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Correlates of genetic monogamy in socially monogamous mammals: insights from Azara's owl monkeys

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Understanding the evolution of mating systems, a central topic in evolutionary biology for more than 50 years, requires examining the genetic consequences of mating and the relationships between social systems and mating systems. Among pair-living mammals, where genetic monogamy is extremely rare, the extent of extra-group paternity rates has been associated with male participation in infant care, strength of the pair bond and length of the breeding season. This study evaluated the relationship between two of those factors and the genetic mating system of socially monogamous mammals, testing predictions that male care and strength of pair bond would be negatively correlated with rates of extra-pair paternity (EPP). Autosomal microsatellite analyses provide evidence for genetic monogamy in a pair-living primate with bi-parental care, the Azara's owl monkey (*Aotus azarai*). A phylogenetically corrected generalized least square analysis was used to relate male care and strength of the pair bond to their genetic mating system (i.e. proportions of EPP) in 15 socially monogamous mammalian species. The intensity of male care was correlated with EPP rates in mammals, while strength of pair bond failed to reach statistical significance. Our analyses show that, once social monogamy has evolved, paternal care, and potentially also close bonds, may facilitate the evolution of genetic monogamy.

1. Introduction

The evolution of mating systems has been a central topic in evolutionary biology for more than 50 years [1,2]. Ever since it was understood that natural selection acts 'at the level of the individual genome' [3, p. 215], it became imperative to examine the genetic consequences of mating and the relationships between social systems and mating systems in order to understand their evolution. Since sexual selection on males and females is greatly influenced by the relationship between the number of mating partners and the reproductive success of males and females [4–6], it also has become clear that extra-pair paternity (EPP) and extra-group paternity (EGP) [7–10] are likely to play an important role in the evolution of mating systems, and that the genetic mating system is more relevant than the social mating system to theories pertaining to the evolution of mating systems.

Unfortunately, the social organization of animals is often a poor indicator of their genetic mating system [7–10]. For example, although the vast majority of passerine birds have traditionally been described as pair-living (Lack, 1968, cited in [8]), in 86% of the species some of the young were not sired by the female's pair-mate and nearly 20% of the broods contained at least one extra-pair chick [8]. These high rates of EPP are not surprising, given theoretical predictions that males most effectively increase their fitness by increasing the number of mating partners [11,12]. More recently, the advantages to females of mating with several males have also become increasingly acknowledged [13–16]. Still, despite this overwhelming evidence of EPP in a broad range of avian taxa, there is still some

evidence for genetic monogamy in a few species [17–21]. While EPPs are widespread among socially monogamous bird species [8], evidence has also started to accumulate in socially monogamous mammals.

Yet, among mammals, social monogamy remains an evolutionary puzzle [22,23]. In not being committed to parental investment through pregnancy and lactation, males may enhance their reproductive success through extra-pair copulations without increasing their parental investment [12]. Still, a small but significant number of mammal species are socially monogamous [24] and genetic monogamy has been reported for four species, the California mouse (*Peromyscus californicus*) [25], Kirk's dik-dik (*Madoqua kirkii*) [26], the Malagasy giant jumping rat (*Hypogeomys antimena*) [27], as well as for pack-living coyotes (*Canis latrans*) [28]. However, several other pair-living species have shown high EPP rates. For example, in the island fox (*Urocyon littoralis*) and the swift fox (*Vulpes velox*), about half of the offspring were not sired by the social father [29,30].

In order to understand the conditions under which genetic monogamy occurs and may have evolved, it is necessary to understand which aspects of social systems are associated with high or low rates of EPP. Among birds, EPP rates were associated with low adult mortality and low levels of male care, even when as much as 50% of interspecific variation was due to differences among taxonomic families or orders [31]. Many other factors have also been related to EPP and EGP rates in birds [32]. Among mammals, EGP was positively correlated with the length of the breeding season, but not the social mating system [9]. By contrast, the social organization (solitary + family-living versus pair-living species), but not the strength of the pair bond, was predictive of EPP rates in allegedly socially monogamous mammals [33].

