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

John Byers* and Stacey Dunn

Sexual selection is driven by competition for mates, and the advantage of a competitor is determined by the number of offspring it produces. Early experiments by Angus Bateman characterized this interaction, and the quantitative relationship between a male's number of mates and number of offspring is known as the Bateman slope. Sexual dimorphism, one of the most obvious results of sexual selection, largely requires a positive Bateman relationship, and the slope provides an estimate of the potential for sexual selection. However, natural selection from the environment can also influence male success, as can random effects, and some have argued for inclusion of the latter in calculations of mate success. Data from pronghorn (*Antilocapra americana*) reveal the presence of a positive Bateman slope in each year of a 10-year study. We found no evidence that random effects skewed male mating success; however, substantial yearly variation in the Bateman slope due to predation on fawns was evident. These results support the validity of the Bateman relationship, yet they also demonstrate that environmental or extrinsic influences can limit the potential for sexual selection.

Angus Bateman's laboratory experiments on *Drosophila melanogaster* provided the first experimental support for Darwin's sexual selection hypothesis (*1*). The results of these experiments described the relationship between male mating success and male number of offspring, and the findings are now codified as the three Bateman principles (*2*): (i) Male variance in number of offspring exceeds that of females; (ii) male variance in number of mates exceeds that of females; and (iii) males show a significant correlation between number of mates and number of offspring, whereas females do not. These conditions, and especially the third, are considered necessary to support the evolution of sexual dimorphism.

Following from these principles, the slope of the linear regression of male number of mates on male number of offspring (called the Bateman slope) indicates the magnitude of the potential for sexual selection. Over time, several comparative studies have investigated whether the Bateman slope predicts the degree of sexual dimorphism, and a recent comprehensive review (*3*) called for a much better understanding of the forces that affect the slope. Two main factors, independent of male competitive success, could influence the

Bateman slope and thus potential for sexual selection. First, factors that reduce offspring survival (and recruitment) could reduce the contribution

of a male to subsequent populations, independent of his quality; thus, environmental conditions could possibly modulate the potential for sexual selection. Additionally, variance in male success (i.e., number of offspring produced) can become greater than female variance solely by random effects when the sexes differ in the latency to remate (*4*, *5*). If random processes such as this drive differential male success, traits from the highest-quality males will not necessarily be passed on to subsequent generations, and selection for reproductively advantageous traits could be swamped.

Here, we used a long-term data set, collected from every individual within the pronghorn (*Antilocapra americana*) population of the National Bison Range (NBR; Northwestern Montana, USA) between 1999 and 2010, to test the random effects hypothesis, ascertain the temporal stability of the Bateman relationship, and determine whether, and to what extent, population and environmental effects altered the magnitude of the Bateman slope. For each year of the study, we knew the number and ages of potentially breeding males and females, the sire and dam of each fawn born, and each fawn's birth mass, foot length, and survival to

Department of Biological Sciences, University of Idaho, Moscow, ID 83844–3051, USA.

*To whom correspondence should be addressed. E-mail: jbyers@uidaho.edu

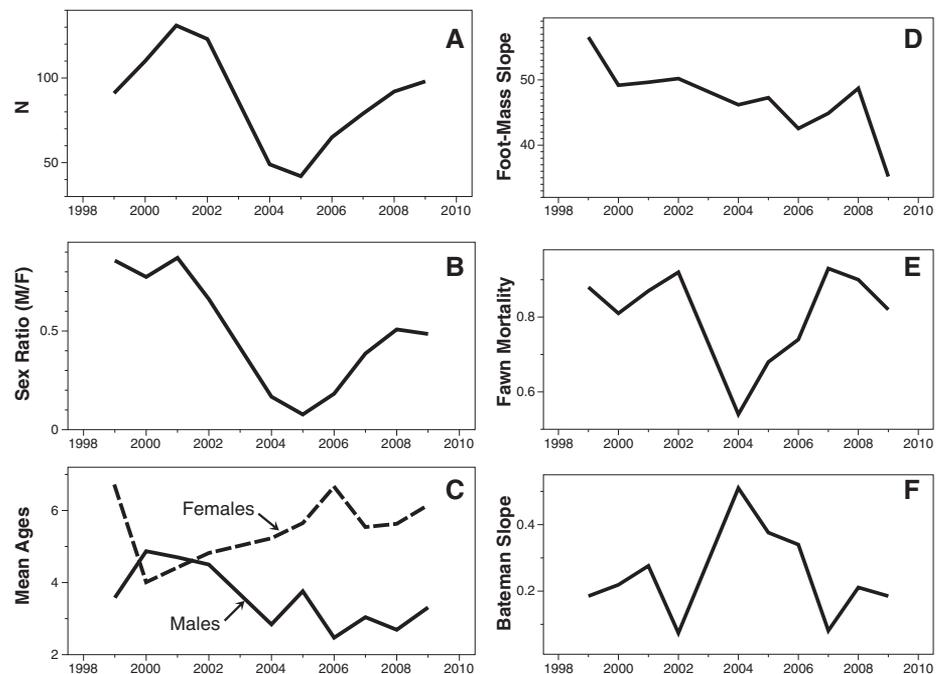**Fig. 1.** Variation in population characteristics. (**A**) Number of breeding-age adults. (**B**) Sex ratio of breeding-age adults. (**C**) Mean ages of males and females. (**D**) Slope of the linear regression of fawn birth mass on foot length. (**E**) Proportion of fawns that died before weaning. (**F**) Slope of the linear regression of male offspring recruited against male number of mates in the previous rut.

