTT, 1996; Sillero-Zubiri and Macdonald, 2004

Nyctereutes procyonoides	0	0	0	1	Sillero-Zubiri and Macdonald, 2004
Vulpes corsac	-	0	0	1	Clark et al., 2009
Vulpes vulpes	1	1	1	1	Iossa et al., 2008; Moehlman and Hofer, 1997; Sillero-Zubiri and Macdonald, 2004; Soulsbury et al., 2008
Vulpes cana	1	1	0	1	Geffen et al., 1992; Geffen and MacDonald, 1992; Sillero-Zubiri and Macdonald, 2004
Urocyon cinereoargenteus	-	0	0	1	Gittleman, 1984; Sillero-Zubiri and Macdonald, 2004
Urocyon littoralis	1	0	0	0	Roemer et al., 2001; Sillero-Zubiri and Macdonald, 2004
Otocyon megalotis	1	0	0	0	Sillero-Zubiri and Macdonald, 2004
Panthera leo	1	0	1	0	Haas et al., 2005; Mosser and Packer, 2009; Rudnai, 1973; Yamaguchi et al., 2004
Panthera pardus	0	0	0	0	Gittleman, 1984
Panthera tigris	0	0	0	0	Gittleman, 1984
Lynx lynx	0	0	0	0	Gittleman, 1984
Lynx rufus	0	0	0	0	Gittleman, 1984
Profelis aurata	0	0	0	0	Gittleman, 1984
Leopardus pardalis	0	0	0	0	Gittleman, 1984
Felis margarita	0	0	0	0	Cole and Wilson, 2015
Felis nigripes	0	0	0	0	Renard et al., 2015
Felis silvestris	0	0	0	0	Corbett, 1979; Natoli et al., 2000
Felis chaus	0	0	0	0	Sunquist and Sunquist, 2017
Caracal caracal	0	0	0	0	Gittleman, 1984
Leptailurus serval	0	0	0	0	Gittleman, 1984
Herpailurus yagouaroundi	0	0	0	0	de Oliveira, 1998; Sunquist and Sunquist, 2017
Puma concolor	0	0	0	0	Gittleman, 1984
Acinonyx jubatus	0	0	0	0	Caro, 1994; Kelly et al., 1998; Krausman and Morales, 2005

<i>Crocuta crocuta</i>	1	0	-	0	Boydston et al., 2001; East et al., 1989; Frank, 1986a, 1986b; Holekamp et al., 1997; Knight et al., 1992
<i>Parahyaena brunnea</i>	1	0	1	0	Mills, 1982; D. Owens and Owens, 1979; Owens and Owens, 1996; D. D. Owens and Owens, 1979
<i>Proteles cristatus</i>	0	0	0	1	Gittleman, 1984
<i>Helogale hirtula</i>	1	1	1	1	Rood, 1986; Schneider and Kappeler, 2014
<i>Helogale parvula</i>	1	1	1	1	Creel et al., 1992; Creel and Waser, 1991; Jennions and Macdonald, 1994; Keane et al., 1994; Rood, 1986; Schneider and Kappeler, 2014
<i>Mungos mungo</i>	1	0	1	0	Cant et al., 2001; Cant, 2003; Gilchrist, 2006a, 2006b; Gilchrist and Russell, 2007
<i>Crossarchus obscurus</i>	1	1	-	1	Goldman, 1987; Schneider and Kappeler, 2014
<i>Suricata suricatta</i>	1	1	1	1	Clutton-Brock et al., 2001a, 2001b, 2004; Clutton-Brock and Manser, 2016; Kutsukake and Clutton-Brock, 2006; MacLeod et al., 2013
<i>Ichneumia albicauda</i>	1	0	0	0	Schneider and Kappeler, 2014
<i>Cynictis penicillata</i>	0	0	0	1	Veron et al., 2004
<i>Paracynictis selousi</i>	0	0	0	0	Veron et al., 2004
<i>Herpestes edwardsii</i>	0	0	0	0	Schneider and Kappeler, 2014; Veron et al., 2004
<i>Herpestes javanicus</i>	0	0	0	0	Schneider and Kappeler, 2014; Veron et al., 2004
<i>Herpestes urva</i>	0	0	0	0	Veron et al., 2004
<i>Herpestes ichneumon</i>	0	0	0	0	Schneider and Kappeler, 2014; Veron et al., 2004
<i>Herpestes smithii</i>	0	0	0	0	Gittleman, 1984
<i>Herpestes vitticollis</i>	0	0	0	0	Veron et al., 2004
<i>Galerella pulverulenta</i>	0	0	0	0	Veron et al., 2004
<i>Galerella sanguinea</i>	0	0	0	0	Veron et al., 2004
<i>Atilax paludinosus</i>	0	0	0	0	Gittleman, 1984
<i>Rhynchogale melleri</i>	0	0	0	0	Veron et al., 2004
<i>Galidia elegans</i>	0	0	0	1	Albignac, 1969
<i>Genetta genetta</i>	0	0	0	0	Bekoff et al., 1984

<i>Genetta tigrina</i>	0	0	0	0	Bekoff et al., 1984
<i>Viverra zibetha</i>	0	0	0	0	Bekoff et al., 1984
<i>Viverra zibetha</i>	0	0	0	0	Bekoff et al., 1984
<i>Viverricula indica</i>	0	0	0	0	Bekoff et al., 1984
<i>Civettictis civetta</i>	0	0	0	0	Gittleman, 1984
<i>Paguma larvata</i>	0	0	0	0	Gittleman, 1984
<i>Nandinia binotata</i>	0	0	0	0	Charles-Dominique, 1978
<i>Cryptoprocta ferox</i>	0	0	0	0	Hawkins and Racey, 2009; Köhncke and Leonhardt, 1986
<i>Bdeogale nigripes</i>	0	0	0	0	Veron et al., 2004
<i>Conepatus chinga</i>	0	0	0	0	Donadio et al., 2001
<i>Conepatus mesoleucus</i>	0	0	0	0	Dragoo and Sheffield, 2009
<i>Felis catus</i>	1	0	1	0	Bradshaw, 2016; Corbett, 1979; Devillard et al., 2003, 2009; Natoli and De Vito, 1991
<i>Genetta angolensis</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta bourloni</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta cristata</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta johnstoni</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta maculata</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta pardina</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta poensis</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta servalina</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta thierryi</i>	0	0	0	0	Bekoff et al., 1984
<i>Genetta victoriae</i>	0	0	0	0	Bekoff et al., 1984
<i>Herpestes auropunctatus</i>	0	0	0	0	Veron et al., 2004
<i>Herpestes brachyurus</i>	0	0	0	0	Veron et al., 2004

<i>Herpestes fuscus</i>	0	0	0	0	Veron et al., 2004
<i>Herpestes naso</i>	0	0	0	0	Veron et al., 2004
<i>Hydrictis maculicollis</i>	0	0	0	0	Kruuk, 2006; Larivière, 2002b
<i>Ictonyx libyca</i>	0	0	0	0	Hoath, 2009
<i>Leopardus tigrinus</i>	0	0	0	0	De Oliveira et al., 2008
<i>Lycalopex gymnocercus</i>	0	0	0	1	Lucherini and Luengos Vidal, 2008
<i>Lycalopex sechurae</i>	0	0	0	0	Cossíos, 2010
<i>Lycalopex vetulus</i>	0	0	0	1	Dalponete, 2009
<i>Martes melampus</i>	0	0	0	0	Powell, 1979
<i>Meles anakuma</i>	1	0	0	0	Cheeseman et al., 1988; da Silva et al., 1993; Kaneko et al., 2014; Kruuk, 1978; Mallinson et al., 1992; Newman et al., 2011; Revilla and Palomares, 2002
<i>Mustela africana</i>	0	0	0	0	Powell, 1979
<i>Mustela felipei</i>	0	0	0	0	Powell, 1979
<i>Mustela itatsi</i>	0	0	0	0	Powell, 1979
<i>Mustela kathiah</i>	0	0	0	0	Powell, 1979
<i>Mustela nudipes</i>	0	0	0	0	Powell, 1979
<i>Mustela strigidorsa</i>	0	0	0	0	Powell, 1979
<i>Nasuella meridensis</i>	1	-	-	0	Whiteside, 2009
<i>Nasuella olivacea</i>	1	0	1	0	Balaguera-Reina et al., 2009; Whiteside, 2009
<i>Neovison vison</i>	0	0	0	0	Kurta, 2017; Thom and Bagniewska, 2015; Zschille et al., 2012
<i>Ommatophoca rossii</i>	0	0	0	0	Seal, 2007; Thomas and Rogers, 2009
<i>Phocarcos hookeri</i>	0	0	0	0	Chilvers and Wilkinson, 2008; Marlow, 1975; Perrin et al., 2009; Wilkinson et al., 2000
<i>Pusa caspica</i>	0	0	0	1	Miyazaki, 2009; Wilson et al., 2017
<i>Pusa hispida</i>	0	0	0	0	Krafft et al., 2007

<i>Pusa sibirica</i>	0	0	0	0	Miyazaki, 2009
<i>Spilogale gracilis</i>	0	0	0	0	Verts et al., 2001
<i>Viverra megaspila</i>	0	0	0	0	Bekoff et al., 1984
<i>Vulpes ferrilata</i>	0	0	0	1	Clark Jr et al., 2008

Our data has been deposited in the Dryad Digital Repository
(<https://doi.org/10.5061/dryad.sxksn02z6>; Federico et al. 2019).

Table 5 - Phylogenetic signal in the traits of interest

	λ	log(L)	log(L ₀)	P
Delayed dispersal	0,89	-28,91	-62,62	2,18E-16
Reproductive suppression	1	8,29	-28,84	6,80E-18
Alloparenting	0,85	-22,31	-48,65	3,93E-13
Monogamy	0,69	-31,37	-68,5	6,82E-18

Note: Pagel's λ was calculated using phylosig in the Phytools package (Revell 2012). Here, log(L) and log(L₀) stand for the log likelihood of the models with the estimated λ and with the λ taken to be null, respectively, while P stands for the P value of the likelihood ratio test between these two models.

Chapter 2 – The coevolution of delayed dispersal and reproductive suppression in primates

Introduction

The evolution of reproductive systems, notably through sexual and kin selection, has a major importance in the evolution of behavioral evolution, population dynamics, and life history. For instance, due to their impact on sexual selection, reproductive systems are widely accepted to influence on the evolution of sexual dimorphism (Willson and Pianka 1963; Björklund 1990; Weckerly 1998; Dunn et al. 2001), especially due to the influence of intra-sexual competition (Clutton-Brock et al. 2006). However, characterizing reproductive systems can prove difficult due to the fact that they encompass both social systems and mating systems. Indeed, social systems are characterized by group composition and organization (Kappeler and Schaik 2002), while mating systems are characterized by how individuals pair to mate (Zveloff and Boyce 1980; Wilson et al. 2017). Focusing on only one of these two components of reproductive systems, several classifications have been proposed (*i.e* social system: Dunbar, 2013; Shultz et al., 2011; Wilson, 1971; *i.e* mating system: Emlen and Oring, 1977). For instance, Shultz et al. (2011) classified Primates into solitary, pair-living, uni-male and multi-male groups, whereas Eisenberg et al. (1972) classified them as aged-graded-male troops when no more than one male in the oldest age bracket is present and as multi-male troops, when several old males are present. Mating systems, on the other hand, are usually classified into four categories - monogamy, polygyny, polyandry and polygynandry - depending on whether individuals of a given sex reproduce with one or several individuals of the other sex (Emlen and Oring 1977; Greenwood 1980). Despite being classified separately, mating systems and social systems are widely thought to interact during the evolution of reproductive systems (see classifications taking into account both group composition and mating systems, *i.e* Clutton-Brock, 1989; Crook et al., 1976; Shuster and Wade, 2003) and previous

research has shown transitions between mating systems to be a key step in the evolution of reproductive systems (Cornwallis et al. 2010). For instance, social monogamy has been suggested to be required for the evolution of cooperative breeding in mammals (Lukas and Clutton-Brock 2012a) and eusociality in insects (Hughes et al. 2008).

So far, studies regarding the evolution of reproductive systems have focused either on social systems (Ebensperger 2001; Ward and Webster 2016; Port et al. 2017) or on mating systems (Emlen and Oring 1977; Edward and Chapman 2011; Lukas and Clutton-Brock 2013). Resource availability, in particular, strongly impacts both aspects of reproductive systems. For instance, resource shortage limits optimal group size (Caraco and Wolf 1975; Brown 1982; Hamilton 2000), and thus favors the restriction of reproduction to dominant individuals (Nichols et al. 2012). However, little attention has been paid to how the combination of two traits ultimately underlies reproductive system: Delayed dispersal and reproductive suppression. First, the composition of social groups is determined by dispersal processes, including natal dispersal, breeding dispersal, presence of one or several adults of each sex in social units is mainly explained by sex-specific delayed dispersal (Ekman et al. 2001a, 2004). Second, the exclusion of certain individuals in the group from reproduction through eviction (Gilchrist 2006a), delayed sexual maturation (Pettitt and Waterman 2011), infanticide (Gilchrist 2006b) or condition-dependent ovulation (Wasser and Barash 1983), known as reproductive suppression, ultimately define reproductive systems. A likely explanation for this process is that competition over resources and care between juveniles may reduce the breeding success of dominants (Hodge et al. 2008; Clutton-Brock et al. 2010; Cant et al. 2014), which may thus have interest in preventing subordinates from breeding. Depending on which individuals access reproduction, a group with several adult individuals of both sexes can eventually display scramble promiscuity if all females are receptive and males are unable to monopolize them, monogamy if a single pair of dominant individuals reproduces, or social polyandry if multiple males mate with the breeding female. Therefore, studying both delayed dispersal and reproductive suppression is crucial to understanding the composition of

social groups and which individuals among them breed, and thus shedding light on reproductive systems.

In addition to being underlied by similar processes, delayed dispersal and reproductive suppression are thought to coevolve. First, the increase in group size caused by delayed dispersal may limit further reproductive opportunities according to the carrying capacity of the species' environment, thus enhancing reproductive suppression (Creel and Macdonald 1995). Second, in species that cooperate or benefit from large group size, delayed dispersal incurs indirect fitness benefits, which may have implications for the evolution of reproductive suppression as well. Indeed, such benefits may mean that individuals do not need to be discouraged from dispersing, in which case dominants have no interest in yielding reproductive concessions to subordinates (Clutton-Brock 2016). However, few studies have extensively studied the coevolution of both processes.

Males and females often display conflicting interests regarding reproductive strategies, including partner choice and mating system (Parker 1979; Chapman et al. 2003; Eberhard and Cordero 2003). Previous research at the intraspecific level suggests a strong evolutionary influence of the conflict of interest between sexes on delayed dispersal and reproductive suppression (Shine et al. 2004). Sex differences in dispersal and reproductive patterns are expected to be linked at the interspecific level as well. For instance, in polygynous species where high maternal investment incurs higher inbreeding costs in females compared to males, females may disperse more and earlier as an inbreeding avoidance mechanism (Waser et al. 1986) but the opposite may occur if female are able to choose their mates, in which case their preference for immigrant males may lead to male-biased dispersal (Lehmann and Perrin 2003). Previous studies in mammals also suggested that male-biased dispersal was ancestral, and that female-biased dispersal mostly occurred in monogamous species (Dobson 1982; Mabry et al. 2013). Despite this, the coevolution of delayed dispersal and reproductive suppression between sexes - and thus the evolutionary pressure of sexual conflict on these traits - has not been extensively studied at the interspecific level yet.

The mammalian order of Primate displays a substantial diversity in social organization, ranging from solitary to pair-living species, uni-male and multi-male groups, with a large proportion of species living in mixed-sex groups (Kappeler and van Schaik 2002; Sussman et al. 2005; Shultz et al. 2011; Dunbar 2013b). Primates also display a wide range of mating systems, including monogamy (Rutberg 1983), polygyny (Clutton-Brock 1985) and polygynandry (Muller et al. 2007). Depending on species, delayed dispersal can be present in both sexes (Pereira et al., 1988), females only (Bennett and Sebastian 1988), males only (Symington 1987), or absent (Fuentes 2000). Thus, the diversity of dispersal and reproductive patterns in both males and females makes primates a group of interest for the study of the coevolution between delayed dispersal and reproductive suppression. Here, we aim at addressing the coevolution of delayed dispersal and reproductive suppression within and between sexes. Given that the mechanisms that may enhance reproductive suppression in groups with delayed dispersal (*i.e* indirect fitness benefits and group size increases) impact both sexes, we predict delayed dispersal to have evolved before reproductive suppression and facilitate its subsequent evolution in both sexes. Based on the previous findings that male-biased dispersal was ancestral, we further predict that delayed dispersal evolved in females before males. To test these predictions, we assess the existence and directionality of potential coevolution between delayed dispersal and reproductive suppression, both within and between sexes.

Material and methods

Assessing the occurrence of delayed dispersal and reproductive suppression in Primate species

We looked for published information on delayed dispersal and reproductive suppression and built a database including 123 species. We used the database compiled by Lukas and Clutton-Brock (2012a) as a starting point, and then reduced the number of species based on the availability of data about delayed dispersal (DD) and reproductive suppression (RS). For each species and each sex, we assessed whether individuals remain in their natal group beyond sexual maturity, whether reproductive suppression of some group members is present. We coded these traits as binary states

(i.e. 0 and 1 standing for the absence and presence of the trait of interest, respectively). We considered delayed dispersal to occur when at least some individuals were explicitly described as remaining in the natal group beyond sexual maturity, in accordance with Ekman et al. (Ekman et al. 2004). Reproductive suppression was considered to occur when either a reproductive skew involving the monopolization of reproduction by dominant individuals and a presence of non-reproductive individuals in the group were observed, or when reproductive suppression mechanisms such as successful monopolization of mating, physiological suppression of reproductive functions, exclusion of pregnant females from their social group, or infanticide were reported. We assumed that a high reproductive skew involved the existence of such mechanisms, even if they were not explicitly described in the literature.

Phylogenetic reconstruction

For phylogenetic reconstruction and to account for phylogenetic uncertainty, we used a consensus tree generated from a set of 100 chronograms generated by the 10kTrees project and pruned to the species of interest (Arnold et al. 2010). For each trait, we calculated the phylogenetic signal as Pagel's λ (Pagel 1999) using *phylosig* from the *Phytools* package (Revell 2012).

