



Comment on "Bateman in Nature: Predation on Offspring Reduces the Potential for Sexual Selection"

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Comment on “Bateman in Nature: Predation on Offspring Reduces the Potential for Sexual Selection”

Göran Arnqvist

Byers and Dunn (Reports, 9 November 2012, p. 802) reported that sexual selection and natural selection are closely related in a wild population of pronghorns. Here, I argue that this conclusion is incorrect. Their main finding is due to the fact that, unsurprisingly, juvenile mortality and juvenile survival are negatively related across years.

The spirit of the Bateman gradient (BG) is to measure how important the number of matings is for reproductive success. It measures sexual selection on mating success (1, 2), and it can be a very useful measure of the strength of sexual selection (3). Following Bateman (4), the BG is estimated as the slope of a regression between “the number of mates and fertility.” Ideally, this involves regressing the relative number of ova sired, for males, or the relative number of ova produced, for females, on relative mating success (e.g., the number of matings performed). This then captures a component of variance in parental fitness (i.e., sexual selection) that is distinct from that which concerns subsequent variance in offspring survival (i.e., natural selection in a narrow sense), although this distinction is not always easy to make (5).

For a correct estimation of the BG in a given population, it is critical to record all matings occurring over the time during which the BG is estimated (1). This is ideally done by direct observations, but when this is impossible, matings are sometimes recorded indirectly by determining mothers and fathers of offspring using genetic markers. The use of genetic markers for estimating the BG can lead to strongly biased estimates, in part because individuals that do not mate may be entirely omitted from the data set (6) and in part because matings that leave no genetic footprint among offspring will be missed (1, 7). Angus Bateman (4) himself did not observe matings but fully realized the gravity of the problem: He spent a great deal of effort to motivate his experimental design and to provide a convincing case that no matings were in fact missed in his data (8). Missed matings lead to errors in the estimation of the BG (1, 6). These problems are greatly exacerbated in species where competitive postmating fertilization success is biased among males, the level of promiscuity is high, and/or brood sizes are small (1, 7).

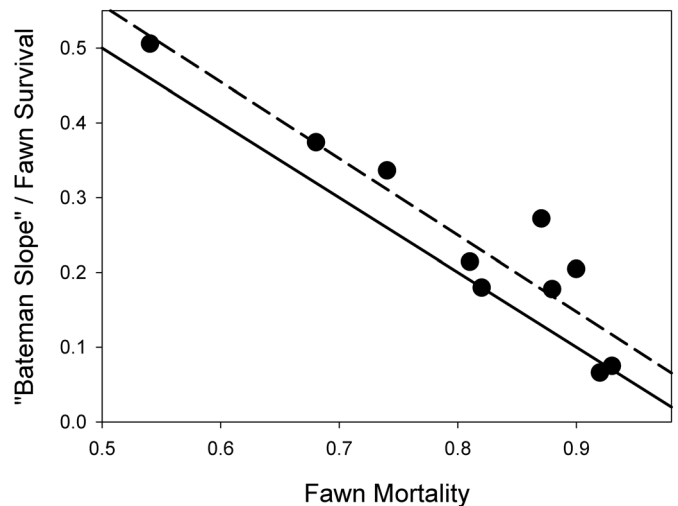
The study by Byers and Dunn of pronghorn (9) reports an interesting and striking difference in the opportunity for selection in males and females. However, their main conclusion is artifactual and the result of three related problems. First, although not stated in the report or its supplementary materials, Byers and Dunn did not observe matings but inferred the number of matings of both sexes from genetic micro-satellite data (10). Although they included males that fathered no offspring in their analysis, an unknown proportion of matings was missed. Pronghorn females invariably give birth to two fawns (9). However, because many sibling pairs have different fathers [44% of all pairs in (11)], most females must mate with several males, and many matings were thus missed.

Second, when comparing BGs across years, populations, sexes, or species, it is imperative that it is estimated based on relativized data (i.e.,

both reproductive success and mating success must be divided by their respective means) (1). In brief, this is because selection acts on relative, and not absolute, fitness (12). Unfortunately, Byers and Dunn based their analyses on absolute rather than relative data (10), although this was not stated in the report or its supplementary materials.

Third, the appeal of the BG is that it scales and incorporates effects of variance in mate fecundity (1), possible parental investment (2), and competitive postmating fertilization success (i.e., sperm competition) (13, 14) on the relationship between reproductive success and mating success. If there is no paternal care, no variance in female fecundity, and females mate only once (i.e., are monandrous), then male reproductive success will be directly proportional to male mate numbers because the former is then built entirely by the latter. Importantly, however, the BG then loses its validity as a meaningful measure of variation in sexual selection: Mate numbers and reproductive success become autocorrelated with an expected BG value of one (for relativized data). Studies on organisms where brood size is small and male mating success is determined by genetic markers in a manner such that matings may be missed are prone to suffer from a related but neglected problem: It becomes difficult to determine whether a variable represents reproductive success, mating success, or both (7), and investigators risk producing uninformative analyses that are generated by autocorrelational relationships between variables. For example, the number of offspring sired could represent male reproductive success but also be seen as a mea-

Fig. 1. The negative relationship between the metric termed “Bateman slope” and fawn mortality in pronghorn. Data are from figure 3 in (9). Neither the slope ($t_8 = 0.18$, $P = 0.86$) nor the intercept ($t_8 = 0.61$, $P = 0.56$) of the observed relationship (dashed regression line) differ from that predicted (solid line) under the relationship $Y = 1 - X$ (i.e., survival equals one minus mortality). Overall, the observations across years have slightly positive “residuals” when compared with the predicted values ($t_9 = 3.21$, $P = 0.011$), which could be due to a minor but systematic inferential bias when estimating the “Bateman slope” (i.e., survival rate). This could be because the estimates of “Bateman slopes” of Byers and Dunn were likely based on data showing heteroskedasticity and containing observations with high leverage, both of which can bias slope estimates in ordinary least squares regression. Additional important statistical problems include severe collinearity, overparameterization in their main inferential model [table 2 in (9)], and a lack of independence of data points because an unknown number of individuals were present during multiple years.



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sure of male mating success, depending on the biology of the taxa studied and the methods used. Because pronghorn lack variance in female fecundity (9) and have a very small litter size, and because Byers and Dunn ignore variance in post-mating fertilization success, this problem is aggravated in their analyses.

The metric termed the “Bateman slope” by Byers and Dunn was calculated as the slope of the regression across males of the absolute number of offspring reaching 12 weeks of age (as a measure of male reproductive success) on the absolute number of offspring that were born (as a measure of male mating success) separately for each year (10), although this was not stated in the report or its supplementary materials. This is not a valid measure of variation in the strength or opportunity of sexual selection among male pronghorn. A somewhat less problematic measure might have been yearly estimates of the standardized variance (i.e., I) in the number of

mates [but see (6)]. The “Bateman slope” of Byers and Dunn is instead a valid population level measure of overall offspring survival during the first 12 weeks of life each year. In fact, this basic inferential rationale (i.e., relating number of individuals at time $t + 1$ to the number at time t) is widely used in ecology to measure and characterize overall survival [e.g., (15)]. The Byers and Dunn “Bateman slope” thus, by necessity, quantifies annual offspring survival rate. The expected value of this metric is one minus fawn mortality rate, and their data match this prediction remarkably well (Fig. 1). Hence, rather than showing that “sexual selection and natural selection are entangled,” Byers and Dunn simply show that juvenile mortality and juvenile survival are negatively related across years.

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