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Multiple paternity and the number of offspring: A model reveals two major groups of species

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Abstract

Parentage analyses via microsatellite markers have revealed multiple paternity within the broods of polytocous species of mammals, reptiles, amphibians, fishes and invertebrates. The widespread phenomenon of multiple paternity may have attending relationships with such evolutionary processes as sexual selection and kin selection. However, just how much multiple paternity should a species exhibit? We developed Bayesian null models of how multiple paternity relates to brood sizes. For each of 114 species with published data on brood sizes and numbers of sires, we compared our null model estimates to published frequencies of multiple paternity. The majority of species fell close to our null model, especially among fish and invertebrate species. Some species, however, had low probabilities of multiple paternity, far from the predictions of the null model, likely due to sexual selection and environmental constraints. We suggest a major division among species' mating systems between those with close to random mating and high levels of multiple paternity, and those with constraints that produce low levels of multiple paternity.

KEYWORDS
Bayesian modeling, brood size, fish species, invertebrate species, mammalian species, MCMC sampling, multiple paternity, negative binomial distribution, reptile species, truncated binomial distribution

MULTIPLE MATING IN VIVIPAROUS SPECIES

Multiple mating can have strong influences on evolution by natural selection. For example, the opportunity for multiple mating could exacerbate the strength of sexual selection, as the limited sex (usually males) vies for reproductive advantages among the members of the limiting sex (usually females) that are available to mate.[1,2] On the other hand, in polytocous species (viz., those producing more than one offspring per reproductive event), multiple paternity could result in a more even distribution of success at paternity among mating males, thus lowering the intensity of sexual selection[3]. Multiple paternity could also reflect post-copulatory sperm competition, as sperm from multiple sires vie for fertilization of eggs[4–8]. Furthermore, the number of sires among a litter, clutch, or brood of offspring influences the degree of relatedness among siblings[9,10], which in turn can influence cooperation between social parents and among offspring via kin selection, the latter yet another form of natural selection.

Multiple mating by females frequently results in multiple paternity of clutches[11–14]. More rarely, but still important, are cases where multiple maternity occurs in species where males gestate offspring[15]. For viviparous (live-bearing) species, the observed probability of multiple paternity should be influenced by at least two factors: the number of mates for females and the number of offspring in clutches[16,17]. As the number of mates increases, multiple paternity should increase; and multiple paternity should also increase as clutch size increases. Examination of genetic parentage of clutches in different groups of vertebrates and invertebrates using analyses of microsatellite DNA are yielding an increased number of species for which rates of multiple paternity and numbers of sires per clutch have been estimated. While these latter two factors appear to co-vary among broadly different

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taxonomic groups such as mammals, reptiles, and fish, they have not shown clear covariation within groups[12]. Avise and Liu[12–15] thus concluded that the benefits of multiple mating must be offset by logistical constraints on the number of mates that the offspring-nurturing sex can have.

Shortcomings of the "Fecundity limitation hypothesis" for multiple paternity

Previous studies inferred multiple mating from genetic parentage analyses (reviewed and analyzed by Avise et al.[12,15,18]; summarized by Avise[19]). These studies reasoned that as the number of offspring for females increases, male competition for access to females should increase as well, so that species with larger brood sizes would have greater competition for matings by the limited sex, and thus greater probabilities of multiple paternity in their populations. Avise and Liu[15] termed their idea the "fecundity limitation hypothesis" and applied it among species by predicting that species with the greatest clutch sizes would have the highest probabilities of multiple paternity. Avise and Liu[12] also described benefits that accrue to the limiting sex from multiple paternity, including increased nuptial gifts, avoidance of mating with sterile males, "good gene" combinations in offspring, and promotion of genetic diversity among offspring. But the strongest benefits, they suggested, accrued to the limited sex (usually males) via increased reproductive success from mating with the most productive members of the limiting sex (usually females). Thus, they were convinced of "near universal" benefits of multiple paternity. The work of Avise and his colleagues was the first attempt at a theoretical approach to multiple paternity, but their framework for testing assumptions about multiple paternity may not have been entirely appropriate[16].

Avise and his colleagues examined results on the number of sires (or dams in male-pregnant species), and not the number of mates per se. However, the probability of multiple paternity in a population depends on the number of mates for the limiting sex and the number of offspring that this choosy sex produces[16,17]. For example, in a study of Soay sheep that produced twins, the rate of multiple paternity was about 74%[20]. Under the assumption of an equal chance of paternity among an average of two mating males, the expected probability of multiple paternity for a litter would be 50%. At an average of four mates per female, however, the expected probability of multiple paternity would be 75%, close to the empirical population average. In both cases, each litter would have one or two fathers, since only cases of two offspring (twins) were examined. But two mates per female implies greater competition for matings than an average of four male mates, other things being equal, and thus stronger sexual selection. Compared to the number of mates for females, the number of sires (the number of successful mates) is a poor predictor of multiple paternity, because more than one sire simply means that multiple paternity exists; there is also no distinction between two or more than two sires when it comes to the rate of multiple paternity. Thus, the distinction between the numbers of mates and sires is important for understanding the evolution of different mating systems among species.