Coevolution and directionality in the evolution of delayed dispersal and reproductive suppression

We performed coevolution analyses on pairs of traits using the DISCRETE method of BayesTraits (Meade and Pagel 2017). Analyses were conducted separately for each sex. For each pair of traits, we tested both dependent models assuming coevolution and independent models in which a trait does not affect the evolution of the other. In agreement with previous evolutionary reconstructions of primate sociality suggesting a solitary ancestor (Shultz et al., 2011), we assumed the most recent common ancestor of primates to lack both traits of interest in males and females. In order to find the impact of this assumption on the results, we also conducted our analyses without any assumption on the ancestral states, which did not change the results. We used a reversible-jump Markov chain Monte Carlo (RJ-MCMC). We ran the chain for 1,000,000 iterations after a burn-in of 10,000 iterations, and sampled the chain at intervals of 1,000 iterations. We used gamma-distributed priors for transition

rates (Currie and Meade 2014). To reduce the uncertainty of choosing priors, we used uniform hyperpriors to draw values for the mean and variance of the gamma parameters. In order to assess the consistency of our results, we ran every model 5 times and verified the convergence of the chain, consistency of transition rates, and alpha and beta parameters of the gamma function. We checked the convergence of the chain by assessing that the distribution of harmonic mean log-likelihoods was approximately normal and that the likelihood traces did not show jumps across runs. We estimated log-likelihoods of each model using a stepping stone sampler with 100 stones per 10,000 iterations (Xie et al. 2010), and calculated the Bayes Factor as twice the difference between the log-likelihoods of the two models, according to Meade and Pagel (2017). Bayes Factor (BF) between the independent and dependent models was used to evaluate whether two traits coevolved. We then characterized transitions between states. Transitions between states (Z scores) that were frequently assigned to zero (approximating independent models of trait evolution) were considered to be unlikely, whereas those only rarely assigned to zero (i.e. approximating dependent models of trait evolution) were considered to be highly likely evolutionary transitions. We further determined the mean \pm SE transition parameter (q value), which indicates the strength of each transition. In order to check for the consistency of our results against phylogenetic uncertainty, we further reconducted our coevolution analyses on the whole set of 100 chronograms and verified that the results remained unchanged.

Results

Distribution of delayed dispersal and reproductive suppression

Among the 122 primate species included in our study, 21 displayed delayed dispersal in both sexes (17%), 16 in females only (13%), 38 in males only (31%) and 47 in neither males nor females (39%). Reproductive suppression was present in both sexes in 7 species (6%), females only in 7 species (6%), males only in 14 species (11%) and neither sex in 94 species (77%).

Coevolution of delayed dispersal and reproductive suppression within sexes

A significant statistical support for the dependent model over the independent one suggested that delayed dispersal and reproductive suppression coevolved in females (marginal likelihood: -110.95 vs -120.32, $BF=18.72^*$, Figure 12). Although delayed dispersal was more likely to evolve first than reproductive suppression, both traits could evolve in the absence of the other ($q_{0 \rightarrow FDD}=0.09 > q_{0 \rightarrow FRS}=0.01$, $Z_{0 \rightarrow FDD}=0.02 < Z_{0 \rightarrow FRS}=0.28$). Transition rates towards reproductive suppression were higher when delayed dispersal was already present ($q_{0 \rightarrow FRS}=0.01 < q_{FDD \rightarrow FDD, FRS}=0.05$, $Z_{0 \rightarrow FRS}=0.28 > Z_{FDD \rightarrow FDD, FRS}=0.15$). Reciprocally, transition rates towards delayed dispersal were marginally higher in the presence of reproductive suppression ($q_{0 \rightarrow FDD}=0.09 < q_{FRS \rightarrow FDD, FRS}=1.00$, $Z_{0 \rightarrow FDD}=0.02 = Z_{FRS \rightarrow FDD, FRS}=0.02$). This strongly suggested that both traits enhanced each other's evolution.

In males, however, we found no support for the dependent model over the independent one, which suggested that delayed dispersal and reproductive suppression evolved independently in males (marginal likelihood: -133.76 vs -132.95, $BF=1.61$ n.s, Figure 12).

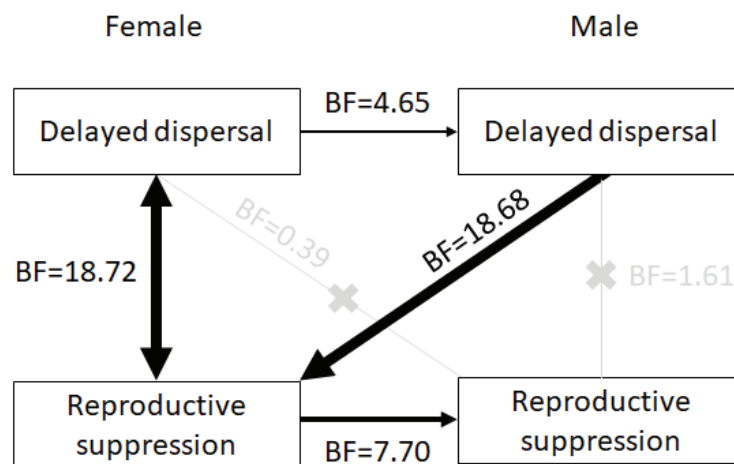


Figure 12 - Between and within-sex coevolutionary relationships between delayed dispersal and reproductive suppression in primates according to the discrete Bayesian method

Double arrows represent the mutual enhancement of two traits, whereas simple arrows represent directional coevolution in which one trait facilitates the further evolution of the other. The thickness of the arrows was scaled to reflect the superiority of the dependent model involving coevolution between the two traits over the independent one, as estimated by the Bayes Factor (BF). Pairs of traits for which there was no significant preference for the dependent model ($BF < 2$) are displayed in gray.

Coevolution of delayed dispersal and reproductive suppression between sexes

Reconstructions conducted on pairs of identical traits in males and females showed that, for both delayed dispersal and reproductive suppression, there was a mild support for coevolution between males and females (delayed dispersal: marginal likelihood -158.76 VS -161.01, BF=4.65*, Figure 12 ; reproductive suppression: marginal likelihood -104.23 VS -108.09, BF=7.70*, Figure 12). Whereas reproductive suppression generally evolved in females first and facilitated the later evolution of reproductive suppression in males, ($q_{0 \rightarrow FRS} = 0.40 > q_{0 \rightarrow MRS} = 0.09$, $Z_{0 \rightarrow FRS} = 0.04 < Z_{0 \rightarrow MRS} = 0.70$; $q_{0 \rightarrow MRS} = 0.09 < q_{FRS \rightarrow FRS, MRS} = 2.48$; $Z_{0 \rightarrow MRS} = 0.70 > Z_{FRS \rightarrow FRS, MRS} = 0.03$), the evolution of delayed dispersal in males was almost impossible without pre-existing female delayed dispersal ($q_{0 \rightarrow MDD} = 0.00$, $Z_{0 \rightarrow MDD} = 0.99$, $q_{FDD \rightarrow FDD, MDD} = 0.60$, $Z_{FDD \rightarrow FDD, MDD} = 0.01$), although the loss of female delayed dispersal resulted in male dispersal only in some species.

A strong statistical support for the dependent model over the independent one showed that male delayed dispersal and female reproductive suppression coevolved (marginal likelihood = -132.57 VS -141.90, BF=18.68**, Figure 12). Transition coefficients indicated that male delayed dispersal typically occurred before female reproductive suppression ($q_{0 \rightarrow FRS} = 0.006 < q_{0 \rightarrow MDD} = 0.916$; $Z_{0 \rightarrow FRS} = 0.81 > Z_{0 \rightarrow MDD} = 0$) and that the two traits mutually enhanced the evolution of each other ($q_{0 \rightarrow FRS} = 0.01 < q_{MDD \rightarrow MDD, FRS} = 2.45$; $Z_{0 \rightarrow FRS} = 0.81 > Z_{MDD \rightarrow MDD, FRS} = 0$; $q_{0 \rightarrow MDD} = 0.916 < q_{FRS \rightarrow FRS, MDD} = 2.45$). This pattern is apparent in the ancestral reconstruction, as occurrences of female reproductive suppression without male delayed dispersal are rare (occurred essentially among the genus *Macaca*, Figure 13) whereas male delayed dispersal without female reproductive suppression is widespread (*Ateles*, *Pithecia*, some great apes such as *Pan troglodytes* and *Gorilla gorilla*, and a few *Macaca* species) and co-occurrences are widely prevalent (see *Alouatta*, *Callithrix*). Inversely, we found no support for coevolution between female delayed dispersal and male reproductive suppression (marginal likelihood = -129.73 VS -129.93, BF=0.39 n.s, Figure 12), which suggests that they evolved independently from each other. Accordingly, the ancestral reconstruction displayed branches where female delayed

dispersal and male reproductive suppression co-occurred (e.g. cooperatively breeding *Callithrix* species, several *Macaca* species such as *Macaca arctoides*, *Mandrillus leucocephalus*, Figure 13) and branches where female delayed dispersal occurred alone (e.g. *Cercopithecus*, Figure 13).

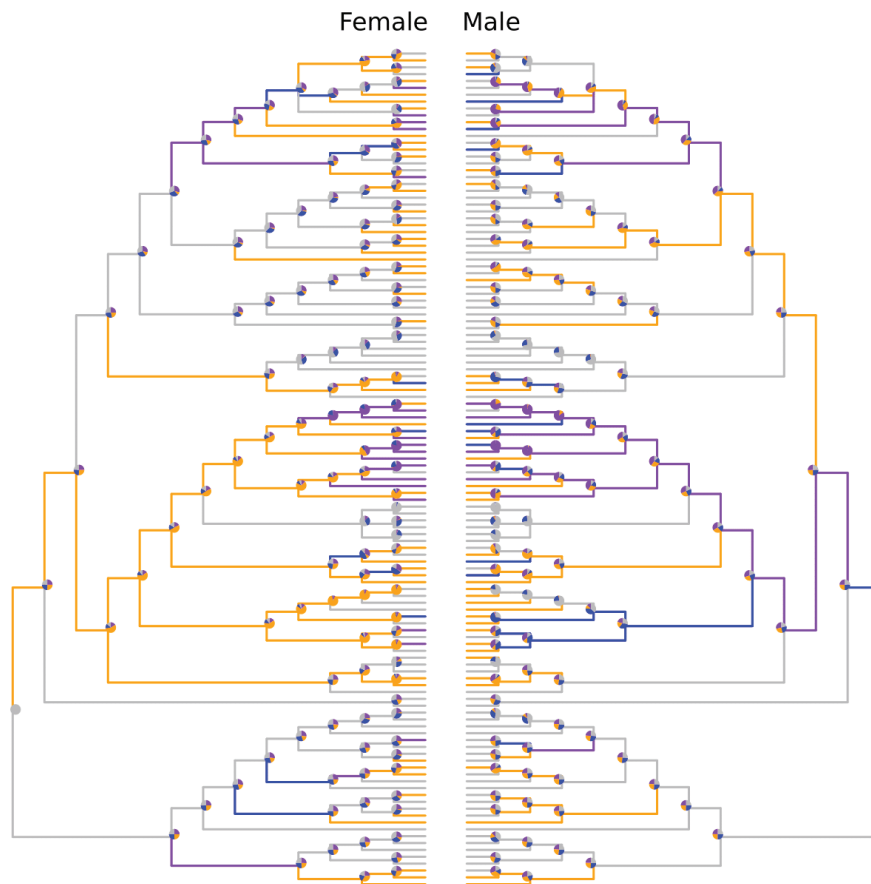


Figure 13 - Female and male primate phylogenies showing ancestral state reconstructions for delayed dispersal and reproductive suppression under the discrete Bayesian models of evolution within each sex

Branches are colored according to the most probable combination of states. The lack of both delayed dispersal and reproductive suppression, delayed dispersal alone, reproductive suppression alone and both traits are respectively displayed in grey, blue, orange and purple. Pies represent the probability distribution of the combinations of traits at each node. The tree topology is the consensus tree obtained from the 10kTrees project posterior distribution. Branch lengths are drawn proportional to time. Given that the model supports a coevolution between the two traits for females but not for males, the displayed ancestral states reconstructions were obtained with the dependent model for females, and the independent model for males.

Discussion

Delayed dispersal evolved in females before males in most branches, which is consistent with the widespread hypothesis that dispersal is mostly male-biased in mammals. Unlike birds, which social systems based on resource defense mostly lead to monogamy and female-biased dispersal, most mammals primarily feature strong sexual competition between males and a male-biased dispersal (Greenwood 1980; Waser 1985). Indeed, the high maternal investment of female mammals incurs high inbreeding costs in the case of inbreeding depression due to the investment being lost on a less fit offspring, which enhances the preference of females for immigrant males (Lehmann and Perrin 2003). Thus, the evolution of delayed dispersal in males may require higher benefits of philopatry and dispersal costs than in females (Pusey 1987; Handley and Perrin 2007), which may explain why the conditions for delayed dispersal to evolve in males were not fulfilled yet when it first occurred in females. Female philopatry may then have increased relatedness enough for benefits of philopatry to further increase to levels that allow for male delayed dispersal (Perrin and Mazalov 2000).

Several non-mutually exclusive hypotheses can explain the finding that delayed dispersal enhances reproductive suppression in female primates. First, delayed dispersal leads to the formation of larger social units such as family groups. Second, philopatry may incur fitness benefits (Koenig et al. 1992; Emlen 1994; Shen et al. 2017) which have been theoretically shown to greatly reduce the incentive for dominants to offer reproductive concessions to retain subordinates in the group (Kokko and Johnstone 1999).

Delayed dispersal can be expected to lead to reproductive suppression due to increase in group size (thus potentially reaching carrying capacity) and increase in group members relatedness (thus leading to increase in indirect fitness benefits if the individual contributes to the group's success - not necessarily directed towards the young - that may allow for the loss of direct fitness benefits). This remains true between sexes - delayed dispersal in males, for instance, still incurs an increase in group

size that may limit the number of births in the group and thus of females that can reproduce, and still increases relatedness, which may incur indirect fitness benefits in females.

Interestingly, while male delayed dispersal enhances female reproductive suppression, female delayed dispersal has no effect on the evolution of male reproductive suppression. A possible explanation for this may be that reproductive suppression is more costly in males, and thus needs more incentives to evolve. Indeed, females may be more prone than males to suppress reproduction as an inbreeding avoidance mechanism when delayed dispersal in the opposite sex increases the relatedness of potential mates. Two main processes underlie this hypothesis: Female choosiness and inbreeding avoidance. First, due to higher breeding costs in females (Kleiman and Malcolm 1981; Clutton-Brock 1991), females are expected to be choosier than males in their mate choice (Burley 1977), especially when mating costs are high (Bleu et al. 2012). In primates, both gestation and lactation are lengthy (Pereira and Fairbanks 2002), resulting in high breeding costs for mothers. Accordingly, female choosiness has indeed been reported in a variety of primate species (Clutton-Brock and McAuliffe, 2009; Eberle and Kappeler, 2004; Small, 1993; Waite et al., 2003; but see Drea, 2005). Second, in species where dispersal is delayed, high relatedness increases the risk of inbreeding, which may lead to inbreeding depression (Pusey and Wolf 1996b; Charlesworth and Willis 2009). Therefore, strong inbreeding avoidance mechanisms are expected in such species (Nichols 2017), including selective mate choice toward non-kin via kin recognition, which has been reported in numerous primate species (Gouzoules 1984; Parr and de Waal 1999b; Dietz 2004) and has been reported in birds to be especially present in cooperative breeders (Jamieson et al. 2009; Riehl and Stern 2015). In some species where such choosiness is present, reproductive suppression when no unrelated partner is available has been observed (Bennett et al. 1996; Cooney and Bennett 2000; O'Riain et al. 2000; Cockburn et al. 2003). Therefore, we can expect that if females are choosier than males, they may specifically suppress their reproduction when the relatedness of potential partners is high due to delayed dispersal, while males maintain reproduction for the same level of relatedness. However, theoretical models have shown that female choosiness is expected to decline rapidly with search costs

such as reproductive delays are present (Lehmann and Perrin 2003). Therefore, further investigation may be needed to investigate the role of female choosiness in the development of female reproductive suppression in species where males delay dispersal.

Chapter 3 - The role of climate in evolutionary pathways to cooperative breeding in Mammals

Abstract

Cooperative breeding, in which social groups include non-breeding individuals which forego dispersal and reproduction and provide alloparental care to the offspring of dominant individuals, evolves from the formation of family groups by delayed dispersal followed by the limitation of reproduction to dominant group members, and is associated with low and unpredictable annual rainfall and polytoccy. Here, we investigate the role of climate and life history on each step of the evolutionary pathway to cooperative breeding in Mammals. We show that low mean annual rainfall is associated with alloparental care, which is present in both cooperative and communal breeders, most likely due to low annual rainfall favoring polytoccy and increasing the benefits of alloparenting. Contrastingly, unpredictable rainfall is associated with reproductive suppression, and may thus be a key factor in determining whether family groups evolve towards cooperative rather than communal breeding. We also surprisingly show an association between habitat heterogeneity and delayed dispersal.

Introduction

Cooperation towards rearing young, which includes a variety of alloparenting behaviors involving fitness costs (Carlisle and Zahavi 1986; Snowdon 1996; Schradin and Anzenberger 2001; Clutton-Brock et al. 2004), is observed in three main cooperative social systems: communal breeding, cooperative breeding, and eusociality (Koenig and Dickinson 2004; Wilson and Hölldobler 2005; Cockburn 2006; Lukas and Clutton-Brock 2012*b*). Communal breeders pool their offspring and share care towards the young, whereas in cooperative and eusocial breeders only dominant individuals breed and are assisted by non-breeding helpers, which are in most cases offspring from the dominant that delay dispersal and reproduction (Lewis and Pusey 1997; Clutton-Brock 2016). Given that alloparenting is only observed in communal breeding, cooperative breeding and eusociality, it is likely that delayed dispersal and reproductive suppression are crucial to the development of alloparental care (Riehl 2013; Griesser et al. 2017). Accordingly, coevolutionary analyses of these constitutive traits show that delayed dispersal precedes the evolution of reproductive suppression and alloparenting in both carnivores (Chapter 1) and primates (Chapter 2), and that the evolution of cooperative and communal breeding follow separate pathways (Chapter 1).

The evolution of cooperative breeding is usually explained by two major hypotheses relying on ecological variables. First, the ecological constraints hypothesis proposes that delayed dispersal occurs when environmental harshness lowers the expected fitness outcomes of dispersal, which leads to the emergence of family groups and the subsequent evolution of cooperative breeding (Emlen, 1994, 1982; Hatchwell, 2009; Koenig et al., 1992). Second, the benefits of philopatry hypothesis argues that nonbreeding helpers remain at home when there is a net fitness benefit to doing so (Stacey and Ligon 1991). While these hypotheses are not mutually exclusive, and are thought to be involved simultaneously (Shen et al. 2017), they both assume cooperative breeding to stem from habitat characteristics.