In the past, theoretical considerations proposed that, in mammals, male care would be associated with high paternity certainty and low levels of EGP ([34–36], but see [37]). A positive relationship between male care and high paternity certainty is usually postulated based on the assumption that the evolutionary benefits to males of providing care will be intimately related to the probability of biological relatedness between the male and the infant [35,37–39]. Under this scenario, one expects male care to be more likely when there is a close connection with the female (i.e. a closer pair bond) that increases the possibilities of monitoring, guarding and preventing her from engaging in extra-pair copulations [34].

Yet, several studies have shown high levels of extra-group copulations despite intense male care (e.g. prairie voles, *Microtus ochrogaster* [40]; fat-tailed dwarf lemurs, *Cheirogaleus medius* [41]; Ethiopian wolves, *Canis simensis* [42]; North American beavers, *Castor canadensis* [43]). The evidence from these empirical studies combined with the findings from phylogenetic analyses [22,44] suggest that, although male care is associated with social monogamy in some cases, it is more likely a consequence of it than a cause [34]. Furthermore, the phylogenetic studies described above have shown that ecological and social factors alone cannot account for the existence of male care since male care is both present and absent in monogamous and polygamous systems [26,45,46].

Given these empirical and theoretical observations, we pursued two goals in this study. First, we conducted a paternity study on Azara's owl monkeys (*Aotus azarae*) [47–49]. Owl monkeys are pair-living and there is never more than one reproductive male and female in a group [47,50,51]. The

adult male contributes intensively to the care of the infant. From the second week of life, the infant is almost exclusively transported by the male, who also plays with and provides solid food for the infant more than the mother [48,49,52–54]. We therefore predicted genetic monogamy or a very low rate of EPP in our study species.

Secondly, we wanted to assess whether the strength of the pair bond and the intensity of male care were associated with genetic monogamy in socially monogamous pair-living mammals. We hypothesized that, given the very high costs to males of providing care to non-related infants, male care should be closely linked to genetic monogamy. To date, no cross-mammal study has investigated whether levels of male care are associated with genetic monogamy (i.e. extent of EPP) in socially monogamous mammals, defined here as a social organization in which an adult individual has only one social adult partner of the opposite sex at a given time [7,55–57]. To examine our hypothesis, we conducted an evaluation of the relationship between genetic monogamy, male care and pair bonds in pair-living mammals using our results on owl monkeys and published data on genetically determined EPP rates. We predicted that a high intensity of male care and a close association between pair partners would be associated with low rates of EPP.

2. Material and methods

(a) Study area and study population

The study area is located in the Guaycolec Ranch, 25 km from the city of Formosa in the Argentinean Gran Chaco of South America (58°11' W, 25°58' S). The local population of Azara's owl monkeys inhabits the gallery forests of the Río Paraguay and its tributaries in the Argentinean provinces of Formosa and Chaco [58]. Most adult individuals in the study population are regularly captured and fitted with radio or bead collars for permanent and unequivocal identification [59,60].

(b) Genetic and parentage analyses

Samples were collected from 128 individuals living in 29 social groups or as solitary floaters [61,62]. All individuals were genotyped for 14 genetic loci (average 13.8 loci, minimum 10 loci; average 4.3 alleles per locus) bearing polymorphic short tandem repeats (electronic supplementary material, tables S1a,b; for more information on methods see the electronic supplementary material, S1).

For 35 infants born to 17 reproducing pairs, the identity of at least one of the two adults present in the group was known, and genetic samples at the time of birth were available. For seven infants, the mothers were known because they were seen nursing them. The adult male present in the group at the time of conception was regarded as the 'social father' of the respective infant. The terms 'group female' and 'group male' include not only known mothers (seen to nurse the infant) and social fathers, but also males and females who were not identified at the time of conception, but were identified and sampled later, when there was no evidence of change of individuals in the group. Maternity and paternity were only assessed for infants for whom the group female or male was sampled. If infants for whom the group male had not been sampled were included in the analysis, then this would necessarily render an extra-group male as the most likely father. As a result, extra-group parentage would have been overestimated.

