Life histories and the evolution of cooperative breeding in mammals

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While the evolution of cooperative breeding systems (where non-breeding helpers participate in rearing young produced by dominant females) has been restricted to lineages with socially monogamous mating systems where coefficients of relatedness between group members are usually high, not all monogamous lineages have produced species with cooperative breeding systems, suggesting that other factors constrain the evolution of cooperative breeding. Previous studies have suggested that life-history parameters, including longevity, may constrain the evolution of cooperative breeding. Here, we show that transitions to cooperative breeding across the mammalian phylogeny have been restricted to lineages where females produce multiple offspring per birth. We find no support for effects of longevity or of other life-history parameters. We suggest that the evolution of cooperative breeding has been restricted to monogamous lineages where helpers have the potential to increase the reproductive output of breeders.

Keywords: cooperative breeding; life history; polytocy; mammals; phylogenetic comparison

1. INTRODUCTION

The evolution of cooperative breeding systems, where breeding females are assisted by non-breeding group members in protecting and feeding their offspring, poses important challenges for the theory of natural selection [1–4]. Recent comparative studies of vertebrates using phylogenetic reconstruction have shown that the evolution of cooperative breeding systems has been confined to socially monogamous species where most recruits to breeding groups have the same father and coefficients of relatedness are high [5,6]. However, cooperative breeding systems have not evolved in all groups of mammals characterized by monogamous mating systems, suggesting that other factors may constrain the evolution of cooperative breeding [7,8].

One possibility that has previously been suggested is that the evolution of cooperative breeding has been restricted to groups where annual mortality is relatively low, so that turnover in breeding positions is slow, and individuals commonly delay dispersal and age of first reproduction [9,10] with the result that the only way of increasing their inclusive fitness open to them is to assist the breeding attempts of relatives. Earlier comparative studies of birds have provided some evidence of an association between cooperative breeding and low mortality [11], however this association has since been questioned [12].

The evolution of cooperative breeding might, alternatively, be restricted to lineages where breeding history allows non-breeding helpers to make a substantial contribution to the reproductive output of breeders [8,13], for example, in species with relatively high fecundity. Previous studies in mammals have shown that females of cooperative breeders commonly have larger litters and shorter inter-birth intervals than non-cooperative social species [14–17]. Although this correlation has normally been interpreted as evidence that cooperative breeding allows reproductive output to increase, helping could also be particularly beneficial in species in which females have particularly large costs of raising offspring: for example, in birds, cooperative breeding appears to have evolved more frequently in altricial than in precocial lineages [18], and in species that depend on scarce or unpredictable resources [19,20].

In this study, we describe phylogenetic comparisons that investigate whether reproductive parameters have restricted the evolution of cooperative breeding in mammals. We first assess whether cooperatively breeding mammals differ from other species in their age of first reproduction, maximum longevity, adult mortality, reproductive investment (neonatal-, litter- and weaning-mass relative to body mass) or reproductive rate (litter size and inter-birth interval). For those parameters that are consistently associated with the presence of cooperative breeding, we subsequently performed phylogenetic reconstructions of the sequence of transitions to detect whether life-history parameters have constrained the evolution of cooperative breeding.

2. MATERIAL AND METHODS

We followed previous authors in adopting a conservative definition of cooperative breeding [5,6,18,21,22], by including species only as cooperative breeders if a proportion of females do not breed regularly and contribute to provisioning or carrying young born to other females. Information on the occurrence of cooperative breeding was collected from reviews and from a systematic search of the available literature on social systems. We identified 34 mammal species as cooperative breeders (see Lukas & Clutton-Brock [6] for details and complete list of species). During the systematic search, we also coded whether species have monogamous mating systems (see [6]). Data for age at first reproduction, longevity, litter size, inter-birth interval and for neonate, weaning and adult body mass were obtained by cross-referencing between published databases [23–25]. We used averages when multiple values for a given parameter for a given species were available. Data on annual adult survival were collected

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from reviews [26–28], and we searched for additional survival values from the primary literature specifically to increase the sample of cooperative breeders [29–31]. Continuous variables were log-transformed prior to analyses. The dated mammalian supertree [32] was used for all phylogenetic informed analyses. The tree was pruned to match the species in the specific datasets by using functions of the package APE [33] in the statistical software R [34].

