

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

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20 **Summary**

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

40

41 **Key words:** *Aotus azarai*; extra-pair paternity; mating system; paternal care; pair
42 bond; pair-living mammals

43

44 **Introduction**

45 The evolution of mating systems has been a central topic in evolutionary
46 biology for more than 50 years [1, 2]. Ever since it was understood that natural
47 selection acts “at the level of the individual genome” [3, p215], it became
48 imperative to examine the genetic consequences of mating and the relationships
49 between social systems and mating systems in order to understand their
50 evolution. Since sexual selection on males and females is greatly influenced by
51 the relationship between the number of mating partners and the reproductive
52 success of males and females [4-6] it also became clear that extra-pair and
53 extra-group paternity [EPP and EGP, 7-10] were likely to play an important role in
54 the evolution of mating systems, and that the genetic mating system is more
55 relevant than the social mating system to theories pertaining to the evolution of
56 mating systems.

57 Unfortunately, the social organization of animals is often a poor indicator
58 of their genetic mating system [7-10]. For example, although the vast majority of
59 passerine birds has traditionally been described as pair-living [Lack, 1968, cited
60 in 8], in 86% of the species some of the young were not sired by the female's
61 pair-mate and nearly 20% of the broods contained at least one extra-pair chick
62 [8]. These high rates of extra-pair paternity are not surprising, given theoretical
63 predictions that males most effectively increase their fitness by increasing the
64 number of mating partners [11, 12]. More recently, the advantages to females of
65 mating with several males have also become increasingly acknowledged [13-16].
66 Still, despite this overwhelming evidence of EPP in a broad range of avian taxa,

67 there is still some evidence for genetic monogamy in a few species [17-21]. While
68 extra-pair paternities are widespread among socially monogamous bird species
69 [8], evidence has also started to accumulate in socially monogamous mammals.

70 Yet, among mammals, social monogamy remains an evolutionary puzzle
71 [22, 23]. In not being committed to parental investment through pregnancy and
72 lactation, males may enhance their reproductive success through extra-pair
73 copulations without increasing their parental investment [12]. Still, a small but
74 significant number of mammal species are socially monogamous [24] and genetic
75 monogamy has been reported for four species, the California mouse
76 [*Peromyscus californicus*, 25], Kirk's dik-dik [*Madoqua kirkii*, 26], the Malagasy
77 giant jumping rat [*Hypogeomys antimena*, 27], as well as for pack-living coyotes
78 [*Canis latrans*, Hennesey et al 2013]. However, several other pair-living species
79 have shown high EPP rates. For example, in the island fox (*Urocyon littoralis*)
80 and the swift fox (*Vulpes velox*), about half of the offspring were not sired by the
81 social father [28, 29].

82 In order to understand the conditions under which genetic monogamy
83 occurs and may have evolved, it is necessary to understand which aspects of
84 social systems are associated with high or low rates of extra-pair paternity.
85 Among birds, EPP rates were associated with low adult mortality and low levels
86 of male care, even when as much as 50% of inter-specific variation was due to
87 differences among taxonomic families or orders [30]. Many other factors have
88 also been related to EPP and extra-group paternity (EGP) rates in birds [31].
89 Among mammals, EGP was positively correlated with the length of the breeding

90 season, but not the social mating system [9]. In contrast, the social organisation
91 (solitary + family-living vs. pair-living species), but not the strength of the pair
92 bond, was predictive of EPP rates in allegedly socially monogamous mammals
93 [32].

94 In the past, theoretical considerations proposed that, in mammals, male
95 care would be associated with high paternity certainty and low levels of extra-
96 group paternity [33-35, but see 36]. A positive relationship between male care
97 and high paternity certainty is usually postulated based on the assumption that
98 the evolutionary benefits to males of providing care will be intimately related to
99 the probability of biological relatedness between the male and the infant [34, 36-
100 38]. Under this scenario, one expects male care to be more likely when there is a
101 close connection with the female (i.e., a closer pair bond) that increases the
102 possibilities of monitoring, guarding, and preventing her from engaging in extra-
103 pair copulations [33].