A new theoretical approach to multiple paternity across species

Our purpose in the present study was to re-evaluate the significance of results from the reviews of Avise et al. [12,15,18], using statistical tools that we developed previously[16] to appropriately construct a null model of multiple paternity. We applied the null model across species to estimate the expected number of mates that females should have under the assumption of an equal likelihood of success at fertilization by all mating males (i.e., each mating male has an equal chance of becoming a sire). The construction of a null model is important for testing the influence of biological mechanisms, including sexual selection and logistical constraints, on multiple paternity. Observed patterns of multiple paternity can then be compared against randomized data in which these mechanisms have been deliberately removed[21–23]. Specifically, we removed potential influences of biological mechanisms such as sexual selection and environmental constraints from multiple paternity by giving all mates an identical probability of siring an offspring in a given clutch. This eliminated such effects from influencing patterns of multiple paternity in the null model. Further, equal likelihood of siring success for the mates of the limited sex is a reasonable null hypothesis for testing alternative hypotheses about the probability of multiple paternity[16]. Large deviations from the null model may indicate parentage patterns that are non-random[23], and thus might be influenced by processes like sexual selection, sperm competition, and environmental factors, all constraints on multiple paternity. We therefore considered several such species and examined specific behaviors that reveal the relationship between sexual selection and observed patterns of multiple paternity in these species.

Our null model approach for mammalian species showed that a positive but curvilinear and weak association of multiple paternity and litter size was predicted[16]. Avise and Liu[12] had predicted a significant positive correlation between probability of multiple paternity and numbers of offspring, and thus tested against a statistical null hypothesis of zero association with no additional information such as expected probabilities of multiple paternity. However, their results revealed a weak correlation that was not significant, close to our null model expectation. Some mammalian species exhibited much lower frequencies of multiple paternity than expected from our null model. It is in this latter group of species in which constraints on multiple paternity are to be found[16]. Constraints might include behaviors associated with sexual selection (e.g., male territoriality, dominance, or mate guarding when females are in estrus), sperm competition (e.g., precedence effects, such as bias for the first or last mating male), or environmental factors (e.g., low density or prolonged mating seasons, perhaps associated with patterns of food resource abundance or availability).

We revealed that for species with numbers of offspring above about 10–12, even low numbers of mating males produced expected probabilities of multiple paternity from the null model that were close to 100%[16]. Since the litter sizes of mammalian species varied from two to about ten, we could not expand the application of the null model to test observed patterns of multiple paternity in species with larger

clutch or brood sizes. Therefore, our primary purpose in the present work was to test the prediction that larger broods than those shown by mammals should exhibit high probabilities of multiple paternity under the null model assumption of an equal likelihood of successful fertilization by all mating males. We did this by reanalyzing the entire collection of datasets that Avise and his colleagues[12,15,18] presented for invertebrate and vertebrate (viz., fish, amphibian and reptile, and mammal) species, which provided a wide range of brood sizes and probabilities of multiple paternity across a variety of viviparous, ovoviviparous (producing live young from internally produced eggs), and oviparous (egg-laying) animals.

THE NULL MODEL FOR MULTIPLE PATERNITY

We began with the mean number of sires, estimated from microsatellite data and reported in the literature. The number of sires cannot be less than one for any clutch in the samples, nor could the number of sires be greater than the size of the clutch. Thus, we could model the number of sires with a zero-truncated binomial distribution[24]. The probability of siring any particular offspring is a function of clutch size and the probability of success among all possible sires, that is among some number of mates. Likewise, the probability of multiple paternity in any given clutch is also a function of clutch size and the probability of siring success given mating[16,17]. The primary assumption of our null model is an equal likelihood of siring success for every mated male (or mated female, for fish species with role-reversed mating systems[25]). Given values for the probability of multiple paternity and clutch size, the probability of success for possible sires can be derived numerically, as there is no closed-form solution. The distribution of the number of mates for clutches follows a negative binomial distribution, with a lower bound equal to the number of sires and no upper bound. The expected number of mates for a clutch of a given size is thus the mean number of sires divided by the probability of success for a mating male. Elsewhere, we gave the derivation of this expectation[16,17].

