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Multiple paternity and number of offspring in mammals

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Many cooperative social attributes are being linked to characteristics of mating systems, particularly to the rate of multiple paternity that typifies a population. Under the logic that greater offspring production by females should engender greater competition among males to mate with females, it is predicted that multiple paternity should increase with litter sizes. We tested the predicted positive association of multiple paternity and litter size with a meta-analysis of 59 species of mammals. The probability of multiple paternity and mean litter size were positively correlated, but not significantly ($Zr = 0.202$). Also, the mean number of sires of litters increased with mean litter size, but not significantly ($Zr = 0.235$). We developed a combinatorial formula for the influence of number of male mates and litter size on the probability of multiple paternity. We used Bayesian Markov chain Monte Carlo simulations to generate an expectation for the form of the relationship between the probability of multiple paternity and mean litter size. Under the assumption of random samplings of numbers of mates, the expected association of the probability of multiple paternity and mean litter sizes among species was positive, curvilinear and relatively high. However, the empirical probabilities of multiple paternities were much less than expected, suggesting that behavioural factors (such as mating-associated behaviours) or ecological characteristics (such as population density) likely limit the number of male mates for reproductive females. The probability of multiple paternity in a population is an estimate of mating patterns that does not closely reflect the number of sires of individual litters. We suggest use of the estimated probability of mating success for males as an alternative measure of their contribution to the mating system.

1. Introduction

The influences of multiple paternity of reproductive success of males (the limited sex, where females are limiting on male reproductive success; *sensu* [1]) within a single breeding season has been examined for monogamous species by Dillard & Westneat [2]. They pointed out that kin selection should influence the evolution of cooperative behaviour quite differently in the presence or absence of multiple paternity. Paternal care of offspring should increase with confidence of paternity, and cooperation among siblings should be most likely when they are full rather than half siblings. Thus, genetic monogamy and some forms of cooperative behaviour should coevolve. The influence of genetic patterns of relatedness may thus influence the evolution of higher levels of social organization. The advent of studies of parentage and relatedness, using molecular techniques such as analyses of DNA microsatellites, may give us insights into social evolution. Dillard and Westneat drew these ideas from basic principles of kin selection [3].

While many genetically monogamous species exhibit high orders of social behaviour, polygynous and polygynandrous (multiple mates in both sexes) species

64 also exhibit cooperative behaviour patterns (reviewed in [4]).
 65 As well, cooperative behaviours and social monogamy have
 66 not always been found associated, and solitary asocial living
 67 may be the ancestral state for socially monogamous species
 68 [5]. So, in addition to possible evolutionary influences on
 69 both genetic monogamy and cooperative social behaviour,
 70 examinations of multiple paternity and associated traits in
 71 polygynous and polygynandrous species may prove illuminat-
 72 ing to the study of social behaviour. The basic principle that
 73 single paternity should favour more genetic polygyny and
 74 associated paternal care and cooperative behaviour among
 75 full siblings is equally compelling in polygynous as in monog-
 76 amous species, since single paternity among littermates raises
 77 the mean coefficient of kinship within litters. Further, the
 78 opportunity for full and half siblings (via a common father
 79 for different litters) in polygynous social species can be used
 80 to test the limits of cooperative nepotism. The same might be
 81 true of full and half siblings in polygynandrous species.

82 Mammals provide an excellent group of species for an
 83 examination of multiple paternity, and both life-history and
 84 social characteristics. The typical mammalian pattern is for
 85 socially polygynous family groups to form around matriloca
 86 females, with highly philopatric females and males that more
 87 often disperse away from their natal homes [6,7]. In such
 88 societies, strong kinship among philopatric females commonly
 89 develops, often with a variety of forms of cooperative behav-
 90 iour. For example, alarm calling to warn close kin of
 91 approaching predators is widespread in small and medium
 92 sized mammals (reviewed in [8]). Some mammalian species
 93 show highly developed care for offspring by sires [9]. In
 94 addition, cooperation among closely related breeding females
 95 forms the basis for several mammalian societies [10].

