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

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Byers and Dunn's (Reports, 9 November 2012, p.802) conclusion that predation constrains sexual selection is problematic for three reasons: their non-standard calculation of Bateman slopes; their assertion that random processes do not influence reproductive success; and the statistically unjustifiable use of six variables to explain just ten observations.

Byers and Dunn (1) contribute to our appreciation of links between sexual selection and environmental variation in nature, tackling this interesting and topical issue using an impressive dataset from a wild mammal population. The major finding of the study is that predation on offspring reduces Bateman slopes for males, and the authors argue that environmental influences limit the potential for sexual selection. While we acknowledge that this fresh perspective may help to grasp the full complexity of the interplay between sexual and natural selection in a wild population (1, 2), we have three concerns that we argue undermine Byers and Dunn's conclusions.

Our first concern is that the Bateman slopes employed by Byers and Dunn are calculated in a non-standard way, since they used the number of fawns recruited (rather than the number of fawns produced) in a given year of the study to measure male reproductive success. If predator-induced mortality among offspring acts independently of sire identity (as Byers and Dunn surmise), this means the y variable of their Figure 3 can be described by:

$$\text{annual Bateman slope} = \# \text{offspring per mate} \times (1 - \text{annual fawn mortality})$$

which is obviously related to the x variable (annual fawn mortality). The two axes are clearly confounded, and so the *null expectation* is a negative slope. The onus is on Byers and Dunn to explain this inevitability or demonstrate that there is something more interesting going on. In other words, since the number of fawns

recruited depends on the intensity of predation, it is hardly surprising that the yearwise regression slopes of “reproductive success” on “mating success” are affected by year-to-year variation in fawn mortality.

Figure 1 illustrates the difference between the conventional way of calculating Bateman slopes *versus* the method of Byers and Dunn. Bateman slopes are usually defined by the slope of a linear regression of the number of zygotes (or number of offspring) on the number of mating partners (3-5), though often (as here) the latter can only be estimated as “genetic mating success” following parentage assignment (but see e.g. 6). Thus Bateman slopes describe the number of additional offspring a male can expect to sire for each additional mate, and should not depend on the intensity of predation on offspring. Byers and Dunn, on the other hand, incorporate this information into their metric, by calculating the number of *surviving* offspring per additional mate. This tells us something about year-to-year variation in reproductive success, but to claim the correlation with mortality offers a major new insight into the conventional Bateman slope is confusing, and risks conflating the potential for sexual selection in one generation with offspring survival in the next.

Second, when considering the potential importance of random processes on male reproductive success, we concur with Byers and Dunn that chance alone seems unlikely to generate the observed variance in male reproductive success (Figure 2 in Byers and Dunn). But finding a deviation from a random distribution does not

exclude an influence of random processes. The randomization analysis merely shows that individual male reproductive success is repeatable across years, hence the highly skewed distribution of reproductive success does not arise by chance alone. However, we fear that their statement “*we found no support for the presence of random effects*” is unjustified.

When discussing random processes that influence the number of offspring, it is important to distinguish sampling variance, an inherent property of processes such as Poisson sampling from an underlying latent variable (7), from “random effect” in the sense of other, not (yet) understood sources of variance. Such random effects can be uncovered, and Byers and Dunn themselves do so by suggesting that predator density affects offspring survival and recruitment. The terminology used by Byers and Dunn does not distinguish sampling variance from other (unexplained) sources of variance and therefore obscures rather than clarifies the random processes issue.

Finally, we worry that the centrepiece of the study, the generalized linear model (GLM) presented in Table 2 of Byers and Dunn, is over-parameterized. This GLM appears to fit 6 variables to explain just 10 datapoints, and extracts offspring mortality as the only significant predictor variable. This leaves two degrees of freedom for the error term. The practice of over-parameterizing models hinders new insight both by reducing power for detecting real effects and by increasing the chance to detect spurious effects (8,9).

In sum, we fear the results presented by Byers and Dunn are clouded by a flawed analysis, including incorporation of the same effect in both the dependent and independent variables, overinterpretation of their data, and overparameterization of the key statistical model. The confusion that is likely to arise from these problems is unfortunate, since the basic idea - that extrinsic factors can limit male reproductive success in some years - does have implications for how we should think about sexual selection. In a long-lived animal such as the pronghorn, it is interesting to speculate for example that, if predation intensity is predictable, this could select for behavioral plasticity to target reproductive effort towards good years (or even alternative reproductive strategies to exploit such a strategy during poor years). We hope that by highlighting the analytical problems we can help to clarify the underlying biology.

References

1. J. Byers, S. Dunn, Bateman in nature: Predation on offspring reduces the potential for sexual selection. *Science* **338**, 802 (2012).
2. M. J. Wade, Constraints on sexual selection. *Science* **338**, 749 (2012).
3. S. J. Arnold, D. Duvall, Animal mating systems: a synthesis based on selection theory. *Am. Nat.* **143**, 317 (1994).
4. A. G. Jones, On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* **63**, 1673 (2009).
5. H. Kokko, H. Klug, M. D. Jennions, Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecol. Lett.* **15**, 1340 (2012).
6. B. Péliissié, P. Jarne, P. David, Sexual selection without sexual dimorphism: Bateman gradients in a simultaneous hermaphrodite. *Evolution* **66**, 66 (2012).
7. S. Nakagawa, H. Schielzeth, Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol. Rev.* **85**, 935 (2010).
8. W. Forstmeier, H. Schielzeth, Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* **65**, 47 (2011).
9. R. Mundry, C. L. Nunn, Stepwise model fitting and statistical inference: turning noise into signal pollution. *Am. Nat.* **173**, 119 (2009).

Figure 1

The standard way of measuring the Bateman slope (usually called the “Bateman gradient”) is to regress the number of offspring at the fertilization stage (dashed line) onto mating success (**A**). The method used by Byers and Dunn is to instead measure reproductive success at the later, recruitment stage (dotted lines), where the difference between the dashed and dotted lines can be interpreted as fawn mortality. In this illustration, different levels of predation affect the number of offspring measured at the recruitment stage but do not affect the number of offspring at the fertilization stage. The consequences of this for the calculated Bateman slopes are shown in (**B**), where predation does not affect the Bateman slope under the standard definition, but necessarily does affect the metric employed by Byers and Dunn. We agree that the dotted line represents a biologically relevant scenario, but suggest that it should not be confused with, and needs to be distinguished from, the dashed line. We suggest a new term such as “effective Batemen slope” (or “effective Bateman gradient”) may be more appropriate when researchers measure a Batemen slope in terms of surviving offspring.

