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Bateman Gradients in Field and Laboratory Studies: A Cautionary Tale

Post Print

ABSTRACT: Since tools of molecular genetics became readily available, our understanding of bird mating systems has undergone a revolution. The majority of passerine species investigated are socially monogamous, but have been shown to be genetically polygamous. Data sets from natural populations of juncos suggest that multiple mating by females results in a sexual selection gradient as steep for females as for males (a result that does not support Bateman's predictions). However, in males, fitness is enhanced directly through fertilization success with multiple matings; in females fitness benefits may be enhanced immediately through direct access to food, protection against predators, or other resources received from males, or they may be delayed through improvement in offspring quality (e.g., through good genes, or greater genetic compatibility between the female and the extra-pair male). But a steep sexual selection gradient for females can be difficult to interpret. If all females copulate with multiple partners that are equally likely to fertilize eggs, then females that produce larger clutch sizes, for any reason, will appear to have copulated with more males. That is, multiple sires have a higher probability of detection in larger clutches than in smaller ones, giving the impression that females that mate with multiple males increase their reproductive success. Yet, in most studies in which there is a correlation between number of offspring produced by females and number of extra-pair males, causation has not been clearly established and other factors may explain the results. Additional complications in understanding male and female reproductive strategies are: (1) Molecular studies cannot detect extra-pair copulations that did not result in fertilizations; yet if a female acquires food or other resources from extra-pair males, such extra-pair matings may have significant effects on female fitness. Thus, molecular studies provide only a conservative estimate of the number of extra-pair copulations or "mates" that a female has. (2) Clutch size affects the probability that any given male will be successful in fertilizing a female's eggs. Specifically, at any given point, a male's chances of fertilizing at least one egg in the female's clutch will be greater as clutch size increases. We predict that in avian species with small clutch sizes, males may be selected to be choosy and avoid extra-pair copulations, while females should be selected to be less discriminating. Moreover, if extra-pair males provide resources that increase female fitness, the females should seek extra-pair copulations, whether or not the males are likely to fertilize any of her eggs.

Laboratory studies with insects have yielded clearer evidence of the causal relationship between multiple mating and increased female fitness. We review studies on a tenebrionid beetle in which female fecundity increases directly with number of mates. In these experiments, the nutritive value of the spermatophores does not fully explain the increase in female reproductive success.

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Molecular approaches have revolutionized our understanding of sexual selection and mating systems. Until the 1980s, most birds were thought to breed in exclusive monogamous male-female partnerships, in which one male and one female pair, build a nest together, and cooperate in raising young. We assumed that each member of the pair mated only with the other. Moreover, in polygynous species, the expectation was that, while males mated with several females, the females mated with only that male. However, molecular studies that allowed the analysis of paternity (e.g., Gowaty and Karlin, 1984; Gibbs et al., 1990; Westneat et al., 1990; Kempnaers et al., 1992; Dixon et al., 1994; Mulder et al., 1994) have demonstrated repeatedly that, in many avian species, females produce broods that are sired by multiple males. In fact, a review by Bennet and Owens (2002) reported that of the socially monogamous passerines in which paternity has been determined using modern molecular techniques, 75–85% engage in EPFs, and true genetic monogamy occurs in less than 7% of species. Thus, while it remains true that most species of birds are socially monogamous (that is, they engage in the social behaviors described above—pairing and raising young together), genetic monogamy (defined as a female and male mating and producing young only with one another) is relatively rare. Here we address whether the actual distribution of reproductive success (RS) among males and females in natural populations causes variance in reproductive success for males and for females to differ from that predicted for truly monogamous systems.

In truly monogamous species, male reproductive success equals female reproductive success, which can be estimated by the number of fledglings produced. However, when alternative reproductive strategies, such as extra pair fertilizations (EPFs) and/or conspecific brood parasitism (CBP), are accounted for, the results are quite different for both males and females. Specifically, male reproductive success is equal to the nestlings in the home nest that are sired by the male, minus the nestlings in the nest that have been sired by a different male (i.e., loss of paternity due to EPF). This can be considered the “home success,” but to this must be added any paternity that the male gains by siring offspring with females other than its mate (i.e., success elsewhere due to EPFs with females at other nests). Likewise, female reproductive success equals the number of her own nestlings at the nest minus any maternity lost to conspecific brood parasitism. This includes quasiparasitism in which other females place eggs fertilized by the resident male into the male’s home nest (although rare, this type of maternity loss has been demonstrated in some species: e.g., Birkhead et al., 1990; Petrie and Moller, 1991; Macedo, personal communication). The resident females’ reproductive success can be reliably quantified by molecular exclusion analysis and can be considered the “home success” for females. However, total female reproductive success also includes success elsewhere, if the female has laid eggs (brood parasitism) in another female’s nest. To determine this component of the equation, it is necessary to find and assign any “missing” parents of the young in a nest.