We first tested whether cooperatively breeding mammals differ from other monogamous or any other mammalian species in each of the variables. Phylogenetically independent contrasts, corrected for branch length, were generated using the function ‘pic’ of the package APE in R. The contrasts of all life-history variables were tested against the contrasts in cooperative breeding in linear regressions forcing the intercept to run through zero. In addition, we used a phylogenetic-generalized least squares (PGLS) approach that estimates the most likely transformation of branch lengths according to Pagel’s lambda to explain the evolution of cooperative breeding while assessing an association with the explanatory terms. We used Akaeke’s information criterion (AIC) to determine which variables best explained the distribution of cooperative breeding. These analyses were performed using the package ‘CAPER’ [35] in R.

Next, we performed multivariate regressions on the life-history variables. Regressions were performed with MCMCglmm [36] in R. MCMCglmm provides an approach to test for the effect of continuous traits on the distribution of a binary trait, including the phylogenetic similarity of species as covariance matrix (see the electronic supplementary material for more information). We first compared models with each life-history factor separately with a null model that included only the covariate monogamy. Significance of terms was assessed based on a comparison of the deviance information criterion (DIC) values. Next, we assessed whether any model that included additive interactions between the factors provided a better explanation of the data. Missing data meant that the sample size of species for which information on all traits was available was small, and the model including all life-history factors would have attempted to explain the distribution of 13 cooperatively breeding species using 11 explanatory variables. We removed those variables with the fewest data points available to retain a dataset that included litter size, longevity, age at first reproduction, inter-birth interval, body mass and monogamy. We used the function ‘dredge’ of the package ‘MUmin’ [37] to compare all possible additive combinations of these variables. This analysis was repeated with a restricted sample which included species that are monogamous only. Finally, we used the function ‘dredge’ to compare all models that include interactions between the factors longevity, litter size and relative neonate mass, the three factors that directly relate to the different predictions.

A series of additional analyses were performed to assess the robustness of these findings. We repeated the analyses using data only from Jones et al. [25], as the authors of the databases that we merged might have relied on different criteria for data selection. As information on longevity can be influenced by sample size, we repeated the analyses with a restricted dataset that only included values of ‘medium’, ‘large’ or ‘huge’ sample size and ‘acceptable’ or ‘good’ quality from the ‘longevity records’ [38]. Tests of independent contrasts are sensitive to the model of evolution of the characters that are tested, and we assessed whether this had strong effects on our analyses by repeating them, using trees with transformed branch lengths all set to ‘1’ or using the ultrametric approach of Grafen [39], and we tested for a correlation between the independent contrasts in cooperative breeding and the remaining variables using the less restrictive non-parametric Spearman’s rho. None of these additional tests changed any of our findings, and we report their results in the electronic supplementary material.

Phylogenetic reconstructions of the sequence of transitions were conducted for the parameters that were found to be associated with cooperative breeding. We used the module DISCRETE [40] of BAYESTRAITS [41] to simultaneously reconstruct the evolution of cooperative breeding and litter size, including 31 cooperatively breeding and 1573 non-cooperatively breeding species. As DISCRETE relies on traits that can be grouped into two distinct categories, we classified all species either as producing a single offspring (monotocous) per birth or as litter bearing (polytocous). The DISCRETE approach makes it possible to assess whether two traits are more likely to have evolved independently or together by assessing the frequency of transitions between the different combined states. It first reconstructs the most likely scenario if two traits evolved independently in the phylogenetic tree and compares this with a scenario in which the two traits are linked in the four possible combinations and where the transitions occur at random. To account for different possible modes of evolution, separate analyses were performed using transformations of the dated trees, creating equal branch lengths and ultrametric branch lengths [39]. The evolution of characters across each of these phylogenies was reconstructed assuming both independent and dependent evolution of the two states. We also allowed the rate of character change to vary for different parts of the tree. Likelihoods for all models were estimated using 25 optimization attempts per run. Significance of results was measured by performing a likelihood ratio test, comparing twice the difference between the independent and dependent model to a chi-square test with four degrees of freedom to reflect the higher number of parameters in the dependent model. Models assuming a dependent model were considered significant at α = 0.05 if the respective likelihood was 4.75 lower than the comparable independent model [40].