104 Yet, several studies have shown high levels of extra-group copulations
105 despite intense male care [e.g., prairie voles, *Microtus ochrogaster*, 39, fat-tailed
106 dwarf lemurs, *Cheirogaleus medius*, 40, Ethiopian wolves, *Canis simensis*, 41,
107 North American beavers, *Castor canadensis*, 42]. The evidence from these
108 empirical studies combined with the findings from phylogenetic analyses [22, 43]
109 suggest that, although male care is associated with social monogamy in some
110 cases, it is more likely a consequence of it than a cause [33]. Furthermore, the
111 phylogenetic studies described above have shown that ecological and social

112 factors alone cannot account for the existence of male care since male care is
113 both present and absent in monogamous and polygamous systems [26, 44, 45].

114 Given these empirical and theoretical observations, we pursued two goals
115 in this study. First, we conducted a paternity study on Azara's owl monkeys
116 [*Aotus azarae*, 46, 47, 48]. Owl monkeys are pair-living and there is never more
117 than one reproductive male and female in a group [46, 49, 50]. The adult male
118 contributes intensively to the care of the infant. From the second week of life, the
119 infant is almost exclusively transported by the male, who also plays with and
120 provides solid food for the infant more than the mother [47, 48, 51-53]. We
121 therefore predicted genetic monogamy or a very low rate of EPP in our study
122 species.

123 Secondly, we wanted to assess whether the strength of the pair-bond and
124 the intensity of male care were associated with genetic monogamy in socially
125 monogamous pair-living mammals. We hypothesized that, given the very high
126 costs to males of providing care to non-related infants, male care should be
127 closely linked to genetic monogamy. To date, no cross-mammal study has
128 investigated whether levels of male care are associated with genetic monogamy
129 (i.e., extent of EPP) in socially monogamous mammals, defined here as a social
130 organisation in which an adult individual has only one social adult partner of the
131 opposite sex at a given time [7, 54-56]. To examine our hypothesis, we
132 conducted an evaluation of the relationship between genetic monogamy, male
133 care and pair bonds in pair-living mammals using our results on owl monkeys
134 and published data on genetically determined EPP rates. We predicted that a

135 high intensity of male care and a close association between pair partners would
136 be associated with low rates of extra-pair paternity.

137

138 **Methods**

139 **Study area and study population**

140 The study area is located in the Guaycolec Ranch, 25 km from the city of
141 Formosa in the Argentinean Gran Chaco of South America (58°11 W, 25°58 S).
142 The local population of Azara's owl monkeys inhabits the gallery forests of the
143 Río Paraguay and its tributaries in the Argentinean provinces of Formosa and
144 Chaco [57]. Most adult individuals in the study population are regularly captured
145 and fitted with radio or bead collars for permanent and unequivocal identification
146 [58, 59].

147

148 **Genetic and parentage analyses**

149 Samples were collected from 128 individuals living in 29 social groups or
150 as solitary floaters [60, 61]. All individuals were genotyped for 14 genetic loci
151 (average 13.8 loci, minimum 10 loci; average 4.3 alleles per locus) bearing
152 polymorphic short tandem repeats (Supplementary Information Tables ESM1_A
153 and ESM1_B; for more information on methods see ESM1).

154 For 35 infants born to 17 reproducing pairs, the identity of at least one of
155 the two adults present in the group was known, and genetic samples at the time
156 of birth were available. For seven infants, the mothers were known because they
157 were seen nursing them. The adult male present in the group at the time of

158 conception was regarded as the 'social father' of the respective infant. The terms
159 'group female' and 'group male' include not only known mothers (seen to nurse
160 the infant) and social fathers, but also males and females who were not identified
161 at the time of conception, but were identified and sampled later, when there was
162 no evidence of change of individuals in the group. Maternity and paternity were
163 only assessed for infants for whom the group female or male was sampled. If
164 infants for whom the group male had not been sampled were included in the
165 analysis, then this would necessarily render an extra-group male as the most
166 likely father. As a result, extra-group parentage would have been overestimated.