For species with a known mean clutch size and mean number of sires per clutch, the above process will yield an expected relationship between the mean clutch size and the probability of multiple paternity. This is the expected relationship under equal likelihood of fertilization among mates, and thus is a "null model" for the probability of multiple paternity given a specific mean clutch size. We used Bayesian analyses with MCMC sampling to investigate the degree to which the real data deviated from the null model. Since multiple paternity studies often only include the number of clutches studied (n), mean clutch sizes (λ_k), and mean number of sires (λ_s), clutches that resembled the observed data were simulated, where $10 \times n$ clutches for each species had clutch sizes randomly generated using a Poisson distribution with mean of λ_k. We similarly generated the number of sires for each clutch from the mean (λ_s) for each species, using a truncated Poisson distribution with the minimum number of sires (s_{min}) equal to one and the maximum number of sires (s_{max}) equal to the generated clutch size. A beta distribution was used with parameters $\alpha = 1$ and $\beta = 1$ to yield an uninformative prior for the distribution of the probability of siring success (q). The generated clutch sizes (K) and number of sires (S) were used to obtain a posterior estimate of the probability of success for each possible sire (q). This value in turn was used to estimate the expected probability of multiple paternity (p_B), given the mean clutch size. This process was applied individually to each species. The Bayesian MCMC estimation process is summarized in Figure 1. The Bayesian analyses used two chains with 1000 burn-in and 10,000 sampling iterations.

The above analytical procedure was applied to data from species that were reported in the literature (datasets from[12,15,18]). We eliminated three invertebrate species from the analyses, because estimated brood sizes were above 25,000 and approximated rather than counted. The samples of species and populations were as follows: mammals (species = 49, populations = 49); herps (species = 16, populations = 18); fish (species = 23, populations = 27); and invertebrates (species = 26, populations = 28). To check the sensitivity of our null model results to the random generation of brood sizes and sires, we reran our analyses 50 times with different seeds and examined the consistency of the estimated probabilities of multiple paternity. Correlations between our original estimates and those subsequently generated were high (minimum $\rho = 0.910$; maximum $\rho = 0.916$; n = 114 species, 122 populations).

REVEALING A PATTERN OF ESTIMATED MULTIPLE PATERNITY ACROSS TAXA

For each studied population, the core variables of the datasets were the proportion of clutches with multiple paternity (p), the mean number of sires per clutch (λ_s), mean clutch size (λ_k), and sample size (n). The major taxonomic groups represented were mammals, viviparous amphibians and reptiles, brooding fish (divided into male and female brooders), and a variety of brooding invertebrates (primarily arthropods and mollusks, with marine species highly represented). Where clutch size was described in words (e.g., "several thousand" or "dozens to hundreds") we approximated values given by Figure 3 of[18] using WebPlotDigitizer software version 4.1 (available at https://automeris.io/WebPlotDigitizer). Fish[15] and invertebrate[18] datasets were provided in tables; and mammal and "herp"[12] data were provided in online supporting information available from the PNAS journal website.

For mammalian species, mean litter sizes varied between two and ten. The mean number of sires for litters of individual species varied from one to 2.8. Many of the observed probabilities of multiple paternity fell below the Bayesian estimated p_B, though a few were above the mean and 95% credible interval expected for the null model (Figure 2). "Herp" species were predominantly reptiles (a single amphibian was included[12]), and clutch sizes varied between about two and 34. The mean number of sires for clutches ranged from one to 4.3. Many of the species had observed probabilities of multiple paternity well below the p_B estimates from the null model, and only a few species were above the estimated null model and 95% credible interval. A cluster of six species in the sample (33% of the sample) exhibited both low clutch sizes and very low probabilities of multiple paternity (Figure 2).