To control for the potentially confounding effect of monogamy, we repeated the analyses using a dataset of species for which information was available on cooperative breeding, monogamy and polytocy. We first tested whether the significant associations between cooperative breeding versus monogamy and polytocy, respectively, could also be detected in this smaller dataset. Next, we combined the information on monogamy and polytocy to create a single binary variable of species either having both monogamous mating and polytocy or missing either of the traits, and compared this against the presence of cooperative breeding. We also tested whether monogamy and polytocy are significantly associated. Finally, we tested whether cooperative breeding and polytocy are associated when only including species with monogamous mating. For all these additional analyses, a phylogenetic tree with branch length set to one was used, because the previous DISCRETE analyses of the association between cooperative breeding and monogamy [6] or polytocy (see the electronic supplementary material) showed this transformation to give the best fit to the data.

3. RESULTS
(a) Associations between cooperative breeding and life-history parameters
We were able to identify 34 mammalian species as cooperative breeders belonging to eight families, all of which
contain socially monogamous species (Muridae, Cricetidae, Castoridae, Hystricidae, Bathyergidae, Cebidae, Canidae, Herpestidae). There are also several mammalian families that contain socially monogamous species but have no cooperative breeders (including Hylobatidae, Indridae, Aotidae, Bovidae, Phyllostomidae, Emperidae).

Our analyses provide no evidence that cooperative breeding is associated with the pace of life histories: both phylogenetic independent contrasts and PGLS (for AIC values see the electronic supplementary material) show that cooperative mammals do not differ significantly from other monogamous or any other mammalian species in age at sexual maturity in females (cooperatively breeding species (coop.): median 350 days, \( n = 25 \) species; monogamous species (monogam.): median 365 days, \( n = 60 \) species, \( F \)-statistic = 0.07, \( t \)-value = -0.27, \( p = 0.79 \); remaining mammalian species (remain.): median 365 days, \( n = 977 \) species, \( F = 0.82, t = 0.90, p = 0.37 \) or in maximum longevity (coop. median 153 months, \( n = 30 \); monogam. median 188 months, \( n = 80 \), \( F = 1.02, t = 1.01, p = 0.32 \); remain. median 155 months, \( n = 1143 \), \( F = 1.95, t = 1.40, p = 0.16 \)).

There is also no association between cooperative breeding and measures of demography: annual adult survival is not significantly different, and while the low sample size might have precluded finding a significant effect, the observed difference is opposite to the prediction of a low turnover in cooperative breeders (coop. median 57\%, \( n = 10 \); monogam. median 69\%, \( n = 6 \), \( F = 0.19, t = 0.43, p = 0.67 \); remain. median 75\%, \( n = 122 \), \( F = 1.09, t = -1.05, p = 0.30 \)).