Accordingly, previous studies have already provided insights regarding the relationship between climate and cooperative breeding. The vast majority of these studies focus on birds and insects rather than mammals, most likely due to the rarity of cooperative breeding in the latter group. However, studies conducted on birds have provided inconsistent results regarding which environments favored cooperative breeding. Cooperative breeding has indeed been suggested to be favored by both harsh, unpredictable environments (Soucy and Danforth 2002; Avilés et al. 2007; Cockburn and Russell 2011; Jetz and Rubenstein 2011) and stable environments (Ford et al. 1988; Arnold and Owens 1999; Rubenstein and Lovette 2007), which may be explained by the differences in grouping benefits between species (Shen et al. 2017). Regarding mammals, Lukas and Clutton-Brock (2017) found that the amount of rainfall to which cooperatively breeding mammals were exposed was both lower on average and more variable between and within year than that of monogamous, non-cooperative species. This result is consistent with findings on birds (Jetz and Rubenstein 2011), and corroborates previous observations on mole rats (Faulkes et al., 1997). Contrastingly, temperature was not found to predict cooperative breeding, and neither temperature nor rainfall predicted group formation (Lukas and Clutton-Brock 2017). Regarding life history, alloparenting has been shown to be associated with polytoccy (Lukas and Clutton-Brock 2012*b*, 2017), as well as lower annual variation of body mass, which is a good proxy for body fat storage. The latter can be explained by reproductive females relying less on their own energetic storage when they are provided help (Heldstab et al. 2017). The strength of this correlation depends on the nature of alloparenting behaviors, with provisioning being more strongly associated with low body fat storage than allonursing (Heldstab et al. 2017). The contradictory findings of studies conducted on other taxa, along with the rarity of studies specifically focusing on mammals, leave room for further investigation regarding the patterns of correlation between climate, life history and cooperative breeding in mammals.

Previous association assessments between group formation and climate variables were specifically conducted on socially monogamous species due to the assumption that social monogamy was a prerequisite to the evolution of cooperative breeding in Mammals (Lukas and Clutton-Brock

2017), whereas recent studies found that monogamy did not necessarily precede group formation by delayed dispersal in evolutionary pathways to cooperative breeding (Federico et al., in press). This is most likely due to the evolution of monogamy and cooperative breeding sharing an array of common causes involved in high dispersal costs and limited reproductive outputs (Dillard and Westneat, 2016). Therefore, restricting analyses to monogamous species may hinder the detection of associations between climate variables and delayed dispersal in branches where monogamy evolved after delayed dispersal. Similarly, in previous studies, the occurrence of alloparental care has only been assessed in groups including non-breeding subordinates, which does not allow for the detection of variables involved in alloparenting in both cooperative and communal breeders, due to groups not involving non-breeding helpers in the latter. Finally, previous research at the interspecific level included Mammalian orders that do not display cooperative breeding at all. This provided important insights regarding the interpretation of patterns, such as arid habitats being mainly occupied by both cooperatively breeding species and orders devoid of cooperative breeding such as ungulates. However, the total lack of cooperative breeding in these orders may mostly be explained by order-specific life history patterns that may prevent cooperative breeding from evolving even in favorable habitats. For instance, unlike carnivores, primate and rodents, most ungulates are fully herbivorous (Hanley, 1982; Pérez-Barberia et al., 2001; Pineda-Munoz and Alroy 2014) which may interfere with the development of sociality given that foraging patterns are thought to be involved in the emergence of sociality (Cantor and Farine, 2018) and are likely to be different depending on diet. Therefore, specifically investigating the orders in which cooperative breeding has been shown to evolve could shed a new light on why some species evolve towards cooperative breeding while others do not.

In this paper, we investigate the role of climate in the evolution of the three constitutive traits of cooperative breeding (delayed dispersal, reproductive suppression and alloparenting) in the main mammalian orders where it occurs (carnivores, primates and rodents). First, we compare the range of climatic variables found in species that display each constitutive trait of cooperative breeding compared to species in which the trait is absent. Second, in order to investigate the further

involvement of climate after the emergence of family groups via delayed dispersal, we compare the occurrence of reproductive suppression and alloparenting according to climate variables in species that already delay dispersal.

Material and methods

Data collection

We used the climate database published by Botero et al. (2014) on Dryad ([http://datadryad.org, doi:10.5061/dryad.sb175](http://datadryad.org,doi:10.5061/dryad.sb175)) as a starting point. This database provides species-level information regarding distribution area size; habitat heterogeneity, calculated as the number of habitat types included in the species' distribution area; and the annual mean, annual variance and between-years predictability of precipitation and temperature for the period of 1901-2009 in the species' distribution area. Botero et al. calculated predictability via Colwell's P (Colwell 1974), which ranges from 0 (unpredictable) to 1 (predictable) and takes into account variation in the onset, intensity and duration of periodic variables. Habitat types were based on the IUCN classification, which classifies habitats into 13 categories (artificial, caves and subterranean, coastal, desert, forest, grassland, intertidal, neritic, oceanic, rocky areas, savannah, shrubland and wetland). In order to focus on the evolution of cooperative breeding, we then pruned this database to terrestrial species from the three mammalian orders where cooperative breeding primarily occurs (Solomon and French 1997). We further reduced the number of species based on the availability of data regarding the occurrence of delayed dispersal (DD), reproductive suppression (RS), alloparenting (A) and monogamy (M) in the species-specific literature, using the database compiled by Lukas and Clutton-Brock (2012a), which includes cooperative breeding, communal breeding and monogamy, as a starting point. These traits were encoded as binary, according to whether the species displayed the trait or not. Our final database includes 232 species, including 110 carnivores, 44 rodents and 78 primates. We assessed for association between social traits using Kendall's rank correlation analysis (Kendall 1948).

Phylogeny

To avoid biased correlations between climate variables and social traits, we controlled all the analyses for shared ancestry between species by using a phylogeny of all involved species. Therefore, we built a phylogeny by pruning the phylogenetic super-tree of mammals published by Bininda-Emonds et al. (2008) to our 232 species. To prune the tree, we used the Brownian correlation structure from the APE package (Paradis et al. 2004).

Interactions between climate, life history and the constitutive traits of cooperative breeding

In order to investigate which climate variables were statistically different depending on the presence of each constitutive trait of cooperative breeding in Mammals, we performed phylogenetic ANOVA (Garland et al. 1993) using the phylANOVA function from the phytools package (Revell 2012) and calculated both F-values and P-values. We controlled for false discovery rate by applying Benjamini and Hochberg's correction to P-values in posthoc tests (Benjamini and Yekutieli 2001). Associations were considered statistically significant when the calculated P-values were inferior to 0.05. In order to assess for climate variables enhancing the evolution of alloparental care or reproductive suppression in species that already delay dispersal, we performed further phylogenetic ANOVA for the former two traits in a subset of species that display delayed dispersal. In order to account for possible differences in the evolutionary patterns according to the orders, we also assessed for phylogenetically corrected correlations between climate variables and constitutive traits of cooperative breeding on three data subsets corresponding to our three mammalian orders (carnivores, primates and rodents), using the same steps described previously.

Results

Data structuration

Among the 232 species of our study, the number of species displaying delayed dispersal, reproductive suppression, alloparenting and monogamy were respectively 80, 37, 36 and 60. Among the 149 species (64.2%) displaying none of the three constitutive traits of cooperative breeding, 28 were monogamous. Our dataset included 24 cooperative breeders, as well as 11 communal breeders. Unsurprisingly, there was positive correlation among the three constitutive traits of cooperative breeding (DD vs RS: $\tau=0.55$, $p<2\times10^{-16}$; DD vs AP: $\tau=0.57$, $p<2\times10^{-16}$; RS vs AP: $\tau=0.59$, $p<2\times10^{-16}$). Monogamy was also positively associated with the traits (DD: $\tau=0.24$, $p=2.9\times10^{-4}$; RS: $\tau=0.46$, $p=4.5\times10^{-12}$; AP: $\tau=0.39$, $p=4.1\times10^{-9}$).

Range habitat heterogeneity, but not total area, is involved in the evolution of delayed dispersal

We found a positive association between habitat heterogeneity and all three constitutive traits of cooperative breeding (DD: $p=0.004$, RS: $p=0.007$, AP: $p=0.003$; Table 6; Figure 14), but not monogamy ($p=0.198$; Table 6). However, habitat heterogeneity was not associated with reproductive suppression and alloparenting in the delayed dispersal subset (RS: $p=0.328$, AP: $p=0.904$, Table 7). The average habitat heterogeneities of cooperative breeders and communal breeders were 2.96 ± 1.83 and 3.00 ± 0.94 , respectively, which was close to the habitat heterogeneity for all species that delayed dispersal (2.77 ± 1.48).

Surprisingly, this pattern of association between habitat heterogeneity and cooperative breeding was not consistent between mammalian orders. No association was found between habitat heterogeneity and any of the three traits in carnivores (DD: $p=0.547$, RS: $p=0.791$, AP: $p=0.497$, M: $p=0.844$, Table 8) and in rodents (DD: $p=0.161$, RS: $p=0.611$, AP: $p=0.881$, M: $p=0.900$, Table 8). Contrastingly the positive association was only found for delayed dispersal and monogamy in primates (DD: $p=0.039^*$, RS: $p=0.235$, AP: $p=0.952$, M: $p=0.012^*$, Table 8).

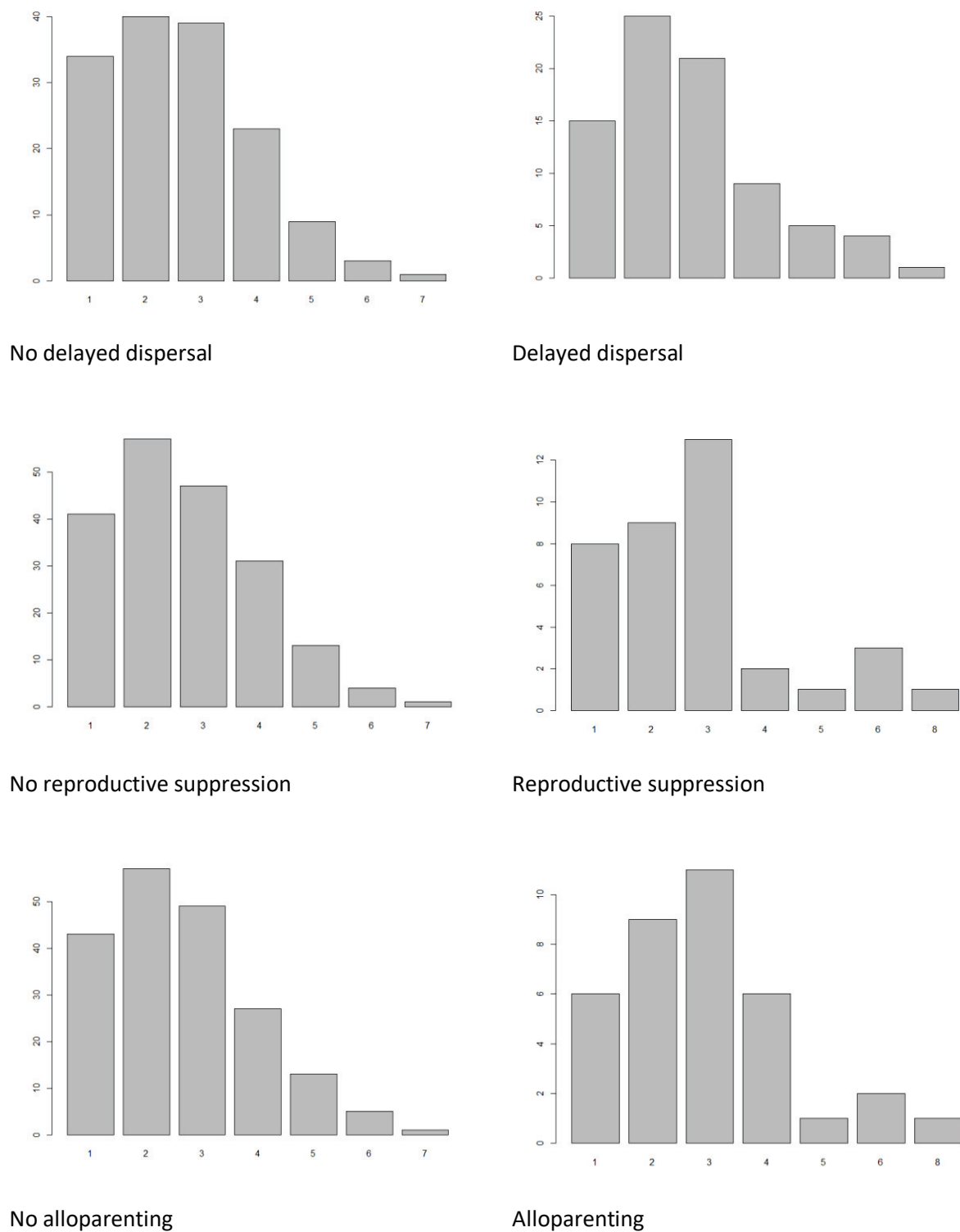


Figure 14 - Distribution of habitat heterogeneity in data subsets according to the status of traits of interest

Each subset only includes species based on whether the trait of interest is present or absent.

Temperature and constitutive traits of cooperative breeding

Neither monogamy, nor the three constitutive traits were associated with temperature patterns in any way in the whole dataset (Table 6). Surprisingly, in the delayed dispersal subset, there was a marginal positive association between temperature predictability and reproductive suppression ($F=5.31$, $p=0.049$, Table 7).

Consistently with these results, neither carnivores nor rodents displayed an association between temperature variables and any of the traits. However, in primates, monogamy was associated with highly predictable temperatures (M: $F=4.46$, $p=0.038^*$, Table 8).

Precipitation variables predict different traits involved in cooperative breeding

As expected, low mean precipitation predicted all three constitutive traits of cooperative breeding (DD: $F=11.95$, $p=0.001$, RS: $F=7.05$, $p=0.003$, AP: $F=6.39$, $p=0.005$, Table 6). Contrastingly, although low between-year predictability predicted reproductive suppression ($F=13.94$, $p<1.0\times10^{-3}$), it was not associated with delayed dispersal ($F=2.7$, $p=0.137$, Table 6). Within-year precipitation variance, on the other hand, did not predict any of the social traits (DD: $F=1.08$, $p=0.297$; RS: $F=0.01$, $p=0.645$; AP: $F=0.04$, $p=0.597$, Table 6, Figure 15).

Among species with delayed dispersal, low predictability of precipitation between years predicted reproductive suppression but not alloparenting (RS: $F=14.21$, $p<1\times10^{-3}$; AP: $F=3.10$, $p=0.095$, Table 2). Contrastingly, low mean precipitation was negatively associated with alloparenting, but not with reproductive suppression (RS: $F=0.48$, $p=0.896$; AP: $F=7.37$, $p=0.033$, Table 7). Surprisingly, despite the lack of correlation between monogamy and any of the climate variables in the whole dataset, high among-year precipitation variance was associated with the occurrence of both alloparenting and monogamy in the delayed dispersal subset (AP: $F=9.60$, $p=0.013$; M: $F=11.49$, $p=0.010$). Monogamy was also predicted by low mean precipitation ($F=11.89$, $p=0.009$).

The association between precipitation variables and traits involved in cooperative breeding also displayed differences between mammalian orders. In carnivores, none of the traits was associated with any precipitation variable (Table 8). In primates, delayed dispersal was associated with mean precipitation (DD: $p=0.008^*$, Table 8) and reproductive suppression with precipitation predictability (RS: $p=0.029^*$), which was consistent with the global pattern. In addition to this, it was the only order to display a slight negative association between monogamy and both reproductive suppression and alloparenting (M: $p=0.038^*$). Contrastingly, in rodents, delayed dispersal and alloparenting displayed a positive association with mean precipitation (DD: $p=0.004$, AP: $p=0.005^*$) and within-year precipitation variance (DD: $p=0.18$, AP: $p=0.029^*$). Precipitation predictability, on the other hand, was lower in monogamous species (M: $p=0.01^*$).