Maternity and paternity of the infants were determined using a Bayesian method that relies on a Markov chain Monte Carlo

(MCMC) approach, using the package MASTERBAYES [63], implemented in program R v. 2.15.2 [64]. This program models the set of joint probabilities of dam–sire pairs for each offspring in a generalized log-linear model as dependent on both genetic and non-genetic data [63]. Treating all theoretically possible candidate parents as equally likely can seriously inflate estimates of EPP rates [63]. Therefore, females were *a priori* excluded as candidate parents if they did not share the same mtDNA haplotype group as the offspring [61]. Similarly, individuals of both sexes were excluded if they were less than 4 years older than the offspring, given the age at first reproduction of owl monkeys (i.e. adults [65]), or if they were known to have died before the year of birth of the offspring.

The analysis also included information on the central location of the territories in which individuals lived. For individuals caught as solitary ‘floaters’ [66], the location where they had been caught was used. Following Hadfield *et al.* [63], the probability of a specific pair of adults being the parents of an offspring born in a particular territory was assumed to be proportional to an exponential function of parameter β times the Euclidean distance between offspring and each of the candidate parents. The exact value of β , genotyping error rates and the number of un-sampled candidate males and females were estimated by the MCMC procedure.

Based on preliminary analyses, the starting values for Markov chains were set as 0.005 for both allelic drop-out rate and genotyping error rate (E1 and E2, respectively), two for the number of un-sampled females, and six for the number of un-sampled males. No mismatch between a candidate parent and offspring were allowed. The number of iterations was set to 1 000 000, whereby the first 50 000 iterations were discarded (‘burn-in’) [67], and the thinning rate (specifying the intervals at which the Markov chain is stored) was set to 10. Tuning parameters were set to $\beta = 100$, and USdam and USsire to 0.1 in order to ensure that Metropolis acceptance rates lay between 0.2 and 0.5, as suggested by the programmer [67].

(c) Pair bonds, male care and extra-pair paternity: comparative analyses

A comprehensive search of the primary literature for genetic studies of paternity in socially monogamous mammal species was conducted. According to the definition provided above, those species with more than 10% of breeding subordinates, or species that commonly have more than two unrelated adults in the group were not considered as socially monogamous. Based on those criteria, 15 pair-living mammal species were identified for which genetic paternity data were available, including this study (electronic supplementary material, table S1c). A recent examination of socially monogamous mammals [33] used a number of species that were not included in our analyses. Explicit criteria for the inclusion or exclusion of species in comparative analyses are paramount to the adequate interpretation of results [68,69]. Thus, the list of those species, and our reasons for their exclusion, are provided in the electronic supplementary material, table S1d, and we further consider the inclusion or exclusion and classifications of species in the Discussion.

Each of the 15 species (owl monkeys and 14 species from the literature) was categorized according to the strength of the pair bond and the extent of male care. Pair bonds were classified as ‘close’ when partners travelled and spent most of the resting/sleeping periods (more than 80% of their active period, at least during mating periods) together. They were classified as ‘dispersed’ when partners shared a common defended territory, but foraged or slept independently during at least 20% of their active period.

Based on this information, the extent of male care in the different species was then classified as either ‘no or moderate

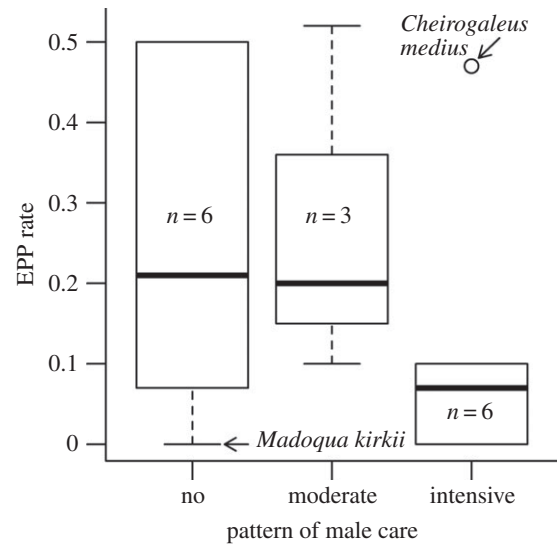


Figure 1. EPP rates for different intensities of male care. For the analysis, the levels of ‘no care’ and ‘moderate care’ were grouped together. Box plots represent median and interquartile ranges (IQR). Whiskers show ranges excluding only values larger than ± 1.5 times the IQR; outliers beyond this range are represented as open circles. *n*, number of species.