There is also no evidence of a consistent association between cooperative breeding and reproductive investment. There is no significant difference between cooperatively breeding and monogamous or polygynous mammals in the absolute weight of neonates (coop. median 40 g, \( n = 25 \); monogam. median 35 g, \( n = 66 \), \( F = 0.04, t = 0.20, p = 0.84 \); remain. median 14 g, \( n = 1044 \); \( F = 0.06, t = 0.24, p = 0.81 \)) or weanlings (coop. median 18 g, \( n = 14 \); monogam. median 182 g, \( n = 21 \), \( F = 0.84, t = -0.92, p = 0.37 \); remain. median 101 g, \( n = 400 \); \( F = 3.28, t = -1.81, p = 0.07 \)), in the weight of offspring relative to maternal body mass (coop. median 6\%, \( n = 25 \); monogam. median 7\%, \( n = 66 \), \( F = 0.86, t = -0.93, p = 0.36 \); remain. median 6\%, \( n = 1044 \); \( F = 0.14, t = 0.37, p = 0.71 \)), in the relative weight of litters at birth (coop. median 18\%, \( n = 24 \); monogam. median 18\%, \( n = 66 \), \( F = 0.50, t = 0.71, p = 0.48 \)); remain. median 10\%, \( n = 798 \); \( F = 2.42, t = 1.56, p = 0.12 \), or the relative weight of weanlings (coop. median 31\%, \( n = 14 \); monogam. median 33\%, \( F = 2.73, t = -1.65, p = 0.11 \); remain. median 31\%, \( n = 400 \); \( F = 0.83, t = -0.91, p = 0.36 \)).

By contrast, there is a strong positive association between the presence of cooperative breeding and reproductive rate. All 34 identified contemporary cooperative breeders produce litters rather than single offspring (range 2–11 offspring per birth, median 3). They have significantly higher values of litter sizes than other monogamous species (range 1–8 offspring per birth, median 2, \( n = 101 \) species, \( F = 8.17, t = 2.86, p = 0.005 \)) or than other mammalian species (range 1–15 offspring per birth, median 2, \( n = 1573 \), \( F = 16.55, t = 4.07, p < 0.001 \); figure 1a). The high reproductive rate of cooperative breeders is also partly owing to short inter-birth intervals (range 3–24 months, median 6 months, \( n = 27 \) species), which are significantly shorter than in other mammalian species (range 2–100 months, median 12 months, \( n = 810 \) species, \( F = 10.1, t = 3.18, p = 0.002 \)), however do not differ from those of other monogamous species (range 2–80 months, median 10 months, \( n = 54 \) species, \( F = 1.09, t = 1.04, p = 0.30 \); figure 1b).

These results are replicated in the MCMCglmm regression approach. Only litter size produces a change in DIC from a null model that includes just monogamy (see the electronic supplementary material). In additive multivariate regressions that combine the life-history parameters (litter size, neonate weight, longevity, age at first reproduction, inter-birth interval, body mass), while including monogamy as a random covariate, including litter size as an explanatory term leads to a decrease in DIC, while including the remaining factors does not (comparing 19 cooperatively breeding species to 463 non-cooperative species; see the electronic supplementary

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**Figure 1.** (a) Litter size and (b) inter-birth intervals in cooperatively breeding and non-cooperatively breeding mammals. Boxplots depict the median species values as well as the quantiles (box: 25–75\%; lines 0–100\%) for (a) the number of offspring a female produces per birth, and (b) the length of the inter-birth interval in number of months. All cooperatively breeding mammals produce two or more offspring per birth. Cooperatively breeding mammals have, on average, inter-birth intervals that are half as long (six months) as compared with the remaining mammalian species (12 months).
Figure 2. Evolutionary model of transitions. The phylogenetical analyses show that cooperative breeding and a high reproductive rate coevolved. Ancestral and extant species can be classified into one of the four trait combinations: monotocous or polytocous, and cooperative breeder or not. Transitions occurring owing to changes in a single trait at a time: horizontal arrows reflect changes between mono- and polytocous species, whereas vertical arrows reflect the gain and loss of cooperative breeding. The line width of the arrows reflects the rate of transition. The most likely evolutionary model shows that transitions to cooperative breeding never occurred in monotocous species, supporting the prediction that polytocy is a necessary condition for the evolution of cooperative breeding. By contrast, it does not support the prediction that the presence of helpers necessarily leads to increases in reproductive rate, as the transition rate to polytocy in cooperative breeders is similar to the transition rate in species that are not cooperative.