weaning (at 12 weeks). An individual that survives to weaning is recruited and is likely to reach breeding age (6). Therefore, for all reproductive-age individuals, we quantified the number of mates (including all males that had no mates) and the number of offspring recruited to the population. These data allowed us to calculate yearly Bateman slopes (from offspring recruited rather than from offspring produced), male and female I (where I is the opportunity for selection, defined as σ^2/mean^2), the breeder sex ratio, the average ages of males and females, yearly fawn condition (least-squares slope of foot length against birth mass), and mortality (Fig. 1).

In an iteroparous species such as pronghorn, the random effects hypothesis can be evaluated by a distribution test. If, in each mating season,

random effects cause the skew in male mating success, then, across several seasons, the mating success of all males will approach a Gaussian distribution (see supplementary materials). If, in contrast, random effects are not important and mating success is caused by male phenotype (i.e., a population subset of males always performs well), then the distribution of mating success across multiple years will remain skewed. Across all years of our study, the frequency distribution of the number of offspring produced by breeding-age males was highly skewed (Fig. 2), significantly different from Gaussian (Doornik-Hansen test for univariate normality $\chi^2 = 1749$, $P < 0.00001$), and significantly different from a Poisson distribution with the same mean [Levene's robust test for the equality of variances W0 = 51.54, df (1, 653), $P < 0.0001$]. The empirical

distribution of male mating success also differed from the expected distribution generated by the random effects hypothesis [empirical median = 0, expected median = 1.5, Levene's robust test W0 = 58.177, df (1, 653), $P < 0.0001$]. Thus, we found no support for the presence of random effects and rather conclude that a population subset of individual males sired most of the offspring. The results also support the three Bateman principles (Table 1). The variance in male number of offspring recruited exceeded the variance in female number of offspring recruited (paired $t = 3.41$, df = 9, $P = 0.008$). Variance in number of mates for males exceeded variance for females by more than two orders of magnitude, and number of recruited offspring produced by males was largely explained by male number of mates (331 male rut years, slope = 0.36, $r^2 = 0.73$). Females usually mated once, but when they mated twice or more so that two males were sires of the two fawn litter, their rates of offspring recruitment did not differ from those of females that mated once ($\chi^2 = 0.24$, $P = 0.89$).

Although we rejected the random effects hypothesis and confirmed the Bateman principles in a species with obvious sexual dimorphism in weapon size, pugnacity, and behavioral focus on copulation, the Bateman slope varied more than fivefold during the decade (Fig. 1F). Thus, our study offered the opportunity to evaluate the environmental and population elements that may affect the maximum intensity of sexual selection and specifically to test the hypothesis that environmentally induced offspring mortality would affect the Bateman slope.

