Estimating a Key Parameter of Mammalian Mating Systems: The Chance of Siring Success for a Mated Male

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Studies of multiple paternity in mammals and other animal species generally report proportion of multiple paternity among litters, mean litter sizes, and mean number of sires per litter. It is shown how these variables can be used to produce an estimate of the probability of reproductive success for a male that has mated with a female. This estimate of male success is more informative about the mating system that alternative measures, like the proportion of litters with multiple paternity or the mean number of sires per litter. The probability of success for a mated male can be measured both theoretically and empirically, and gives an estimate of the intensity of sperm competition and of a male's "confidence of paternity" upon mating. The probability of success for mated males for ten "exemplar" species of mammals is estimated and they are compared for insights into the functioning of their mating systems.

1. Introduction

One of the central topics in behavioral ecology is the evolution of mating systems, such as monogamy, polygyny, and polyandry.[1] In these mating systems, exclusive mating occurs between a male and female, a male and more than one female, and more than one female and a single male, respectively. Such relationships can be social or genetic, but only the latter truly describes the genealogical relationships that mating systems produce.[2] In turn, the transition of genes that individuals carry from one generation to the next produces changes in the frequencies of traits that evolve by natural selection.[3] Social associations of mating individuals may

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approximate genetic mating associations, but with notable exceptions. For example, Alpine marmots exhibit a socially monogamous mating system, but about 20% of litters have young produced by the paired male and one or more males other than the social male partner.[4] The rate at which the genetic pattern of mating differs from social monogamy is influenced by the social setting, specifically the number of subordinate males nearby,[5] and even by conditions associated with climate change.[6]

This phenomenon of social monogamy associated with multiple sires within some litters of young occurs in several mammalian species.[7] These authors could divide socially monogamous mammal species into those that typically show true genetic monogamy, and those that show some degree of multiple paternity. Multiple paternity occurs when more than one male turns out to sire offspring in the litter of a particular female. Naturally, this can only occur in species in which more than a single offspring is produced at a time by reproductive females. Multiple paternity is extremely widespread in nature. It occurs in litters and clutches of a broad diversity of viviparous animals (reviewed by refs. [8–11]). Multiple paternity also occurs in many species of oviparous animals (e.g., ref. [12]). While some individual females may produce offspring that share a single sire, others have litters or clutches fertilized by multiple males. Thus, most species may have some frequency of multiple parentage by the mates of females that are producing offspring during a single reproductive event (or males when they carry broods[9]). If both males and females have multiple mates, the social mating system is termed "polygynandrous,"[2] and this mating system is likely widespread among animal species.

Thus, the simple division of mating systems into monogamy, polygyny, and polyandry needs to be re-evaluated. Studies of multiple parentage were stimulated by the advent of molecular techniques, primarily analyses of microsatellite DNA but in the future perhaps single nucleotide polymorphisms (SNPs), that allowed assessment of paternity (reviewed by ref. [13]). Molecular studies document the proportion of litters or clutches with multiple paternity and the number of sires that contribute to each of the broods. The proportion of multiply fertilized litters or clutches is a characteristic of a population. The number of sires is measured for individual females, and is usually presented as a population mean and variance in molecular studies. When applied to mammalian species, paternity studies have shown that the phenomenon of multiple paternity of litters of offspring is extremely

widespread.[14] While these species are primarily socially polygynandrous, genetically we could say that males are polygynous and females are polyandrous. Of course, along with this, we would want to know the proportion of multiple paternities in a population, and the mean and variance of the number of sires.