Table 6 - Phylogenetically corrected ANOVA correlations between climate variables and constitutive traits of cooperative breeding

	DD		RS		AP		M	
	F	p	F	p	F	p	F	p
Mean precipitation	11.95	0.001*	7.05	0.003*	6.39	0.005*	2.10	0.351
Var precipitation	1.08	0.297	0.01	0.645	0.04	0.597	2.54	0.295
Pred precipitation	2.74	0.137	13.94	0.000*	8.39	0.005*	2.14	0.130
Mean temperature	0.83	0.305	0.87	0.473	0.47	0.417	1.50	0.186
Variance temperature	0.15	0.594	2.70	0.251	1.15	0.527	0.59	0.760
Pred temperature	0.48	0.459	2.49	0.170	0.73	0.504	0.14	0.492
Range area	0.10	0.714	0.01	0.854	0.02	0.954	0.05	0.860
Habitat heterogeneity	7.12	0.004*	5.50	0.007*	6.29	0.003*	0.77	0.198

Table 7 - Phylogenetically corrected ANOVA correlations between climate variables and constitutive traits of cooperative breeding in species that display delayed dispersal

	RS		AP		M	
	F	p	F	p	F	p
Mean precipitation	0.48	0.896	7.37	0.033*	11.89	0.009*
Variance precipitation	3.94	0.161	9.60	0.013*	11.49	0.010*
Pred precipitation	14.21	0.000*	3.10	0.095	0.26	0.773
Mean temperature	1.78	0.223	0.20	0.649	0.11	0.743
Variance temperature	4.72	0.103	3.57	0.159	5.30	0.081
Pred temperature	5.31	0.049*	3.08	0.153	3.10	0.185
Range area	0.06	0.843	0.70	0.422	0.23	0.680
Habitat heterogeneity	0.70	0.328	0.02	0.904	1.01	0.447

Table 8 - Phylogenetically corrected ANOVA correlations between climate variables and constitutive traits of cooperative breeding in carnivores, primates and rodents

	DD		RS		AP		M	
	F	p	F	p	F	p	F	p
Carnivores								
Mean precipitation	0.09	0.848	1.75	0.561	1.46	0.522	1.07	0.758
Var precipitation	0.20	0.789	0.57	0.711	0.06	0.897	0.20	0.897
Pred precipitation	0.13	0.837	0.75	0.685	1.27	0.541	0.07	0.94
Mean temperature	3.85	0.255	1.03	0.629	1.05	0.575	0.02	0.967
Variance temperature	4.00	0.242	1.51	0.561	1.43	0.505	0.18	0.906
Pred temperature	3.61	0.265	1.87	0.553	2.79	0.379	0.43	0.85
Range area	0.00	0.98	1.05	0.632	0.43	0.725	2.21	0.657
Habitat heterogeneity	1.10	0.547	0.32	0.791	1.49	0.497	0.46	0.844
Primates								
Mean precipitation	7.53	0.008*	2.98	0.088	1.77	0.188	3.27	0.074
Var precipitation	1.87	0.175	1.81	0.182	2.40	0.125	0.20	0.659
Pred precipitation	3.66	0.059	4.94	0.029*	0.06	0.808	2.47	0.120
Mean temperature	3.67	0.059	0.01	0.922	0.53	0.470	3.69	0.059
Variance temperature	3.01	0.087	0.01	0.934	0.87	0.354	4.46	0.038*
Pred temperature	6.58	0.012*	1.13	0.291	0.89	0.347	1.34	0.250
Range area	4.75	0.032*	0.21	0.647	0.95	0.333	2.48	0.120
Habitat heterogeneity	4.39	0.039*	1.43	0.235	0.00	0.952	6.70	0.012*
Rodents								
Mean precipitation	7.53	0.004*	0.81	0.349	10.43	0.005*	1.35	0.39
Var precipitation	4.93	0.018*	1.46	0.221	6.84	0.029*	3.69	0.13
Pred precipitation	1.21	0.266	1.91	0.183	2.10	0.247	12.57	0.01*
Mean temperature	0.01	0.916	0.07	0.787	0.07	0.837	0.18	0.78
Variance temperature	0.09	0.777	0.16	0.713	1.01	0.440	0.23	0.74
Pred temperature	0.17	0.690	0.44	0.472	1.35	0.310	0.77	0.54
Range area	4.09	0.037*	0.53	0.468	0.33	0.615	0.00	0.96
Habitat heterogeneity	2.08	0.161	0.26	0.611	0.03	0.881	0.03	0.90

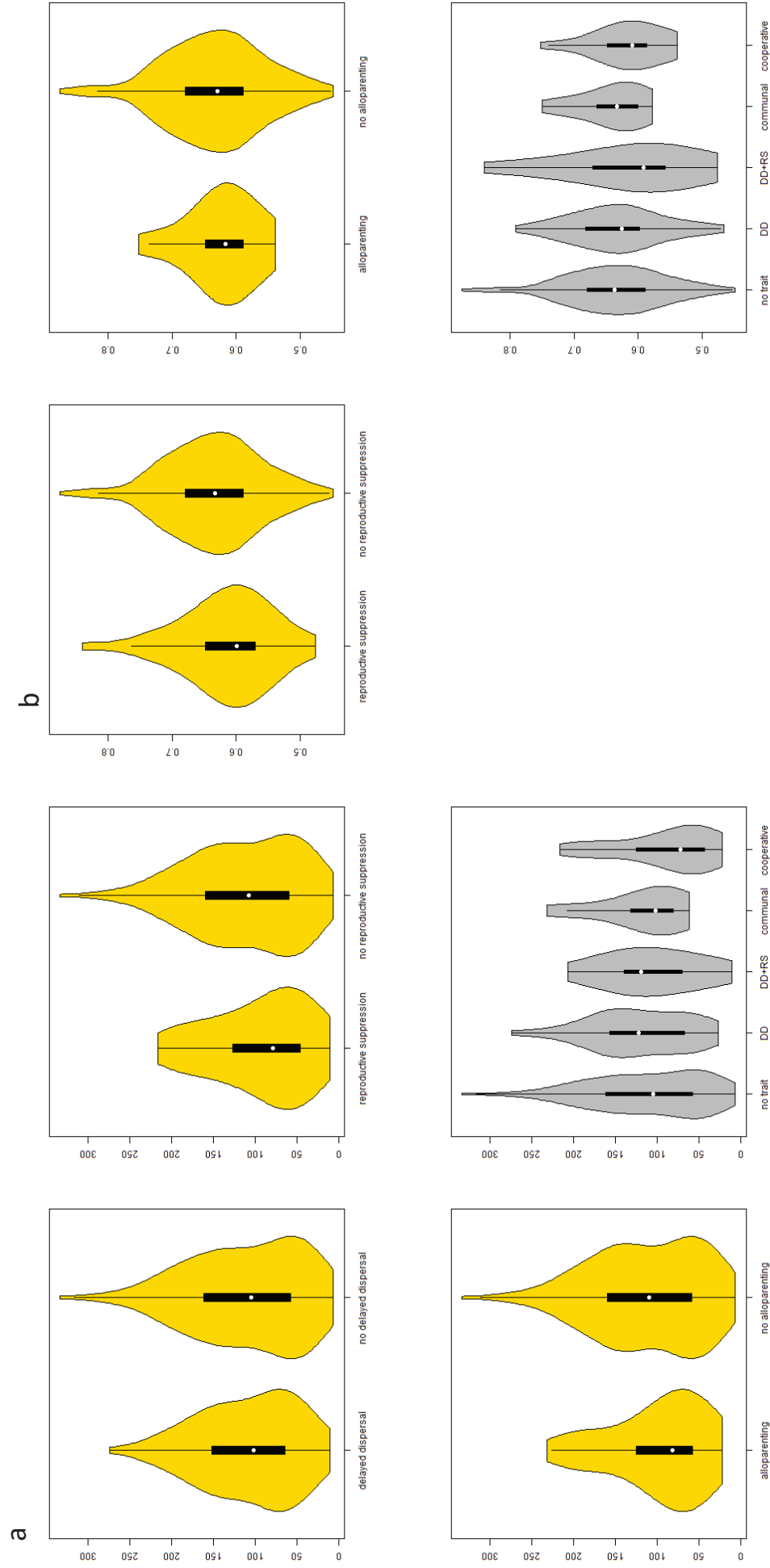


Figure 15 - Distribution of annual mean (a) and between-year predictability (b) of precipitation in species according to their social traits. Annual mean and variance are displayed in millimeters. Precipitation predictability is displayed as Colwell's P. The distribution of species according to the most common combinations of social traits are displayed in grey. In this panel, “No trait” refers to species lacking all three traits, whereas DD and RS refer to delayed dispersal and reproductive suppression. Communal and cooperative refer to the breeding systems of the species; communally breeding species thus displaying delayed dispersal and alloparenting but not reproductive suppression, and cooperatively breeding species displaying all three traits.

Discussion

In accordance with previous research (Lukas and Clutton-Brock. 2017), our results indicate a strong association between cooperative breeding and both the annual mean and predictability of rainfall, as well as habitat heterogeneity. However, we found that these variables were associated with different constitutive aspects of cooperative breeding, which include delayed dispersal, reproductive suppression and alloparenting. Low annual rainfall is associated with all three constitutive traits of cooperative breeding, which suggests that it may be involved at an early stage in the pathway to cooperative breeding, such as in the transition to delayed dispersal. However, the correlation between low annual rainfall and alloparenting remains strong within species that delay dispersal, in contrast to the correlation with reproductive suppression, which suggests a further role in the evolution of alloparenting behaviors in both cooperative and communal breeders. Contrastingly, rainfall predictability is associated with reproductive suppression and alloparenting, and its association with reproductive suppression subsists within species that delay dispersal. Therefore, it may be key in the evolution of reproductive suppression in species that delay dispersal, and thus play a crucial role in the evolution towards cooperative breeding rather than communal breeding. Interestingly, habitat heterogeneity shows association to all three constitutive traits of cooperative breeding, but correlates with neither reproductive suppression nor alloparenting within species with delayed dispersal, which suggests a role in the evolution of delayed dispersal only. Finally, we found no correlation between monogamy and any of the climate variables in the dataset that included all species, whereas monogamy was associated with a high annual mean and within-year variance when the dataset was restricted to species with delayed dispersal. These results obtained on mammals from all three orders that display cooperative breeding do not reflect the patterns that underlie each order, which suggests that they reflect the relative weight of the three orders in the database rather than a global pattern. In carnivores, only habitat heterogeneity is associated with the traits of interest. Finally, rodents display an intriguing reverse pattern, in which none of the variables is involved in delayed dispersal,

and homogenous climates with high precipitation levels and stable temperatures are associated with reproductive suppression and alloparenting.

Species that display both delayed dispersal and reproductive suppression, which groups can either breed cooperatively or include non-breeders that do not help, are exposed to significantly less predictable rainfall than species that delay dispersal but share reproduction between all group members. Therefore, low between-year predictability in rainfall may play a key role in the evolution towards cooperative breeding rather than communal breeding after the evolution of delayed dispersal (Figure 16) which is consistent with its association with cooperative breeding (Lukas and Clutton-Brock. 2017). However, while Lukas and Clutton-Brock suggest that the association between rainfall and cooperative breeding may result from the association between low rainfall and polytocy, polytocy is also associated with allonursing in species without reproductive suppression (MacLeod and Lukas. 2014), and thus with communal breeding. Therefore, polytocy is unlikely to be the sole explanation behind the association between rainfall patterns and cooperative breeding. It is possible that, due to the association between rainfall and primary productivity (Pandey and Singh. 1992; Yang et al.. 2008), the carrying capacity can be low some years in unpredictable environments. Low carrying capacity may result in the restriction of reproduction to dominant individuals due to maximal group size being reached easily, especially in species that display polytocy and/or delayed dispersal, both of which increase group size. However, this interpretation is subject to caution due to the limits of rainfall as a predictor of primary productivity and carrying capacity, especially in worldwide analyses including a wide range of habitats and climates. Indeed, the positive correlation between annual rainfall and primary production levels off when annual rainfall is high (Yang et al.. 2008), and in some cases soil moisture is a much better predictor of primary productivity than rainfall itself (Nippert et al.. 2006).

Unexpectedly, high rainfall with a high within-year variance suggesting seasonality is associated with alloparenting and monogamy only in species that already delay dispersal (Figure 16). This association was not found in previous research restricted to family groups (Lukas and Clutton-

Brock. 2017). A possible explanation for this may lie in the restriction of this analysis to monogamous species in this previous work. Indeed, due to the presence of additional group members, the social systems of monogamous species that also delay dispersal are widely different from those of monogamous species that disperse at sexual maturity: the former are mostly cooperative breeders, whereas the latter are pair-living. Therefore, it can be hypothesized that high seasonal rainfall is specifically associated with the evolution of cooperative breeding, whereas it is not involved in pair-living.

One of the most important findings of this study is that the patterns of association between climate variables and social traits are highly variable according to mammalian orders, and do not necessarily reflect the results obtained on all mammals. In rodents, reproductive suppression appears to be unaffected by climate variables, whereas delayed dispersal and alloparenting are favored by stable, benign environments with high precipitation levels. While the implications of this result are unclear, it may imply that mammalian orders are affected by different evolutionary hypotheses, in which case there may be no global explanation that applies to all mammalian orders simultaneously. The ecological constraints hypothesis, which argues that cooperative breeding stems from harsh environments in which dispersing to breed independently incurs severe fitness losses, may apply better to primates, in which cooperative breeding is favored by harsher conditions (low and unpredictable precipitation), and less to rodents (Shen et al., 2017). It is also possible that group formation processes other than delayed dispersal are more involved in rodents than in other groups. In primates, on the other hand, alloparenting appears to be surprisingly unaffected by climate variables whereas reproductive suppression is favored by unpredictable environments and delayed dispersal is favored by drought, thus reflecting the early steps of the evolutionary route. Finally, no association between climate and constitutive traits of cooperative breeding was found at all in carnivores. This might suggest that evolutionary hypotheses relying on environmental conditions, such as ecological constraints and benefits of philopatry, play a weaker role than previously thought in the evolution of cooperative breeding in carnivores. Other factors underlying the evolution of cooperative breeding,

such as indirect fitness benefits, may play a stronger role, which would be consistent with delayed dispersal being a prerequisite to the evolution of the two other traits (Chapter 1). This also suggests that the global pattern highly relies on results found in other taxa, and that investigating the evolutionary patterns of cooperative breeding on very large interspecific scales such that of all mammals may lead to attribute patterns to all taxa. We recommend future investigations at the interspecific level on cooperative breeding in mammals to pay close attention to the possible heterogeneity of evolutionary relationships between orders, and conducts analyses on subsets of carnivores, primates and rodents separately.

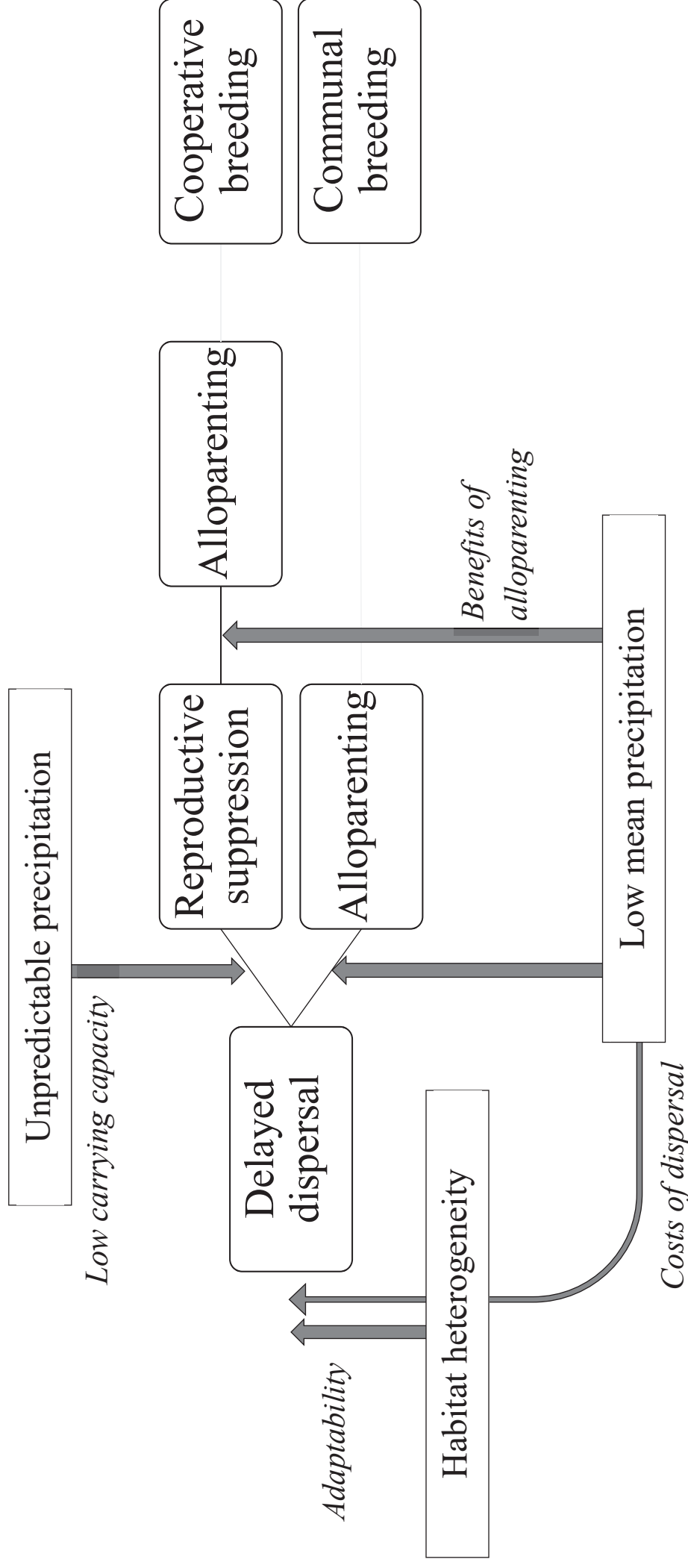


Figure 16 - Roles of climate variables on evolutionary pathways to communal and cooperative breeding in Mammals

Evolutionary pathways to communal and cooperative breeding involve delayed dispersal followed by alloparenting alone or reproductive suppression and then alloparenting respectively (accordingly with Chapter 1). Grey arrows represent the probable involvement of climate variables in evolutionary transitions as suggested by their association with constitutive traits of cooperative breeding. Association with all traits suggests that the variable played a role in the onset of delayed dispersal whereas specific association with reproductive suppression and/or alloparenting suggests a role in the evolutionary transitions of these traits. The main evolutionary hypotheses involved in the roles of climate variables are displayed in italics next to the arrows.

Discussion

Why are coevolutionary patterns different between taxa?

Comparison of the evolution of cooperative breeding in primates and carnivores

Surprisingly, although delayed dispersal and reproductive suppression coevolved in both carnivore and primate females, they evolved independently in primate males. Given that only females engage in alloparenting in the vast majority of cooperatively breeding carnivores, this result may stem from female specificities, such as the higher reliability of maternal recognition clues (Hepper 2005) or the specifically female reproductive strategies (Robert 1972; Emlen and Oring 1977; Parker 1979; Andersson 1994), rather than differences between taxa. When delayed dispersal and reproductive suppression indeed coevolved, delayed dispersal was the first trait to evolve. However, although this was an obligatory first step in carnivores, reproductive suppression could evolve without delayed dispersal in some branches of primates. Another major difference lied in the stability of intermediate configurations, i.e social systems involving at least one of the three traits of interest but neither classified as communal nor as cooperative breeding. Only 12 % of carnivores displayed such configurations, whereas 41% of primates displayed them in males and 29% in females. This was further reflected in the transition coefficients from intermediate configurations, which were much higher in carnivores than in primates. This has major implications for the evolution of cooperative breeding in each group, and may explain the differences in the number of evolutionary transitions to alloparenting, which was usually the last trait to appear in both groups. In carnivores, the evolution of delayed dispersal almost always incurred the further evolution of either alloparenting, or reproductive suppression followed by alloparenting, most likely in a very short timeframe given the instability of intermediate states, hence the high number of evolutionary transitions to alloparenting, which appeared to be a direct consequence of delayed dispersal. Contrastingly, in primates, branches could maintain delayed dispersal alone, or delayed dispersal and reproductive suppression, without triggering the further evolution of alloparenting. This resulted in a very low number of evolutionary transitions to alloparenting, despite the higher frequencies of delayed dispersal and reproductive suppression than in carnivores, which were shown to facilitate transitions to alloparenting. Delayed dispersal was also less likely to result in the further evolution of reproductive suppression. These differences between primates and carnivores are summarized in Table 9.