Numerous studies of passerine birds show that, with regard to “home success,” males have a paternity loss to EPFs of approximately 28% (Bennet and Owens, 2002), and it is the distribution of this 28% among EPF sires that determines the consequences for variance. The loss of maternity due to CBP for females in the same studies of passerine birds is approximately 3%, and likewise the distribution of this 3% among actual mothers affects variance in RS. Clearly, the potential effect is greater in males than in females.

If one considers the possible relationships between the number of mates and reproductive success (Bateman's sexual selection gradients: Bateman, 1948; Arnold and Duvall, 1994), three outcomes are possible:

1. Lack (1968) suggested that both sexes can be constrained by monogamy, such that both males and females have relatively low, but equivalent reproductive success. In this case, the critical point is that males and females mate only with one other partner and both are the genetic parents of all young produced. Note that, in this case, it is not possible to ask whether there is a sexual difference in variance of reproductive success based on the number of mates because both sexes mate with only one other individual—that is, there is only one mate and this is true of both males and females. This would be the case in genetically monogamous species.

2. Alternatively, as proposed by Bateman (1948), males are constrained by access to females and male RS increases with the number of mates. Females, however, are constrained by the ability to produce and rear offspring. Under the assumption that one male produces enough sperm to fertilize all of a female's eggs, Bateman reasoned that females reach their peak of RS after mating with only one male; mating with additional males has no effect on a female's RS.

3. A third possibility is that RS responds equally to mating success (for the sake of simplicity defined here as number of mates; but see discussion below) in both sexes. Under this scenario, both males and females increase RS with number of mates.

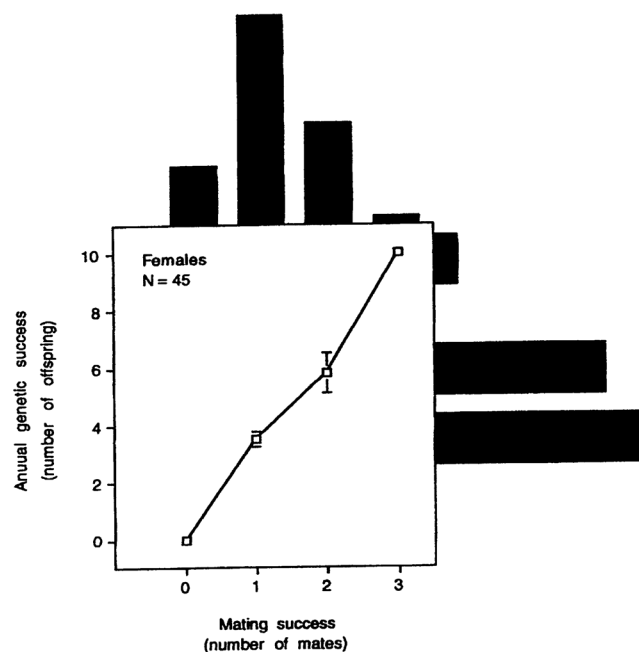


FIG. 1. Relationship between mating success (defined as number of sires as determined by DNA paternity analysis) and reproductive success (number of offspring) in female dark-eyed juncos. Top histogram is a frequency distribution of numbers of females with 0 to 3 mates; right hand histogram is a frequency distribution of total numbers of offspring produced by females with 0 to 3 mates. From Ketterson et al. (1998).