We evaluated the magnitude of possible effects using a generalized linear model (GLM), in which the yearly Bateman slope was the dependent variable and the independent variables were population size, sex ratio, average ages of both sexes, fawn mortality, and condition slope (slope of the yearly least-squares regression of foot length on fawn mass). Density, sex ratio, and age structure are commonly predicted to be population characteristics that could alter the Bateman slope (7), and fawn condition is potentially important as a yearly indicator of the overall probability of survival to recruitment. The result (Table 2) showed clearly that one variable, fawn mortality, affected the Bateman slope. The effect of fawn mortality on the Bateman
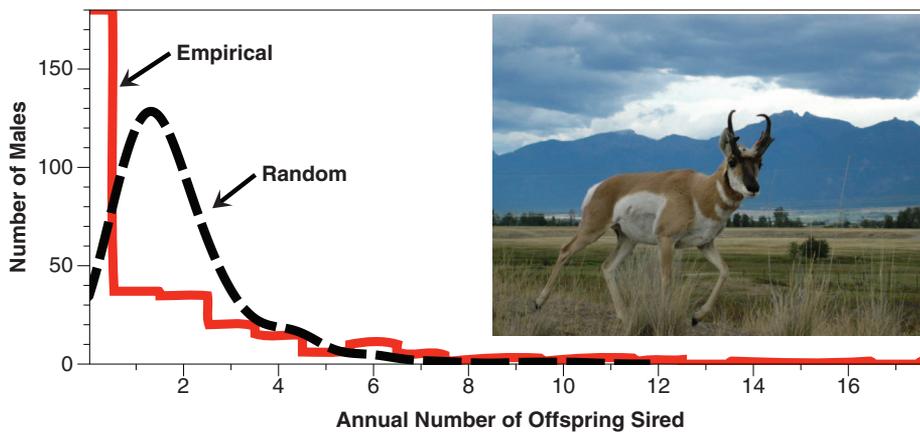

Fig. 2. The red line shows the annual distribution of individual male mating success summed across all years of the study. The dashed black line shows the expected distribution generated by simulations that followed the assumptions of the random effects hypothesis (see supplementary materials).

Table 1. Bateman principle statistics. I, the opportunity for selection, is the standardized variance.

Bateman principle	Males	Females
Offspring recruited: male σ^2 > female σ^2	$I = 4.84$	$I = 2.29$
Number of mates: male σ^2 > female σ^2	$I = 3.73$	$I = 0.09$
Correlation between number of mates and number of offspring recruited: male > female	$r = 0.85$	One mate: $I = 1.80$ Two mates: $I = 2.06$

Table 2. Results of a GLM analysis in which the yearly Bateman slope was the dependent variable.

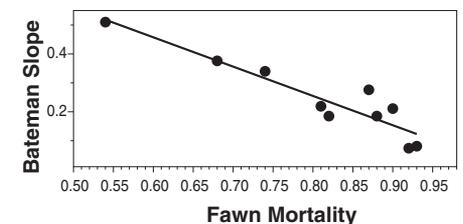| Independent variable	Coefficient	SE	z	P
Population size	0.0013	0.0030	0.43	0.66
Breeding adult sex ratio	−0.015	0.2770	−0.06	0.95
Mean male age	−0.035	0.0531	−0.67	0.50
Mean female age	−0.991	0.0477	−0.03	0.97
Fawn mortality	−1.201	0.3418	−3.51	>0.001
Fawn foot-mass regression slope	0.004	0.0068	0.69	0.49
Constant	1.023	0.5601	0.68	0.07

Fig. 3. Yearly proportion of fawns that died before weaning plotted against the Bateman slope for that year. Each point represents a year.

slope was negative, linear, and very strong (Fig. 3, $r^2 = 0.87$).

The interpretation of this finding rests upon understanding the causes of fawn mortality. If fawn mortality has a largely environmental cause, then our hypothesis that environmental mortality can affect the Bateman gradient is supported. In our population and across western North America, evidence points to coyotes (*Canis latrans*) as the primary cause. On the NBR and elsewhere, rates of fawn survival are directly related to rates of coyote removal practiced by state and federal agency personnel (*8*). Additionally, fawn survival in Yellowstone National Park is predicted by local wolf density and winter snowpack, two factors that reduce local coyote density (*9*). Finally, in the NBR population, fawn survival increases with maternal age, although the magnitude of maternal expenditure does not (*6*). With age, females appear to gradually improve the complex behavior of the hiding strategy, the mechanism to conceal fawns from predators during the first 3 to 4 weeks of life (*10*). Environmental characteristics that may affect the rate of coyote predation on pronghorn fawns include the density and litter sizes of territorial coyote pairs; the density of floaters; the densities of alternative prey, such as rodents of the genus *Microtus*; and the magnitude of spring precipitation, which can influence rodent densities as well as the quality of pronghorn milk and the concomitant change in fawn growth rates (*11*).