167 Maternity and paternity of the infants were determined using a Bayesian
168 method that relies on a Markov chain Monte Carlo (MCMC) approach, using the
169 package MasterBayes [62], implemented in programme R version 2.15.2 [63].
170 This programme models the set of joint probabilities of dam-sire pairs for each
171 offspring in a generalised log-linear model as dependent on both genetic and
172 non-genetic data [62]. Treating all theoretically possible candidate parents as
173 equally likely can seriously inflate estimates of extra-pair paternity rates [62].
174 Therefore, females were *a priori* excluded as candidate parents if they did not
175 share the same mtDNA haplotype group as the offspring [60]. Similarly,
176 individuals of both sexes were excluded if they were less than four years older
177 than the offspring given the age at first reproduction of owl monkeys [i.e., adults,
178 64], or if they were known to have died before the year of birth of the offspring.

179 The analysis also included information on the central location of the
180 territories in which individuals lived. For individuals caught as solitary 'floaters'

181 [65], the location where they had been caught was used. Following Hadfield et al.
182 [62], the probability of a specific pair of adults being the parents of an offspring
183 born in a particular territory was assumed to be proportional to an exponential
184 function of parameter β times the Euclidean distance between offspring and each
185 of the candidate parents. The exact value of beta, genotyping error rates, and the
186 number of un-sampled candidate males and females were estimated by the
187 MCMC procedure.

188 Based on preliminary analyses, the starting values for Markov chains were
189 set as 0.005 for both allelic drop-out rate and genotyping error rate (E1 and E2,
190 respectively), two for the number of un-sampled females, and six for the number
191 of un-sampled males. No mismatch between a candidate parent and offspring
192 were allowed. The number of iterations was set to 1,000,000, whereby the first
193 50,000 iterations were discarded ('burn-in') [66], and the thinning rate (specifying
194 the intervals at which the Markov chain is stored) was set to 10. Tuning
195 parameters were set to beta=100, and USdam and USSire to 0.1 in order to
196 ensure that Metropolis acceptance rates lay between 0.2 and 0.5, as suggested
197 by the programmer [66].

198

199 **Pair bonds, male care, and EPP: comparative analyses**

200 A comprehensive search of the primary literature for genetic studies of
201 paternity in socially monogamous mammal species was conducted. According to
202 the definition provided above, those species with more than 10% of breeding
203 subordinates, or species that commonly have more than two unrelated adults in

204 the group were not considered as socially monogamous. Based on those criteria,
205 15 pair-living mammal species were identified for which genetic paternity data
206 were available, including the present study (Table ESM1_C). A recent
207 examination of socially monogamous mammals [32] used a number of species
208 that were not included in our analyses. Explicit criteria for the inclusion or
209 exclusion of species in comparative analyses are paramount to the adequate
210 interpretation of results [67, 68]. Thus, the list of those species, and our reasons
211 for their exclusion, are provided in Table ESM1_D, and we further consider the
212 inclusion or exclusion and classifications of species in the Discussion.

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

220 Based on this information, the extent of male care in the different species
221 was then classified as either 'no or moderate care', or 'intensive care'. Preliminary
222 analyses had suggested that the categories 'moderate' and 'no care' could be
223 merged in a single category since they were not statistically different (Welch's
224 two-sample t-test: $t=-0.3$, $d.f.=5.5$, $p=0.55$; see also Fig 1 to see the similarity
225 between these two categories). Species were classified as providing 'no care' if
226 the male did not provide any infant care. 'Moderate care' was considered when

227 males performed some basic infant care like huddling or grooming, but the
228 studies did not report a statistically significantly increase in infant survival due to
229 male care. Species were classified as having ‘intensive male care’ if males
230 contributed direct care (e.g., infant carrying or food provisioning) as much or
231 more than the mother, if male care had been reported to be associated with
232 infant survival (e.g., a comparison of infant survival raised with or without a male
233 present), or if the care provided entailed a cost to the male (e.g., a statistically
234 significant loss in body mass of caring males compared to non-caring males;
235 References in Table ESM1_C).