(b) Reconstruction of the sequence of transitions
To assess whether the high reproductive rate of females represents the ancestral condition we performed phylogenetic reconstructions. ‘DISCRETE’ models assuming a dependent evolution of cooperative breeding and polytocy (litter-bearing) had a significantly higher likelihood than the models assuming an independent evolution of the two traits for five of the six models (changing the branch lengths and the rate variation; electronic supplementary material, table S1). According to the most likely model, cooperative breeding systems have never evolved in mammalian lineages where females produce a single offspring per birth (figure 2). The model also suggests that cooperative breeding is rapidly lost if species change from polytocy to producing a single offspring per birth. For example, this seems to have been the case for Goeldi’s monkey, Callimico goeldii, which, unlike other Callitrichids, produces single young and breeds communally, but is probably derived from a cooperatively breeding ancestor [42].

We subsequently investigated whether the association between polytocy and cooperative breeding is independent of the relationship between monogamy and cooperative breeding. Information on all three parameters is available for 1059 species. In this restricted dataset, too, dependent models are significantly more likely and predict that transitions to cooperative breeding never occurred if either monogamy or polytocy was absent (electronic supplementary material, table S2). In addition, there is no association between monogamy and polytocy, providing further support that both traits independently influence the evolution of cooperative breeding. We also tested for an association between polytocy and cooperative breeding in a restricted dataset that included the 34 cooperative breeders and 182 monogamous species and here, again, the dependent model is significantly more likely than independent evolution and transitions to cooperative breeding never occurred in monogamous lineages where females are monogamous.

4. DISCUSSION
Our results suggest that polytocy is a necessary pre-condition for the evolution of cooperative breeding in monogamous mammals. This is probably because the presence of helpers is only likely to generate effects on the reproductive output of breeders that are large enough to offset the costs of breeding in polytocous species that breed multiple times per year. The association between cooperative breeding and polytocy may not have been noticed previously, because the production of single eggs is rare in birds [43,44] and in insects groups where eusocial breeding has evolved [45]. Cooperative breeding may also lead to secondary increases in reproductive rate. Intraspecific comparisons show that increases in the number of resident helpers are commonly associated with reductions in inter-birth interval, larger litters and higher annual rates of survival [46–48]. In addition, comparative studies of several mammalian groups have suggested that cooperative breeding is associated with increases in the reproductive rate of females. For example, females have larger litter sizes in canid species with reproductive suppression [14], and females have relatively short inter-birth intervals in primate species where offspring receive care from individuals besides their mother [16,17]. While it is not yet clear whether alloparental care can lead to increases in reproductive rate, our observation that none of the traits besides
litter size is consistently associated with cooperative breeding suggests that benefits might be lineage-specific.

We found no support for the prediction that cooperative breeding is a consequence of contrasts in longevity or in opportunities for sub-adults to obtain breeding positions. Cooperatively breeding mammals do not exhibit lower mortality than non-cooperative breeders. For mammals, these factors have been suggested to explain the evolution of monogamous mating systems [49], but they do not necessarily seem to predict why, in some species, subordinate individuals become helpers, while in others, they do not provide support (e.g. marmots [50] and Siberian jays [51]). There is also no association between cooperative breeding and species differences in age of first reproduction or longevity, and a previous study between longevity and group size also suggested that differences in the pace of life are not linked to the evolution of sociality in mammals [52].

Most attempts to explain the distribution of cooperative breeding have focused on the effects of variation in $r$ in Hamilton’s equation [4] rather than upon the variation in the $b$ and $c$ terms. Our results provide one example where variation in the benefits of helping appear to have an important influence on the evolution of cooperative breeding but other recent studies have suggested that variation in the costs or benefits of cooperation are likely to play an important role in its evolution and maintenance. For example, among birds, cooperative breeding is commonly found in species living in habitats where annual rainfall is low and unpredictable, conditions that are expected to increase the potential benefits of cooperation [20]. Similarly, among the mole rats, cooperative or eusocial breeding is associated with unpredictable habitat [53]. These results suggest that future work exploring the evolution of cooperative breeding would benefit from including factors likely to affect the benefits or costs of delayed reproduction and allomaternal care.

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