Ketterson et al. (1998) tested these three possible outcomes in socially monogamous dark-eyed juncos (*Junco hyemalis*). As expected, male reproductive success increases with number of mates. Moreover, males that sire young on other territories have enhanced reproductive success. For male juncos there was little evidence of a tradeoff where males traded success at home for success elsewhere. Instead, males that suffered few EPF losses at home were those that gained the most through EPFs elsewhere. Concomitantly, males that suffered more in EPF losses seldom had EPF gains elsewhere. This means that the variance of male RS was more extreme than predicted by monogamy, and the standardized variance in male RS rose 32%, from 0.54 (apparent success) to 0.72 (actual success). A more unexpected finding was that females that had higher mating success (defined as females whose clutches were sired by more than one male) also showed increased reproductive success (Fig. 1). In other words, females who had young sired by extra-pair males, or who changed mates during the season, also had higher RS.

Several hypotheses propose that females seek extrapair males and mate with them because this increases the female's RS (e.g., see reviews by Gowaty, 1985; Westneat et al., 1990; Birkhead and Moller, 1992; Kempenaers and Dhondt, 1993; Petrie and Kempenaers, 1998; Kempenaers et al., 1999; Griffith et al., 2002; Westneat and Stewart, 2003). The Ketterson et al. (1998) study did not examine the mechanisms responsible for greater RS in females that mated with more than one male, nor did it test any of the relevant hypotheses. Potentially, by mating with extra pair males, females could gain both immediate social benefits for herself, as well as delayed genetic benefits for her offspring. For example, females could obtain social benefits such as additional resources, assistance with feeding young, or protection in the form of vigilance against predators. Moreover, it is important that such benefits are likely to be independent of whether the extra-pair male sires any of the female's offspring (assuming that males cannot recognize own young). As one example, Tryjanowski and Hromada (2005) recently reported that in the great grey shrike (*Lanius excubitor*) extra-pair males provide food of significantly higher size and energy value to their extra-pair mates, as compared to their social mates. Thus, it can be expected that females in this species benefit from mating with extra-pair males (EPCs), whether or not EPFs occur. Another possible immediate benefit to females, which does depend on fertilizations, is insurance against sterility of the social mate. Proposed genetic benefits (all of which require fertilization rather than simply extra-pair copulations) assume that the female gains in RS by obtaining genes that increase viability or attractiveness of her offspring, that increase genetic diversity in a clutch, or that are more "complementary" or compatible with the female's own genes (Mays and Hill, 2004). Thus, depending on the circumstances, a female may mate with extra-pair males that are genetically more similar or more dissimilar to herself. For example, females may mate with certain males to preserve co-adapted gene complexes, or to increase MHC variation in her offspring. In a relevant study, Kempenaers et al. (1999) suggest that female tree swallows (*Tachycineta bicolor*) may benefit by mating with genetically compatible extra-pair males; clutches with extra-pair young had higher hatching success than clutches sired by only one male.

Although at times, social and genetic benefits are treated as dichotomous alternatives, in some species females may simultaneously gain both types of benefits from extra-pair matings. For example, if females choose extra-pair males that provide high quality

resources, are adept at feeding young, or are particularly skilled at detecting and defending against predators, and if these males actually fertilize some of the female's eggs, the female could gain "good genes" for her offspring as long as the male's traits are heritable. Thus, social and genetic benefits could be simultaneously important and are not necessarily mutually exclusive.

In considering the relationship between the number of extra-pair mates and female reproductive success, mating and fertilization are often confounded. Although invaluable in determining rates of extra-pair fertilizations, molecular studies cannot provide information about number of mates or EPCs. Failure to detect extra-pair paternity cannot be taken as conclusive evidence that females are not engaging in extrapair matings. In fact, in much of the literature, since Bateman (1948), there has been confusion about the definition of "mating success"; many authors define it as "number of mates," while others equate it to the number of sires that have fertilized a female's eggs. The inability to determine actual number of mates (as opposed to sires) is not trivial because females may benefit simply from mating with multiple males, even if the males do not fertilize any of her eggs. Therefore, caution is necessary when we analyze female reproductive success as a function of "number of mates" when what we really mean is "number of males that sired young in a clutch" (see also Dewsbury, 2005). For example, since their molecular methodology could not provide information on the total number of extrapair males that a female mated with, Ketterson et al. (1998), were rightly cautious and accurate in defining mating success as the number of males that sired young with a given female. In summary, it is extremely difficult to observe extra-pair copulations under most field conditions. Consequently, most of the time we have little to no reliable information on how many males a female copulates with, or on how those copulations (particularly those that do not result in fertilizations) may impact her reproductive success. Assuming that EPCs did not occur, because we do not have behavioral or molecular genetic evidence for them, is likely to lead to incorrect conclusions and confound our understanding of female mating strategies.

