

Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough-skinned newt

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Few studies have influenced thought on the nature of sexual selection to the extent of the classic paper of A. J. Bateman on mating patterns in *Drosophila*. However, interpretation of his study remains controversial, and a lack of modern empirical evidence prevents a consensus with respect to the perceived utility of Bateman's principles in the study of sexual selection. Here, we use a genetic study of natural mating patterns in the rough-skinned newt, *Taricha granulosa*, to investigate the concordance between Bateman's principles and the intensity of sexual selection. We found that males experienced strong sexual selection on tail height and body size, while sexual selection was undetectable in females. This direct quantification of sexual selection agreed perfectly with inferences that are based on Bateman's principles. Specifically, males (in comparison with females) exhibited greater standardized variances in reproductive and mating success, as well as a stronger relationship between mating success and reproductive success. Overall, our results illustrate that Bateman's principles provide the only quantitative measures of the mating system with explicit connections to formal selection theory and should be the central focus of studies of mating patterns in natural populations.

Keywords: Bateman gradient; mating system; microsatellites; paternity; parentage; sexual selection

1. INTRODUCTION

In his 1948 article, Bateman (1948) articulated three specific points, eventually referred to as 'Bateman's principles' (Arnold 1994; Arnold & Duvall 1994), with respect to mating patterns and sexual selection in the fruitfly *Drosophila melanogaster*. These principles have been extremely influential to the development of sexual-selection theory over the last three decades (Trivers 1972; Andersson 1994). While Bateman discussed his study in terms of a species in which sexual selection acts most strongly on males, his principles are germane to sexual selection acting on either sex (Arnold 1994; Arnold & Duvall 1994). Arnold (1994) recently enumerated Bateman's original principles, so here we focus only on their modern manifestations. Bateman's three principles contend that:

- (i) the sex experiencing the strongest sexual selection has the higher standardized variance in reproductive success (total number of offspring) (Wade 1979; Wade & Arnold 1980);
- (ii) the sex experiencing more intense sexual selection exhibits a greater standardized variance in mating success (number of mates) (Wade 1979; Wade & Arnold 1980); and
- (iii) the slope of the regression relating reproductive success to mating success is larger in the sex experiencing stronger sexual selection (Arnold 1994; Arnold & Duvall 1994).

For most taxa, males experience stronger sexual selection

than females, a pattern that Bateman interpreted as an ultimate consequence of anisogamy (Bateman 1948). However, ecological and social constraints can cause a reversal in the direction of sexual selection (Trivers 1972; Oring 1986; Berglund *et al.* 1986), and Bateman's principles are equally valid under such circumstances (Jones *et al.* 2000, 2001*b*).

The value of Bateman's principles is that they are the only proposed statistical measures of mating patterns with clear connections to formal selection theory (Wade & Arnold 1980; Arnold & Duvall 1994). Several other measures of sexual selection have been proposed, such as relative parental investment (Trivers 1972), the operational sex ratio (Emlen & Oring 1977), and potential reproductive rates of the sexes (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992), but they do not possess a simple relationship to selection theory. To see the connection between Bateman's principles and selection theory, we first need to appreciate that sexual selection arises as a result of competition for access to mates and hence includes only those aspects of fitness related to offspring production (Darwin 1871; Andersson 1994). Thus, Bateman's first principle, the standardized variance in reproductive success (I , the opportunity for selection), represents the maximum strength of selection acting on a population with respect to numerical offspring production (placing an upper bound on the strength of sexual selection) (Crow 1958; Wade 1979; Wade & Arnold 1980). As sexual selection involves competition for access to mates, Bateman's second principle, the standardized variance in mating success (I_s , the opportunity for sexual selection), indicates the maximum strength of *sexual* selection acting in a population (Wade 1979; Wade & Arnold 1980). Finally, for sexual selection to operate, success in mating competition must translate into increased fitness.

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As a consequence, Bateman's third principle, the relationship between mating success and reproductive success (β_{ss} , the Bateman gradient), provides the final path to fitness for all sexually selected traits (Arnold & Duvall 1994).

