Repetition of Bateman challenges the paradigm

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It is impossible to overestimate the impact that Bateman's 1948 paper (1) has had on theoretical and empirical studies of sexual selection and, by extension, also on the study of parental investment theory, evolution of mating systems, evolution of sexual dimorphism, and male-female differences in sexual behavior. In fact, the study by Bateman (1) is a foundational paper and has served as a cornerstone and underpinning for vast areas of behavioral ecology. Bateman's ideas and conclusions, codified as "Bateman's principles" by Arnold (2), have helped to define what we mean by sexual selection and how best to measure it. So-called "Bateman gradients" are routinely used to estimate the strength of sexual selection and which sex is more subject to selection. Although Bateman's results have been repeatedly questioned since the 1980s (e.g., 3–6), there had been no known attempt to replicate his study. A paper by Gowaty et al. (7) in PNAS repeats Bateman's experiments, using the same *Drosophila* strains and methodology employed in the original study. The authors report that they cannot confirm Bateman's conclusions and find no evidence for sexual selection.

The three basic conclusions of Bateman (1), which he applied almost universally to all sexually reproducing animals, were that:

i) Male reproductive success (RS) increases with the number of mates, whereas female reproductive success does not; female RS presumably reaches a peak after mating with only one male. This relationship between RS and number of mates is represented in the typical Bateman gradient: The slope for females remains flat after one mating, whereas the slope for males rises steeply with number of mates.

ii) Males have greater variance in RS than do females; this is because, presumably, some males mate with many females but others mate with few or none, whereas all females are believed to mate (typically with a single male).

iii) The sex with the greater variance in RS, which Bateman believed was the male sex, is more subject to sexual selection. Bateman used anisogamy (differences in the size of male and female gametes) as the basis for his conclusions. Because sperm are small and numerous, the assumption was that they cost little; males could thus afford to mate with as many females as possible, thereby increasing their RS. Eggs, on the other hand, are large and nutrient-filled; therefore, they are expensive. Because of this high maternal investment in eggs, females were predicted to be very choosy in selecting a mate; a female should mate with only one "best" male, and he would be capable of fertilizing all her eggs. Behaviorally, this translated into predictions of choosy and coy females and indiscriminate and promiscuous males.

Bateman's studies were conducted using various different mutant strains of flies.

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Because molecular biology did not exist in 1948, Bateman could not use DNA markers to estimate the number of offspring produced by each of his mutant crosses; instead, he used phenotypic markers (each mutation served as a marker). Thus, the calculations that lead to his conclusions on differences in male and female mating success and greater variances in male RS were based on determining parentage by counting the number of offspring from each cross that exhibited specific mutant phenotypic markers. Consequently, the validity of Bateman's conclusions is completely dependent on the accuracy of his counts. In their replicate of Bateman's study, Gowaty et al. (7) find that nearly 25% of the offspring suffered from lower viability because they were double mutants. Individuals that died would not have been counted by Bateman because they died before eclosion, and Bateman based his counts on adult flies. Thus, the results of this study provide an unassailable argument that challenges Bateman's primary conclusions.

Reexamining the Paradigm

Bateman's paradigm had already been undergoing reevaluation (6, 8) because when viewed through the lens of modern findings, so many aspects of his predictions do not appear to be accurate. A number of theoretical studies suggest that the results reported by Bateman (1) could have been attributable to stochastic and nonheritable factors (3–5) rather than to sexual selection. For example, Sutherland (3) constructed a model that included such factors as searching time for new mates, handling time of matings, and random rates of mating encounters. He concluded that Bateman's differences in mating success between males and females could have occurred by chance alone. Subsequently, Hubbell and Johnson (4) extended Sutherland's model by examining lifetime mating success as affected by survival rates over time and the fact that in populations of sexually reproducing organisms, the mean mating success for the two sexes must necessarily be the same. They concluded that nonheritable, stochastic factors can have profound influences on time allocation budgets for mating. The results of this theoretical model further eroded confidence in Bateman's findings. Additionally, Gowaty and Hubbell (5), based on a simulation model called DYNAMATE, concluded that many of the factors described previously, alone or in combination, can affect whether a male or female is choosy or indiscriminate; sex role switching is common, with males sometimes being choosy and females behaving more indiscriminately.