Table 9 - Coevolutionary patterns of constitutive traits of cooperative breeding in carnivores and primates

For carnivores, only female data is displayed due to the extreme rarity of male alloparenting behaviors. Coevolution between delayed dispersal and reproductive suppression, as well as the first step of the evolutionary pathway to cooperative breeding and whether this first step is necessary for the two other traits to evolve, were assessed in chapters 1 and 2.

		Carnivores	Primates	
			Females	Males
Coevolution between delayed dispersal and reproductive suppression		Dependent	Dependent	Independent
First step		Delayed dispersal		NA
Necessity of the first step for the further evolution of the other traits		Yes	No	
Frequency of the traits	Delayed dispersal	0,21	0,30	0,48
	Reproductive suppression	0,10	0,17	0,11
	Alloparenting	0,12	0,10	0,12
Intermediate configurations		Unstable	Stable	
Number of evolutionary transitions to alloparenting		8	3	1

Behind the stability of intermediate combinations

The results presented in the two first chapters show that the stability of intermediate combinations displaying some, but not all, constitutive traits of cooperative breeding is vastly different between carnivores and primates. In the former, such combinations are highly unstable and either evolve toward cooperative or communal breeding or revert to the absence of all traits. Communal and cooperative breeding are stabilized by interactions between traits (Chapter 1). Contrastingly, primates display a vast range of stable intermediate combinations of some but not all traits involved in cooperative breeding. Delayed dispersal and reproductive suppression display stabilizing interactions, but these interactions are much weaker than those observed in carnivores.

Group hunting and coevolution between delayed dispersal and reproductive suppression

An explanation for this might be that in carnivores who feed on large prey, hunting success and prey size are low in solitary attempts and grows higher with the number of individuals involved in the

hunting (Fanshawe and Fitzgibbon 1993; Creel and Creel 1995; MacNulty et al. 2014). This advantage of group living is especially high in species that frequently take multiple prey (Packer and Rutten 1988; Courchamp and Macdonald 2001). Therefore, benefits of philopatry may be higher in group-hunting carnivores than in primates, and thus weaken the incentive for dominants to share reproduction with subordinates as the latter already highly benefit from staying in the group even if they forego reproduction (Clutton-Brock, 2016). This would provide an explanation for a stronger relationship between delayed dispersal and reproductive suppression in carnivores than in primates. It may also explain the higher number of transitions to alloparenting in carnivores. However, we performed a complementary analysis that showed no relationship between the prey/predator size ratio and any of the three constitutive traits of cooperative breeding. Thus, group hunting may have limited explicative power on the evolution of constitutive traits of cooperative breeding. However, this analysis was performed on carnivores only due to the lack of data on primates, and its conclusions may not apply to comparisons between carnivores and primates.

Alloparental behaviors and evolutionary pathway to cooperative breeding

Another possible explanation for the stronger facilitating effect of delayed dispersal on the evolution of alloparenting may lie in the differences in alloparental care between cooperatively breeding carnivores and primates. Indeed, while food sharing with non-offspring infants is widely documented in carnivores (Clutton-Brock et al. 2001a; Courchamp and Macdonald 2001), primates mostly provide alloparental care in the form of allocarrying (Goldizen 1987). Although cooperatively breeding primates may forage in groups (Garber, 1997) and use vocal cues to trigger food transfers to juveniles (Brown et al. 2004), food transfers to non-offspring juveniles are rarely observed, even in species where adults widely display allogrooming, allocarrying and play towards them (Welker et al. 1987). Although there are exceptions such as communally breeding *Microcebus murinus*, where mothers were regularly observed to nurse non-offspring despite their ability to discriminate their own young (Eberle and Kappeler 2006), alloparenting is mostly performed in the form of allocarrying or protection. It is possible that the young benefit less from these behaviors than from allofeeding. If alloparental care is more beneficial to the young in carnivores than in primates, it may evolve more easily in group-living species than it does in primates, thus making group-living, non-cooperative configurations unstable. However, some studies suggest that, in some species such as saddle-back tamarins, allocarrying may be important to the extent that successful offspring rearing is impossible without alloparenting behaviors from other group members (Goldizen et al. 1996).

Delayed dispersal as an obligatory or facultative first step

Non-kin group formation and further evolution of reproductive suppression and alloparenting in primates

A possible explanation for delayed dispersal being an obligatory prerequisite to the two other traits in carnivores and not primates could be that, unlike carnivores that primarily rely on philopatry for group formation, non-kin group formation evolves in primates by recruitment of unrelated adults (Kinzey 1997). Such group formation paves the way for the evolution of other features such as reproductive suppression or alloparenting, without delayed dispersal being involved beforehand. The lesser importance of external recruitment in carnivores may stem from low general tolerance toward other individuals, due to the more recent transitions to multi-male, multi-female groups in primates (75 million years ago in Anthropoidea and 40 million years ago in Prosimii, Shultz et al., 2011) compared to carnivores, where sociality is likely to be more recent than the evolution of Caninae and Herpestidae (cf Chapter 1). This hypothesis involves the possibility for reproductive suppression and alloparenting to evolve in primate groups without kinship being the sole explanation. This is obviously the case for reproductive suppression, given that the incentive for individuals that control reproduction to shed concessions to non-kin is weaker due to the lack of indirect benefits that would compensate for the loss of individual reproductive success. The issue is more complex for alloparenting. Indeed, a wide range of research suggests that kinship remains a key mechanism behind cooperation between primates. First, kin recognition mechanisms based on familiarity (Bernstein 1991; Silk 2009) or phenotypic cues (Parr and de Waal 1999a; Widdig 2007) are indeed widespread in primates (Rendall 2004), which suggests that cooperation and affiliative behaviors may be specifically be directed toward kin. Second, behavioral biases toward kin have been described in a wide range of non-cooperatively breeding primate social systems, including non-gregarious dwarf lemurs displaying kinship structures (Kappeler et al. 2002), or female baboons preferentially grooming kin and reconciling conflicts at higher rates with kin (Silk 2002; Kapsalis et al. 2004). Thus, it is highly likely that lower kinship in some group-living primates cannot explain alone why delayed dispersal is not an obligatory prerequisite for the evolution of reproductive suppression and alloparenting in primates.

A stronger competition over reproduction in primates

Another possibility is that competition over reproduction could be stronger in primates than in carnivores, thus leading reproductive suppression to evolve more easily in primates, even in absence of kinship making up for the loss of direct fitness. However, the importance of reproductive competition in the evolution of reproductive skew has been increasingly disputed. Indeed, if dominant individuals fail to control the reproduction of other group members, strong reproductive competition

may instead lead to a balanced reproductive share (Nonacs et al., 2011). Therefore, these hypotheses should be treated with caution, especially in species where the relative competitive ability of dominant and subordinates is unclear or where the bias towards dominants is low.

What predictions can be made about rodents?

How stable are intermediate configurations in rodents?

Regarding the stability of combinations, many rodent species display intermediate configurations involving some but not all constitutive traits of cooperative breeding, like primates (see Chapter 2) and unlike carnivores (see Chapter 1). Thus, we do not expect the ratio of transition rates from and to intermediate states to be as high in rodents as in carnivores, neither do we expect communal and cooperative breeding to be the only stable social systems involving delayed dispersal. This may first come off as surprising due to the prevalence of allonursing in rodents, which might incur high benefits like those observed in carnivores, and thus lead to patterns where alloparenting evolves easily enough to make group-living, non-cooperative configurations unlikely. However, as already pointed in the introduction, the costs of allonursing may be high enough to outweigh the benefits in many rodent species (Rogowitz 1996), and allonursing may thus stem from the inability of mothers to discriminate their own offspring rather than actual net benefits in rodents (Manning et al. 1995). The net benefits of allonursing may therefore be much lower in rodents than in carnivores, thus providing an explanation to why many rodent species actually display intermediate configurations involving group-living but not alloparenting.

Is delayed dispersal more likely to be an obligatory or a facultative first step in rodents?

Likewise to carnivores, natal philopatry is by far the main mechanism of group formation in rodents (Solomon 2003). Thus, it could be hypothesized that delayed dispersal is prerequisite to cooperative breeding in rodents, given that it is a prerequisite to group-living. However, unlike in carnivores in which the philopatric sex (females) is also the alloparenting sex, male alloparenting is widespread in rodents (Allainé and Theuriau 2004), although females are vastly the philopatric sex. Therefore, it is possible that male delayed dispersal is not required for male alloparenting to evolve.

Furthermore, evidence for benefits of philopatry in rodents, which may provide a strong argument for delayed dispersal being a prerequisite to cooperative breeding, is contrasted. Indeed, territory inheritance occurs in some species such as yellow-bellied marmots (Armitage 1991), but not others such as prairie voles (McGuire et al. 1993). In both cases, monitoring nearby territories for

potential vacancies may provide philopatric individuals with further opportunities for territory acquisition (Arnold 1990; McGuire et al. 1993). Similarly, direct fitness has been shown to both increase (Armitage and Schwartz 2000) and decrease with group size (Hoogland 1995) depending on the species. Therefore, it is difficult to make predictions regarding the role of philopatry in the evolution of cooperative breeding in rodents.

Lack of cooperative breeding in other taxa

In contrast to birds, in which cooperative breeding has evolved in a wide range of orders, cooperative breeding is mostly restricted to three taxa in mammals. There are several possible explanations for this.

The occurrence of monogamy

First of all, the distribution of monogamy between taxa has been shown to be extremely uneven. For instance, while 29% of primates and 16% of carnivores are monogamous, only 3% of artiodactyles display this mating system (Lukas and Clutton-Brock 2013). Given the role of monogamy in the evolution of cooperative breeding, it could be hypothesized that monogamy is simply not frequent enough in other taxa to allow for the evolution of cooperative breeding. However, we showed in Chapter 1, in accordance with Dillard and Westneat (2016), that monogamy may share with cooperative breeding an array of common causes thought to be involved in high dispersal costs and limited reproduction rather than be a preliminary cause. Therefore, those mechanisms, which could include scarce food resources, harsh environments (Emlen and Oring 1977; Barlow 1988), limited nest sites and predation pressure (Dillard and Westneat 2016; Groenewoud et al. 2016), may explain both the low occurrence of monogamy and the absence of cooperative breeding in other mammalian taxa.

The occurrence of sociality

Similarly, it is possible that orders where cooperative breeding did not evolve are orders where sociality does not evolve easily. Indeed, in addition to cooperative breeding involving a high degree of sociality, there are common mechanisms behind the evolution of cooperative breeding and the evolution of sociality in general, which is consistent with the conception of sociality as a spectrum with cooperative breeding, also described as semisocial in insects, being one of the most social states (Wilson 1971). Indeed, high benefits and/or low costs of close association with conspecifics both increase the incentive to form social groups and the compensation for foregoing reproduction temporarily and permanently. Such benefits include but are not limited to protection from predators, access to resources, mating opportunities, reduced heat loss, or lower vulnerability to infanticide

(Krause et al. 2002). Therefore, it could be hypothesized that transitions to both sociality and cooperative breeding are rarer in orders where the extent of these benefits are low, for instance if resources are abundant and predation risk is low. However, sociality is widespread in all major lineages of mammals. In addition to primates, carnivores and rodents, sociality is well-documented in cetaceans (Mann et al. 2000), ungulates (Jarman 1974), lagomorphs (Chapman and Flux 1990) and a wide range of mammalian orders. Therefore, the lack of the factors enhancing sociality cannot explain the lack of cooperative breeding in most mammalian orders.

The lack of low-risk breeding opportunities

A possible explanation for the evolution of cooperative breeding being mostly restrained to carnivores, primates and rodents lies in the lack of low-risk breeding opportunities outside the natal group. Indeed, although all groups include social species, not all social species delay dispersal and/or restrain reproduction to a limited number of individuals. Given that this lack of low-risk breeding opportunities can stem from difficult ecological conditions, and that Chapter 3 evidenced the role of climate in the evolution of reproductive suppression in species that already delay dispersal, this hypothesis could be further investigated by assessing the differences in climate patterns at the order level.

Towards a comparison with birds

Cooperative breeding in birds

Most studies regarding evolutionary pathways to cooperative breeding in birds suggest that, similarly to mammals, alloparental care mostly evolved within family groups formed through delayed dispersal (Stacey and Ligon 1991; Ligon and Burt 2004; Brown 2014), and within kin neighborhoods formed by short-distance dispersal (Dickinson and Hatchwell 2004). Life history also played a key role in the evolution of cooperative breeding in birds.

In contrast to these similarities, avian and mammalian cooperative breeding display a number of differences. Unlike in mammals, the distinction between cooperative and communal breeding is not always clear in birds due to the lack of distinction between non-breeders and potential breeders in many cases (Cockburn 1998). Indeed, in many species, groups include several breeders of each sex in addition to non-breeding helpers (Hatchwell, 2009), and cases where all individuals are potential breeders, such as dunnocks (*Prnuella modularis*), are even more difficult to classify_ (Davies 1992). Furthermore, avian cooperative breeding systems are rarely obligate. Although a tiny number of species cannot breed without helpers, such as white-winged choughs that do not produce more than

one young per year when there are less than seven individuals in the group (Heinsohn 1992), reproductive success in pairs without helpers has been reported in a majority of cooperatively breeding birds. Pairs form the majority of groups in a proportion of them, thus blurring the frontier between pair-living and cooperative breeding. This leads to further discrepancies in the classification of avian cooperative breeders. For instance, Cockburn (2006) classified as pair-living 150 species with rare instances of cooperative breeding, although some of them were classified as cooperative breeders in other research (Arnold and Owens 1998; Brown 2014). Therefore, some bird species are classified as cooperative breeders in key studies although as few as 10% of nests are actually attended by two adults (Cockburn 2006).

Avian cooperative breeding is also comparatively rarer in islands. A possible explanation for this may be that colonization is facilitated by dispersal of both sexes, in contrast to species in which one or both sexes are philopatric (Cockburn et al. 2003).

The rarity of cooperative breeding in mammals

Cooperative breeding is displayed in less than 1% of mammal species (Clutton-Brock 2016), whereas its occurrence in birds has been estimated to 9% in an extensive dataset of 9456 bird species assigned to 188 families (Cockburn 2006), and has evolved at least 28 independent times (Ligon and Burt 2004). There are several possible explanations for the rarity of cooperative breeding in mammals compared to birds.

Family living is more frequent in birds

First, family living, which is the main mechanism leading to the evolution of cooperative breeding, may be more frequent in birds than in mammals. In birds and mammals, a similar high proportion (96% in birds and 90% in mammals, respectively) of species living in multigenerational family groups further evolve towards cooperative or communal breeding (Krebs et al. 1993). Therefore, there is most likely no obstacle for family-living mammals towards the evolution of cooperative breeding compared to birds, and the higher proportion of cooperative breeding in birds mostly stems from the higher prevalence of family living. The link between multigenerational family groups and cooperative breeding is actually stronger in mammals than in birds. Indeed, 95% of cooperatively breeding mammals live in such groups, whereas it is the case of 88% of birds (Krebs et al. 1993). In a more recent estimation, Riehl estimated that 15% of known cooperatively breeding birds nested with non-kin, and 30% nested with both kin and non-kin (Riehl 2013). Therefore, in addition to the higher frequency of family living species in birds, the prevalence of cooperative breeding in birds should also be explained by a higher occurrence of non-kin cooperative breeding than in mammals.

Altriciality may enhance cooperative breeding in birds

A vast body of literature suggests altriciality to have played a role in the evolution of cooperative breeding in birds. Indeed, altriciality requires a high level of parental investment, and is thus likely to increase the benefits gained by the offspring in the presence of helpers (Ligon and Burt 2004). This hypothesis is backed by the higher prevalence of cooperative breeding in altricial species (11%) than in precocial species (4%) (Cockburn 2006). Altriciality is also thought to be ancestral in most extant bird lineages (Starck and Ricklefs 1998). If altriciality is indeed ancestral in birds, it may have facilitated the evolution of avian cooperative breeding. In contrast, although altriciality is also widespread in mammals, the relationship between cooperative breeding and developmental mode appears to be less clear, presumably due to precocial offspring also needing parental care in the form of nursing in mammals (Scheiber et al. 2017). However, although there are examples of both precocial (i.e. *Fukomys damarensis*) and altricial (i.e. *Heterocephalus glaber*) species among cooperative or eusocial mammalian breeders, it should be noted that cooperative breeding evolved in orders with mostly altricial species such as Primates, and not in orders with mostly precocial species such as Artiodactyls.

Stronger augmentation benefits in birds

In addition to kin groups being more frequent in birds and thus enhancing the evolution of cooperative breeding, the processes driving the evolution of non-kin cooperative breeding may be stronger in birds as well. For instance, they may increase their survival via group augmentation benefits, or increase their probability of inheriting a breeding position and/or their reproductive success once they breed, more than mammals. Several empirical studies support this hypothesis. First, some birds in groups have significantly higher survival than those that breed alone (Walters et al. 1992; Khan 1999). Strong group augmentation benefits would also provide a strong explanation to the occurrences of adults kidnapping and raising unrelated juveniles in white-winged choughs (Heinsohn 1991).

Intraspecific brood parasitism

Another possible explanation is that non-kin cooperative breeding in birds may have evolved via intraspecific brood parasitism (Vehrencamp and Quinn 2004). Indeed, in some bird species, mostly species where egg size relative to body size is small enough to allow for the incubation of a larger clutch than what a female can lay, a female lays her eggs in another's nest without providing any parental care after hatching. The adoptive birds benefit from the presence of additional young via the predator illusion effect, which decreases the odds for their own offspring to be predated (Vehrencamp and Quinn, 2004). These benefits usually outweigh the costs of caring for additional young. Despite the lack of direct evidence for this hypothesis, theoretical studies suggest that a transition between intraspecific brood parasitism and cooperative breeding is likely (Zink 2000; Riehl 2013). Furthermore,

intraspecific brood parasitism is common in species in which females primarily breed in joint nests, which suggests a high flexibility in the choice of strategy (Riehl 2010). Given that intraspecific brood parasitism is impossible in mammals, its possible involvement in the evolution of non-kin cooperative breeding in birds may explain why non-kin cooperative breeding did not evolve in mammals.