While these quantitative measures of the mating system, by virtue of their ties to selection theory, potentially provide insights into the nature of sexual selection, they have been criticized on numerous grounds (Sutherland 1985*a,b*; Grafen 1987; Kokko *et al.* 1999). Most criticisms of the measures have been constructed on the basis of plausibility arguments or untested assertions, and we will return to this issue in § 4, where we show that the denigration of measures based on Bateman's principles has not produced a convincing case for their invalidation. Importantly, empirical datasets have not yet been used to show that variance-based measures are unrelated to the intensity of sexual selection. In addition, measures of the mating system based on Bateman's third principle have not yet been criticized (but neither have they been explicitly tested using data from natural populations). Consequently, we see the utility of Bateman's principles in the study of sexual selection as an unresolved empirical issue.

Our goal was to identify a natural system in which sexual selection was thought *a priori* to be stronger on males than on females and to test the concordance of measures based on Bateman's principles with direct measures of the intensity of selection on sexually selected traits. No published studies have yet quantified these three measures of the mating system along with direct estimates of selection intensities. Our focal organism is the rough-skinned newt (*Taricha granulosa*), which provides an excellent model for the study of mating patterns in nature. In winter, these newts migrate to ponds to breed. Males arrive before females, who trickle into the pond in small numbers (Pimentel 1960). The operational sex ratio is therefore male biased and sexual selection appears to act strongly on males (Janzen & Brodie 1989). The discrete nature of these aggregations facilitates complete sampling of the breeding adults, and all parameters relevant to Bateman's principles and the intensity of sexual selection can be measured from a complete study of parentage in one of these breeding groups. Thus, the outcome of our study of parentage in newts is relevant to the debate regarding the utility of Bateman's principles for research on sexual selection and should contribute to the development of a consensus method for the characterization of mating patterns in nature.

2. MATERIAL AND METHODS

(a) Collection of samples

We built a one-way drift fence around a pond (44°41'18" N, 123°12'29" W) in the E. E. Wilson Wildlife Area near Corvallis, Oregon. The pond, which holds water all year round, was created in the 1950s when the foundation of a demolished building became inundated with water. Cement walls surround the pond on three sides, and we built a fence of aluminium flashing to blockade the fourth side. Ultimately, barriers were arranged so that newts could enter the pond easily but could not exit. Despite its unusual origin, the pond housed an amphibian community that was typical of Oregon's Willamette Valley, including

breeding populations of *T. granulosa*, the long-toed salamander *Ambystoma macrodactylum*, the Pacific treefrog *Hyla regilla* and the bullfrog *Rana catesbeiana*.

We collected adult newts from the pond from 4 April to 9 June 2000, by submerging four plastic minnow traps in the water. Most females enter ponds in January and February (Pimentel 1960) and conclude their mating activity shortly thereafter (Propper 1991). They then lay eggs singly in vegetation over the course of several weeks or months (Twitty 1966). Thus, we caught newts during the egg-laying phase of the reproductive cycle, after breeding had been completed. We continued to trap newts until catch rates dropped to zero. A total of 96 adult males and 42 adult females were collected, and 78% of the captures occurred before the end of April. The dramatic decline in capture rates in May and June indicates that we sampled all (or nearly all) newts from the pond. Newts were measured with respect to mass, snout to vent length (SVL), tail length (TL), tail height (TH), limb diameter and head width. A small amount of tissue (2–5 mm) was excised from the tip of each tail for DNA analysis. The females were isolated in water-filled plastic shoeboxes equipped with artificial turf and were injected with 10 μ l of a 0.5 mg ml⁻¹ solution of luteinizing hormone-releasing hormone (des-Gly¹⁰-[D-His(Bzl)⁹]LH-RH ethylamide) to induce egg laying (Jones *et al.* 2002). Eggs were raised to hatching, and hatchlings were preserved at -70 °C for microsatellite assay.