236 For comparative purposes with other studies (Table EMS1_C), the
237 proportion of EPP infants was estimated, rather than the proportion of litters in
238 which at least one infant was sired by an extra-pair male. These proportional data
239 were arcsine-transformed to normalize them. Inspection of residuals vs. fitted
240 values did not suggest a strong deviation from normality for the overall model. A
241 generalized least square model (phyGLS) with a phylogenetic correlation
242 structure was fitted to the data, using a Brownian motion model of character
243 evolution, and variables or the interaction term were deemed statistically
244 significant if $p < 0.05$ [69]. Details about the different taxon-phylogenies on which
245 the overall phylogeny were based are presented in ESM1 and Fig ESM1_1.

246 Because reported divergence times and methods varied considerably
247 between studies [e.g., 70, vs. 71], the robustness of our results was checked in
248 several ways. First, 16 trees of the same topology were constructed in which
249 branch lengths were randomly changed by some value between -20 and +20

250 MYA, with the restriction that no negative divergence times were allowed and the
251 general topology had to remain the same. Likewise, 15 trees (with the original
252 topology) were constructed based on only 14 species, with each of the 15
253 species being removed in turn to check for the effects individual species might
254 have on the phyGLS results, essentially a [branch removal] boot-strapping
255 approach. We also fitted a model to data including three additional species that
256 were not included in the analyses even when they might be considered pair-
257 living: *Microtus ochrogaster* [72], *Hylobates lar* [73], and *Canis latrans* [74].
258 (Table ESM1_D provides the reasons these were not considered pair-living for
259 the analyses).

260 Different models of the phyGLS were compared by choosing the model
261 with the lowest AIC variance structure [75]. We checked whether changing
262 variance structures for either or both variables would increase the model fit [76].
263 Because AIC levels were higher for models with differing variance structures
264 (AIC=115.1 to 117.1) than for the simpler model (AIC=114.9), we assumed
265 similar variance structures. When the interaction term was not statistically
266 significant (which was the case for all models), it was removed. The two variables
267 were retained for the final model, even if not statistically significant since they
268 were of primary interest. Statistical analyses were conducted in R [63], using the
269 packages 'ape' [77] and 'nlme' [78].

270

271

272 **Results**

273 **Genetic monogamy in owl monkeys**

274 Our analyses are strongly indicative of genetic monogamy in owl
275 monkeys. All of the 32 group females and 30 group males for which genetic
276 information was available could not be excluded as parents of the offspring in
277 their group because they exhibited no mismatches (Table ESM1_E; the
278 genotypes of all monkeys are given in ESM2). The Bayesian analysis identified
279 all females, and all but one male in the group of the infant, as the most likely
280 parents. In one case, no most likely sire was found. This result was likely due to
281 both the group male and a direct neighbour not having any mismatches with the
282 offspring, and no group female being sampled. For 53% of the females and 57%
283 of males, the likelihood estimates for these assignments lay at least in the 95%
284 confidence interval, and 66% of dams and 73% of sires had an assignment with a
285 confidence interval of 85% or higher (Table ESM1_E). The MCMC approach
286 estimated genotyping error rates to be even lower than originally assumed with
287 0.002 (SD=0.0021) for E1 and 0.002 (SD=0.0018) for E2, respectively. Here, the
288 number of un-sampled females was 2.0 (SD=1.01), the number of un-sampled
289 males was 6.4 (SD=3.2), and β was -0.026 (SD=0.013).

290

291 **Relationship between pair bonds, male care and EPP**

292 Species with intense male care had lower levels of EPP than those without
293 intense male care (Fig. 1, Table 1). While most species with close bonds had
294 lower levels of EPP than those with dispersed ones, this difference was not

295 statistically significant (Fig. 2, Table 1). There was also no statistically significant
296 interaction between male care and pair bond type (Table 1).