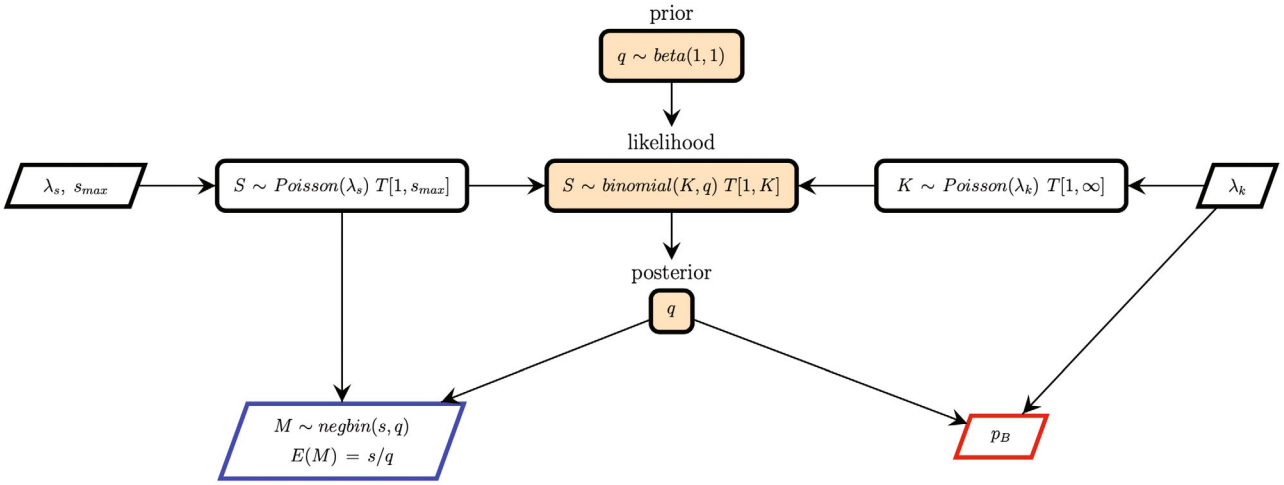

FIGURE 1 Bayesian process of estimating the success rate of mates (q). The Bayesian MCMC estimated number of mates (M) is calculated using the mean of the negative binomial distribution, which uses the generated number of sires (S) and Bayesian estimated q to generate a null distribution of the expected number of mates under the assumption of equal likelihood of successful fertilization by competing mates. The Bayesian estimated probability of multiple paternity (p_B) is calculated using the known litter or clutch size (λ_k) from the data and Bayesian estimated q. $T[a, b]$ indicates the distribution is truncated to produce values in the interval $[a, b]$. K is the generated litter or clutch size.

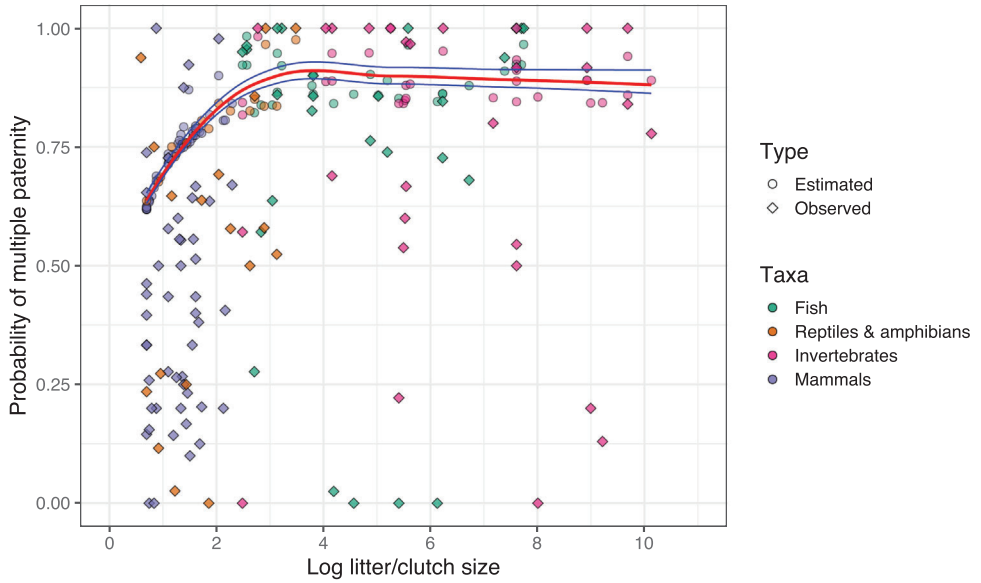

FIGURE 2 Bayesian MCMC estimated probability of multiple paternity (p_B) across litter sizes for all species (circles). The solid red line is a loess smoother of p_B. Blue solid lines represent the upper and lower limits of the 95% credible intervals. Diamonds are the original data values, and colors differentiate the four major taxonomic groupings.

Fish species contained examples of both male and female brooders, with clutch sizes ranging from about 12 to 2300. The mean number of sires (or dams, for role-reversed species) varied between one and nearly five. Over the range of clutch sizes, Bayesian estimates of probabilities of multiple paternity from our null model were flat, at about 90%. Only a few species fell well below the estimated p_B and credible 95% interval (Figure 2). Finally, invertebrate species contained a haphazard sample of marine and a few terrestrial species, with clutch sizes varying between about 12 and 25,000 (three species with vague larger brood sizes were omitted). Mean number of sires per clutch ranged from one to nearly 20, and the Bayesian-estimated probabilities of multiple paternity from the null model were fairly flat and constant at about 90%. Again, only a few species data points fell below the estimates of p_B from the null model and its 95% credible interval (Figure 2).