96 The purpose of our study was to begin an exploration of life-
 97 history traits associated with multiple paternity of mammalian
 98 litters. Avise & Liu [11,12] suggested that increased degrees of
 99 multiple paternity should be associated with increased num-
 100 bers of offspring and termed this the fecundity limitation
 101 hypothesis. They reasoned that opportunities for multiple inse-
 102 mination should be more apparent when more offspring are
 103 available for fathers in the litters of individual females, and
 104 that several benefits should accrue to both sexes under multiple
 105 mating. Other things being equal, when females have greater
 106 numbers of offspring, then the potential gain in fitness for
 107 each mating male increases. Thus, the intensity of competition
 108 for mates (via sexual selection) increases. This should encourage
 109 more males to vie for mating with each female; and thus, favour
 110 multiple paternity. Other benefits included enhanced reproduc-
 111 tive success with increased partners, increased genetic diversity
 112 of offspring, and direct benefits such as nuptial gifts. Avise and
 113 Liu [11–13] did not find significant support for their hypothesis
 114 within major taxonomic groups of viviparous species and
 115 offered the following *post hoc* explanation. The degree of mul-
 116 tiple paternity is a balance between two factors: the universal
 117 advantages of mating multiply and logistic constraints on
 118 mate acquisition.

119 In a population that is not rapidly increasing or decreasing,
 120 the survival of young and adults will be close to demo-
 121 graphically balanced, to produce an equilibrium number of
 122 individuals in each age class. Males may gain a reproductive
 123 advantage by mating with females that are in better condition
 124 because they produce larger numbers or higher quality of off-
 125 spring. This reasoning, however, does not correspond to a
 126 clear expectation for an among-species comparison. Because

sexual selection occurs within populations, there is not a clear
 relative fitness advantage with respect to average number of off-
 spring among species, since males of different species do not
 compete with respect to mating opportunities. Thus, there
 may not be a universal advantage in terms of sexual selection
 to mating multiply, when comparing different species. If so,
 sexual selection is not expected to produce an association of
 mean litter sizes and mean rates of multiple paternity, even if
 such an advantage occurred within the individual species.
 Within species, however, extreme competition among males
 for female mates and strong female choice for particular male
 traits might well produce low rates of multiple paternity.

Any test of a relationship between multiple paternity and
 numbers of offspring needs to be compared to an appropriate
 null hypothesis. Avise & Liu [12] used linear regression and a
 null hypothesis of zero association to test the significance of
 association of these two variables. Specifically, they predicted
 a significant positive correlation of the degree of multiple
 paternity and mammalian litter size. Using the literature on
 mammalian species, we re-examined the relationship between
 the average degree of multiple paternity and the mean number
 of offspring for females. The opportunity for multiple paternity
 should increase with number of offspring, but the number of
 sires in a litter also depends on the number of males mating
 with females. For example, with two males mating and
 random fertilization, litters of two might be expected to have
 50% multiply sired litters. If sperm from four potential sires
 were available to mating females with two offspring, however,
 the likelihood of multiply inseminated litters would be
 expected to increase to 75%. In general, under the assumption
 that each mating male has an equal probability of siring each
 offspring of a mated female, the probability of multiple pater-
 nity, denoted by p , depends on the number of offspring and
 number of mating males, given by the combinatorial formula:

$$p = \frac{m^k - m}{m^k} = 1 - \frac{m}{m^k}, \quad (1.1)$$

where m is the number of males that contribute sperm (*viz.*,
 mating males) and k is litter size. Here m^k is the number of
 ways (combinations) that m mates can be assigned to k
 offspring in a litter, and m/m^k is the probability of singly inse-
 minated litters. Since only one value of p was available from the
 data, using equation (1.1) to specify the null hypothesis with a
 fixed p constraint would mean that increasing litter size k is
 associated with decreasing mating males m , which is counter-
 intuitive. For this reason, data from the theoretical statistical
 distributions of the relevant quantities were generated using
 a Bayesian MCMC simulation, which were then used to specify
 the null hypothesis.