care’, or ‘intensive care’. Preliminary analyses had suggested that the categories ‘moderate’ and ‘no care’ could be merged in a single category since they were not statistically different (Welch’s two-sample *t*-test: $t = -0.3$, d.f. = 5.5, $p = 0.55$; see also figure 1 to see the similarity between these two categories). Species were classified as providing ‘no care’ if the male did not provide any infant care. ‘Moderate care’ was considered when males performed some basic infant care like huddling or grooming but the studies did not report a statistically significant increase in infant survival due to male care. Species were classified as having ‘intensive male care’ if males contributed direct care (e.g. infant carrying or food provisioning) as much or more than the mother, if male care had been reported to be associated with infant survival (e.g. a comparison of infant survival raised with or without a male present), or if the care provided entailed a cost to the male (e.g. a statistically significant loss in body mass of caring males compared with non-caring males; references in the electronic supplementary material, table S1c).

For comparative purposes with other studies (electronic supplementary material, table S1c), the proportion of EPP infants was estimated, rather than the proportion of litters in which at least one infant was sired by an extra-pair male. These proportional data were arcsine transformed to normalize them. Inspection of residuals versus fitted values did not suggest a strong deviation from normality for the overall model. A generalized least square model (phylGLS) with a phylogenetic correlation structure was fitted to the data, using a Brownian motion model of character evolution, and variables or the interaction term were deemed statistically significant if $p < 0.05$ [70]. Details about the different taxon-phylogenies on which the overall phylogeny was based are presented in the electronic supplementary material, S1 and figure S11.

Because reported divergence times and methods varied considerably between studies (e.g. [71] versus [72]), the robustness of our results was checked in several ways. First, 16 trees of the same topology were constructed in which branch lengths were randomly changed by some value between -20 and $+20$ MYA, with the restriction that no negative divergence times were allowed and the general topology had to remain the same. Likewise, 15 trees (with the original topology) were constructed based on only 14 species, with each of the 15 species being removed in turn to check for the effects individual species might have on the phylGLS

results, essentially a (branch removal) boot-strapping approach. We also fitted a model to data including three additional species that were not included in the analyses even when they might be considered pair-living: *Microtus ochrogaster* [73], *Hylobates lar* [74] and *Canis latrans* [75]. (The electronic supplementary material, table S1d provides the reasons why these were not considered pair-living for the analyses).

Different models of the phyIGLS were compared by choosing the model with the lowest AIC variance structure [76]. We checked whether changing variance structures for either or both variables would increase the model fit [77]. Because AIC levels were higher for models with differing variance structures (AIC = 115.1 to 117.1) than for the simpler model (AIC = 114.9), we assumed similar variance structures. When the interaction term was not statistically significant (which was the case for all models), it was removed. The two variables were retained for the final model, even if not statistically significant, since they were of primary interest. Statistical analyses were conducted in R [64], using the packages ‘ape’ [78] and ‘nlme’ [79].