Loss of kinship in cooperatively breeding birds

Finally, it has been hypothesized that non-kin cooperative breeding evolved from kin cooperative breeding in birds. Under that hypothesis, kin selection initially played a key role in the evolution of cooperative breeding, and kinship has subsequently been lost due to immigration, promiscuity or brood parasitism (Cornwallis et al. 2010; Cockburn 2013). Given the involvement of promiscuity in the switch to non-kin cooperation, the stabilization of monogamy by cooperative breeding in some mammals (Chapter 1) may explain why cooperatively breeding groups of mammals stayed highly related through evolution, contrary to birds. Furthermore, the absence of brood parasitism may also translate into the lack of a key mechanism in kinship decrease in cooperative breeders, thus providing a supplementary explanation to the lack of non-kin cooperative breeding in mammals. However, this hypothesis can explain why there are non-kin cooperative breeders in birds and not in mammals, it focuses on species that already breed cooperatively, and thus does not provide any explanation for the higher frequency of cooperative breeding in birds compared to mammals.

Possible explanations for different evolutionary patterns of cooperative breeding in mammals and birds

In addition to being rarer in mammals than in birds, the evolution of cooperative breeding displays slightly different patterns in the two taxa.

While monogamy is crucial to the evolution of cooperative breeding in both mammals and birds (Cornwallis et al. 2010; Lukas and Clutton-Brock 2012a), the possibility for monogamy to be a step rather than a prerequisite in the pathway to cooperative breeding (Chapter 1) may also apply to birds. Thus, ancestral reconstructions of combinations of monogamy and constitutive traits of cooperative breeding in birds may shed light on whether monogamy evolved before or after traits such as delayed dispersal and reproductive suppression. However, it should be noted that monogamy is very common in birds, where as much as 90% of species can be considered socially monogamous (Cockburn 2006), whereas this is only the case for 9% of female mammals (Lukas and Clutton-Brock 2013).

Evolution of delayed dispersal and reproductive suppression: Could resource defense cause differences?

In most bird species with female-biased dispersal, males defend critical resources and compete for females via their ability to hold these resources, which provides limited opportunities for male dispersal (Greenwood 1980). Indeed, males may benefit from the familiarity with their natal territory while acquiring resources that are necessary to building a breeding territory, as well as be advantaged against other males when they compete over an area where they were already present. Females may also display a preference for local males. This remains true in migratory species, in which fledglings of the dispersing sex, usually females, either disperse before migration, or return to breeding sites farther from their natal site than their siblings of the philopatric sex (Wolff and Plissner 1998). A few exceptions can be found, such as in the family of Anatidae, where pair formation may occur during migrations, in which case males return to females' territories, rather than their own, to breed (Cooke et al. 1975).

These differences may also explain why monogamy impairs the dispersal of males in mammals while no coevolution between sex-biased dispersal and monogamy was found in birds (Mabry et al. 2013).

The role of ecology and life history traits: The dual benefits framework may provide an explanation to the discrepancies between taxa

Regarding environmental variables and life history traits involved in the evolution of cooperative breeding, there are notable differences between mammals and birds. Although longevity has been shown to be correlated with higher rates of cooperative breeding in bird families (Arnold and Owens 1998), there is no such correlation in mammals (Lukas and Clutton-Brock 2012b).

The dual benefits framework proposed by Shen and his colleagues may shed light on these differences between mammals and birds (Shen et al. 2017). According to this model, grouping benefits can be classified into resource defense benefits (RD), which are obtained from defending resources as a group, and collective action benefits (CA), which result from social interaction between group members. Spatial variation (habitat heterogeneity) mostly increases RD benefits, and favors delayed dispersal in temporally stable environments. When habitat heterogeneity is low, delayed dispersal is favored in favorable environments. Contrastingly, temporal variation (low predictability) and environment harshness (*i.e* low mean annual rainfall) increase CA benefits. Given the key role of resource defense in the evolution of dispersal patterns (Greenwood 1980) and cooperative breeding (Canestrari et al. 2008) in birds, it can be hypothesized that RD benefits mostly apply to birds, whereas CA may apply more to mammals. Thus, the dual benefits framework may explain the specific role of longevity in birds. Indeed, while high adult mortality and low longevity play a crucial role in the RD-driven life history hypothesis, their involvement in collective action benefits is less clear. As a conclusion, our

results suggest that, while some bird families may have evolved cooperative breeding via high resource defense benefits, thus explaining the correlation with life history, cooperative breeding may have mostly evolved via collective action benefits, in which predictability is crucial.

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Appendix: The estimation of mammalian sex ratios: a critical reappraisal

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Abstract

Adult sex ratio (ASR) is a fundamental concept in population demography, and interspecific variation in ASR may have strong implications for behavioral evolution and biodiversity conservation. However, providing reliable ASR estimations at the species level is widely thought to be laden with difficulties stemming from both intraspecific variation in ASR and variation in detection bias depending on estimation methods. Here, we provide a critical evaluation of ASR estimations, using data from 100 populations of 51 mammal species. We evaluate the repeatability of ASR estimates at both species and population levels using a GLM approach, and identify which factors, including estimation method, body size, sex-biased dispersal and mating system, underlie high within-species variation in ASR. We find that the repeatability of ASR estimates is satisfying at the species level ($r=0.600$), and close to that observed in birds, including species where estimations were performed in different populations or methods. We find no effect of sex-biased dispersal and mating system on within-species ASR variation. However, using capture-based methods rather than censuses may help reduce within-species variation in ASR estimates, especially on smaller species. We conclude that ASR estimates are reasonably accurate in most cases, and can widely be considered as a species-specific parameter in further studies regarding conservation and behavioral evolution.

KEYWORDS

Sex ratio, adult sex ratio, mammals, capture, census

Introduction

Adult sex ratio (ASR; the proportion of males in the adults of a population) is a fundamental demographic property of a population (Székely et al. 2014). Due to greater mating opportunities for the rarer sex compared to the supernumerary sex, ASR is a key factor of behavioral evolution. ASR is indeed thought to influence mating systems, intrasexual competition, parental care and behavioral differences between sexes (Kokko and Jennions 2008; Jennions et al. 2017; Schacht et al. 2017). Imbalanced ASR may even have major implications for dispersal patterns and sociality in humans (Kramer et al. 2017). Variation in ASR may also influence key aspects of life histories, such as survival and reproductive success, by modifying investment in parental care, mate competition and harassment (Székely et al. 2014). Finally, ASR is also crucial in population dynamics and conservation. Strongly unbalanced ASRs, in particular, may cause a major risk of population extinction or collapse, due to behavior-related increase in mortality (Galliard et al. 2005), lower effective population size (Frankham 1995) or decrease in reproductive success (Solberg et al. 2002). Therefore, accurate estimates of ASR are crucial to understanding the relationship between ASR and behavior, life history or evolution at the species level or above.

ASR varies widely in wild populations, ranging from heavily female-biased populations to largely male-biased ones (Donald 2007). For instance, an extreme male-biased ASR was found to be persistent over years in a population of Kentish plover *Charadrius alexandrinus* (Kosztolányi et al., 2011), whereas the presence of male-killing *Wolbachia* allows for the persistence of a 100 females per male sex-ratio in a natural population of the butterfly *Hypnolimnas bolina* (Dyson and Hurst 2004). Such variation may result from intrinsic characteristics of the species. Indeed, ASR emerges from differences in birth sex ratio (BSR), sex differences in juvenile and adult mortality, different maturation rates for males and females or sex-biased dispersal. These factors underlying variation in ASR can be highly dependent on species. However, previous studies conducted on the same species indicate significant within-species variation in ASR estimates. Such variation raises major issues in the use of ASR studies as a species characteristic.

Two major, non-exclusive hypotheses may underlie the within-species variation in ASR estimates. First, obtaining accurate ASR estimates can be challenging (Ancona et al. 2017). Field estimations of ASR are usually obtained either by counting individuals (census), by trapping unmarked individuals (capture), or by using mark-recapture methods. More rarely, other methods such as counting carcasses (Norbury et al. 1988; Takeuchi and Koganezawa 1994) or performing molecular analyses of biological samples such as feces or hair (Kruckenhauser et al. 2009; Tredick and Vaughan 2009) can provide ASR estimates. Depending on sex differences in behavior, morphology and habitat, different methods of estimation

may produce discordant ASR estimates. For example, different patterns of activity or bait sensitivity between sexes may incur differences in catchability, leading to a bias in capture-based estimates (Drickamer et al. 1995; Domenech and Senar 1998; Solmundsson et al. 2003). Morphological sexual dimorphism may increase the observability of one sex and induce a bias in census estimates (Ancona et al. 2017). Simulations from previous studies thus suggest that methodological bias may vary according to species, depending on sex differences in movement pattern and detectability (Rodrigues and Coelho 2016). Second, it is possible that within-species differences in ASR estimates result from an actual variability in ASR between populations rather than method bias. Indeed, inter-population variation in environmental conditions, population size, dispersal opportunities or resource availability may affect males and females differently. Such variation may influence sex differences in mortality, maturation rates or dispersal, and therefore result in changes in sex ratio (*i.e* Bókony et al., 2019). In order to understand the origin of within-species variability of ASR estimates, it is crucial to assess inter-population variation and how the method influences these estimations.

Mammals are optimal to conduct a study on ASR estimations. Indeed, mammals display huge diversity in a number of traits that may affect the reliability of observed ASR at the species level, such as social organization (Clutton-Brock 2016), physical and behavioral sexual dimorphism (Weckerly 1998; Lindenfors et al. 2007), sex-biased dispersal (Greenwood 1980), and inter-population variation. Furthermore, imbalanced ASR can result from selective harvesting and are suspected to raise major conservation issues in mammals (Ginsberg and Milner-Gulland, 1994; Marealle et al., 2010; McLoughlin et al., 2005; Solberg et al., 2002). However, ASR estimates are often suspected to be unreliable in mammals. Sex differences in home range, preferred foraging areas, activity patterns and vigilance make males easier to detect than females in a number of mammalian species. However, sex ratio estimates of ungulate populations are thought to be frequently biased towards females due to imperfect detection (McCullough et al. 1994), which can be accounted for with accurate estimators (Weaver and Weckerly 2011). In most mammalian groups, males are on average significantly larger than females, which may add bias to ASR estimates (Szekely et al. 2007). Therefore, assessing the accuracy and factors of variation of ASR estimates in mammals is crucial to the understanding of demographic and social questions in mammals.

In this paper, we aim at providing guidelines to produce accurate estimates of ASR in wild mammalian populations. We perform an analysis of the factors underlying intraspecific variation in ASR. Such factors include variation between populations and method. We assess if these factors influence ASR measures differently depending on order, body size, sexual dimorphism and social system.

Material and methods

Data collection

We extensively searched the primary literature in order to collect ASR data from published sources. Search was not restricted to any mammalian taxon and effort was made to cover as many mammalian taxa as possible. We only searched for a species if the key variables (see below, mating system, male and female body mass, sex-specific dispersal) for that species were all available in the literature. We aimed at collecting several ASR estimates per species, if they were available. Multiple ASR estimates could be extracted from the same study (e.g. if a study investigated two populations of a given species, or ASR was estimated separately for each year of study) or from different studies of a given species. For most studies, ASR was stated in the original source, although 26 ASRs were calculated using the data provided by the source study using the number of adults of each sex. Our final database includes 233 ASR estimates from 51 species (4.57 ± 4.60 estimates per species). The median number of individuals for ASR estimates was 77.5 individuals, although a few studies used large sample sizes, notably in ungulates and rodents (*Connochaetes taurinus*, *Kobus kob*, *Mastomys natalensis*) so that both the mean and variance of sample size are high (665.64 ± 2168.00 individuals per species).

ASR is given as the proportion of adult males in the population (number of adult males / total number of adults, Ancona et al. 2017). For each ASR estimate, we report sample size, as well as the population ID so that to compare within-population and among-population variation in ASR. To investigate the influence of ASR estimation method on the reliability of ASR estimates, we also report the method of estimation classified as census (i.e., observing and counting unmarked individuals), capture (trapping and assessment of individuals without further recapture), capture-recapture, carcasses (counting dead individuals) or molecular (using genetic sexing of samples such as feces).

Mating system was defined as polygynous, promiscuous or monogamous (Clutton-Brock 1989) and sex bias in dispersal as male-biased or female-biased ? (Handley and Perrin 2007). Sexual size dimorphism (SSD) was estimated as the logarithm of the ratio of male body mass over female body mass.

Consistency of ASR estimates

We performed a repeatability analysis using the R package rptR (Stoffel et al. 2017). In order to assess which parameters influence repeatability, we investigated three orders separately given that these orders have ASR data from at least 8 species per order (Artiodactyla, Primate and Carnivora); mating system, sex bias in dispersal and sexual size dimorphism. For sexual size dimorphism, species were divided into three categories: No sexual dimorphism, low sexual dimorphism and high sexual dimorphism. The threshold between low and high SSD was placed at 0.17 in order for the low

and high datasets to include the same number of species (see Supplementary data for the distribution of SSD among species). In order to assess the role of small sample sizes in extreme observed ASR values, we calculated a phylogenetic Spearman correlation coefficient between sample size and deviation from mean ASR (Revell 2010).

Influence of mating system, sex-specific dispersal, population and estimation method on within-species ASR variation

We separately calculated within-species and within-population relative variability of ASR as the coefficient of variation (CV) of ASR estimates for each species (Abdi 2010). We then estimated the influence of mating system, sex-biased dispersal, SSD, method and population variation on relative ASR variability. In order to investigate the effect of the species bias in method selection, we performed both generalized least squares uncorrected for phylogeny (GLS) and phylogenetic generalized least squares (PGLS).

We use the mammalian supertree (Bininda-Emonds et al. 2008) and pruned it to our set of species. For the latter, we used the Brownian correlation structure from the APE package (Paradis et al. 2004). We compare coefficients of variation based on whether the estimates for these species were obtained on one or multiple populations, whether they were estimated with multiple methods (in which case the method of estimation was classified as “multiple”, otherwise we reported the method of estimation for this species). We also compare species regarding their mating system (monogamous, promiscuous or polygynous, as no strict polyandrous species was included in the dataset), their sex-bias in dispersal (male-biased, female-biased or unbiased) and their SSD.

Finally, we fitted both phylogenetically corrected and uncorrected GLMs using the package *phylolm* (Ho et al. 2018) on both within-species and within-population coefficients of variation, respectively, to identify which of the aforementioned variables correlated with them. In order to investigate the interactions between significant predictors ($p < 0.05$), they were included in a further GLM allowing for interactions.

For both phylogenetically corrected and uncorrected analyses, we removed one species from the dataset (*Cervus elaphus*) because its extremely high coefficient of variation in ASR (CV = 115.13%) obtained on three observations induced correlations that were not robust to the removal of the species.

Results

Distribution of ASR

Adult sex ratios were female-biased in most mammals (0.45 ± 0.13 , median ASR = 0.47, one-sample t-test $p = 0.007$, $n = 51$ species : they ranged from heavily female-biased (e.g. 0.14 in *Kobus kob*) to male-biased (e.g. 0.65 in *Vulpes vulpes*). Within-species variation in ASR (measured by CV) did not correlate with the mean ASR ($r = 0.23$, $p = 0.57$, $n = 51$ species, Supplementary figure 1b), which suggests that male-biased ASR were not more subject to high within-species variation than female-biased ones. Surprisingly, we found a positive correlation between sample size and the deviation from the mean ASR, ($r = 3.79 \pm 1.1$, $p < 0.001$, $n = 51$ species), which indicates that extreme ASRs were not caused by a low sample size: on the contrary, large sample sizes were primarily observed for species with extreme ASRs. However, this positive correlation depended upon 3 extremely large sample sizes since it was not present when they were removed (Figure 1). Orders showed substantial differences in both mean ASR and mean CV. For instance, ASR were mostly balanced in primates and carnivores (carnivores: ASR = 0.55 ± 0.15 ; primates: ASR = 0.49 ± 0.10) whereas they were female-biased in artiodactyles (ASR = 0.34 ± 0.17). Within-species variation was lower in primates (CV = 14.61 ± 8.36) than in carnivores (CV = 22.24 ± 26.80) and artiodactyles (CV = 32.39 ± 32.98).

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Figure 1 – Funnel plot displaying ASR estimates in relation to sample size. Each dot represents an ASR estimate and is colored according to the method of observation. The red straight line represents the mean ASR of our dataset, while the yellow and blue lines represent the 80% and 95% confidence limits, respectively. 30 sample sizes larger than 500 (ranging from 513 to 19,965) were not included in this relationship

Repeatability of ASR

ASR estimates were highly repeatable ($r_{ICC} = 0.600$, $P < 0.001$, $n=51$ species, Figure 2a). The repeatability of ASR estimates observed within population was even higher ($r_{ICC} = 0.787$, $P < 0.001$, $n=172$ populations, Figure 2b). At both levels, the repeatability was higher than the repeatability measures performed from permuted datasets (Figure 2).

However, there was an extensive variation across species in the amount of within-species variation in ASR. Within-species CV in ASR ranged from 1.21% to 115.13%, with a median of 16.99%. In particular, two species displayed exceptionally high CV (*Otaria byronia*: CV = 79.37%, and *Loxodonta africana*: CV = 66.54%, Supplementary figure), which indicates extremely discordant ASR estimates among populations. Accordingly, repeatability measures slightly differed between orders (carnivores: $r_{ICC} =$

0.670, $P < 0.001$, $n=8$ species; artiodactyles: $r_{ICC} = 0.665$, $P < 0.001$, $n=9$ species; primates: $r_{ICC} = 0.745$, $P < 0.001$, $n=9$ species).

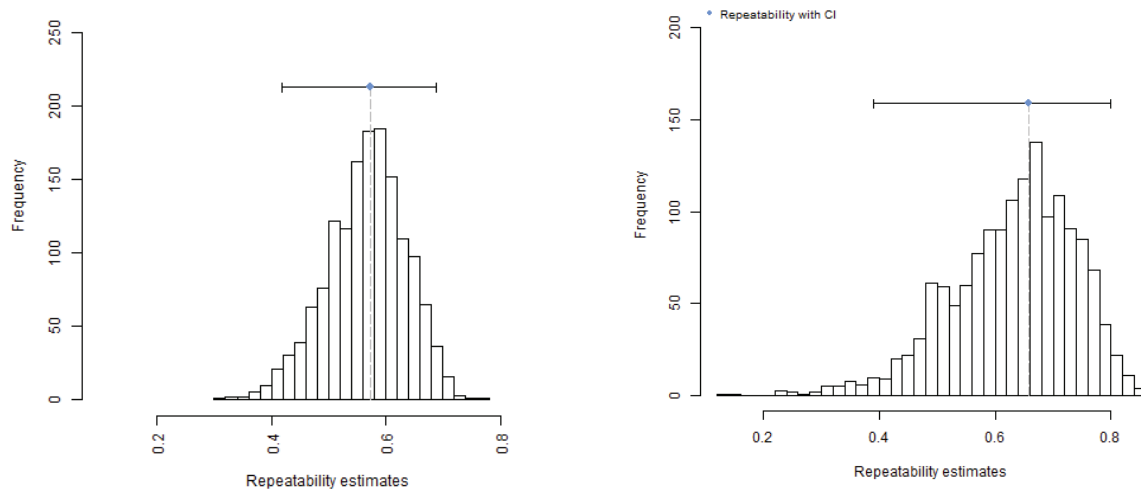


Figure 2 – Distribution of the repeatability measures within species (a) and within populations (b). The blue dots and bars represent the median and 95% confidence intervals, respectively for 51 species and 172 populations. We obtained both distributions using 1500 bootstrap samples.