We conducted a meta-analysis of studies that reported
 mean values of multiple paternity, litter size, and number of
 sires, to evaluate the influences of number of offspring and
 number of male mates for females on the likelihood of multiply
 inseminated litters among species of mammals. Probabilities of
 multiple inseminations were estimated, under the simplifying
 assumption of an equal chance of paternity of individual off-
 spring for each mating male. A relationship was derived for
 the expected number of male mates given the observed proba-
 bilities of multiply inseminated litters. Markov chain Monte
 Carlo (MCMC) sampling methods for a Bayesian analysis
 were used to obtain the estimated number of mates for various
 litter sizes, which were compared to field-estimated means for
 the number of sires and litter size for each species. From these

analyses, we re-examined the expected and actual associations of probability of multiple inseminations and litter sizes among mammalian species. We used this comparison to indirectly tested the hypothesis that there are logistical limits on the number of male mates for females among mammalian species. Further, we quantified the difference between the actual and expected probabilities of multiple paternity for the populations of various mammalian species, revealing those species that should strongly reflect social or ecological constraints.

2. Methods

On 10 January 2018, a search of 'Web of Science' with the option 'All Databases' found 327 publications under the keywords 'multiple paternit*' and 'mammal*'. Of these, 60 studies contained data on both multiple paternity and litter size for populations of mammalian species. From literature cited in these 60 articles, we extracted an additional six studies not listed in the web search. Our final sample total was 66 studies with 62 population samples, and 59 species (three species were studied twice). For each population sample, one or two studies provided the following information: number of litters examined (n), mean litter size (λ_k); and from analyses of microsatellite DNA, proportion of multiple paternity (p) within the sample of litters and mean number of sires per litter (λ_s). Two of the sampled populations did not have the mean number of sires per litter and were thus not used in some analyses. All data, original references and code are available on Dryad.

Associations of variables were assessed with correlational analyses, the correlation coefficient serving as an indicator of effect size [14]. The Z_r statistic was used, rather than unadjusted correlation values. Because the analysis revealed likely autocorrelation between the effects of mating males and litter sizes, the expected association of these variables and the rate of multiple paternity was positive. Nonetheless, the number of mates for mating females was unknown, making it difficult to specify the null hypothesis for the influence of litter size on the rate of multiple paternity. The Bayesian analysis was employed to estimate the number of mates for mating females and specify this null hypothesis.

The empirical variables included the mean number of sires per litter for 60 samples and 57 species. The number of sires cannot be less than one or more than the litter size. Given a litter size of $K = k$, the number of sires S can thus be anywhere between 1 and k , and follows a zero-truncated binomial distribution [14] with probability mass function:

$$P(S = s|k, q) = \frac{\binom{k}{s} q^s (1-q)^{k-s}}{1 - (1-q)^k}, \quad s = 1, 2, \dots, k, \quad (2.1)$$

where q is the probability of success at paternity for each possible sire. The probability of multiple paternity p is

$$p = P(S > 1|k, q) = 1 - P(S = 1|k, q) \\ = \frac{1 - kq(1-q)^{k-1}}{1 - (1-q)^k}. \quad (2.2)$$

For given values of p and k , equation (2.2) can be solved for q numerically, as there is no closed form solution for q . Increasing litter size (k) for fixed probability of multiple paternity (p) lowers the probability of success at paternity for each possible sire (q). On the other hand, increasing p for fixed k increases q . Given q , the probability of success, and $S = s$ the number of sires, the distribution of the number of mates, M , is a negative binomial with parameters s and q . Theoretically, the negative binomial distribution for M describes the required number of independent trials each having a probability of success q to succeed s times.