The Ketterson et al. (1998) study on dark-eyed juncos found a clear relationship between reproductive success and extra pair fertilizations, suggesting that females benefit from mating with multiple males. However, other interpretations are possible because specific hypotheses predicting increased female RS as a result of extra-pair matings were not tested. Specifically, on closer inspection, the results obtained by Ketterson et al. (1998) do not necessarily mean that mating success (number of mates or extra-pair sires) caused the increase in female RS. Instead, the relationship between female mating success and reproductive success may be confounded because the probability of detecting an EPF depends on the reproductive success of a female; the greater the RS of a female, the more likely that an extra-pair sire will be detected (Burley and Parker, 1998). Thus, the implied causal relationship between mating behavior and reproductive success may be spurious.

In other words, if all females engage in EPCs at the same rate, additional males will be detected at higher rates in broods of more successful females, regardless of the cause of the female's success. For the standard clutch size (4–5 chicks) produced by dark-eyed juncos (Ketterson et al., 1998), the probability of detecting the second, extra-pair, male depends on the background rate of EPCs and EPFs (Fig. 2; Burley and Parker, 1998). Burley and Parker (1998) illustrate this point by considering the following scenario. If one assumes that all females in a population engage in within-pair and

extra-pair copulations at the same rate, and that all copulations are equally likely to fertilize eggs, then the

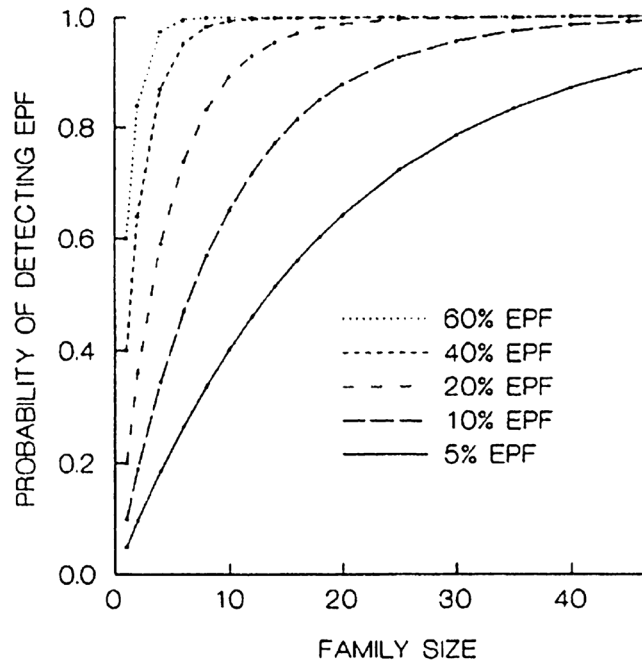


FIG. 2. The probability of detecting at least one extra-pair fertilization (EPF) as a function of family size (number of offspring produced in a season), when each female participates in extra-pair copulations (EPCs) at the same rate. Curves represent different populations, each at the constant EPF rate indicated. See text for calculation of probability of detecting at least one EPF in a family. From Burley and Parker (1998).

probability, P , that a clutch (or family) of size n will contain only young sired by the social mate is w (defined as the proportion of copulations that are within-pair). P decreases with family size, but the probability that families contain one or more extra-pair young ($1 - w^n$) increases asymptotically with family size.

Here we apply this scenario to juncos, where there is a 28% EPF rate and a 72% within-pair fertilization (WPF) rate. Assuming all females engage in 28% EPCs, the probability of detecting a second, extra-pair sire increases with number of offspring in a clutch, as shown in Figure 3. By reversing the axes and comparing the increment in RS between one and two mates for female juncos (Fig. 4), the increment in RS from 3.2 to 5.9 is associated with a 32% increase in probability of detection from 0.65 to 0.86. This analysis suggests cautious interpretation of the Ketterson et al. (1998) results, which showed that the proportion of young sired by EPFs increased significantly as the annual reproductive success of females increased. It is difficult to determine how much of the increase in female RS is due to the increase in number of mates.