Factors influencing variation in ASR

Estimation method

There was no correlation between the use of census as a method to estimate ASR and the observed variation in ASR when accounting for phylogeny ($F = 2.58 \pm 7.88$, $p=0.75$, Table 1), although the use of census-based methods led to high intraspecific variation in ASR ($F=11.72 \pm 6.11$, $p=0.05^*$, Supplementary) in non phylogenetically corrected analyses, which suggests that census methods may be preferentially used for species that display high variation in ASR, difficulties in obtaining reliable ASR estimates, or both. Most unusually high variation in ASR was observed in species for which census was the only estimation method used (Figure 3). However, there was no statistically significant increase in ASR variation when multiple estimation methods were used to produce the different estimates within a given species ($F=11.76 \pm 6.74$, $P=0.06$, Figure 3). This suggests that there is no major discrepancy between the estimates provided by different methods when applied to the same species.

The GLM model suggests that a weak interaction occurred between ASR estimation method and log body mass. Large size combined with census method correlated positively with the amount of observed variation in ASR ($F=7.33 \pm 3.60$, $p=0.05^*$). GLM models provided no support for interactive effects between method and SSD, method and mating system, or method and amount of sex-biased

dispersal, which suggests that the lower repeatability of census-based ASR estimates is a specific feature of this method of sampling ASR and is independent on the species life style, except for body mass (Table 1)

Sexual size dimorphism

GLS estimates showed that the within-species variation in ASR increased with SSD ($F = 58.53 \pm 17.79$, $P=0.02^*$, Table 1). Strongly dimorphic species displayed high mean CV in ASR ($cv_{high\ SSD} = 26.32\%$), whereas non-dimorphic and lowly dimorphic species displayed similar lower CV ($cv_{no\ SSD} = 15.93\%$, $cv_{low\ SSD} = 16.17\%$). When restricted to species with strong SSD, the repeatability of ASR was not statistically different from 0, suggesting that ASR estimations may not be repeatable for highly dimorphic species (Supplementary figure).

Social traits

Neither the dispersing sex nor the mating system influenced the amount of ASR variation (both $P > 0.05$, Table 1; Figure 3). Accordingly, the subsets based on sex-biased dispersal (male or both) or mating system (monogamous, polygynous or promiscuous) all showed detectable repeatability (ranging from 0.34 – promiscuous subset – to 0.70 – single population subset -, $P < 0.001$, Supplementary figure).

Population variation

Unexpectedly, estimating ASR for one species using all available ASR estimates from a single population did not provide a lower variation in ASR than using estimates from different populations ($F = -9.45 \pm 5.06$, $P=0.07$, Table 1). Therefore, within-population variation does not significantly increase within-species variation in ASR. Furthermore, we did not find evidence that any tested factor of variation influenced within-population variation in ASR (Table 1).

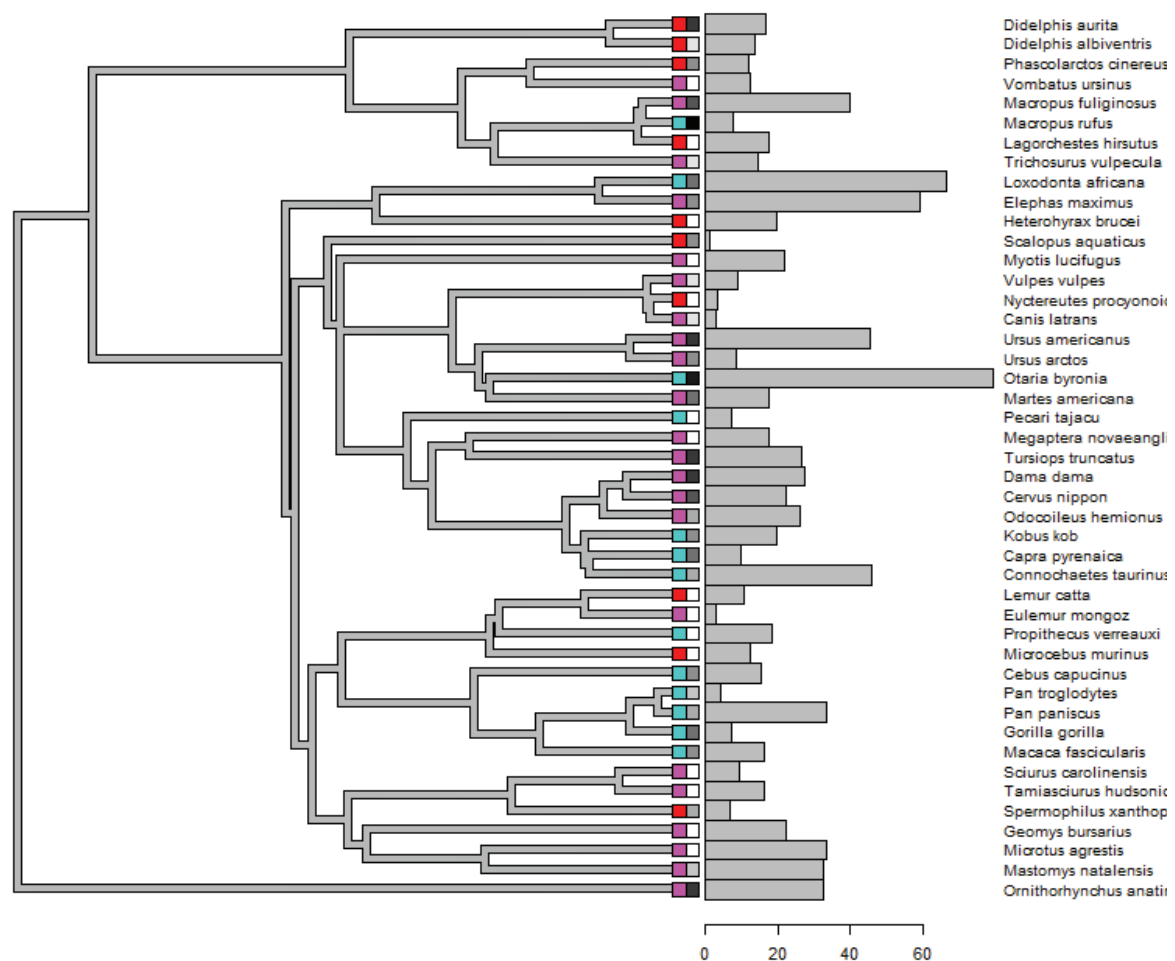
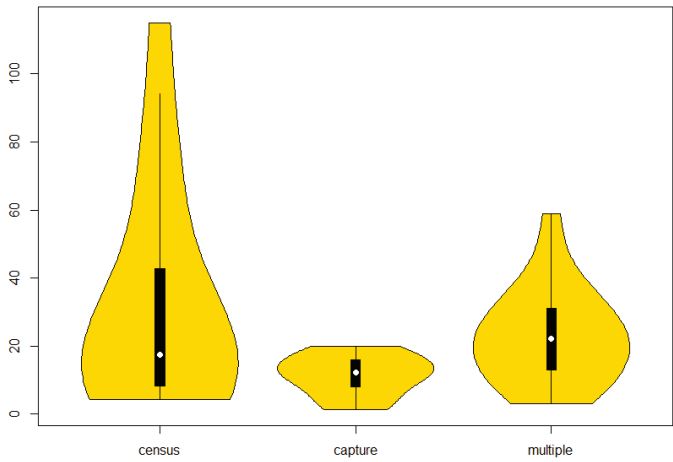


Figure 3 – Phylogenetic distribution of ASR estimation methods, SSD and ASR variation among mammals. Estimation methods and SSD are represented by the squares on the immediate right of the tree. Species where only census, only capture or different methods have been used to produce ASR estimates are displayed by the left square in blue, red and purple, respectively. Darker shades of grey in the right square stand for higher sexual size dimorphism in favour of males. Intraspecific variation in ASR, calculated as the coefficient of variation of ASR estimates in a given species, is displayed in the distribution on the right of the tree.

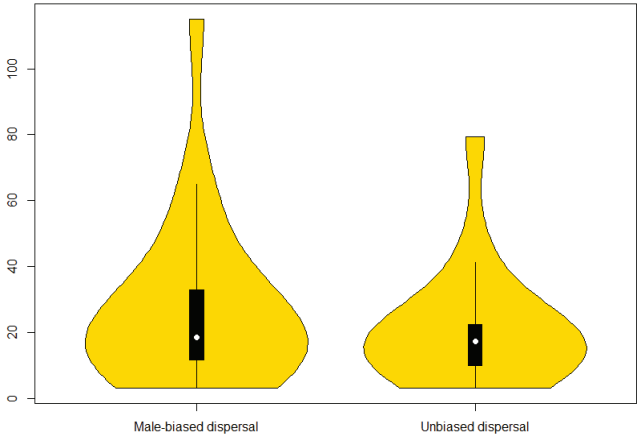
Table 1 – Phylogenetically corrected within-species variation in ASR in relation to estimation method, mating system, sex-biased dispersal, body mass, SSD and whether estimates were conducted on the same population. ASR variation (response variable in all models) is measured by the coefficient of variation (CV) of ASR measures within species (a, n=51 species) or population (b, n=38 populations),

	Coefficient	SE	p
Estimation method			
Census	2.58	7.88	0.74
Multiple	5.92	5.93	0.32
Mating system			
Promiscuous	6.77	16.49	0.68
Polygynous	17.02	16.06	0.30
Monogamous	-0.36	23.57	0.99
Sex-biased dispersal			
Male	1.45	6.78	0.83
Body mass			
	1.24	1.38	0.22
SSD			
	22.66	21.26	0.29

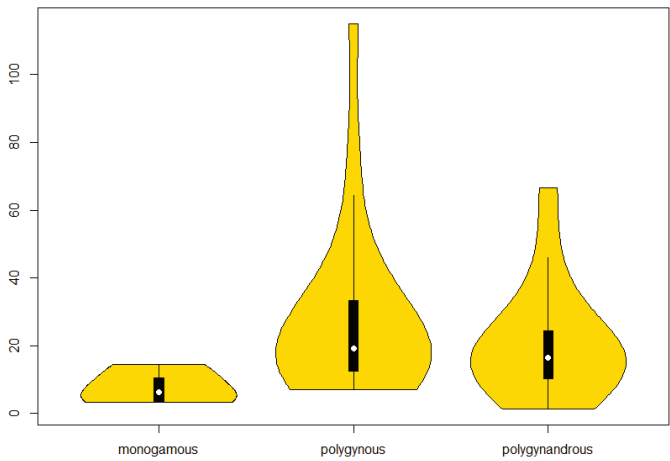
Method



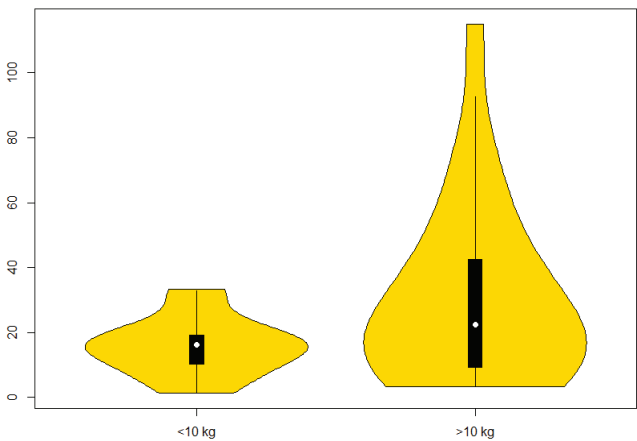
Dispersing sex



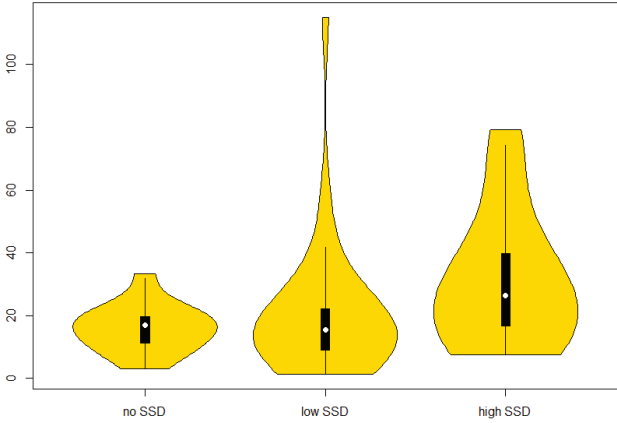
Mating system



Body mass



SSD



Number of populations

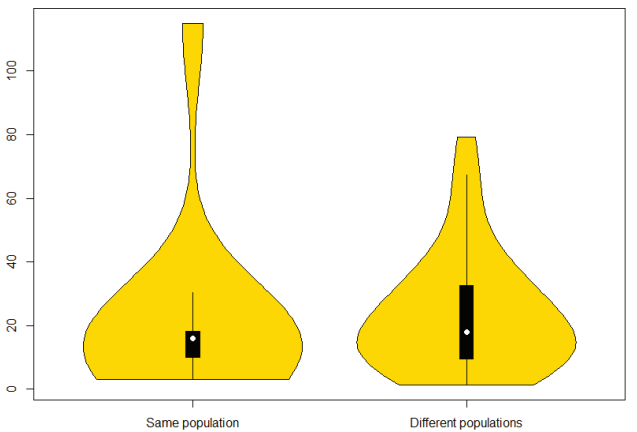


Figure 4 – Distribution of intraspecific relative variabilities of ASR estimates in data subsets. Each subset only includes species with identical methods, dispersing sex bias, mating systems, body size classification, SSD classification or number of populations classification. Relative variability is equal to the coefficient of variation (CV) of ASR measures within species (n=51 species)

Discussion

Although there was substantial within-species variation, ASR estimates were highly repeatable for a given species. The consistency of ASR estimates at the species level in mammals we found here was only slightly lower than that recently reported in birds (Ancona et al. 2017). Consequently, despite the difficulties inherent to data collection on the field and variable sex differences in detection rates caused by sexual size and behavioral dimorphism, ASR estimates were not only accurate in most cases but can be considered as a species-specific parameter such as survival or reproduction. Indeed, between-species differences account for a much larger part of observed ASR variation than within-species variation generated by differences in local conditions shaped by the local context or by methodological issues. Thus, field observations of ASR do provide insightful information for studies of behavioral evolution and population dynamics, including across species comparisons.

However, in a number of cases the reliability of ASR measures can be further improved. For instance, ASR repeatability is higher within population than among populations, which suggests that ASR variations between populations of the same species should not be overlooked. Furthermore, we call attention to the critically high ASR variation in some outlier species, for which it is impossible to detect whether ASR is biased or not, even at the species level. Therefore, we recommend to check systematically the literature for high ASR variation when estimating ASR for a given species, and to use ASR with extreme caution if intraspecific variation is very high, such as in *Cervus elaphus* ($cv=115.13$).

All methods provided consistent ASR estimates, including simple censuses of individuals from field observations. These methods are widely used because they require less effort than capture-based surveys, but have been the object of several concerns regarding the quality of produced observations (Ancona et al. 2017). Indeed, unlike capture-recapture estimates, censuses do not account for sex differences in detection rates, and are also more likely to miss, double-count or misidentify individuals, which leads to bias the ASR estimates. The existence of a correlation between the use of census methods and ASR variation in the non-corrected model, which vanished when using the phylogenetically-corrected model, suggests that the difference in repeatability between census and capture methods is most likely due to the fact that census methods are most often used in taxa with

high intra-specific variation in ASR. Therefore, in most situations where capture-based surveys require too much effort or are technically impossible, censuses remain a useful tool for getting reliable ASR estimates. However, this should not discourage researchers to use detection-based models instead than simple counts when possible. We should also keep in mind that the choice of the method to estimate ASR is typically adjusted to the target species. For instance, census is generally used for large species that are sexually dimorphic in size and hard to capture (e.g. large herbivores), but cannot be used for small and/or monomorphic species (e.g. rodents). Therefore, observed variation in intraspecific variation in ASR according to the method is actually caused by interspecific differences in ASR, rather than by low quality estimates of ASR when using some methods. Finally, we did not find sufficient data during our literature survey to investigate some methods that have only been rarely used, such as molecular analyses of feces or hair. Therefore, further investigation will be needed to provide guidelines on whether such methods could be used reliably or not.

We found a positive correlation between body size and intraspecific variation in ASR. The interaction between large body size and census methods also increases intraspecific variation in ASR. A possible explanation for this may be that it is harder to produce reliable estimates on large species due to difficulties in using more reliable methods such as captures.

We found that intraspecific variation in ASR was higher in species with high SSD. Two main hypotheses may underlie this result. First, high SSD might lead to unreliable observations. In this case, potential difficulties associated with high SSD might depend on the method, which would lead to increase the variance among ASR values estimated from different methods. In capture surveys, high SSD would only induce bias in ASR estimates when coupled with behavioral dimorphism. When using census methods, females might be either less noticeable than males due to their small size, or easier to detect due to their smaller home range. In both cases the ASR estimate will be biased and the magnitude of this bias will vary among habitats sampled. The other possible explanation for higher intraspecific variation in ASR in highly dimorphic species is related to spatial and temporal variation in ASR, which is indeed higher in such species. Thus, higher sensitivity to environmental variables in males may lead to stronger increase in mortality in males than in females during harsh years (Toïgo & Gaillard 2003), and thus lead to high between-year variation in ASR. Such differences are well known to exist in several highly dimorphic and polygynous species. For instance, high population density and high winter rainfall negatively affect the proportion of males at birth (Kruuk et al. 1999), which may have repercussions on ASR. Survival rates of male Soay sheep are influenced by weather throughout winter, whereas those of females are mostly influenced by rainfall at the end of winter (Coulson et al. 2001). Such differences have also been reported to be high in dimorphic bird species in relation to the higher energy demands during growth, which makes the larger sex more vulnerable to a shortage of resources, thus incurring

a strong correlation between SSD and sex-specific mortality, as well as female-male difference in fledging mass change (Benito and González-Solís 2007; Kalmbach and Benito 2007).