(b) Parentage analysis

The paternity of hatchlings was determined by the use of six polymorphic microsatellite loci. Details of the primer sequences, microsatellite amplification protocols and DNA extractions are provided elsewhere (Jones *et al.* 2001*a*, 2002). A total of 30 females laid eggs, and we assayed an average of 25.4 offspring per female. All six loci were used to assay adults, each of which exhibited a unique genetic profile. Most hatchlings were genotyped at three loci, and paternity was assigned with a combination of two analytical techniques. For most females, we reconstructed paternal genotypes from progeny arrays using the program GERUD1.0 (Jones 2001), and we identified fathers by matching reconstructed genotypes to those of sampled males. For cases in which paternal genotypic reconstructions were ambiguous, paternity was assigned by complete exclusion, with data from four to six loci, using the computer program CERVUS (Marshall *et al.* 1998). These techniques resulted in the unambiguous assignment of paternity (to either known or unknown males) for 756 of the 762 assayed offspring. The genotypes of the remaining six offspring were consistent with their being the full siblings of other offspring from their mother, so we treated them as offspring of the same sire as their apparent full-sibling clutch mates.

(c) Selection analysis

We used the techniques developed by Lande & Arnold (1983) to calculate selection differentials and gradients for male and female phenotypic traits. All phenotypic measurements were log transformed and standardized to have a mean of zero and a variance of one. We initially focused on three traits (SVL, TL and TH) that seemed probable targets of sexual selection. We performed two analyses, using either mating success or reproductive success as our measure of fitness. We also performed an analysis of selection gradients using principal components of all measured phenotypic traits.

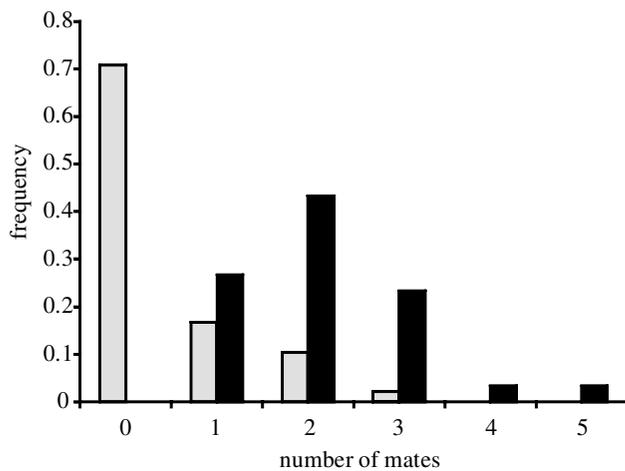


Figure 1. Distributions of genetically documented mating events for male and female newts. Grey bars, males; black bars, females.

3. RESULTS

(a) Parentage analysis

Our microsatellite-based study of parentage resulted in a very complete picture of mating patterns in this population of *T. granulosa*. As females laid their eggs in captivity, the maternity of each hatchling was known with certainty, and we obtained a precise description of female mating and reproductive success. On average, a female used sperm from 2.1 males to fertilize her eggs, resulting in 64 distinct mating events in our dataset. We identified the father from our pool of candidate males for 42 of these successful inseminations. The remaining inseminations clearly involved sperm from males that did not reside in our pond. This result is not surprising, because newts were able to enter the pond during the breeding season. Some females clearly carried stored sperm from neighbouring ponds into our breeding group. While we cannot completely rule out the possibility that some females left our pond, most of the reproductive success of our resident males should have been retained within the pond by the one-way drift fence. A small number of missing females will have a negligible effect on our overall conclusions. Mating success histograms for males and females are shown in figure 1.

(b) Selection analysis

Our selection analysis, with respect to male mating success, revealed highly significant selection on TH and marginally significant selection on body size (table 1). We see a similar pattern for male reproductive success (table 1), indicating that positive sexual selection is operating on either male SVL or TH (or, most probably, both). Similar conclusions are obtained whether we look at selection differentials or selection gradients (which correct for correlated responses to selection). Females, however, display a very different pattern of selection than males (table 1). In terms of mating success, we found no evidence for selection on any trait in females (table 1), and all point estimates of female selection coefficients are less than one-fifth of the corresponding values for males. For female reproductive success, we did find some evidence for selection. Significant selection differentials indicate that larger

females produce more offspring (table 1), which is not surprising given that a positive correlation between female size and fecundity is a common pattern in amphibians.