3. Results

(a) Genetic monogamy in owl monkeys

Our analyses are strongly indicative of genetic monogamy in owl monkeys. All of the 32 group females and 30 group males for which genetic information was available could not be excluded as parents of the offspring in their group because they exhibited no mismatches (electronic supplementary material, table S1e; the genotypes of all monkeys are given in the electronic supplementary material, S2). The Bayesian analysis identified all females, and all but one male in the group of the infant, as the most likely parents. In one case, no most likely sire was found. This result was probably due to both the group male and a direct neighbour not having any mismatches with the offspring, and no group female being sampled. For 53% of the females and 57% of males, the likelihood estimates for these assignments lay at least in the 95% confidence interval, and 66% of dams and 73% of sires had an assignment with a confidence interval of 85% or higher (electronic supplementary material, table S1e). The MCMC approach estimated genotyping error rates to be even lower than originally assumed with 0.002 (s.d. = 0.0021) for E1 and 0.002 (s.d. = 0.0018) for E2, respectively. Here, the number of un-sampled females was 2.0 (s.d. = 1.01), the number of un-sampled males was 6.4 (s.d. = 3.2) and β was -0.026 (s.d. = 0.013).

(b) Relationship between pair bonds, male care and extra-pair paternity

Species with intense male care had lower levels of EPP than those without intense male care (figure 1 and table 1). While most species with close bonds had lower levels of EPP than those with dispersed ones, this difference was not statistically significant (figure 2 and table 1). There was also no statistically significant interaction between male care and pair bond type (table 1).

Qualitatively, the results were very robust, whether using phylogenies with different branch lengths, removing each species in turn, or adding the three additional species excluded from analyses (electronic supplementary material, table S1g). Male care was negatively correlated with EPP rates in all models (all $p < 0.03$, electronic supplementary material, table S1g), while the interaction term was never statistically

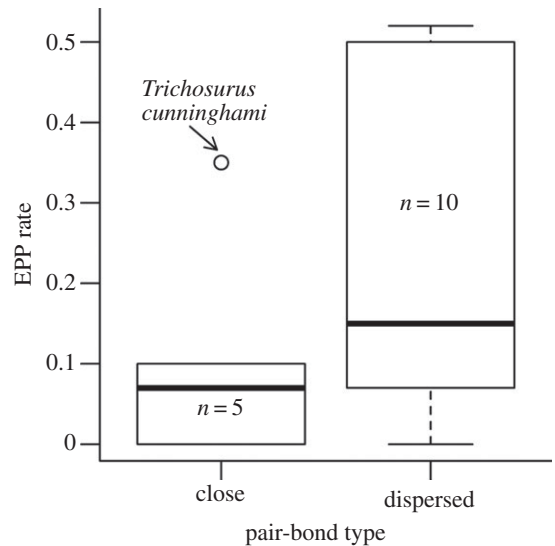


Figure 2. EPP rates in species with close and dispersed pair bonds. Box plots represent median and IQR. Whiskers show ranges excluding only values larger than ± 1.5 times the IQR; outliers beyond this range are represented as open circles. n , number of species.

Table 1. Model coefficients for the phylogenetic generalized least square model.

AIC = 114.1	value	s.e.	t-value	p-value
intercept ^a	26.5	14.7	1.8	0.10
pair bond	7.5	6.7	1.1	0.29
(dispersed) ^a				
male care	-17.8	4.0	-4.4	0.001
(intense) ^a				
pair bond :	-10.2	15.0	-0.7	0.51
male care				

^aValues from the model *not* including the interaction term.

significant. Close pair bonds were significantly associated with low EPP rates only in one tree with random branch length, and even removing *Trichosurus cunninghami*, a species that has close bonds but also high EPP rates from the analysis (figure 2), did not result in a statistically significant relationship. However, the direction of the association, with close pairs having lower EPP rates than dispersed species, was the same in all models (electronic supplementary material, table S1g).

4. Discussion

(a) Genetic monogamy in Azara's owl monkeys

Our findings on genetic monogamy in Azara's owl monkeys provide a potential explanation for a most remarkable and unusual commitment to paternal care shown by the species. Ever since paternal care was first described in owl monkeys, various hypotheses were evaluated to account for its evolution and maintenance [80,81]. Given the social proximity, sharing of space and coordination of activities that is characteristic of owl monkey pair-mates, it was reasonable to predict high paternity certainty and low levels of EPP through successful mate guarding by males. On the other hand, we could also expect that the

regular presence of intruders and the competition with extra-group males [66] would generate opportunities for extra-pair copulations that could lead to EPP. Not surprisingly, it was the suggested examination at the level of the individual genome [3] that provided the conclusive answer.