Some empirical studies also have failed to support critical aspects of Bateman's conclusions and predictions. For example, a number of studies on a variety of species and taxa have now found that both males and females increase their RS with the number of mates (e.g., 9–11), a result contrary to those predicted by Bateman gradients. Moreover, in some of these species, there is little or no difference between the sexes (11), and in at least one species of katydid, females have steeper gradients than males (12). Moreover, it is also well known that females in the majority of sexual species mate multiply and often take the lead in seeking additional copulations with different males, a behavior that also violates Bateman's predictions (5). Contrary to the assumption made by Bateman (that males should always copulate with as many females as possible), males in many species do not

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mate indiscriminately and, in some cases, may actually refuse to copulate with willing females (13, 14). We now know that sperm depletion is a problem for many males (15) and that this shortage of sperm can result in sperm allocation (males may give more sperm to certain females based on their size, mating status, or health, a form of mate choice, and can otherwise behave very selectively when choosing a mate). Moreover, methodological and statistical reanalyses of Bateman's experimental design and data have revealed numerous and serious problems, including rampant pseudoreplication, mathematical mistakes, and sampling biases (5, 16).

Supporting Data

However, it is fair to say that some studies also have supported key conclusions advanced by Bateman. Specifically, Arnold (2), working with a theoretical model, concluded that Bateman's ideas have significant merit. Likewise, some empirical studies have reinforced the importance and accuracy of some of Bateman's predictions. For example, in a study on the rough-skinned newt (*Taricha granulosa*), Jones et al. (17) used genetic paternity analysis to construct Bateman gradients. They found that males had greater variance in both RS and number of mates and that the Bateman gradients were consistent with Bateman's predictions: significantly steeper for males than for females. In another study, Jones et al. (18) investigated the pipefish (*Syngnathus typhle*), a sex role-reversed species in which females compete for males and males are choosy. In this case, female RS increases with number of mates and is significantly steeper than that for males precisely in the manner predicted by Bateman for such species, suggesting that sexual selection in females is stronger than it is in males. In another notable study, Bjork and Pitnick (19) attempted a partial replicate of Bateman's study. Using several different species of fruit flies, including *Drosophila melanogaster*, they generated Bateman gradients. They found greater differences between males and females in more anisogamous species (i.e., species in which there is a greater difference in the size of eggs vs. sperm) and more similar gradients when species were more isogamous (i.e., species in which the size of eggs and sperm is more similar). These results, including those for *D. melanogaster*, were consistent with Bateman's findings.

Conclusions

Taken together, all the preceding studies, along with the replicate by Gowaty et al. (7) in PNAS, suggest that, at best, Bateman's principles should be considered hypotheses and approached with great care. For example, it is fairly common for studies of Bateman gradients to disregard alternative explanations, including the null hypothesis that stochastic and nonheritable factors can produce results similar to Bateman's (5, 20). Ideally, future studies based on Bateman's classic paper (1) will explicitly consider and test such alternative explanations.

Replication is a critical part of the scientific process because it can lead to the refutation of results that cannot be repeated. It is interesting that for more than 60 y, Bateman's ideas served as a paradigm and were accepted fairly uncritically without any known attempts at replication. The results obtained by Gowaty et al. (7) are a major contribution that is likely to lead to a paradigm shift in the study of sexual selection and related topics. At a minimum, the demonstration of viability effects that bring into question the validity of Bateman's reported gradient poses a major challenge to the Bateman paradigm and indicates that it is imperative that his contributions and predictions be reexamined.

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