297 Qualitatively, the results were very robust, whether using phylogenies with
298 different branch lengths, removing each species in turn, or adding the three
299 additional species excluded from analyses (Table ESM1_G). Male care was
300 negatively correlated with EPP rates in all models (all $p < 0.03$, Table ESM1_G),
301 while the interaction term was never statistically significant. Close pair bonds
302 were significantly associated with low EPP rates only in one tree with random
303 branch length, and even removing *Trichosurus cunninghami*, a species that has
304 close bonds but also high EPP rates from the analysis (Fig 2), did not result in a
305 statistically significant relationship. However, the direction of the association, with
306 close pairs having lower EPP rates than dispersed species, was the same in all
307 models (Table ESM1_G).

308

309 **Discussion**

310 **Genetic monogamy in Azara's owl monkeys**

311 Our findings on genetic monogamy in Azara's owl monkeys provide a
312 potential explanation for a most remarkable and unusual commitment to paternal
313 care shown by the species. Ever since paternal care was first described in owl
314 monkeys, various hypotheses were evaluated to account for its evolution and
315 maintenance [79, 80]. Given the social proximity, sharing of space, and
316 coordination of activities that is characteristic of owl monkey pair-mates, it was
317 reasonable to predict high paternity certainty and low levels of extra-group

318 paternity through successful mate guarding by males. On the other hand, we
319 could also expect that the regular presence of intruders and the competition with
320 extra-group males [65] would generate opportunities for extra-pair copulations
321 that could lead to EPP. Not surprisingly, it was the suggested examination at the
322 level of the individual genome [3] that provided the conclusive answer.

323 Owl monkeys are then the sole primate taxon, and only the fifth socially
324 monogamous mammal, for which genetic monogamy has been reported based
325 on the empirical examination of adequate sample sizes. A study of the Bornean
326 gibbon (*Hylobates muelleri*) did not find evidence of EPP, but the small sample
327 size (n=4 infants) limits the conclusions to be drawn from it [81]. Although owl
328 monkeys are an excellent model for studying the functioning and maintenance of
329 social and genetic monogamy [22, 43], a single-species approach cannot
330 elucidate the processes that may have led to the evolution of genetic monogamy
331 in owl monkeys. For this reason, we conducted a comparative phylogenetic
332 analysis to explore these issues more expansively.

333

334 **Genetic monogamy, male care and pair bonds in mammals**

335 Our comparative phylogenetic analyses explored under what
336 circumstances social monogamy, an already intriguing and rare social system
337 among mammals, may lead to genetic monogamy, a mating system where the
338 limitations on male reproductive potential take on an extreme form. Our study is
339 the first to provide evidence that, within pair-living species, male care is linked to
340 the genetic mating system. Low rates of EPPs are expected in species with male

341 participation in infant care for at least two reasons that may imply a different
342 causal directionality: the paternity certainty associated with low EPP may
343 promote male care [34, 35], or male care may enhance possibilities of mating
344 monopolisations and, thus, reduce EPP rates [33].

345 Intense male care was strongly related to low levels of EPP, whereas the
346 strength of the pair bond was not, even when most species with strong bonds
347 had low rates of EPP rates. An earlier study of the relationships between extra-
348 group paternity rates and their breeding system found that the variation in EPP
349 was better explained by the social structure than by the type of pair bonding [32].
350 However, these authors did not consider paternal care in their analyses and
351 included cooperative breeders and other species that are not pair living in their
352 comparisons. These differences underscore the importance of explicit and clear
353 definitions of categories when species are classified for comparative analyses
354 (see below). When considering birds, our results fit partly with theoretical
355 considerations and empirical findings where low rates of EPP are also associated
356 with high rates of male care [30]. In dispersed bird pairs, though, the opportunity
357 for extra-pair copulations is higher than in species with close bonds where
358 partners can monitor each other more easily and effectively.

359 There are still some notable exceptions among the 15 pair-living species
360 analysed; species that do not conform to the general association of either
361 intensive male care with close pair bonds, or no care and dispersed bonds.
362 For example, male Kirk's dik-diks do not seem to provide much infant care, but
363 have been described as genetically monogamous [26] and fat-tailed dwarf lemurs

364 have nearly 50% EPP rates, but still show male care. It is possible that the
365 influence of pair bonds and infant care are affected at different levels of influence
366 in these species. The strength of the pair bond represents a proximate influence
367 where mates with close bonds are guarded more closely, and the opportunities of
368 extra-pair copulations are more limited. Directly measured rates of mate guarding
369 should provide much needed behavioural data that will allow a more fine-tuned
370 exploration of this relationship. In contrast, the relationship between male care
371 and EPP rates may be indirect.