Unlike the number of sires, we assumed no upper bound on the number of mates. Thus, the probability of m mates is

$$P(M = m|s, q) = \binom{m-1}{s-1} q^s (1-q)^{m-s}, \quad m = s, s+1, \dots \quad (2.3)$$

and the expected number of mates is

$$E(M|s, q) = \frac{s}{q}. \quad (2.4)$$

We examined the fit of the data from the literature to our proposed expectation under random mating using a Bayesian analysis with MCMC sampling for the 60 samples (57 species) that included mean number of sires per litter. Our purpose was to test the accuracy of the random models for describing the data-sets. This was accomplished by visual inspection of the real data for the probability of multiple paternity and the mean number of sires, and the expected values at different litter sizes. Litters were randomly generated for each sample population with proportion matching each sample's proportion of examined litters n , where the litter size $K \in \{1, 2, \dots, \infty\}$ followed a truncated Poisson distribution with parameter $\lambda_k =$ average litter size from the data. The number of sires for each litter, $S \in \{1, 2, \dots, K\}$, were similarly generated from a truncated Poisson distribution with $\lambda_s =$ average number of sires, given in the data. We used the beta distribution with parameters $\alpha = 1$ and $\beta = 1$ as an uninformative prior distribution of the probability of success for each sire, q . The generated litter size K and number of sires S were used to obtain a posterior estimate of q for each species by maximizing the likelihood given in equation (2.1) that describes the relationship between q , S and K . For species with more than one sample population in the original data, all randomly generated litters of the same species were combined to obtain the species' posterior estimate of q . This posterior estimate of q was used to calculate the estimated probability of multiple paternity p_B for each sample population using $k = \lambda_k$ in equation (2.2). The Bayesian analysis used two chains and 1000 burn-ins monitored for 10 000 simulations. Sensitivity of the Bayesian modelling was evaluated by repeating the process a total of 50 times.

The observed proportion of multiple paternity p and the total number of litters n given in the literature were used to calculate approximate 95% confidence intervals for probability of multiple paternity as $p \pm 1.96p(1-p)/n$. These intervals were subtracted from p_B as $(p_B - p) \pm 1.96p(1-p)/n$ to provide an approximate 95% confidence interval for the deviations from the expected null model. The mid-points of these intervals $p_B - p$ were differences of the true values of multiple paternity from the expected values derived from the null model for each species. These deviations potentially reflect logistical constraints on multiple paternity (after [12]). The deviations were used to fit a meta-analytic random-effects model with restricted maximum likelihood (REML) estimation. All analyses were conducted in R using packages rjags, R2OpenBUGS, and coda [15–18]. The meta-analysis was performed using the metafor package [19] of R.

3. Results

The association of the proportion of multiple paternity among litters with the mean number of offspring per successful breeding (viz., litter size) for females was positive, weak, and not significant (figure 1a, one-tailed test, $Z_r = 0.202$, ± 0.130 s.e., $N = 62$). Also, association of the mean number of sires per litter and litter size was not significant (figure 1b, one-tailed tests, $Z_r = 0.235$, ± 0.132 s.e., $N = 60$). The effect sizes of these associations were small (i.e. $r < 0.3$; [14]). The scatters for these associations were broad and exhibited no obvious outliers, though observations appear clumped at lower litter sizes and at low mean numbers of sires.