A drawback of molecular studies, however, is that the frequency of multiple paternity depends not on the number of sires, but on the number of mates that females have[14] (see Equation (1) below). For a few species, the number of mates can be monitored with detailed behavioral observations. But such reports are not available for most species, because matings occur either in secretive, protected microhabitats (small animals) or across vast areas of habitat that are difficult to observe (large animals). Molecular studies document paternity, not the number of males that compete for reproductive success through the avenue of successful mating (viz., insemination), but fail to fertilize the female that they mated. Nonetheless, with some straightforward assumptions and modeling of the relationship between multiple paternity, number or sires, and the size of litters among species of mammals, we were able to estimate the probability of siring success for a male that has mated with a female.[14]

For each of the mammalian species studied, we used the mean probability of a male successfully siring offspring with a female that he mated, and estimated the expected numbers of mates for breeding females. From the probability of male siring success, we also estimated a "null" expectation of the proportion of multiple paternity, under the assumption of random fertilization by each of the mating males. This null expectation is the statistical hypothesis that a pattern of multiple paternity should be tested against, to determine whether the proportion of multiple paternity in a population or species is what might be expected under the condition of random fertilization. We could then compare the actual value of multiple paternity to the null expectation given the mean litter size in each species. Deviations from the null expectation could then be attributed to the influences of factors that cause deviations from random fertilization. Such factors might include the timing of copulation with respect to ovulation by the female, the rapidity of copulations by different males, or the length of the period during which fertilizations can occur.

The key to these analyses was the estimation of the probability of male siring success given mating.[14] We calculated this variable under the assumption of random fertilization by mating males, thus producing an average value for each species that was studied. In this essay, we argue that the probability of siring success for a mated male may help to discern the nature of a species' mating system and can be modeled further at the population level. As an initial step, our purpose in the present study was to estimate the probability of siring success when there is variation in the mean number of sires per litter, variation in the number of male mates that fail to sire offspring, and variation in litter size. We also estimated the variance in male success within ten species of mammals from our earlier study,[14] for females that have variable numbers of mates. Estimation of the probability of siring success includes males that mate but fail to produce offspring. Empirical evidence for this quantity is difficult to obtain and is often not reported. We considered failures by mating males in a Bayesian framework to estimate the probability of male siring success, and thus took a step toward solving this problem. All procedures and analyses were performed in R.[15]

2. Probability of Siring Success

2.1. A Null Model for the Influence of Litter Size on Multiple Paternity under Random Fertilization

We considered a null hypothesis for the expected relationship between multiple paternity and litter size in which male sperm from inseminations mixes so that paternity is random among mating males.[14] For each population or species, the proportion of litters that show multiple paternity (p) can be determined from the number of mates (m) that females have and the size of their litter (k) using the combinatorial formula

$$p = \frac{m^k - m}{m^k} = 1 - \frac{m}{m^k} \tag{1}$$

The value of p increases when m increases, k increases, or both m and k increase. If we again make the same assumption that male sperm mixes so that paternity is random among mating males, then the probability of siring success for a mated male (q) would be calculated as

$$q = 1 - \left(\frac{m-1}{m}\right)^k \tag{2}$$

In this case, q increases when k increases for a fixed m but decreases when m increases for a fixed k. Equations (1) and (2) work only under idealized conditions of random fertilization among mating males, and cannot be used when there are differences in siring success of mated males due to differences in sperm quality among males and precedence (e.g., fertilization advantage by the first-male or last-male to inseminate).[16–19] Note that neither formula takes the number of sires per litter into account. This latter information is, however, available in paternity analyses that use molecular data, where studies of multiple paternity generally record mean litter size, mean number of sires per litter, and the proportion of litters that show multiple paternity.

Dobson et al.[14] used published data on multiple paternity in a meta-analysis of mammalian mating systems. We generated patterns of multiple paternity and expected number of mates from the observed number of sires and litter sizes. These were used to set the null distributions for testing the expected relationship between multiple paternity and number of offspring in a litter. In earlier studies, Avise and Liu[9,11] predicted that the relationship between percent multiple paternity and litter size should be positive and monotonic, because in species with greater litter of clutch sizes, males should compete more strongly for matings. In turn, this greater competition was hypothesized to produce greater degrees of multiple paternity, an idea termed the "fecundity-limitation hypothesis." We examined whether the prediction of a positive association of multiple paternity and litter size would be expected under an appropriate null model.