TESTING AGAINST THE NULL MODEL

The key to understanding species with lower-than-expected multiple paternity values from our null model lies in non-random mating that

causes a strong bias in the distribution of siring success. With this in mind, we turn to a case consideration of studies where the probability of multiple paternity is especially low and contrast them with species not dissimilar from the null model. For this, we identified species that deviated from the null model by looking at the effect size (Hedges' *g*) of the difference between the null model estimated p_B and the observed probability of multiple paternity *p* in the studied populations (Figure 3). Random effects meta-analyses using the method of restricted maximum likelihood (REML) were used to calculate overall differences for the groups. We examined Hedges' *g* to eliminate bias due to differences in sample size among studies[26]. We report its mean and 95% confidence interval. Species with 100% and 0% observed multiple paternity values from the data were excluded from the meta-analyses, since for these species there was no variation in multiple paternity. All meta-analyses were performed using the *metafor* package[27] in R.[28]

The link with sexual selection – mammalian case studies

The observed multiple paternity of a small mammal, the red squirrel (*Tamiasciurus hudsonicus*), was very close to the expected probability of multiple paternity from our null model. The species is polygnyandrous, in which both males and females mate with multiple sexual partners during an annual mating season[29]. Males and females of this species live on solitary territories and are generally considered asocial[30]. Females are in estrus for a single day, and they are subjected to "mating chases" by several males[31]. An average of about six males mate per estrous female, with an average of about 23 copulations. Litter size averages about three offspring, and each litter has an average of 2.3 sires. The sexes are very similar in size[32,33], as expected for mammalian species when sexual selection is extremely weak[34]. The deviation of the probability of multiple paternity from that expected under our null model is trivial (Hedges' $g = 0.02$; Figure 3).

The red squirrels contrast with Columbian ground squirrels (*Urocitellus columbianus*), a polygynandrous species in which both males and females are capable of both single and multiple mating[35] (F.S. Dobson, personal observations). Females live in small matrilineal groups of adjacent but individually territorial close relatives ("kin clusters"[36,37]), and subadult males are the predominant dispersers (reviewed by[38]). Males are combative when females are in estrus, and attempt to guard them from other males, but with limited success[39] (F.S. Dobson, personal observations). Adult females mate with from one to up to eight males when in estrus and have an average of three offspring per litter[35]. Significant but mild sexual size dimorphism favors males[40] and likely indicates sexual selection on male body size[41]. The probability of multiple paternity is significantly different from that expected under the null model, but the size of the effect is small to moderate (Hedges' $g = 0.30$; Figure 3).

Among mammals, European wild boar (*Sus scrofra*) contrast strongly with the two squirrel species in the probability of multiple paternity. Wild boar exhibit a common social pattern among mammalian species of local social groups that contain closely associated females, likely matrilineal relatives[42], and adult males that are unrelated immigrants[43]. Litter size is high for the size of the species, at an average of 5.5 piglets per birth[44]. Males are highly aggressive and much larger and different in external appearance (a mane runs down the back), compared to females[45,46], thus likely reflecting strong sexual selection[34]. Although several males within a locality can be successful at producing offspring, there is a low probability of multiple paternity[43], perhaps facilitated by intrasexual aggression and mate guarding among the males. The deviation of the probability of multiple paternity from that expected from the null model is high and has a very large effect size (Hedges' $g = 2.17$; Figure 3). While anecdotal, the comparison of the squirrels and wild boar reflects our expectation for low multiple paternity associated with evidence of relatively strong sexual selection.

Another contrast to the polygynandrous squirrel species is the European brown bear (*Ursus arctos*). Brown bears in Scandinavia are large-bodied, solitary carnivores[47] that occur at very low spatial densities[48]. Although they exhibit a slight matrilineal social structure, with kin females settling nearby one another and males dispersing widely, the mean home range covers more than 400 km^2 and overlap of female ranges is only about 25%[47]. Even though average litter size is relatively low at a little less than two and a half young, the estimate of multiple paternity is relatively low at 14.5% of litters[49]. Males are usually about twice the body mass of females[50]. The deviation of the probability of multiple paternity from that expected from the null model is high and has a very strong effect (Hedges' $g = 1.36$; Figure 3). Although lacking the group-based social structure of the wild boar, brown bears similarly deviate strongly from the null model, perhaps due to being so thinly spread over their landscape and strong sexual selection.