Owl monkeys are then the sole primate taxon, and only the fifth socially monogamous mammal, for which genetic monogamy has been reported based on the empirical examination of adequate sample sizes. A study of the Bornean gibbon (*Hylobates muelleri*) did not find evidence of EPP, but the small sample size ($n = 4$ infants) limits the conclusions to be drawn from it [82]. Although owl monkeys are an excellent model for studying the functioning and maintenance of social and genetic monogamy [22,44], a single-species approach cannot elucidate the processes that may have led to the evolution of genetic monogamy in owl monkeys. For this reason, we conducted a comparative phylogenetic analysis to explore these issues more expansively.

(b) Genetic monogamy, male care and pair bonds in mammals

Our comparative phylogenetic analyses explored under what circumstances social monogamy, an already intriguing and rare social system among mammals, may lead to genetic monogamy, a mating system where the limitations on male reproductive potential take on an extreme form. Our study is the first to provide evidence that, within pair-living species, male care is linked to the genetic mating system. Low rates of EPPs are expected in species with male participation in infant care for at least two reasons that may imply a different causal directionality: the paternity certainty associated with low EPP may promote male care [35,36], or male care may enhance possibilities of mating monopolizations and, thus, reduce EPP rates [34].

Intense male care was strongly related to low levels of EPP, whereas the strength of the pair bond was not, even when most species with strong bonds had low rates of EPP rates. An earlier study of the relationships between EGP rates and their breeding system found that the variation in EPP was better explained by the social structure than by the type of pair bonding [33]. However, these authors did not consider paternal care in their analyses and included cooperative breeders and other species that are not pair living in their comparisons. These differences underscore the importance of explicit and clear definitions of categories when species are classified for comparative analyses (see below). When considering birds, our results fit partly with theoretical considerations and empirical findings where low rates of EPP are also associated with high rates of male care [31]. In dispersed bird pairs, though, the opportunity for extra-pair copulations is higher than in species with close bonds where partners can monitor each other more easily and effectively.

There are still some notable exceptions among the 15 pair-living species analysed: species that do not conform to the general association of either intensive male care with close pair bonds, or no care and dispersed bonds. For example, male Kirk's dik-diks do not seem to provide much infant care, but have been described as genetically monogamous [26], and fat-tailed dwarf lemurs have nearly 50% EPP rates but still show male care. It is possible that the influence of pair bonds and infant care are affected at different levels of influence in these species. The strength of the pair bond

represents a proximate influence where mates with close bonds are guarded more closely, and the opportunities of extra-pair copulations are more limited. Directly measured rates of mate guarding should provide much needed behavioural data that will allow a more fine-tuned exploration of this relationship. By contrast, the relationship between male care and EPP rates may be indirect.

To further explore this possibility, it would be valuable to have individual-based data for more species in order to disentangle individual effects from species-level effects [35]. This approach may help to explain why cross-species approaches consistently find that reduced mean paternity covaries with reduced male care [35,36,83], whereas within-species studies produce contradictory results (e.g. [37,84–87]). The need for more and better behavioural data on mating patterns has been already raised in the avian literature, where a better understanding of the causes of EPP is being limited by a lack of adequate information on the behavioural events that affect paternity [27]. Following an exponential growth in the number of genetic studies that revolutionized the study of avian mating systems, it is now becoming clear that the proper interpretation of the correlates of paternity will require detailed information on mating patterns.

Our analyses identified a relationship between EPP rates and male care, but whether male care drove the evolution of social monogamy or genetic monogamy remains unclear. Some authors have concluded that paternal care was not important in driving the evolution of social monogamy because it evolved more frequently in the absence of male care than in its presence [88]. Indeed, in at least three major lineages among the primates (lemurs, tarsiers and platyrrhines), pair-living seems to have evolved before male care [89].