We used Markov chain Monte Carlo (MCMC) methods to estimate the probability of siring success for a mated male (q) and the number of mates (m) within each of 60 mammalian species.[14]

The probability that the number of sires is $S = s$, given values of k and the probability of siring success for a mated male (q), follows a truncated binomial distribution[20]

$$P(S = s|k, q) = \binom{k}{s} q^s (1-q)^{k-s} / (1 - (1-q)^k), \, s = 1, 2, \ldots, k \tag{3}$$

Since we had empirical evidence of the mean numbers of sires from the paternity studies, we estimated q from the method of maximum likelihood applied to empirical mean values of s and k. Assuming a Poisson distribution for k (a count datum), we truncated k to be no less than 1 and generated 10 000 random integer-valued litter sizes from the mean value of k for each species. The number of sires for each litter cannot be less than 1 nor more than k. Under this restriction and assuming a truncated Poisson distribution of s between 1 and k, we randomly assigned sires to each randomly generated litter. We then solved for q numerically, since there is no closed solution for q from Equation (3). We calculated mean estimates of q, and repeated the procedure for each of the species that had been subjected to paternity studies.

From these values and the assumption that male sperm mixes so that paternity is random among mating males, we estimated the expected probability of multiple paternity (p) from the truncated binomial distribution as well as the probability that the number of mates per female is $M = m$, and the expected number of mates from the negative binomial distribution[21] as

$$p = P(S > 1|k, q) = 1 - P(S = 1|k, q)$$
$$= \left(1 - kq(1-q)^{k-1}\right) / \left(1 - (1-q)^k\right) \tag{4}$$

$$P(M = m|s, q) = \binom{m-1}{s-1} q^s (1-q)^{m-s}, \, m = s, s+1, \ldots \tag{5}$$

$$E(M|s, q) = \frac{s}{q} \tag{6}$$

The negative binomial distribution is used as a model for the number of attempts required to achieve a fixed number of successes for a given success probability. Here we can see first important conclusion about q. Once we know q, we can estimate the value of p without knowing the value of m. Though of course the expected number of mates for females (m) is still an important aspect of the mating system, and it is easily estimated from the empirical value of the average number of sires among litters (s) and the probability of success for a mated male (q). Our null model of the expected number of mates revealed a pattern of increase in multiple paternity with litter size that was similar to what was found empirically, and identified species that differed strongly from the expectation of multiple paternity under the assumption of random success among mating males.[14] Species that deviate strongly from the null model were presumably influenced by factors in the ecological or social environments (termed the "logistical constraints hypothesis" in ref. [10]).

## 2.2. Mates That Fail to Sire and Litter Size Govern the Pattern of Siring Success

For an initial simulation, we used MCMC in a Bayesian analysis to study changes in the probability of siring success for a mated male (q) as litter size increased, where mean litter size varied from about 2 to 10. We chose two ranges for the average number of sires: close to the minimum (S_{LO}) and maximum (S_{HI}) reported number of sires in the mammalian data. Mean values of S produced by the truncated binomial distribution in the simulations varied. We used the same number of failed mates (viz., males that mated but did not sire offspring) for both cases, a range from 1 to 5. We considered $n = 100$ litters and generated the litter sizes using a zero-truncated Poisson distribution with the average litter sizes ranging from 2 to 10.

The number of sires was generated using the Poisson distribution with mean in the ranges S_{LO} and S_{HI} but truncated at 1 on the lower end and the litter size at the higher end. Since in the truncated Poisson distribution the mean is a function of the variance, restricting the upper bound of the distribution by a litter size that changed in every iteration meant that we could not fix the mean number of sires. However, the mean number of sires was restricted in the two ranges S_{LO} and S_{HI} (1.39 ≤ S_{LO} ≤ 1.87 and 1.77 ≤ S_{HI} ≤ 3.43), representing potentially low and high rates, respectively, of siring success for a mated male, if the total number of mated males per female were a fixed value. This latter, however, was not strictly possible, because the total number of mates is the sum of number of mates that failed to sire (f) and the number of sires (s). We varied f within each range of s and studied how q varied with k for relatively equal numbers of successes. We intuitively expected the probability of successful mating to increase with the number of offspring that a female birthed, *ceteris paribus*. The probability of success for mated males increased with litter size in the simulation, and more strongly when the mean number of sires was greater (**Figure 1**).