The link with sexual selection – case studies for reptiles and fish

In reptiles, southern water skinks (*Eulamprus tympanum*) are polygynandrous and fit fairly close to the expected probability of multiple paternity from our null model. In water skinks, both overlapping male and female territories occur, as well as "floaters" of both sexes that do not defend territories (a majority, 72.5% of the population, are floaters[51]). Estimates of multiple paternity vary between about 65% and 82%, relatively high for a species with a mean clutch size of only 3.2 offspring[52]. Further, the mean number of sires for these small clutches averages around 1.7. Although males exhibit tactics to limit access to females, such as territorial behaviors, multiple mating by females does not appear to be significantly constrained by low densities[51]. Although the probability of multiple paternity is slightly different from that expected under the null model, the effect is small (Hedges' $g = 0.21$; Figure 3).

We contrast the strongly polygynandrous mating system of southern water skinks with the largely monogamous mating system of Cunningham's skinks (*Egernia cunninghami*). The latter species lives in groups of eight to nine adults but has only slight polygyny (four

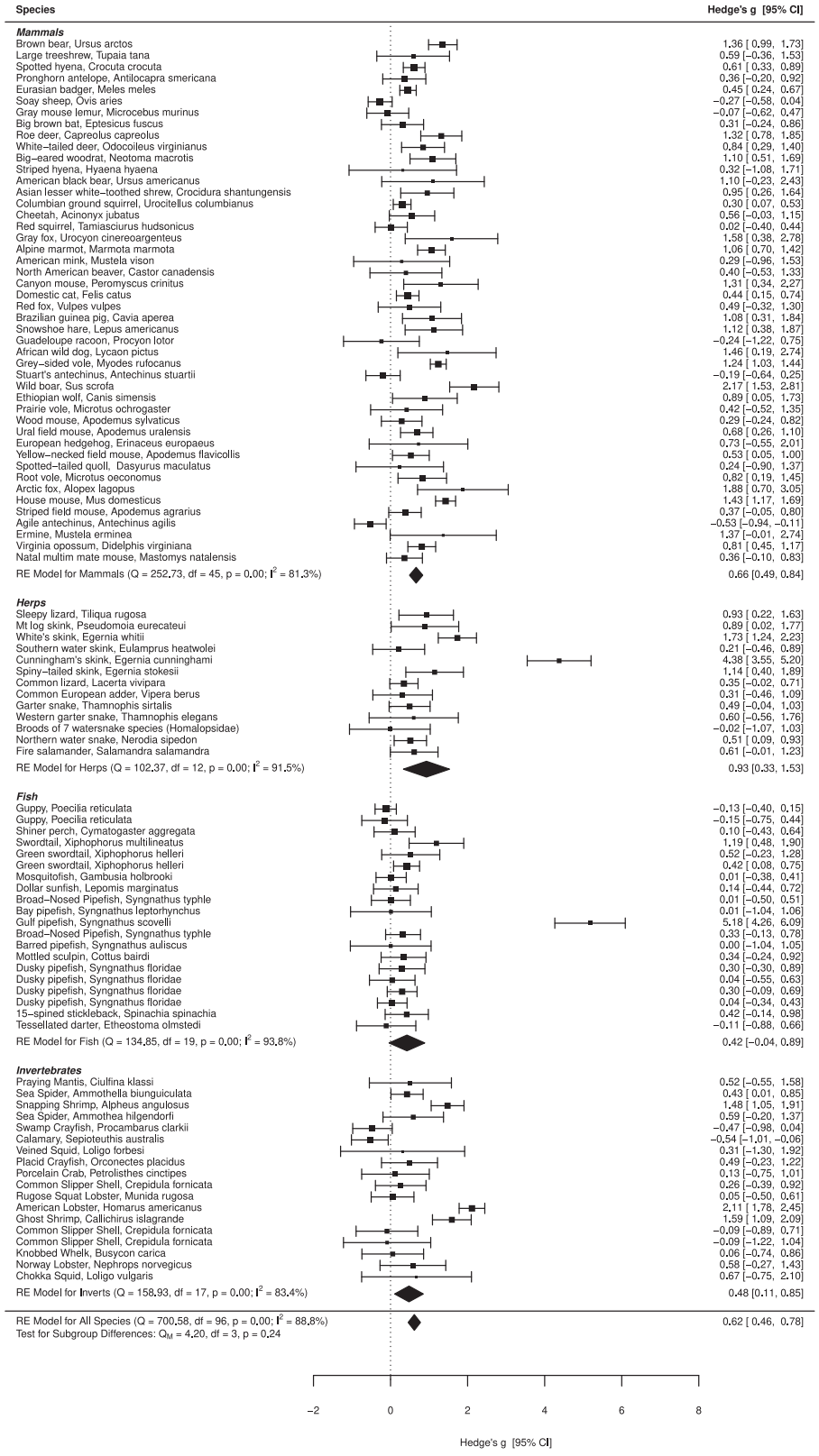

FIGURE 3 Hedges' effect sizes and 95% confidence intervals for the difference of the observed probability of multiple paternity (p) from the Bayesian MCMC estimated probability of multiple paternity (p_B) calculated for each population within mammals, reptiles and amphibians, fish, and invertebrates. Species with 100% and 0% observed multiple paternity values were excluded. Species are ordered by increasing average clutch size.