As suggested by Ketterson et al. (1998) there are three scenarios that are consistent with the results of this study: (a) more sires were detected as family size or number of offspring increased; (b) more fecund females attracted and mated with more males, resulting in higher rates of EPFs; (c) there is an advantage to females in mating with multiple males. At present, it is not possible to distinguish among these three alternatives and the relevance of the Ketterson et al. (1998) study to "Bateman's

Principle” remains ambiguous. Specifically, in the case of the first two scenarios, the data are uninformative with regards to Bateman’s Principles and cannot be used to reject Bateman’s predictions. The third explanation would be contrary to the assumptions made by Bateman about the relationship between number of mates obtained by a female and that female’s reproductive success.

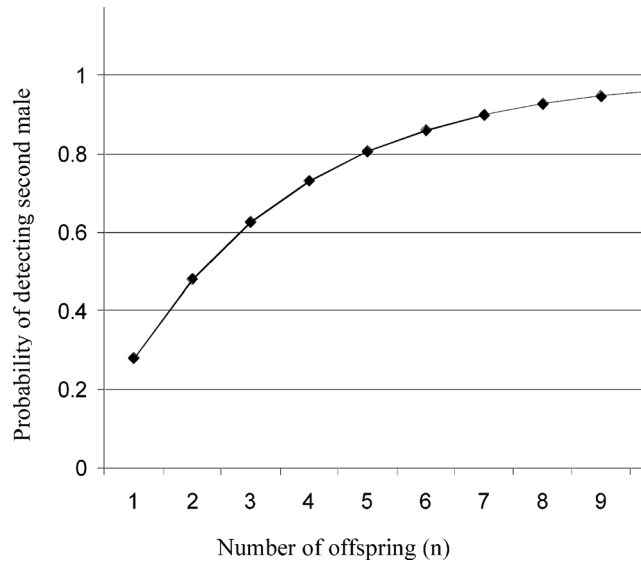


FIG. 3. Probability of detecting at least one extra-pair fertilization (EPF), as a function of family size (number of offspring) in darkeyed juncos, assuming that all females engage in a 28% rate of extrapair copulations (EPCs).

Many studies of extra pair copulations assume that extra-pair matings by females are costly and that, therefore, multiply-mating females must be obtaining some benefit. Thus, if a study shows a positive relationship between number of extra-pair sires and female reproductive success, it is assumed that the relationship is a causal one and that females necessarily benefit by mating with extra-pair males. Certainly, this may be true, in which case Bateman's predictions would be falsified. However, alternative explanations rarely are considered; instead, it is merely assumed that extra-pair fertilizations have a causal positive effect on female fitness. Thus, because results