We used an alternative reparameterization of the negative binomial distribution[21] to model the number of failures among the male mates (F) as a function of the number of sires (s) and the probability of success for each mating male (q), that has a likelihood described by the probability mass function

$$P(F = f|s, q) = \binom{f + s - 1}{s} q^s (1-q)^f \tag{7}$$

Here, f is the number of failures, which we varied from 1 to 5, and s is the number of sires from the data. For each f, we generated a complete sample of n litters with mean litter size and mean number of sires fixed at a given range of data values. For this second simulation, we varied the number of failed mates and used only the S_{HI} range for average sires. Changing the number of failed mates indicates the range of changes in q that are possible in mating systems in which f is variable (S_{HI} was used for illustration, and both S values were arbitrary from the larger sample of 60 mammalian species from ref. [14]). Naturally, as more males failed, a given male's probability of success declined (**Figure 2**). Nonetheless, at every value of failures for a mating, the probability of success increased with litter size.
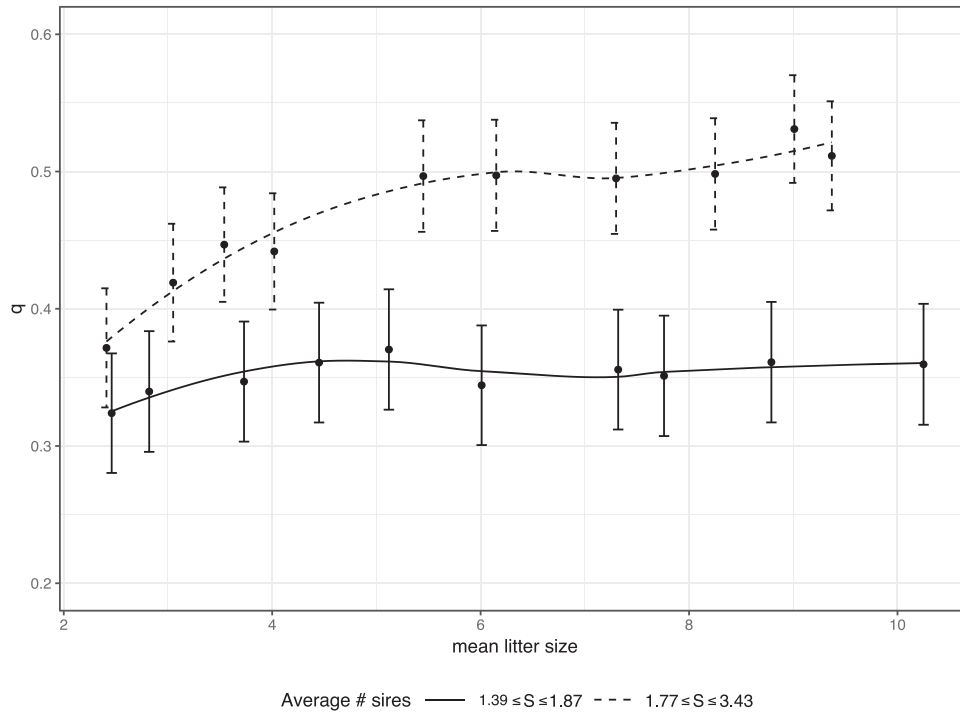
Figure 1. Simulated probability of siring success for mated males at relatively low and high numbers of sires at litter sizes of 2–10. The number of mating males that failed to produce young was varied from 1 to 5 for each litter size and numbers of sires. S was produced by a truncated binomial distribution, resulting in a range of S values in the simulations, as shown below the graph. Means shown by dots, bars indicate 95% credible limits of variation.
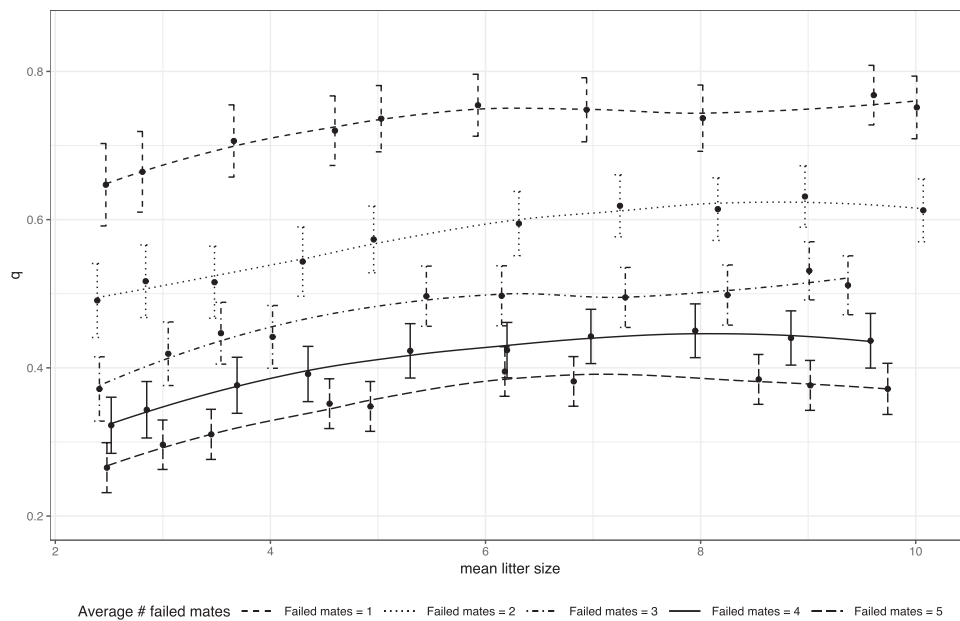
Figure 2. Simulated probability of siring success for mated males at relatively low and high numbers of sires at litter sizes of 2–10. The number of mating males that failed to produce young was varied from 1 to 5 for each litter size and numbers of sires. Means shown by dots, bars indicate 95% credible limits of variation.