Our analysis of selection gradients using principal components of all measured phenotypic traits yielded similar results. In males, we detected significant selection on the first principal component (which can be interpreted as an index of overall body size) with respect to both mating success and reproductive success, whereas in females we documented significant selection on overall body size with respect to reproductive success but not with respect to mating success. Overall, these results indicate that phenotypically superior males enjoy increased mating success and increased reproductive success within a breeding season. By contrast, female mating success is unrelated to any measurable aspect of the phenotype, but larger females produce more offspring. Thus, sexual selection, which is based on competition for access to mates, appears to be strong in males, but undetectable in females (at least with respect to the phenotypic attributes that we were able to measure).

One important consideration is that we measured the phenotypic attributes of males and females only once during the course of this study. If trait values change dramatically and unpredictably during the course of the season, then the interpretation of our results could be compromised. The trait most prone to vary is TH in males (males develop a tail crest only during the breeding season), so to address this issue we measured TH for a sample of male newts from the focal population as part of a pilot mark-recapture study. Each male (marked with a passive integrated transponder tag) was measured in either February or March of 1999 and again in either April or May of the same year. While TH decreased over this period (from a mean of 13.4 to 11.4 mm), we found a highly significant correlation between TH late in the breeding season and TH early in the season ($N = 16$, $r = 0.84$, $p < 0.001$). These results show that phenotypic measurements collected late in the breeding season accurately reflect relative values during the breeding season. While changing phenotypic attributes will add some noise to the estimation of selection coefficients, our observation that the phenotype changes predictably justifies the approach that we used to study our focal population of newts.

(c) Bateman's principles and sexual selection

Given that sexual selection appears to be stronger in male than female newts, we wished to calculate the measures of sexual selection based on Bateman's principles and compare them between the sexes. The first two measures based on Bateman's principles are standardized variances in reproductive and mating success (table 2). Females exhibited higher mean mating success and reproductive success than males, a necessary consequence of the severely skewed sex ratio (table 2). The standardized variance in reproductive success for males is about 19 times that for females, and the male's standardized variance in mating success is about seven times that of the females (table 2). Hence, the relative values of these measures in males as compared with females are similar to the relative values of the selection coefficients on phenotypic traits. The third measure of sexual selection is given by the least-squares regression of reproductive success on mating suc-

Table 1. Estimates of the coefficients of selection on SVL, TL and TH in male and female newts from the pond.

(The selection differentials (s') are given by the covariance between the trait and fitness. We performed two analyses, in which fitness was equated with either mating success or reproductive success. Selection gradients (β') are estimated using a multiple regression approach. All phenotypic measurements were natural-log transformed before analysis, and selection coefficients have been standardized so that their units are phenotypic standard deviations. p -values are given for tests of the null hypothesis that coefficients do not differ from zero.)

character	fitness = mating success				fitness = reproductive success			
	s'	p	β'	p	s'	p	β'	p
male								
SVL	0.48	0.005	0.61	0.06	0.60	0.005	0.96	0.02
TL	0.29	0.11	-0.47	0.13	0.33	0.14	-0.67	0.09
TH	0.65	< 0.001	0.56	0.004	0.60	0.005	0.41	0.09
female								
SVL	0.06	0.49	0.03	0.87	0.18	0.04	-0.06	0.72
TL	0.05	0.55	-0.02	0.93	0.21	0.01	0.24	0.18
TH	0.11	0.20	0.10	0.29	0.15	0.08	0.09	0.35

Table 2. Quantitative measures of the genetic mating system of newts based on Bateman's principles.