372 To further explore this possibility, it would be valuable to have individual-
373 based data for more species in order to disentangle individual effects from
374 species-level effects [34]. This approach may help to explain why cross-species
375 approaches consistently find that reduced mean paternity co-varies with reduced
376 male care [34, 35, 82], whereas within-species studies produce contradictory
377 results [e.g., 36, 83-86]. The need for more and better behavioural data on
378 mating patterns has been already raised in the avian literature, where a better
379 understanding of the causes of EPP is being limited by a lack of adequate
380 information on the behavioural events that affect paternity [27]. Following an
381 exponential growth in the number of genetic studies that revolutionized the study
382 of avian mating systems, it is now becoming clear that the proper interpretation of
383 the correlates of paternity will require detailed information on mating patterns.

384 Our analyses identified a relationship between EPP rates and male care,
385 but whether male care drove the evolution of social monogamy or genetic
386 monogamy remains unclear. Some authors have concluded that paternal care

387 was not important in driving the evolution of social monogamy because it evolved
388 more frequently in the absence of male care than in its presence [87]. Indeed, in
389 at least three major lineages among the primates (lemurs, tarsiers, and
390 platyrrhines), pair-living seems to have evolved before male care [88].

391 Similarly, recent comparative studies of primates and other mammals also
392 concluded that, when paternal care is associated with social monogamy, it is
393 more likely as a consequence of its evolution rather than a cause [22, 43]. These
394 studies on the evolution of social monogamy analysed the correlated evolution of
395 social monogamy with the traits 'male care', 'grouping structure of females' and
396 'infanticide risk' within primates [43] and mammals [22]. Opie et al. [43],
397 concluded that male infanticide is the most compelling explanation for the
398 appearance of monogamy, a conclusion that may warrant further examination
399 given that their results show similar support for a relationship to biparental care
400 and female ranges [90]. In contrast, Lukas and Clutton-Brock [22] suggest that
401 social monogamy evolved where males were unable to defend multiple females
402 and conclude that its evolution was not associated with a high risk of male
403 infanticide. Thus, social monogamy likely evolved, and may be maintained, for
404 different reasons and along different pathways in various species [88, 89].

405

406 **Classification issues and robustness results**

407 Comparative analyses based on dichotomized marker traits (e.g., care vs.
408 no care) are likely to be significantly influenced by how species are classified.
409 Potentially dismissed as an obvious methodological consideration to be

410 addressed at an early stage of research design, the issue has lately been
411 receiving proper, and much needed, attention following the publication of two
412 large comparative analyses on social monogamy. For example, Dixson [68]
413 suggested that some of the findings from the study on the evolution of social
414 monogamy in primates [43] were based on comparing “apples with oranges”,
415 whereas de Waal and Gavrilets [90] found the contrast in conclusions by the two
416 research teams “disturbing”.

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

425 Our inclusion of *Cheirogaleus medius* strengthens our findings because
426 this species does not conform to the general trend, and its exclusion would
427 therefore result in less noise in the analyses. Indeed, our analyses excluding
428 each of the species in turn showed that our results robustly exhibited the same
429 trends (Table ESM1_G). Likewise, the classification of some species as having
430 moderate or intensive male care is not always straightforward. Again, our
431 analyses dropping these species still provide significant results.

432 A further difficulty is defining criteria for a minimal sample size for each
433 species. A genetic study on Müller's Bornean gibbon [*Hylobates muelleri*, 81] was
434 not included because it did not find evidence of EPP based on only four infants,
435 whereas a study on fork-marked lemurs that was based on only five pairs was
436 included [91]. Although the finding of EPP in a socially monogamous species
437 clearly rejects the null-hypothesis that the species is also genetically
438 monogamous, the lack of evidence for EPP based on only four infants cannot
439 convincingly reject the alternative possibility.