Table 1. Basic data on ten species of mammals: number of litters (**n**), mean litter size (**k**), mean number of sires (**s**), and frequency (probability) of multiple paternity (**p**) are from microsatellite DNA studies in the literature; the difference between a null model estimation of **p** and the actual value of **p** is from ref. [14]; estimated probability of siring success for a mated male (**q**) and number of mates (**m**) from this study with 95% confidence intervals in parentheses.

Species	No. of litters	Average litter size	Average no. of sires	P = probability of multiple paternity	p(null) − p(data)	Mean estimated q (95% CI)	Estimated no. of mates (95% CI)
Agile antechinus, *Antechinus agilis*[a]	47	7.7	2.8	0.978	−0.149	0.590 (0.540, 0.641)	7.51 (3.20, 12.33)
Stuart's antechinus, *Antechinus stuartii*[b]	39	4.4	2.8	0.923	−0.140	0.822 (0.758,0.878)	3.87 (1.21, 7.42)
Eastern chipmunk, *Tamias straitus*[c]	43	2.8	2.5	0.860	−0.150	0.894 (0.836,0.940)	3.05 (1.10, 4.88)
Red squirrel, *Tamiasciurus hudsonicus*[d]	215	3.0	2.0	0.727	−0.002	0.321 (0.252,0.395)	3.66 (2.54, 9.23)
Columbian ground squirrel, *Urocitellus columbianus*[e]	29	2.8	1.9	0.724	−0.014	0.636 (0.606,0.665)	2.88 (1.52, 6.21)
Columbian ground squirrel, *Urocitellus columbianus*[f]	147	3.0	1.8	0.578	0.147	0.636 (0.606,0.665)	2.88 (1.52, 6.21)
Virginia opossum, *Didelphis virginiana*[g]	64	8.7	1.4	0.406	0.426	0.147 (0.118,0.177)	8.61 (5.67, 21.65)
Alpine marmot, *Marmota marmota*[h]	69	3.5	1.3	0.265	0.488	0.401 (0.339,0.465)	3.40 (2.18,6.92)
Red-backed vole, *Myodes rutilus*[i]	44	4.3	1.2	0.232	0.549	0.642 (0.606,0.676)	3.37 (1.50, 6.50)
Brown bear, *Ursus arctos*[j]	68	2.0	1.1	0.145	0.478	0.539 (0.457,0.620)	2.03 (1.62, 3.88)
Wild boar, *Sus scrofa*[k]	30	4.5	1.1	0.100	0.685	0.250 (0.178,0.329)	4.24 (3.04, 7.31)