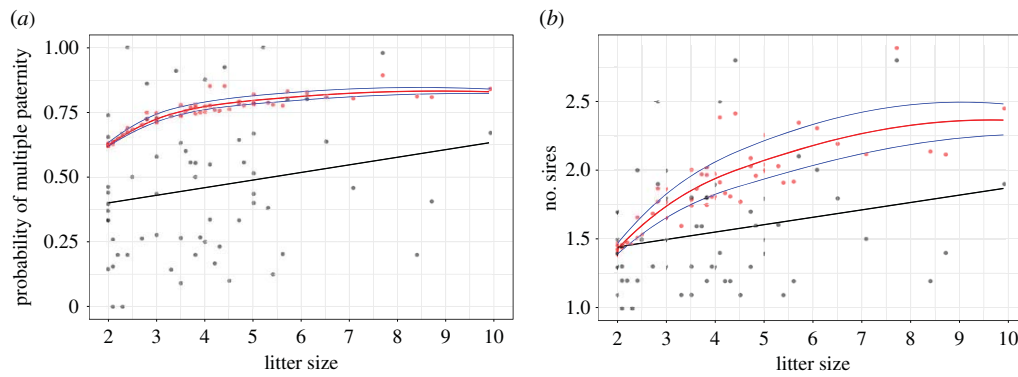


Figure 1. (a) Bayesian MCMC estimated probability of multiple paternity (p_B) across litter sizes for mammalian species (red points). The solid red line is the predicted probability of multiple paternity using equation (2.2). (b) Estimated number of sires as calculated by the mean of the zero-truncated binomial distribution in equation (2.1). Blue solid lines represent the upper and lower limits of the 95% credible intervals. Black points are the original data values, and the black line is a linear regression through those data.

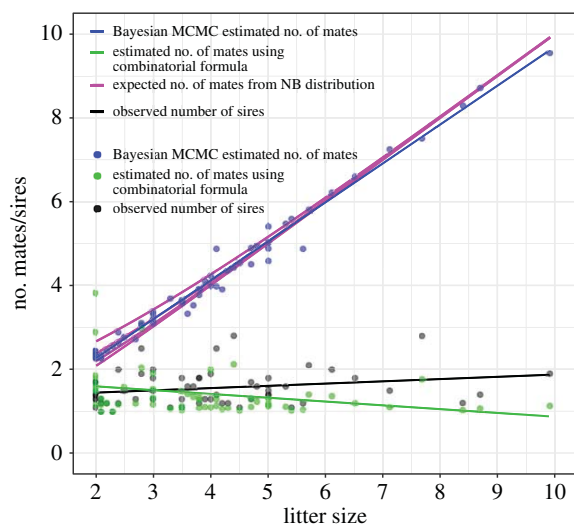


Figure 2. Bayesian MCMC estimated number of mates from the mean of the negative binomial distribution in equation (2.4) (in blue). A blue linear regression line is plotted through these points. The expected number of mates under different values of q (magenta line, from lowest line up, $q = \{0.8, 0.7, 0.6, 0.5\}$) from the negative binomial distribution in equation (2.3). Observed number of sires from the literature is shown as black points with a black linear regression line drawn through those points. The number of sires estimated using the combinatorial formula in equation (1.1) are shown as green points with a green linear regression line drawn through those points.

The expected number of sires calculated using the mean of the zero-truncated binomial distribution for different litter sizes given in the data increased with litter size, but very slowly (figure 1b). Additionally, the expected number of sires was typically higher than the true number of sires. The Bayesian MCMC simulation of the negative binomial distribution produced an expectation for the number of mates that increased with litter size and closely matched the theoretical expectations (figure 2). Predicted values for p_B at each litter size along with 95% credible limits were calculated using Bayesian MCMC, and the curve was overlaid on the observed data (figure 1a). The estimated probability of multiple paternity rose slowly with litter size and tapered off for large litter sizes. Only a few of the observed proportions of multiple paternity were larger than the Bayesian-estimated p_B (8 of 60, i.e. 13% of the

data points), and of those five of the Bayesian-estimated p_B values were significantly smaller than the observed proportion of multiple paternity (figure 3). The estimated number of mates derived from equation (2.4) increased linearly and matched theoretical expectations (figure 2). Additionally, the combinatorial average number of mates calculated from equation (1.1) gave a decreasing relationship with litter size (figure 2), which did not match theoretical expectations from the negative binomial distribution of equation (2.3), but rather matched the expected counterintuitive association with litter size. Comparison of the estimates for p_B with the 50-run estimates for p_B using Spearman's rank correlation statistic showed high correlation ($\rho_{\min} = 0.996$, $\rho_{\max} = 1.000$), indicating that the Bayesian analysis was not sensitive to minor fluctuations in K and S in the random data generation. Within-species variability accounted for only 0.4% of the total variability in the 50 replications.

Differences between the Bayesian estimates and actual values of the proportion of multiple paternity were significantly positive for 62% of the observed populations (figure 3), and the mean difference was also significantly positive (0.293 ± 0.034 s.e., $p < 0.001$, $N = 60$). Litter size had a nonsignificant impact on the mean difference (0.003 ± 0.019 , $p = 0.861$, $N = 60$).