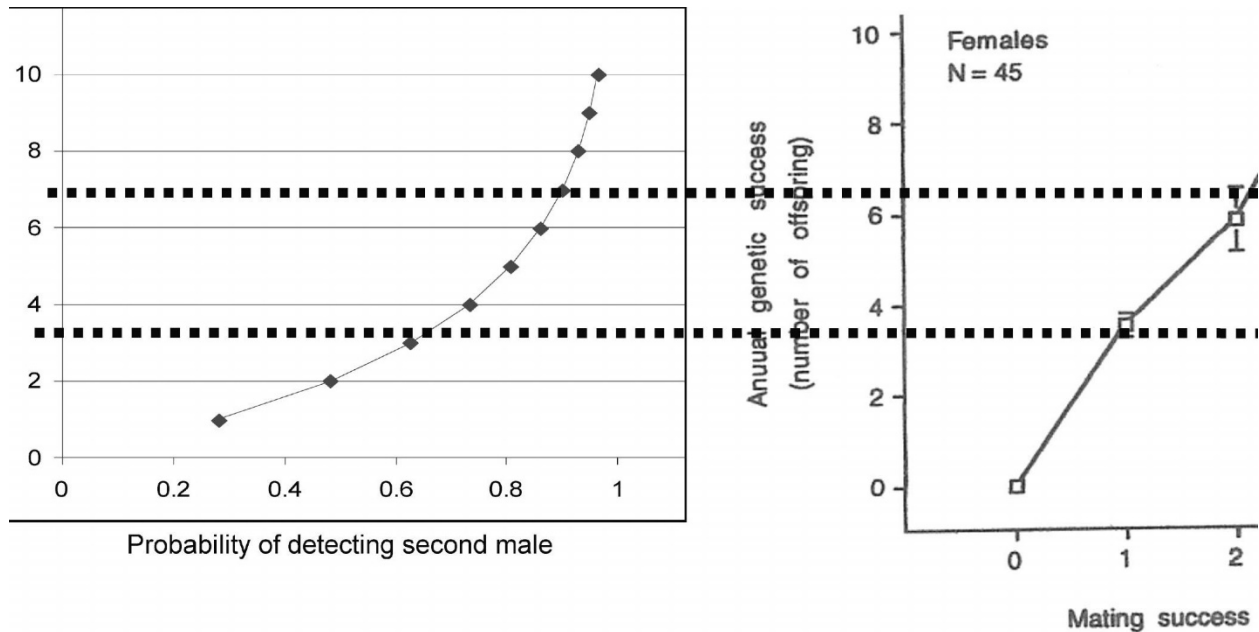


FIG. 4. A comparison of the probability of detecting at least one extra pair sire as a function of number of offspring (reversing axes in Fig. 3) and number of offspring as a function of mating success in female dark-eyed juncos (Fig.1). Horizontal dotted lines connecting graphs bracket the most common annual numbers of offspring in the dark-eyed junco study population and show that the inference of increased RS from MS on the right graph is confounded by rising probability of detection over that same range in the left graph.

superficially fit with current assumptions about benefits to female as a result of extra-pair matings, few studies adequately test whether the relationship is real (i.e., causal) or only coincidental. The primary purpose of this analysis is to stress that there are potential pitfalls when researchers assume that females gain in RS as a result of obtaining EPFs. Too often, such a relationship is presumed to indicate a causal relationship such that extra-pair copulations by females generate direct (immediate social) or indirect (delayed genetic) benefits that increase the females' RS. However, as we have demonstrated above, other explanations are also possible.

FACTORS INFLUENCING EXTRA-PAIR COPULATIONS BY MALE BIRDS

Bateman (1948) and Trivers (1972) theorized that male reproductive success is limited only by access to females; thus, under most conditions, males should always seek to mate with as many females as possible. This prediction was based, in part, on

the assumption that production of sperm is inexpensive and that males can always produce unlimited numbers of gametes. Recent evidence suggests that this is far from being the case (Wedell et al., 2002; see also Tang-Martinez, 2005). Mating with multiple females may well be costly to males and may result in male choice. In addition to increased vulnerability to predators, costs of multiple mating for males may include sperm depletion, time and energy spent searching for females (particularly if females are widely dispersed or difficult to find), and exposure to parasites and/or sexually transmitted diseases. Consequently, it should come as no surprise that males often allocate sperm based on the health, age, or status of females, and presence of competitors (Wedell et al., 2002); in some species, males have even been reported to refuse to mate with certain females (Pinxten and Eens, 1997; Saether et al., 2001).

Shortly after Trivers (1972) published his seminal paper on parental investment theory, Maynard Smith (1977) pointed out that males should abandon their original mate to seek other females only when the male's overall reproductive success would be higher than if he had not deserted his mate. Factors that influenced male reproductive success in Maynard Smith's models included the probability of finding a new mate, fertilizing the new female, and successfully producing offspring with her.

Maynard Smith's analysis is interesting because, even though he was considering only complete abandonment of presumably monogamous females by their original mate, some of the factors he discusses also are relevant in the case of extra-pair copulations by males and females. Specifically, his arguments suggest that, in certain situations, males should not seek additional females with whom to mate because it is too costly to do so and there is no guarantee of increased reproductive success.

One dynamic that has not been widely recognized is that a male's probability of fertilizing a female's eggs will depend on clutch size. The more eggs that a female produces, the higher the likelihood that a single copulation will result in a successful fertilization. At one extreme, in species that produce only one egg, only one male will be successful, regardless of how many males the female mates with. At the opposite extreme, in species that produce very large numbers of eggs, any given male will have a higher probability of fertilizing at least one egg, up to the point that all the female's eggs have been fertilized. This suggests that, whether or not males engage in extra-pair copulations should depend on the mean number of eggs that the females of the species produce, as well as on the presence of other males who may already have mated with the female. If the number of eggs produced is small and the female is already in a socially monogamous relationship, or if there are other males (whether the social mate or others) already present in the vicinity of the female, we predict that males should be less likely to engage in repeated and indiscriminate extra-pair copulations. The reasons are two-fold: First there are the costs associated with any copulatory attempt (as discussed previously). Second, the male would risk squandering sperm with little likelihood of success, leading to possible sperm depletion. In these types of circumstances, males may actually incur lower reproductive success by mating indiscriminately with as many females as possible. Thus, males of some species, and under some circumstances, should be cautious when engaging in extra-pair copulations. Moreover, female clutch size may be one important factor, among others, influencing male reproductive strategies.