[a] Ref. [22] [b] Ref. [23] [c] Ref. [24] [d] Refs. [25,26] [e] Ref. [27] [f] Ref. [19] [g] Ref. [28] [h] Ref. [5] [i] Ref. [29] [j] Ref. [30] [k] Refs. [31,32] Species appear in the order of Figure 3, from the top of the graph to the bottom. Data and results are from Dobson et al.[14] and analyses described in the text, except where noted.

2.3. Siring Success and Number of Mates Can Be Estimated Indirectly Using Molecular Data

For each of ten "focus groups" of mammalian species, one or two studies provided information on mean and maximum litter size. For the ten species studied, mean litter size varied between 2 and 8.7 (**Table 1**). A larger sample of 60 species had mean litter sizes that varied between 2 and 9.9.[14] The mean number of sires per litter varied from 1.1 to 2.8. The proportion of litters with multiple paternity among our ten species varied from 10.0% to 97.8%. Thus, our exemplar species covered a broad range of mammalian mating patterns (see also refs. [10,14]).

For our primary analysis, we generated **n** litters from truncated Poisson distributions for **k** with mean litter sizes from the literature and maximum litter sizes being restricted to reported values. Here, **n** was equal to the real sample size of litters for the species. These studies also provided estimates of the mean number of sires in the actual litters which were used to generate numbers of sires for the generated litters via truncated Poisson distributions. For the Columbian ground squirrel, that had two microsatellite DNA studies (Table 1), two samples of size **n** were generated and combined. The generated number of sires and litter sizes were used in the truncated binomial distribution given in Equation (3) to estimate, using Bayesian MCMC analysis, the mean probability of success for each mating male (**q**) as a function of litter size (**k**) and the number of sires (**s**). We then plugged this estimated mean **q** and mean **s** from the literature into Equation (6) to calculate the numbers of mates (**m**) for females of the species considered (**Figure 3**).

In a secondary analysis of the ten exemplar species of mammals (Table 1), we varied the number of males that failed to sire offspring from mating with a female at 1–5. With this information and the mean number of sires and litter sizes from the data, we maximized the negative binomial likelihood given in Equation (7) in a Bayesian MCMC. This provided the changes in the probability of male success as the mean number of mates (the sum of the mean number of sires and the number of mates that failed to sire offspring) increased for the ten species. Of course, since the mean number of sires was fixed, increased number of mates reflected adding mating males that failed to sire offspring. We plotted the relationship of the probability of male success to the mean number of mates from the secondary analysis (Figure 3). Because six of the species had very similar trends in the relationship between mean number of mates and probability of male success, we did not plot three of the species for clarity. Exclusively using this **q** versus **m** relationship from the secondary analysis, we predicted the probability of siring success at the mean number of mating males estimated using the primary analysis with the mean litter sizes and mean number of sires reported in the literature.

We plotted these values (asterisks) along with the estimated mean **q** for the calculated **m** obtained from the primary analyses (circles with pluses), and the two estimates showed close agreement (Figure 3). For all exemplar species, the empirical patterns exhibited a strong trend toward the expected negative pattern (Equation (2); see Table 1). Estimated values of the probability of siring success for mated males (**q**) varied between 0.147 and 0.894. From the mean values of **q** and **s**, we also estimated the mean number of mates for a mating female (**m**), which varied between 2.03 and 8.60.