4. Discussion

Avise & Liu [11] suggested that there are universal benefits to multiple mating, including increased fecundity for some males at higher litter or clutch sizes. This idea suggests that the intensity of sexual selection is stronger at larger litter sizes. From the idea of universal benefits to both males and females of mating with multiple partners, especially the benefit to males of mating with females that produce larger litters, they predicted a positive association of probability of multiple paternity and mean litter size among species. As a *post hoc* hypothesis, they also suggested that there are logistic constraints on the number of mates that females could acquire, and these constraints might be different in different species [12,13]. This, they explained, may have caused the probability of multiple paternity in mammal species that exhibit mean litter sizes above one to increase, but not significantly. Such constraints would cause greater variation among the species with respect to multiple paternity, because females of some species would have greater access to multiple male mates than in other species, due to social or

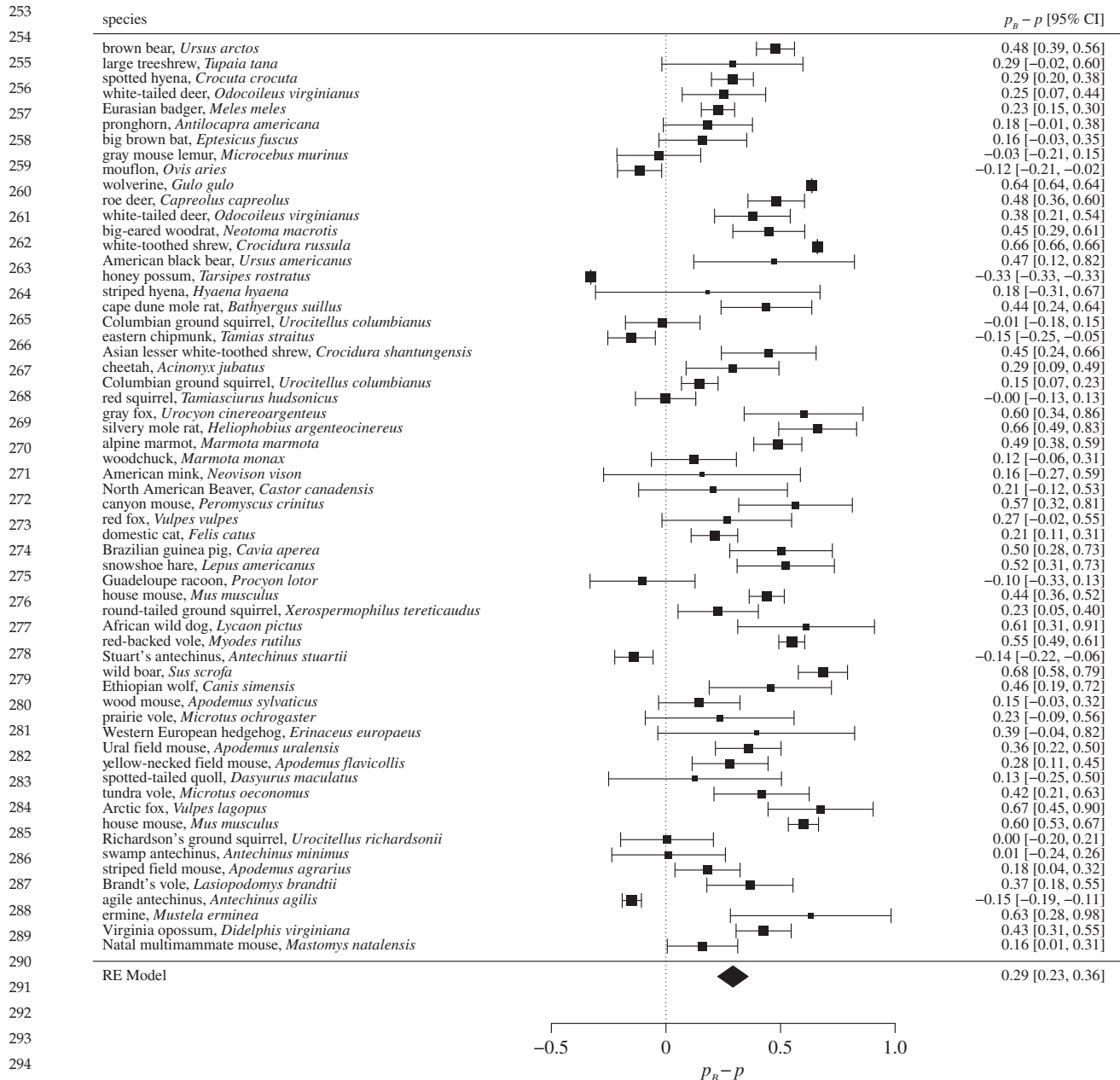


Figure 3. Effect sizes for each population calculated as difference between observed probability of multiple paternity (p) and Bayesian MCMC estimated probability of multiple paternity (p_B). Species are ordered by increasing average litter size.

ecological circumstances. With the increase in variation that such constraints would cause, the correlation between multiple paternity and litter size would be in the correct direction (positive, as predicted), but as they found, not statistically significant.

Another suggested possible advantage of increased mean numbers of offspring was simply the increase in mean litter size itself [11]. Increased opportunity to observe multiple paternity when litter sizes are large, however, is not necessarily advantageous in an evolutionary sense. Equation (1.1) shows that the probability of multiple paternity is expected to increase with both the number of male mates for females and with litter size, on average and among species. Thus, increases in multiple paternity with litter size among species are expected as a null hypothesis, and should occur even without dramatic excesses in the number of mating males or changes in the intensity of

competition for mates. As well, increases in the number of males mating with females might also produce an increase in the rate of multiple paternity, even if the increase did not produce stronger sexual selection, such as from demographic shifts or changes in population density. Obviously, population parameters, mating parameters and natural selection are interwoven. But changes in the rate of multiple paternity with litter size need not result from specific causal relationships (e.g. sexual selection) among the three variables of multiple paternity, litter size, and number of mates. Rather, a relationship is expected from the combinatorial formula, though at the largest litter sizes little change is expected (i.e. the expected rate of multiple paternity at large litter sizes is close to 100% for all numbers of mates greater than one).