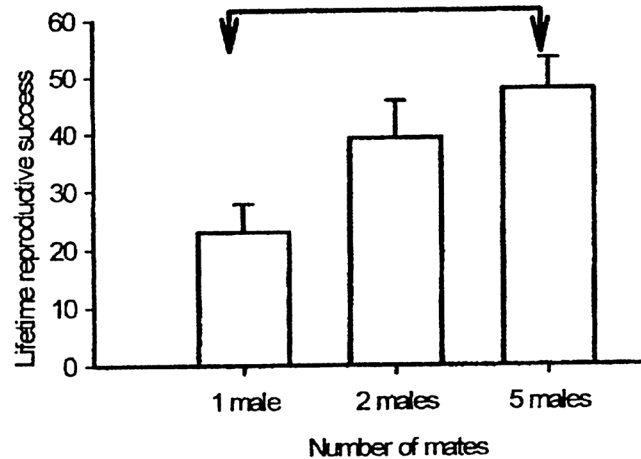


FIG. 5. Lifetime reproductive success of female mealworm beetles mated with 1, 2 or 5 males. From Worden and Parker (2001).

The flip side of this argument is that extra-pair males in species with small clutch sizes also should be less likely to continue provisioning the female or providing other services. In other words, because extrapair males would have a low probability of siring young in small clutches (and concomitantly, a high uncertainty of paternity), they should be reluctant to invest further in the female or her offspring (e.g., bringing food to the female, provisioning young, or defending against predators), even if they had mated with the female.

It is interesting that even when males have little chance of successfully inseminating a female's eggs, females may still seek extra-pair copulations if by doing so they gain direct benefits such as food, vigilance against predators, or other resources. Moreover, in such cases, cryptic female choice could add an additional layer of exploitation with a female mating with many different males and then selecting the father(s) of her offspring. Therefore, it is possible to envision situations in which females could be selected to mate indiscriminately, while males, particularly if they provide direct benefits, could be selected to be more cautious and circumspect about seeking out multiple females. In this scenario, males would be selected to be less promiscuous and, therefore, less likely to be exploited by females. (See Gowaty, 1997 for a deeper discussion of sexual conflicts of interest between males and females).

STUDIES ON MEALWORM BEETLES

Unlike some of the uncontrolled variables and ambiguities that can arise in field research, lab studies allow for clear controls and the standardization of other sources of variation in RS. Worden and Parker (2001) conducted a series of experiments with mealworm beetles (*Tenebrio molitor*) that clearly showed that, contrary to Bateman's predictions, female RS increases as a function of number of mates.

Female mealworm beetles mating with multiple males under controlled conditions, laid significantly more eggs than females that mated with only a single male. Specifically, virgin, 8-day old females were reared under identical conditions and mated to virgin, 8-day old male beetles. Females were mated sequentially to one male, two males, or five

males. Females mated with 5 males produced approximately twice as many eggs as females that had mated only with one male (Fig. 5).

These initial results led to two other experiments aimed at determining the reasons for the increased RS of females that mated with multiple males in the first experiment. One question was whether females that are nutritionally limited benefit disproportionately from multiple matings. This could be the case if, by mating multiply, females gain access to male resources in the form of spermatophores. A second question asked whether females that mate with the same male four times benefit less than females that mate with four different males (assuming that one controls the total number of copulations in both instances). These questions were addressed by maintaining two groups of females: one group was nutritionally deprived (kept on a poor diet), while the other was maintained on a rich diet. Females from both types of diet were then subjected to four different treatment groups: (a) females were allowed to mate once with only one male and did not encounter any other males; (b) females mated once with only one male but had social interactions (but no mating) with three other males; (c) females were allowed to mate four times with the same male; and (d) females were allowed to mate once but with four different males. There were no significant differences among females that mated with only one male, regardless of the females' nutritional condition or social interactions with additional males. However, there was a significant difference between females that mat-