2.4. Probability of Siring Success is More Informative Than Probability of Multiple Paternity

The probability that a mated male is successful at siring one or more offspring in the litter of a female is a useful variable that can give us insights about mating systems. When this value is high, most mating males are successful each time they mate; and the opposite when the value is low. As a population mean with a range of values, it indicates species that experience relatively low or high sperm competition, respectively. The degree
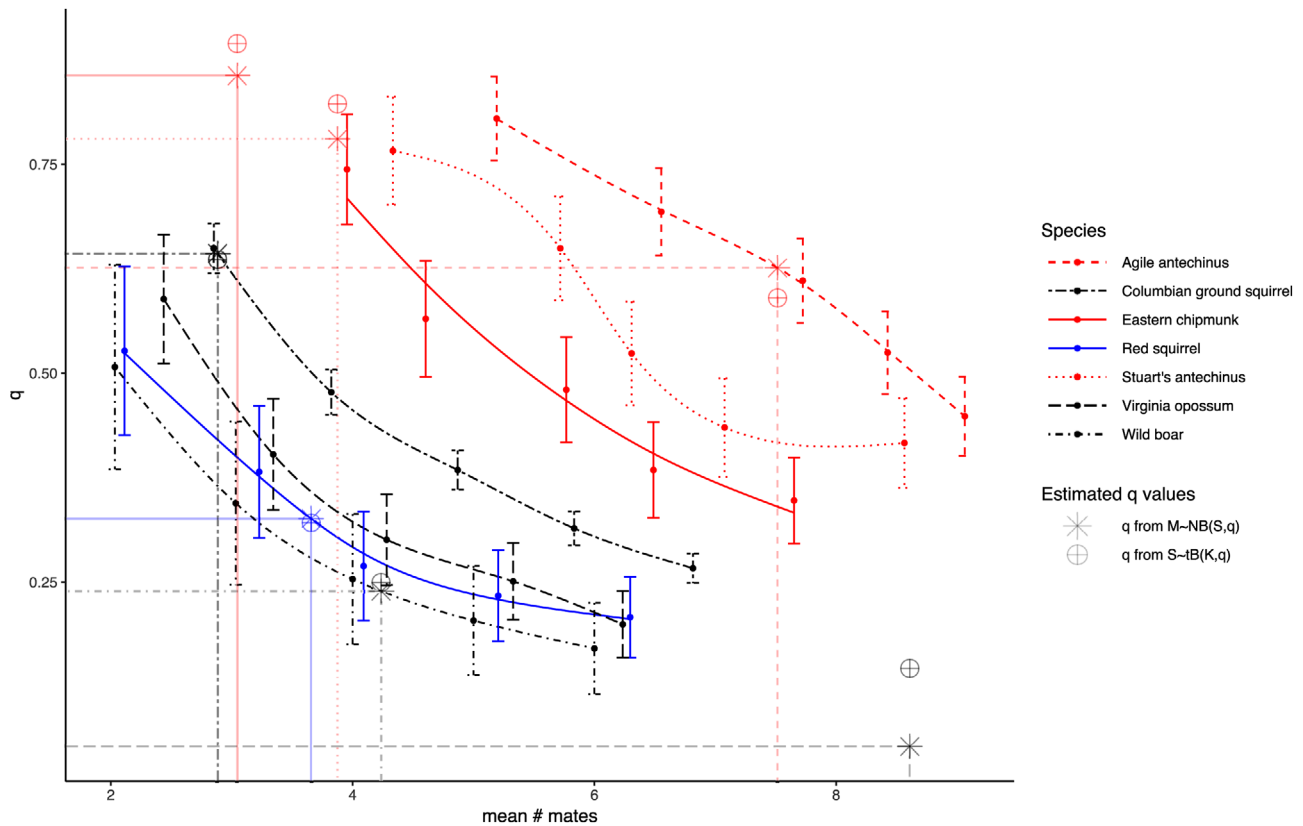
Figure 3. For exemplar species (see Table 1), probability of siring success for mated males and number of mating males. Curves, dots, asterisks, and 95% credible intervals from simulations in which the number of males that failed to produce young was varied from 1 to 5 for each litter size and numbers of sires. Circles with an internal plus are empirical mean estimates for each species (from the primary analysis described in the text), given in Table 1. Asterisks joining horizontal and vertical lines with the same identity as the curves give the *q* and *m* values for the former estimates (from the secondary analysis described in the text).

of sperm competition may influence the evolution of reproductive traits.[18,33] It is more informative than the usually reported proportion of litters with multiple paternity, because the latter is a population parameter that gives no information about individuals and is thus reported without information about variance. The mean number of sires is also usually reported, but it at best poorly describes the competitive environment for mating males. The probability of siring success is also a rough measure of confidence of paternity in a litter (*sensu*[34]), at least when comparing among populations or species.