(The opportunity for selection (I) is the variance in reproductive success (σ_{rs}^2) divided by mean reproductive success (\bar{X}_{rs}) squared. Similarly, the opportunity for sexual selection (I_s) is the variance in mating success (σ_{ms}^2) divided by its mean (\bar{X}_{ms}) squared. The Bateman gradient (β_{ss}) is given by the least-squares regression of reproductive success on mating success (figure 2). The last column shows the 95% confidence intervals for the male and female Bateman gradients.)

sex	\bar{X}_{rs}	σ_{rs}^2	I	\bar{X}_{ms}	σ_{ms}^2	I_s	β_{ss} (95% CI)
male	33.8	5122.4	4.48	0.43	0.58	3.06	74.6 (63 to 86)
female	161.9	5928.8	0.23	2.13	0.95	0.44	22.2 (-7 to 52)

cess (figure 2). In males, the regression is significantly positive ($y = 74.6x + 1.2$; $r = 0.80$, $N = 96$, $p < 0.001$), whereas the female's slope did not differ significantly from zero ($y = 22.2x + 114.5$; $r = 0.28$, $N = 30$, $p = 0.13$). If we consider only the point estimates of β_{ss} (table 2), we arrive at comparable conclusions to those provided by the other measures of sexual selection—the intensity of sexual selection acting on males is at least several times that acting on females.

4. DISCUSSION

This first comprehensive genetic study of parentage for any newt or salamander clearly shows that sexual selection is acting on male rough-skinned newts in nature. Positive sexual selection seems to be acting on both male body size and male TH, and this result is consistent with inferences based on visual observations of newts mating in the wild (Janzen & Brodie 1989). Confirmation and quantification of the nature of sexual selection in this population were necessary to accomplish the main goal of this study, which was to compare inferences based on Bateman's principles with the direct measurement of sexual selection. The results of these comparisons shed light on the utility of Bateman's principles for the study of sexual selection, and they illustrate the explicit connections between selection theory and these measures of the mating system.

One undeniable aspect of the genetic mating system is that for sexual selection to operate (with respect to offspring numbers), all of the measures of sexual selection based on Bateman's principles must be nonzero (Wade

1979, 1987; Wade & Arnold 1980; Arnold & Duvall 1994). Male newts satisfy this test. They exhibit high standardized variances in mating success and reproductive success, and their significantly positive Bateman gradient verifies that the observed variance in mating success is related to variance in fitness. Thus, all lines of evidence agree that sexual selection acts on male newts in our study population. By contrast, females show very small standardized variances in mating and reproductive success, and we were not able to show that their Bateman gradients differ significantly from zero. Consequently, females appear to experience little or no sexual selection. The only apparent selection operating on females is fecundity selection on body size, which is not part of the sexual-selection process (Darwin 1871; Andersson 1994). Inferences based on selection coefficients measured for particular phenotypic traits agree perfectly with these conclusions based on Bateman's principles, both in direction and magnitude. Regardless of the measure used, the data indicate that sexual selection on males is 4–20 times more intense than sexual selection on females.

As noted above, explicit measures of the mating system based on Bateman's first two principles have been heavily criticized over the past two decades (Andersson 1994). Most criticisms fall into two major categories:

- (i) factors other than sexual selection can contribute to variances in mating success and reproductive success (Clutton-Brock 1983; Sutherland 1985_{a,b}, 1987; Koenig & Albano 1986; Grafen 1987, 1988; Hubbell & Johnson 1987); and