440

441 **Conclusions**

442 To our knowledge, this is the most complete data set for studying genetic
443 paternity in socially monogamous (i.e., pair-living) mammals. While the results
444 are robust in terms of statistical analyses and margin of error with respect to
445 certain classifications, it should still be noted that the analyses were based on
446 only 15 species, for some of which sample sizes are rather small.

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

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

463

464

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483

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- 741

742 Tables:

743

744 **Table 1: Model coefficients for the phylogenetic generalized least square**
745 **model.**

AIC=114.1	Value	Std. error	t-value	p-value
Intercept *	26.5	14.7	1.8	0.10
Pair bond (dispersed) *	7.5	6.7	1.1	0.29
Male care (intense) *	-17.8	4.0	-4.4	0.001
Pair bond : Male care	-10.2	15.0	-0.7	0.51

746 * Values from the model *not* including the interaction term.

747

748

749 Figure Legends:

750

751 **Figure 1: Extra-pair paternity rates for different intensities of male care.** For

752 the analysis, the levels of 'no care' and 'moderate care' were grouped together.

753 Box plots represent median and interquartile ranges (IQR). Whiskers show

754 ranges excluding only values larger than ± 1.5 times the IQR; outliers beyond this

755 range are represented as open circles. N = number of species.

756

757 **Figure 2: Extra-pair paternity rates in species with close and dispersed pair**

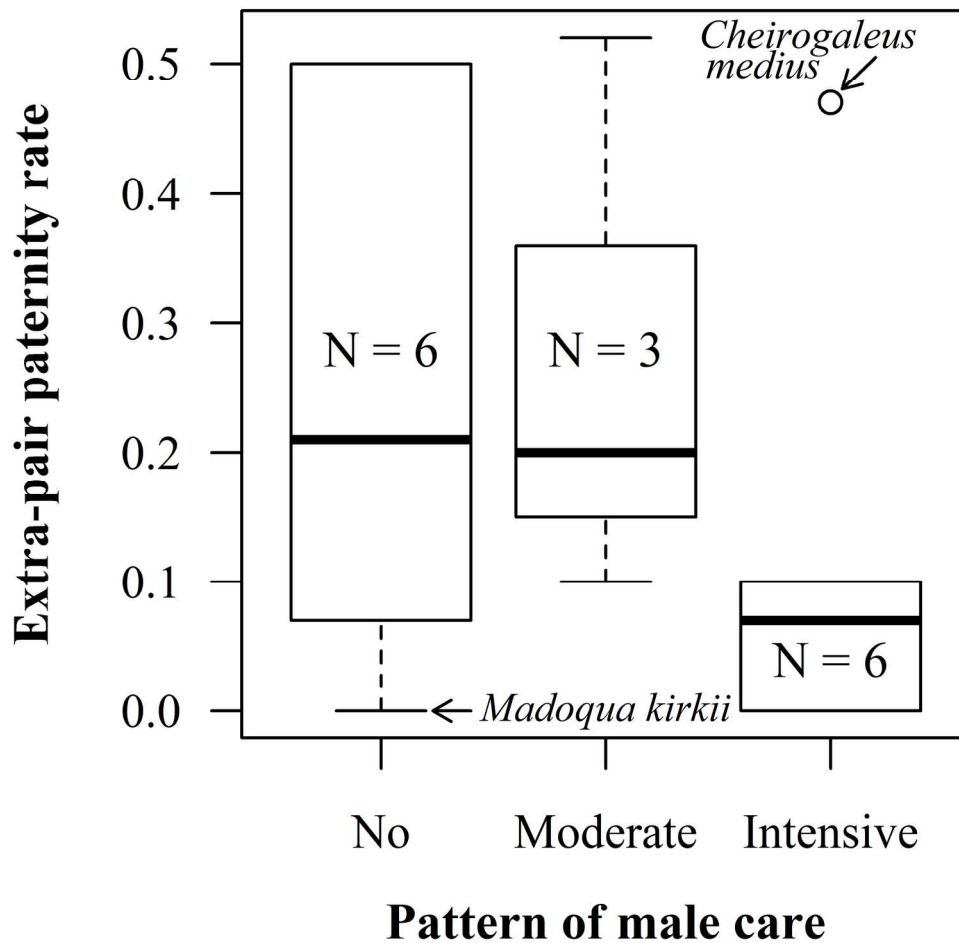
758 **bonds.** Box plots represent median and interquartile ranges (IQR). Whiskers

759 show ranges excluding only values larger than ± 1.5 times the IQR; outliers

760 beyond this range are represented as open circles. N = number of species.