The estimates of number of male mates for females in the Avise and Liu [11–13] reviews were from the observed

number of male *sires*, and not the actual number of males that mated with females. While multiple paternity is associated with the presence of multiple sires, the probability of multiple paternity depends on the number of male *mates* that females have, as demonstrated by equation (1.1). The actual number of mates, however, might still be influenced by social and ecological factors that affect access to male mates for mating females. Limitation of male mates for females can occur due to low densities with respect to sparse environmental resources, for example [1,20]. Thus, the actual number of male mates should reflect constraints on mating patterns, as well as any possible competitive influence of sexual selection.

In our dataset on 60 mammalian populations, we found the same pattern of increase in number of sires of litters with increasing litter size that Avise & Liu [12] documented, with positive correlations, though insignificant values. After accounting for bias in the correlation coefficients by using the *Zr* statistic and calculating confidence intervals changes in proportion of multiple paternity with litter size, and mean number of male sires in litters with litter size were not significant (figure 1*a,b*). The effect sizes were small but showed the expected positive associations.

While our correlative analyses were similar to the previous analyses of Avise & Liu [12], equation (1.1) yields more insight into the relationship between the probability of multiple paternity in populations from different species and the number of offspring. Specifically, we should expect the relationship to be nonlinear (figure 1*a*). Thus, while correlations provide a rough idea of effect size of the relationship, a lack of significant association under the null hypothesis of $r = 0$ is not appropriate for testing significant deviation from the expected pattern. At a given number of mates for females, on average, increasing mean litter size produces a curved distribution of probability of multiple paternity. This presented us with a quandary with respect to the null hypothesis of the expected influence of litter size on probability of multiple paternity, since the expected number of mates was unknown. Nonetheless, we concluded with confidence that the expected among-species pattern of the probability of multiple paternity over different mean litter sizes should be both positive and nonlinear.