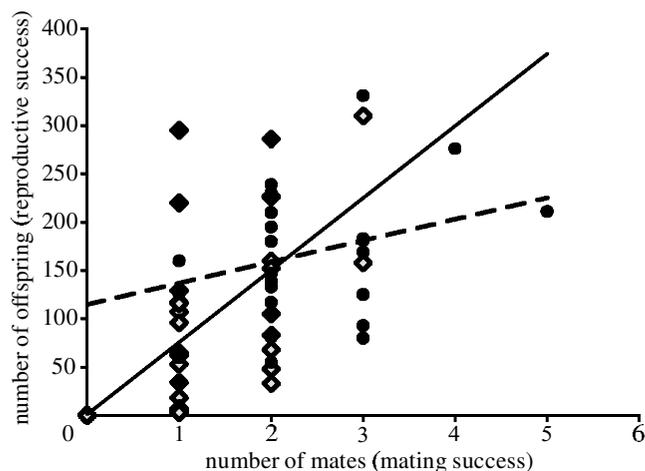


Figure 2. A plot of reproductive success versus mating success for newts from our focal population, showing Bateman gradients (also known as sexual-selection gradients) for males (solid line) and females (dashed line). The Bateman gradient is calculated by a least-squares regression, which facilitates simple statistical comparison. In this case the male's Bateman gradient is significantly larger than the female's (ANCOVA, $p < 0.001$), indicating that sexual selection acts more strongly on males in this population of newts. Diamonds, males; circles, females.

- (ii) variance may not be the best way to characterize the differences among sexes or populations with respect to the outcome of a nonrandom mating process such as sexual selection (Koenig & Albano 1986; Grafen 1987; Sutherland 1987; Kokko *et al.* 1999; Fairbairn & Wilby 2001).

However, although these criticisms are based on logical arguments, they employ models with untested assumptions, and none of them show definitively that a relationship between Bateman's principles and sexual selection is impossible or improbable (see below). In fact, the only widespread, well supported point of agreement seems to be that the standardized variances in mating and reproductive success *do* represent the maximum strength of sexual selection (Clutton-Brock 1983; Partridge & Endler 1987; Wilkinson *et al.* 1987; Grafen 1988; Fairbairn & Wilby 2001), as originally shown by Wade (Wade 1979; Wade & Arnold 1980).

For the sake of brevity, we will deal here with only the two most popular categories of criticism. A longer treatment of these and related issues will be presented elsewhere. The first class of argument contends that many factors other than sexual selection can contribute to variances in mating success and reproductive success. These factors include chance (Sutherland 1985*a,b*, 1987), environmental effects (Clutton-Brock 1983), lifespan (Grafen 1987; Hubbell & Johnson 1987; Clutton-Brock 1988) and selection on other traits (Koenig & Albano 1986). As a consequence, the variance in mating success (or variance in reproductive success) will tend to overestimate the actual intensity of sexual selection (Wade 1987; Partridge & Endler 1987). However, variance-based measures should be interpreted as indicators of the opportunity for sexual selection rather than infallible measures of its intensity. Although chance and other factors can in

principle contribute to variance-based measures, it remains to be seen whether such contributions undercut the value of these in practice. The utility of variance-based measures of sexual selection remains an empirical issue.

The second major class of criticisms for variance-based measures of the mating system argues that variance is not the best way to characterize nonrandom mating (Koenig & Albano 1986; Grafen 1987; Sutherland 1987; Kokko *et al.* 1999; Fairbairn & Wilby 2001). Some authors believe that it may be easier to measure other aspects of the mating system, such as time spent mating (Sutherland 1985*a,b*, 1987), potential reproductive rates of the sexes (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992) or operational sex ratios (Emlen & Oring 1977). These measures either require assessment of the reproductive status of individuals from nature or intensive laboratory experiments of reproductive potential. Most species are not amenable to such studies. By contrast, with the recent advent of powerful molecular techniques, variance-based measures of the genetic mating system are actually more tractable in most natural populations. Furthermore, the proposed alternative measures of mating systems are linked to the intensity of sexual selection through their effect on variances in mating success. For example, a male-biased operational sex ratio (or a higher potential reproductive rate or shorter mating time in males) is expected to increase the intensity of sexual selection, and this increase in intensity is invariably accompanied, at least in theoretical models, by an increase in variances in mating and reproductive success (Wade 1987; Arnold & Duvall 1994).