Similarly, recent comparative studies of primates and other mammals also concluded that, when paternal care is associated with social monogamy, it is more likely to be as a consequence of its evolution rather than a cause [22,44]. These studies on the evolution of social monogamy analysed the correlated evolution of social monogamy with the traits 'male care', 'grouping structure of females' and 'infanticide risk' within primates [44] and mammals [22]. Opie *et al.* [44] concluded that male infanticide is the most compelling explanation for the appearance of monogamy, a conclusion that may warrant further examination given that their results show similar support for a relationship to biparental care and female ranges [90]. By contrast, Lukas & Clutton-Brock [22] suggest that social monogamy evolved where males were unable to defend multiple females and conclude that its evolution was not associated with a high risk of male infanticide. Thus, social monogamy probably evolved, and may be maintained, for different reasons and along different pathways in various species [89,91].

(c) Classification issues and robustness of results

Comparative analyses based on dichotomized marker traits (e.g. care versus no care) are likely to be significantly influenced by how species are classified. Potentially dismissed as an obvious methodological consideration to be addressed at an early stage of research design, the issue has lately been receiving proper, and much needed, attention following the publication of two large comparative analyses on social monogamy. For example, Dixon [69] suggested that some of the findings from the study on the evolution of social monogamy in primates [44] were based on comparing 'apples with

oranges', whereas de Waal & Gavrillets [90] found the contrast in conclusions by the two research teams 'disturbing'.

Our analyses also depend on various underlying classifications. These include whether to consider the species to be socially monogamous or not, whether a species has a dispersed or close pair-bond, whether male care is considered as intense or only moderate and how EPP rates are calculated. Frequently, cut-off values are arbitrary, and estimates of proportions can be unreliable, if based on small sample sizes. Thus, when considering the inclusion or exclusion of a species, it is advisable to make the decision so that if there is an effect it is counter to the one 'expected'.

Our inclusion of *Cheirogaleus medius* strengthens our findings, because this species does not conform to the general trend, and its exclusion would therefore result in less noise in the analyses. Indeed, our analyses excluding each of the species in turn showed that our results robustly exhibited the same trends (electronic supplementary material, table S1g). Likewise, the classification of some species as having moderate or intensive male care is not always straightforward. Again, our analyses dropping these species still provide significant results.

A further difficulty is defining criteria for a minimal sample size for each species. A genetic study on Müller's Bornean gibbon (*Hylobates muelleri*) [82] was not included because it did not find evidence of EPP based on only four infants, whereas a study on fork-marked lemurs that was based on only five pairs was included [92]. Although the finding of EPP in a socially monogamous species clearly rejects the null-hypothesis that the species is also genetically monogamous, the lack of evidence for EPP based on only four infants cannot convincingly reject the alternative possibility.

5. Conclusion

To our knowledge, this is the most complete dataset for studying genetic paternity in socially monogamous (i.e. pair-living) mammals. While the results are robust in terms of statistical analyses and margin of error with respect to certain classifications, it should still be noted that the analyses

were based on only 15 species, for some of which sample sizes are rather small.

After recognizing that social monogamy is no guarantee for genetic monogamy [8,10], ornithologists have accumulated an impressive amount of genetic data for a broad range of species over the last two decades. Yet, the number of genetic studies of allegedly socially monogamous mammal species remains surprisingly scant. We hope that work on socially monogamous mammals will be expanded to produce a more comprehensive database that combines behavioural, demographic and parentage data with a judicious use of statistical and analyses tools.

Finally, the findings from both evolutionary approaches (e.g. [22]) and our study suggest that, once social monogamy evolved, unaffected by male care patterns, the likelihood of genetic monogamy evolving was linked to male care. These results also suggest there is a relationship between genetic monogamy and the strength of the pair bond. Male care and potentially the intensity of the pair bond, as well as subsequent opportunities for close surveillance of the mating partner, would then have reinforced the maintenance of a monogamous social organization.

The collection of samples, and all subsequent related research, was approved by the corresponding animal research committees of the University of Pennsylvania and the Zoological Society of San Diego, and was done in adherence to the legal requirements of both Argentina and the USA.

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