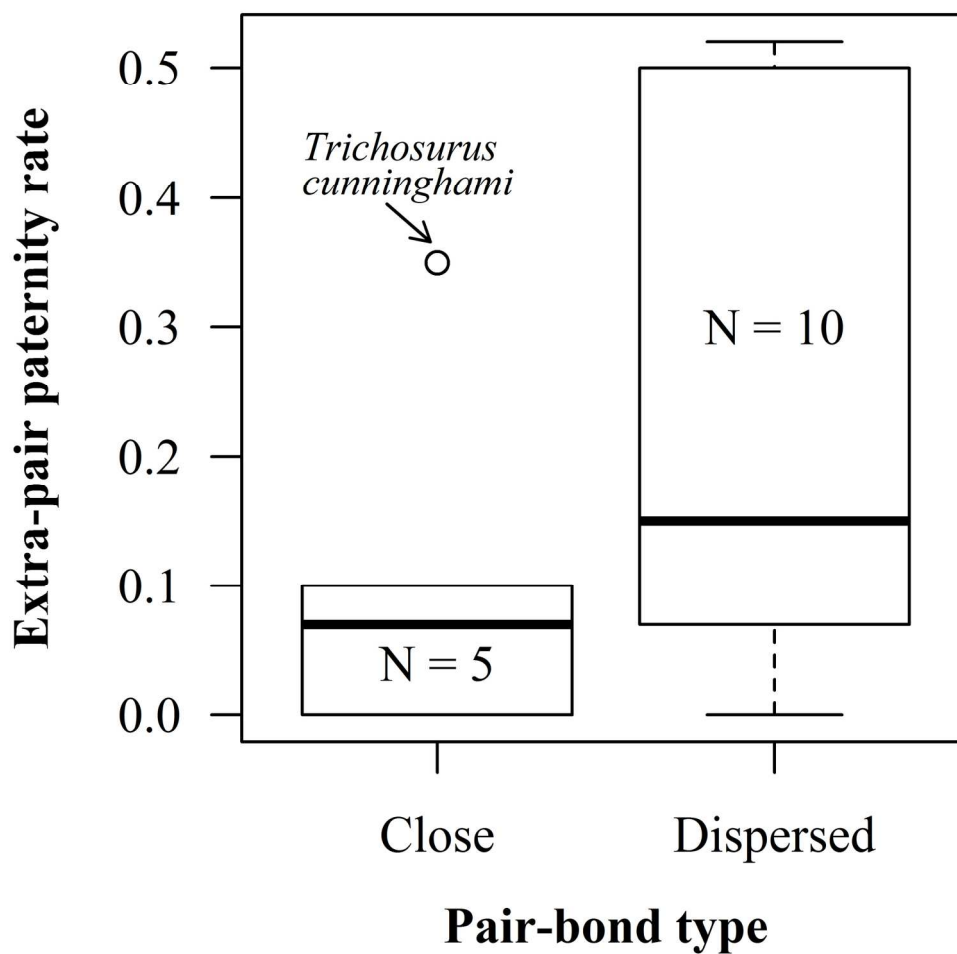
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Extra-pair paternity rates for different intensities of male care. For the analysis, the levels of 'no care' and 'moderate care' were grouped together. Box plots represent median and interquartile ranges (IQR). Whiskers show ranges excluding only values larger than ± 1.5 times the IQR; outliers beyond this range are represented as open circles. N = number of species.

83x83mm (600 x 600 DPI)



Extra-pair paternity rates in species with close and dispersed pair bonds. 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.
83x83mm (600 x 600 DPI)