Our exemplar species showed general patterns of influence on a mated male's probability of successful reproduction. For example, the two antechinus species have very similar proportion of multiple paternity and mean number of sires. Yet, the probability of siring success for a mated male is much higher for Stuart's antechinus. This results because the agile antechinus has a larger number of estimated male mates per reproductive female. Since the mean number of sires is very similar in the two species, this translates into more failed mates and a lower probability of siring success for a mated male in the agile antechinus. This difference was not captured by the original estimates of multiple paternity and mean number of sires. Similarly, brown bears and wild boar have low proportions of multiple paternity and very similar mean numbers of sires, but wild boar have larger litter

sizes, more estimated numbers of mates (and thus more failed mates), and a much lower estimated probability of siring success for mated males.

The relationship between multiple paternity (*p*) and the probability of siring success for mated males (*q*) is not obvious. Both *p* and *q* increase with litter size (*k*), showing the most substantial increases at low values of litter size. On the other hand, *q* should decrease substantially with increases in the number of mates for a female, reflecting increased competition among males for successful matings and increased intensity of sperm competition. Sperm competition should be strongest at low values of *q*. As *q* declines, mating males are getting a low rate of success from their matings. At the same time, a few successful males may obtain high numbers of offspring via mating, as is the case in highly polygynous species. Cases of strong sperm precedence would produce this sort of mating pattern (e.g., 1st male advantage in Columbian ground squirrels; Table 1).[19,35] As *q* nears one, on the other hand, every male has a roughly equal chance of reproducing when mating with a female. At this extreme, both genetic and social monogamy or polygyny may occur, where mate defense restricts mating males to guarding one or a few females and mating with them, depending on the adult sex ratio.[2] As *q* declines from one, some degree of social polygynandry should produce relatively strong rates of multiple paternity.

Finally, Avise and Liu[10] developed a "fecundity-limitation hypothesis" for species with multiple paternity, based on the idea that competition for mating with females that produce larger litters should be more intense. The idea is that males have a greater chance of being successful (that is of being sires) when more offspring are likely to be produced by the female. While this rationale might occur within species, it is not a logical process among species. Males of different species do not compete with each other for mates and the reproductive fitness that females offer. Our previous study of 60 mammalian species suggested that multiple paternity should increase among species simply as a result of increased opportunities for males to sire one of the offspring, such that species with a relatively high litter sizes give males more chances to sire offspring if they can mate.[14]

Within species, however, males might compete more strongly for mating with females that produce the largest litters, in order to sire the greatest number of offspring. This possibility, however, must be balanced against the increased chance of multiple paternity at larger litter sizes. In any case, there would have to be some mechanism for males to discern the later reproductive success of the females, but females should vary in body size or condition and these traits are often associated with increased reproductive success (e.g., refs. [36,37]). For at least some species of mammals, low probability of siring success for mated males at the largest mean litter sizes suggests support for the idea that sperm competition might be more intense for these species.

3. Conclusion

The widespread occurrence of multiple paternity in the animal kingdom mandates a reconsideration of the diversity of mating systems and their evolution. Important evolutionary phenomena like sperm competition can be better understood as depending on both the number of mates for females and the number of offspring that females produce when reproducing. We have argued that the probability of siring success for a mated male is both a fundamental property of a mating system, especially the polygynandrous systems typical of most mammalian species, and an important and useful theoretical variable. The probability of siring success is a post-copulatory variable, however, and must be considered with pre-copulatory variables in the social and ecological environments that may influence mating systems.

Conflict of Interest

The authors declare no conflict of interest.

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