A more appropriate null hypothesis can be obtained from the distribution of the mean number of sires in litters among species (figure 1*b*), under random fertilization, where each mating male has equal chance of paternity of an individual offspring. As litter size increases, the minimum number of sires cannot be less than one. The maximum number of sires is equal to the litter size. Under these conditions and within each species, the distribution of the number of sires over litter sizes follows a zero-truncated binomial distribution. We used this distribution to estimate the number of sires for females with different litter sizes using Bayesian estimation with MCMC sampling. The number of mates cannot be less than the number of sires and follows a negative binomial distribution. We used this distribution to estimate the expected number of mates from the distribution of the number of sires. These estimates are approximately linear and increasing for the Bayesian MCMC simulation (figure 2).

Comparison of the empirical data to expectations from the simulation (figure 1*a*), suggested that much lower rates of multiple paternity occur in most mammal species than one would predict from the null hypothesis of equal chance of paternity for each mating male. This appears to be consistent for the

entire range of mean litter sizes. This occurs in part because the expected probability of multiple paternity approaches a high percentage with increasing litter size. Reductions from the expected probability of multiple paternity might involve several processes, as well as constraints on mating systems. Indeed, since probabilities of multiple paternity from the data are below expected values for most species, the empirical number of mates, if known, would likely also be lower than expected. Sexual selection might well limit the number of males that females have available to them when they are in oestrus. While in some species females are thought to exert strong female choice, male defence of individual or grouped females is thought to be common in mammals [1,6,10]. Such defence may occur via behavioural dominance or territorial behaviour in areas where females are active. Density of mates in the ranges that females occupy may also be low in some species, thus making it difficult for oestrous females to contact high numbers of mates [1,20]. The largest deviations between the expected probability of multiple paternity from the Bayesian analysis and the actual data values indicates those species that should exhibit the greatest reductions in multiple paternity due to social or ecological constraints (figure 3). Overall, these deviations strongly support the logistical constraints hypothesis. Several Carnivora, which occupy higher trophic levels, have large deviations that might reflect the ecological constraint of relatively low population densities. It is also possible that historical (phylogenetic) influences occur, though some Carnivores had neutral or even negative deviations.

The probability of multiple paternity is widely reported, but it lacks important information about the mating system: namely the number of mates per litter. Although the number of sires is also widely reported (in our study, in 60/62 populations = 97% of the time), it also does not reflect the number of mates for females. The estimated chance of successful mating for each reproductive male (q), however, is a reasonable reflection of a male's chances of producing offspring. Once estimated, the chance of success per male q and the mean number of sires from the actual data can be used to estimate the mean number of mates for breeding females (from equation (2.4)). Thus, q is an extremely useful value for describing, in part, the form of a mating system.

Reductions in opportunities for multiple mating may be counter-balanced by female preference for multiple mates. Increases in the number of mates for females has several likely causes [1]. One possibility is high population density, so that many males are available to females for matings. Most mammals are polygynandrous [20], so increasing population density should make it more difficult for males to economically defend females during the mating season. Another possibility is the genetic benefits of multiple mating for females (reviewed in [21]), including the possible benefit of genetic diversity among offspring in uncertain environments. While a balance between benefits, costs and constraints on the number of mates for females likely occurs in all mammalian species, our results show that increases in litter size among species should result in increased probabilities of multiple paternity, other things being equal; and that for most species, this potential is seldom met.

Ethics. All data for the study were obtained from the scientific literature, and include no research on humans, or living or dead animals.

Data accessibility. All data and code are available on Dryad.

379 **Authors' contributions.** F.S.D. conceived the research, conducted initial
380 analyses and wrote the manuscript. A.A. conceived the modelling,
381 **Q6** analysed data and contributed to writing. H.C. contributed to mod-
382 elling, analysed data and contributed to writing. C.K. and B.Z.
383 contributed to modelling.

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