Our findings suggests that, in general, ASR estimations are repeatable at the species level in mammals, including those obtained with census methods. ASR can thus be considered a species trait and used in studies at the interspecific level. However, some species, especially those with high sexual size dimorphism or large body size, should be treated with specific caution as intraspecific variation may be higher in such species.

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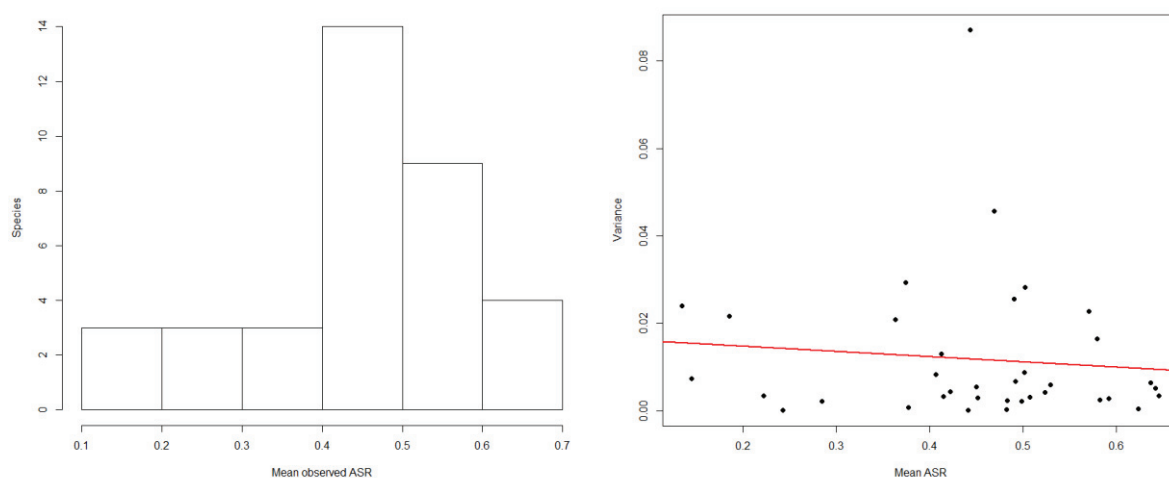
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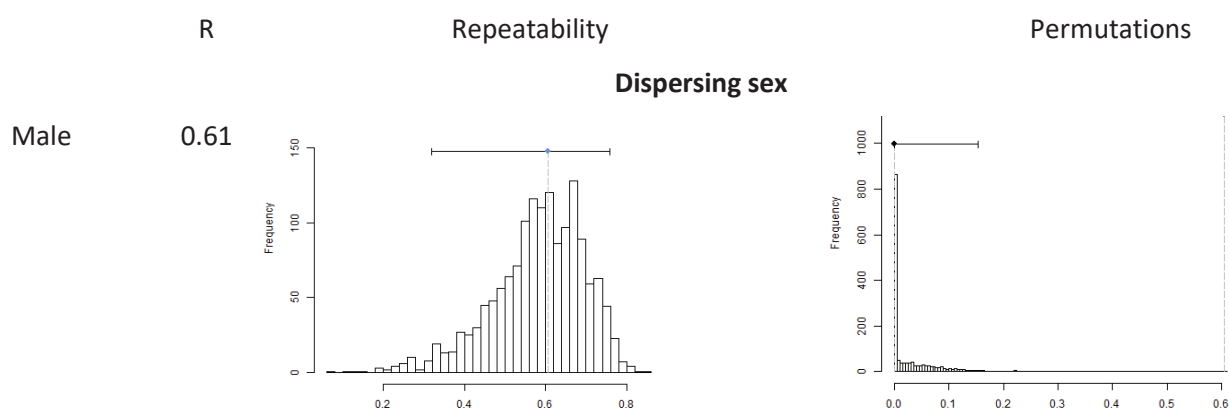
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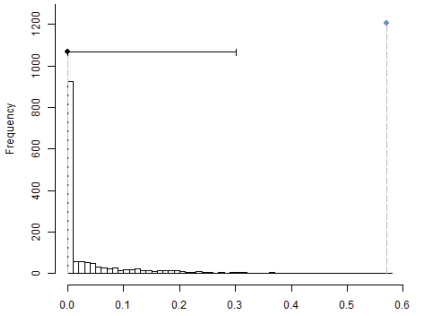
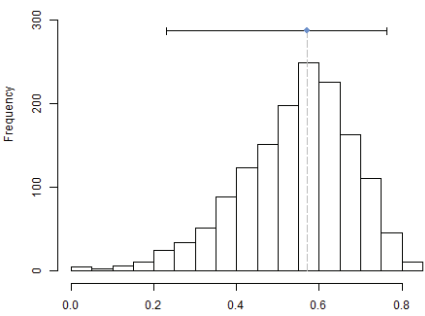
Supplementary data



Supplementary figure 1 – Distribution of mean observed ASR within species

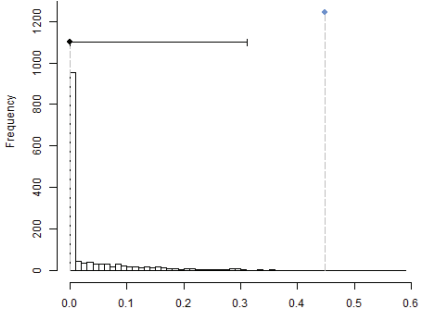
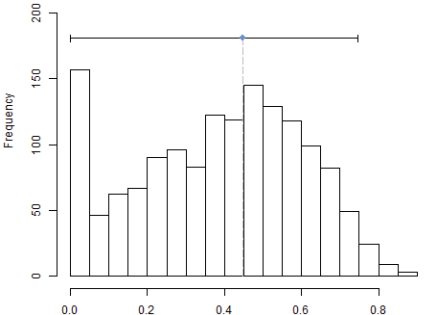


Both 0.57

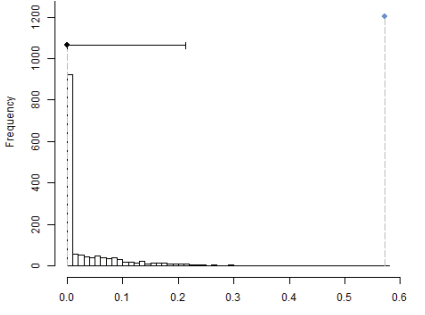
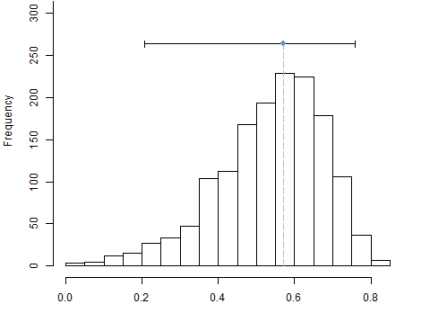


Mating system

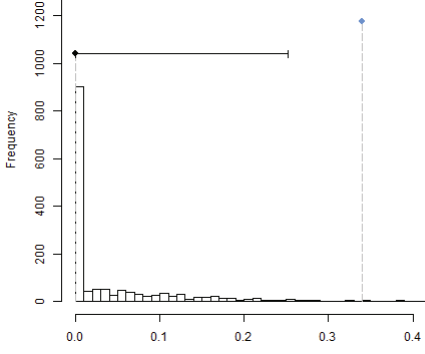
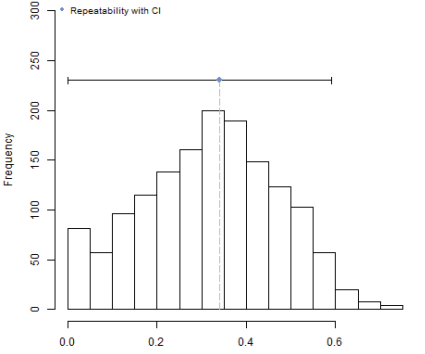
Monogamy 0.44



Polygyny 0.57

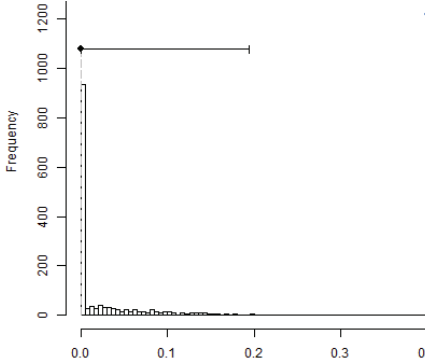
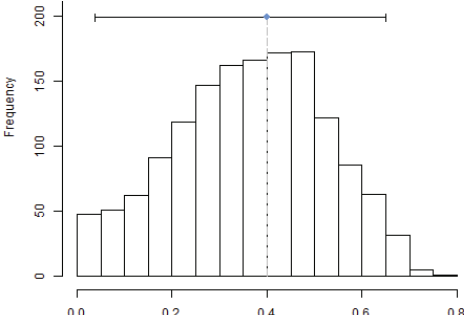


Promiscuity 0.34

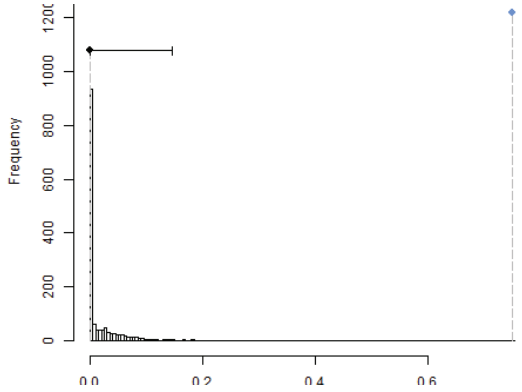
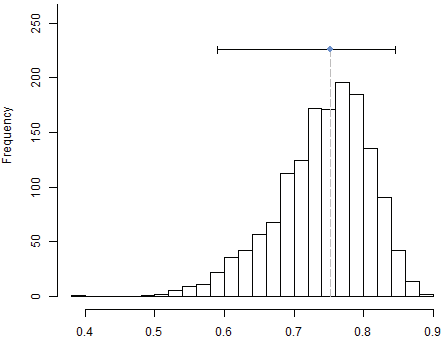


SSD

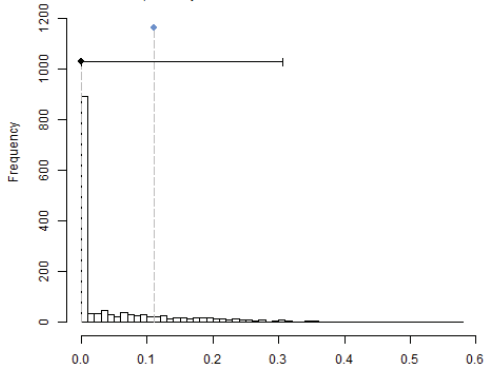
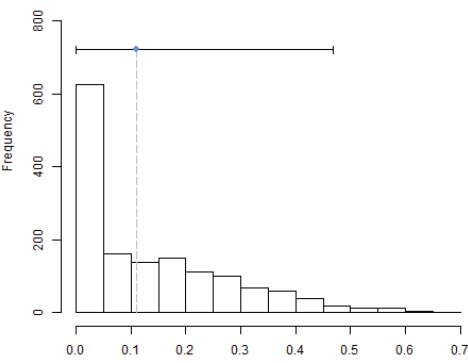
None 0.40



Small 0.75

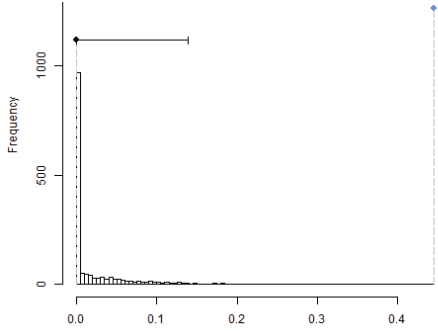
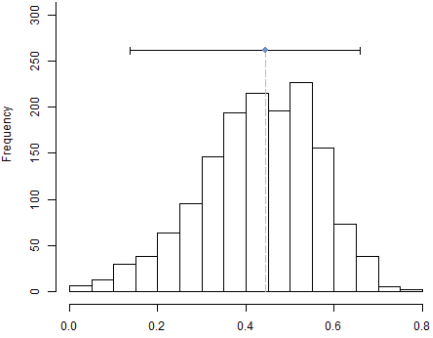


Large 0.11

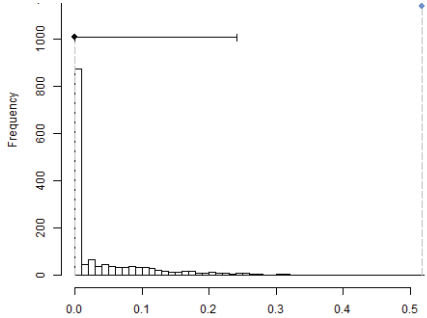
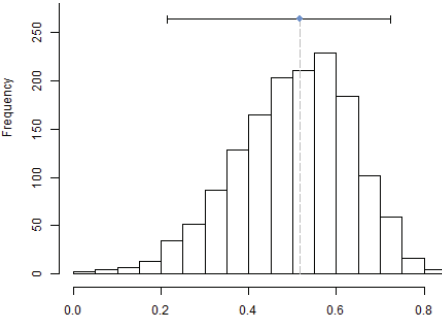


Body mass

<10 kg 0.44



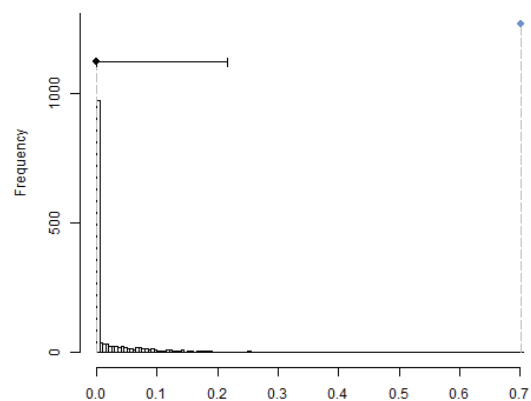
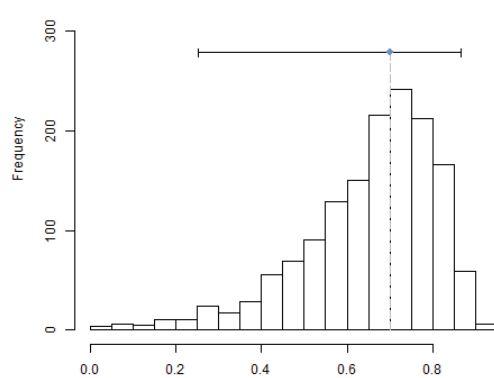
>10 kg 0.52



Number of studied populations

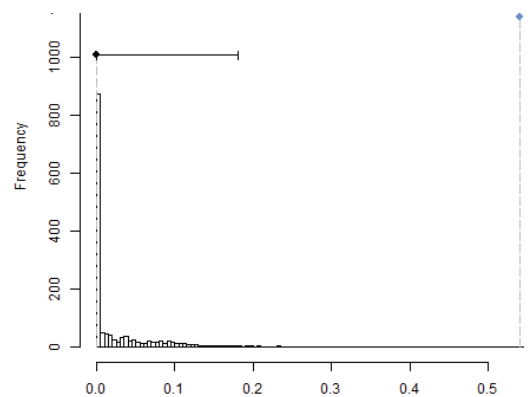
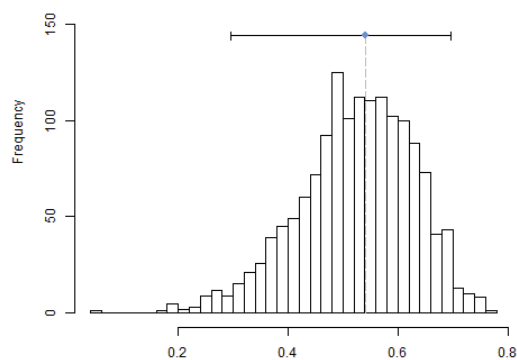
1

0.70



>1

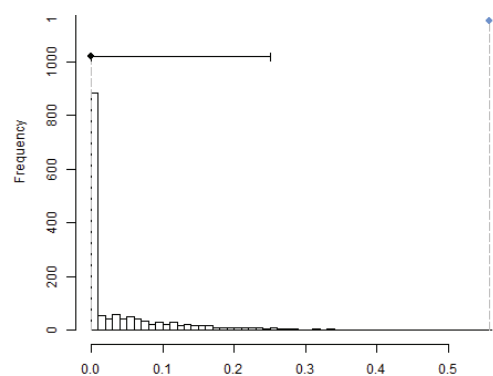
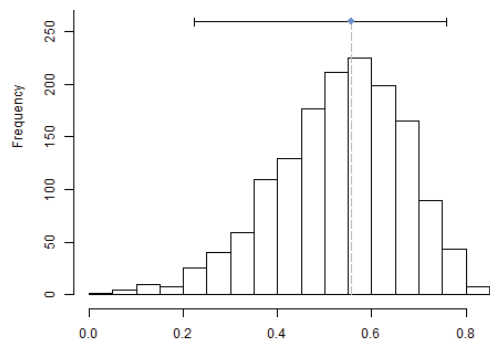
0.54



Number of methods

>1

0.56



Within-species variation in ASR without phylogenetic correction in relation to estimation method, mating system, sex-biased dispersal, body mass, SSD and whether estimates were conducted on the same population. ASR variation (response variable in all models) is measured by the coefficient of variation (CV) of ASR measures within species (a, n=51 species) or population (b, n=38 populations),
Without phylogenetic correction

(a)			
	<i>Coefficient</i>	<i>SE</i>	<i>p</i>
Estimation method			
Census	11.72	6.11	0.05 *
Multiple	11.76	6.74	0.06 .
Mating system			
Promiscuous	13.39	9.37	0.16
Polygynous	16.44	8.97	0.07
Monogamous	-4.45	18.62	0.81
Sex-biased dispersal			
Male	3.41	5.37	0.53
Body mass	1.98	0.72	0.01 **
SSD	58.53	17.79	0.02 **
Estimates conducted on the same population	-9.45	5.06	0.07 .
(b)			
	<i>Coefficient</i>	<i>SE</i>	<i>p</i>
Estimation method	-1.19		0.24
Census	0.43	6.68	0.95
Multiple	-1.60	10.61	0.88
Mating system			
Promiscuous	10.529	10.704	0.33
Polygynous	9.82	10.16	0.34
Monogamous	-5.03	20.73	0.81
Sex-biased dispersal			
Male	-3.10	6.65	0.65
Body mass	7.92	2.46	0.003 **
SSD	46.08	23.92	0.06