Some recent studies have indicated that indices of inequality, such as the index of Morisita (1962) or the index of resource monopolization (Green 1966), may be more useful than variance-based measures to explore the potential for sexual selection (Kokko *et al.* 1999; Fairbairn & Wilby 2001). The problem with these measures is that they do not possess a clear relationship to selection theory and are therefore extremely difficult to interpret with respect to the sexual-selection process (Kokko *et al.* 1999; Fairbairn & Wilby 2001). Furthermore, as indirect measures of the potential for sexual selection, they suffer many of the same drawbacks as the variance-based measures. Thus, the clear connections between the measures based on Bateman's principles and the process of sexual selection justify their use for the statistical characterization of genetic mating systems in natural populations (Wade 1979; Wade & Arnold 1980; Arnold & Wade 1984*a,b*; Arnold 1986; Arnold & Duvall 1994). Other proposed measures lack this connection to selection theory.

While the variance-based measures are useful, our study shows that all three measures should be calculated and considered with respect to their implications for the sexual-selection process. In fact, the most revealing measure of the intensity of sexual selection may be the Bateman gradient (Arnold 1994; Arnold & Duvall 1994), because it represents the final statistical path to fitness for all sexually selected traits. This measure has neither been tested widely nor criticized extensively, so its utility for the study of sexual selection has yet to be confirmed empirically. Nevertheless, the few studies such as ours that have characterized Bateman gradients find good agreement between the expected intensity of sexual selection and

inferences based on the gradients (Arnold & Duvall 1994; Jones *et al.* 2000; Garant *et al.* 2001).

In the present study, we have sidestepped two very important issues that should be taken into consideration in future studies. First, we have intentionally ignored the influence of mate quality or offspring quality on the measurement of sexual selection. While the numerical production of offspring is probably far more important to the intensity of selection in a species with no paternal investment in offspring like a newt, in some species the major fitness benefit to success in mating competition may stem from variation in the quality of mating partners (Clutton-Brock 1988; Andersson 1994). Separate studies, beyond the simple characterization of the genetic mating system, are required to establish the importance of mate quality to sexual selection for any particular biological system. Only then can measures of the mating system and effects due to mate quality be integrated into a more complete understanding of the sources of fitness variation for sexually selected traits.

Second, as in most other studies of mating patterns in natural populations, we have ignored the important issue of age structure. In most studies, including ours, this shortcoming is a result of logistical constraints. However, variance-based measures of the mating system, Bateman gradients and selection coefficients should be calculated in a way that accommodates age-specific effects (Wade 1979; Wade & Arnold 1980; Lande 1982; Arnold & Duvall 1994). Ideally, all of these measures should be based upon data on lifetime mating and reproductive success. Failing that, the data can be corrected for age structure. We were unable to include age structure in our analysis, mainly as a consequence of sample size considerations. This shortcoming should have resulted in overestimates of mating-system measures as well as selection coefficients and consequently should not affect the major conclusions of this study, which are based upon comparisons of relative values between the sexes. Nevertheless, a major goal of future studies of mating patterns in nature should be to integrate the genetic mating-system data with data on age structure.

In summary, our results indicate that inferences based on Bateman's principles are perfectly concordant with direct measurement of selection on phenotypic characters. Thus, Bateman's principles reflect the intensity of sexual selection in the absence of any information about the phenotypes of individuals. Such a use of Bateman's principles has been criticized in the past (Sutherland 1985*a,b*; Grafen 1987; Andersson 1994). However, the foundation of selection theory upon which these measures of sexual selection rest boasts at least as much theoretical support as the criticisms that have been levelled. Thus, the question of the utility of Bateman's principles is an empirical issue, and our results indicate that these measures may be extremely useful. In fact, in some ways they surpass the direct measurement of sexual selection with respect to particular phenotypic traits in that they:

- (i) require no knowledge of the phenotype;
- (ii) represent a composite measure of all sexual selection acting in a population (including that on unmeasured or immeasurable traits);

- (iii) provide a basis for comparison among systems in which homologous traits may not exist; and
- (iv) can be quantified relatively easily from genetic studies of mating systems.

Wider adoption of these measures will facilitate a more standard approach to the characterization of mating systems, which will permit better comparative studies and an improved synthesis of mating systems, ecology and sexual selection.

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