In all years of our study, the result of the fall rut was substantial variance in male mating success. However, mating success translated directly into reproductive success only when the rate of coyote predation was relatively low. When the rate was higher, fawn mortality eliminated most incipient variation in male reproductive success. Long-term studies show that the intensity and the direction of natural selection fluctuate with environmental conditions (*12*) and that the target of sexual selection varies with the nature of female mate choice (*13*). We now show that the maximum possible rate of evolutionary change under sexual selection varies with predator-driven offspring mortality. Bateman was a pioneer in the study of sexual selection (*14*) who established important principles that continue to guide empirical work. However, our study shows that single point estimators of the Bateman principles may be misleading and that ecological forces can modulate the potential for sexual selection. Sexual selection and natural selection are entangled.

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Corals Chemically Cue Mutualistic Fishes to Remove Competing Seaweeds

Danielle L. Dixson and Mark E. Hay*

Corals in the genus *Acropora* generate much of the structural complexity upon which coral reefs depend, but they are susceptible to damage from toxic seaweeds. *Acropora nasuta* minimizes this damage by chemically cuing symbiotic goby fishes (*Gobidon histrio* or *Paragobidon enchinocephalus*) to remove the toxic seaweed *Chlorodesmis fastigiata*. Within minutes of seaweed contact, or contact from only seaweed chemical extract, the coral releases an odor that recruits gobies to trim the seaweed and dramatically reduce coral damage that would otherwise occur. In turn, chemically defended gobies become more toxic after consumption of this noxious alga. Mutualistic gobies and corals appear to represent a marine parallel to terrestrial ant-plants, in that the host provides shelter and food in return for protection from natural enemies.

Coral reefs are in global decline, with seaweeds commonly replacing corals. Coral cover has decreased by ~80% in the Caribbean (*1*) and by ~50% along the Great Barrier Reef (*2*). Drivers of decline are debated, but all major stresses—including overfishing of herbivores, pollution, ocean heating, acidification, and disease (*3, 4*)—suppress corals, enhance seaweeds, and result in greater seaweed-coral competition.

For reefs to flourish, rapidly growing, branching corals such as Acroporids are critical because they create much of the topographic complexity upon which other species depend (*4, 5*). Other species, such as herbivorous fishes, then enhance reef resilience by grazing on competing algae and facilitating the colonization and growth of corals after disturbances (*3, 4, 6*). In the Caribbean, when two dominant *Acropora* species declined, structural complexity was lost across the entire region with likely effects on fishes, fisheries, biodiversity, coastal protection from wave damage, and ecosystem function in general (*7, 8*).

Reef-scale herbivory facilitates coral growth and maintenance by removing competitively superior seaweeds (*3, 4, 9, 10*), as exemplified by herbivore-rich reefs and marine protected areas that are higher in coral and lower in macrophyte cover, whereas overfished reefs with fewer herbivores have fewer corals and more macroalgae (*3, 9, 10*). However, individual corals are damaged only by adjacent seaweeds. Thus, critical aspects of competition occur at coral edges, a spatial scale over which corals might exert influence. Recent studies of seaweed-coral competition emphasize effects of seaweed allelopathy (*11, 12*) (chemical suppression of competitors), seaweeds vectoring coral diseases (*13, 14*), and near-contact creating anoxic zones or enhancing detrimental microbes on corals (*14, 15*). These mechanisms all require close contact for seaweeds to damage corals. Thus, millimeter- to centimeter-scale differences in proximity may cause large differences in coral health (*11, 12, 15*). Just as mutualist ants on *Acacia* trees protect their host by removing nearby competitors (*16*), we reasoned that the goby or pomacentrid fishes that shelter in many Acroporid corals (*17*) might play a similar function and remove seaweed competitors from coral edges.

We therefore focused on the common coral *Acropora nasuta* and asked the following: (i) whether commensal fishes sheltering in *Acropora* suppressed an allelopathic seaweed competitor, (ii) whether different commensal fish species varied in the protection they provided the coral, (iii) whether the interaction was affected by a specialist crab that lives only in the allelopathic sea-

School of Biology and Aquatic Chemical Ecology Center, Georgia Institute of Technology, 310 Ferst Drive, Atlanta, GA 30332, USA.

*To whom correspondence should be addressed. E-mail: mark.hay@biology.gatech.edu