cases among 34 males) and even rarer multiple paternity of the small clutches that females produce (clutch size averages 3.4, and a single case of multiple paternity occurred among 38 clutches = 2.6% multiple paternity[53]). Further, most surviving pairs stay together for a subsequent annual breeding season (26 of 30 couples = 88.9%). Cunningham's skink exhibits a probability of multiple paternity that is very different from that expected under the null model, as reflected by a very large effect size (Hedges' $g = 4.38$; Figure 3).

Finally, a comparison of gulf and dusky pipefish (*Syngnathus scovelli* and *S. floridae*, respectively) is instructive, as both species are male-pregnant and exhibit "role reversal" in sex roles of breeding adults. Gulf pipefish had an extremely low probability of multiple maternity (25.0%), far below the expected value from our null hypothesis (a very large effect size for the difference, Hedges' $g = 5.18$, Figure 3). Dusky pipefish, on the other hand, have a high rate of multiple maternity (72.7%–84.6%) at near the predicted value from the null model (small to moderate effect sizes, Hedges' $g = 0.04$–0.30, Figure 3). Both species have a mating system based on the male pouch-brooding eggs that they receive from females, so the intensity of sexual competition for mates should be indicated by sexually selected dimorphism of the females[54]. Evidence from sexual dimorphism suggests that female gulf pipefish have been under stronger sexual selection, with choosy males and displaying females, thus indicating an association of sexual competition among females for male mates[54,55]. Dusky pipefish, on the other hand, exhibit little dimorphism, at least in size[56]. So, it appears that the mating system of gulf pipefish, which is characterized by matings of single males and females, likely has strong sexual competition that contributes to a low probability of multiple maternity. Density is unlikely to play a major role in availability of male mates for females, since the density of gulf pipefish is much higher than the more polygynandrous dusky pipefish[57].

Distance from the null is important for a theory of multiple paternity

These case studies reflect a general pattern that ranges from species with expected high rates of multiple paternity to species with socially or spatially restricted opportunities for matings that lead to low rates of multiple paternity. The key to limitation of multiple paternity appears to be success of males at limiting the number of potential mates of females, likely through behavioral means. Cases far from the null model predictions of p_B have low values of not only p, but also of s. These cases appear to be associated with behavioral tactics that restrict not only the number of sires, but also the number of likely mates. These include aggressive social dominance (wild boar[43]), mate guarding (Columbian ground squirrels[39]), and probably territorial behavior (Columbian ground squirrels[58,59]). For large and asocial mammalian carnivores, low local population densities may limit the number of male mates available to females (brown bears[49]) and provide examples of logistic constraints on multiple paternity[16]. These types of behavioral and environmental influences on matings of receptive females, when unsuccessful, can lead to more broadly dispersed reproductive success among males, such as the mating chases of red squirrels and the highly mobile behaviors of floaters among southern water skinks.

THE RACE FOR MATES: SUCCESS MATTERS

For many species, we found that the probability of multiple paternity was in fairly close agreement with our null model, which indicates that we cannot reject the null hypothesis that these species have mating patterns that exhibit close to what we would expect if there were equal likelihood of fertilization success among competing mates. Thus, our primary conclusion is that expected rates of multiple paternity are widespread and high among most polytocous species. However, several species showed lower than expected rates of multiple paternity that likely reflect social or environmental limits on the success of mates. In every major taxon that Avise and his colleagues examined[12,15,18], we found species for which the probability of multiple paternity was far below what would be expected from their clutch size and estimated number of mates (the latter based on equal probability of success of males, which was estimated from the mean number of sires). The discovery of multiple paternity was considered exciting, because it showed that multiple sires were possible, hence implying possible influences on competition for mates and associated phenomena like sperm competition. But perhaps behavioral ecologists should have been surprised that the phenomenon of multiple paternity was not more widespread among polytocous species, as our null model suggests.

Our specific prediction from analyses of mammalian species[16] was that the expected probability of multiple paternity, given the litter size and estimated number of mates for each species, would be close to 100% when clutch sizes were over about 10–12 offspring. In the combined analysis of species from a variety of major taxa, the clutch size above which the highest rates of multiple paternity would be expected is slightly over 100. The mammalian species in[12] had a range of mean litter sizes from two to about 10 (the mean for 49 species was about four). In this case and with an equal likelihood of siring success among males, we found a positive association of the probability of multiple paternity and mean litter size (Figure 2). For reptiles, the range of mean clutch sizes was about two to 33 (the mean across 18 species was about 10), again with an increasing association with the probability of multiple paternity, given the assumption of equal likelihood of fertilization success. For viviparous fish, the expected association of probability of multiple paternity and clutch size under an equal chance of success among mating males was relatively flat and maximal. The range of mean clutch sizes was 13 to 40,000 (the mean for 29 species was about 1850). For a variety of invertebrate species in several major taxa and with even more extreme brood sizes, the probability of multiple paternity again fell within the plateau of high expected values across different brood sizes[18].