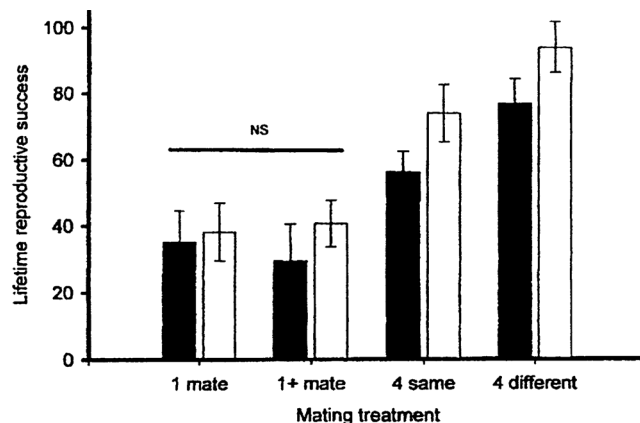


FIG. 6. Lifetime reproductive success of female mealworm beetles mated with 1 male (1 mate), with one male and also allowed social interactions but no additional matings with another 3 males (1+ mate), four times to the same male (4 same), or with 4 different males (4 different). Solid bars indicate females kept on a poor diet; open bars indicate females kept on a richer diet. From Worden and Parker (2001).

ed four times with the same male and those that mated four times but with a different male each time; diet did not have an effect (Fig. 6). Thus, these results demonstrate that the nutritive value of the spermatophore does not fully explain the enhanced reproductive success of multiply-mating females. Females on poor diets did not benefit significantly as compared to those on rich diets in any of the four mating treatments. However, females mating multiply with the same partner had greater RS than those mating only once, indicating resource limitation (either nutrients or sperm) in singly-mating females. Even so, mating with multiple partners did increase female RS disproportionately. Females may have gained superior or complementary genes, or fertilization insurance, by mating with more than one male. Regrettably, the mechanism

for the increase in RS of female mealworm beetles as a result of multiple matings with different males has not been determined. Also unfortunate is that molecular techniques were not used to determine paternity. Therefore there is no information on sperm competition or on possibly cryptic mechanisms of female choice that might have resulted in skewed paternity favoring certain males.

CONCLUSIONS

In the studies reviewed above, females that mate with multiple males show an increase in reproductive success, a finding which is contrary to Bateman's predictions. Nonetheless, in field studies of birds, measuring effects of multiple mating and the resulting variance in male and female RS is not always straightforward. In contrast, controlled laboratory experiments on insects yield more unequivocal results.

In the few studies of avian species in which paternity can be assigned, female RS is positively correlated with mating success (number of sires in a clutch). However, interpretation of these results is complicated by a possible statistical confound. Because annual RS in Passerine birds is low (typically clutch size or family size is less than 10), the positive relationship between mating success and RS is confounded because the probability of detecting extra-pair fertilizations is affected by female RS. Therefore, it is difficult to conclude with certainty that female passerines benefit specifically as a result of mating with multiple males. Although the positive increase in female RS with increasing number of mates appears, at first glance, to contradict Bateman's prediction that females achieve peak RS after mating with only one male and that acquiring additional mates will not improve female RS, other factors may be affecting this relationship and the increase in RS may not be caused by mating success. What cannot be denied, however, is that socially monogamous females of many avian species routinely mate with multiple males and actively seek extra-pair copulations.

We also predict that clutch size should affect a male's likelihood of engaging in extra-pair copulations and providing additional food or services to his extrapair mates. In fact, under certain conditions that include small clutch sizes and even moderate levels of sperm competition, males should evolve to be cautious and choosy in seeking extra-pair mates. On the other hand, as long as females gain direct benefits in the form of food or assistance in raising young, they may well evolve to be more indiscriminate and promiscuous in seeking extra-pair copulations, even when extrapair males have little or no probability of fertilizing a female's eggs.

In contrast to the uncertain interpretation of the results obtained in the bird studies, lab studies of mealworm beetles clearly show enhanced female RS as a function of mating success. When other relevant variables are controlled, females that mate with more males produce significantly larger numbers of eggs. This advantage to female fecundity appears to be genetic in origin, but the exact mechanisms are unknown. In conclusion, both passerine and insect females show an increase in reproductive success with increasing number of mates. However, while the results in insects are in clear contradiction to the predictions made by Bateman (1948), the results obtained with birds are still open to multiple interpretations.

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