Avise and Liu[12,15] suggested that multiple paternity should have competitive advantages for both males and females via the process of sexual selection, but also perhaps be constrained logistically by the life history and ecology of particular species. The idea was that males

would compete more for highly productive polytocous females, and that this would lead to higher probabilities of multiple paternity in populations. Faced with a lack of increases in probabilities of multiple paternity with clutch size, they suggested that there must be balancing logistical constraints. Our null model suggests, however, that high probabilities of multiple paternity is what we would expect if the likelihood of success of mating males was even, given the basic results presented in paternity studies: mean litter size, mean number of sires among clutches, and percent of multiple paternity in populations. Further, our null model explains the basically flat relationship that was found for fish species[12] and invertebrates[18]. What needs explanation is not those cases in which the probability of multiple paternity is high or fairly constant among species with high clutch sizes, but cases where it is especially low.

We suggest that both intra-sexual competition before mating and sperm competition after mating should result in lower probabilities of multiple paternity. But these two processes should have profoundly different influences. Before mating, competition among the limited sex (usually males) limits the number of mating males. When these males are successful, female choice becomes relatively limited, and the mean number of potential sires decreases. Thus, sexual selection acts against a high probability of multiple paternity. When males are unsuccessful at sequestering female mates, however, more males may potentially mate and the probability of multiple paternity may be quite high. Whether the potential for more mating males is met, however, depends on female choice. Thus, it is not the intensity of competition per se that influences multiple paternity, but how successful males are in their intra-sexual competition for access to female mates. In addition, those species with logistical constraints such as low population densities, widespread and non-overlapping ranges of the sexes, or other ecological characteristics that limit mating contacts, should also exhibit relatively low rates of multiple paternity. In this way, the influences of sexual selection and logistical constraints should produce the same effect: a lowering of the probability of multiple paternity. Sexual competition and logistical constraints might likely be reflected through a reduction in number of mating males with individual females.

Sperm competition, and thus the distribution of the number of sires, could be influenced by the timing, duration, and frequency of mating events. Mate guarding may limit the number of mates (and thus sires), but it also changes the timing of mating with other males, perhaps increasing the success of the guarding male. In this case, his sperm get an advantage, even though the female may go on to mate with other males. Cases of first and last mating male fertilization advantage may be produced by such male and female behavior (e.g., females may accept or avoid such guarding). So, the distribution of male success at mating may be influenced by the behaviors of both males and females, as well as by sperm characteristics[2].

CONCLUSIONS AND OUTLOOK

Our thesis going forward is that the major division in mating systems may not be the difference between monogamy and polygyny, as has traditionally been envisioned[1]. This division is simply between a male's sequestering ability or female preference for a single mate, whether this results in a single female or a few females per male. Rather, the more fundamental division is perhaps between those species in which male and female matings produce polygynandry, a phenomenon in which both sexes mate with several partners (and with high rates of multiple paternity), and largely exclusive mating partners that exhibit either male sequestering or female choice for a single partner. Our examples show how the latter can come about when behavioral tactics of males or female preference for single males results in mating patterns that are non-random.

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CONFLICT OF INTEREST

The authors have declared no conflict of interest.

AUTHOR CONTRIBUTIONS

Hannah Correia, Ash Abebe, and F. Stephen Dobson designed the research and analyzed the data, and all authors contributed to writing the paper.

DATA AVAILABILITY STATEMENT

All data are previously published and available in the following articles: Avise, J.C., and Liu, J.X. (2010). Multiple mating and its relationship to alternative modes of gestation in male-pregnant versus female-pregnant fish species. *Proceedings of the National Academy of Sciences of the USA*, 107, 18915–18920. Avise, J.C., and Liu, J.X. (2011). Multiple mating and its relationship to brood size in pregnant fishes versus pregnant mammals and other vivparous vertebrates. *Proceedings of the National Academy of Sciences of the USA*, 108, 7091–7095. Avise, J.C., Tatarenkov, A., and Liu, J.X. (2011). Multiple mating and clutch size in invertebrate brooders versus pregnant vertebrates. *Proceedings of the National Academy of Sciences of the USA*, 108, 11512–11517.

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