

Original Article

Reinterpreting Bateman gradients: multiple mating and selection in both sexes of a songbird species

Gerlach, N.M.^a McGlothlin, J.W.^b Parker, P.G.^c and Ketterson E.D.^a

^aDepartment of Biology, Indiana University, 1001 E. 3rd St., Bloomington, IN 47405, USA, ^bDepartment of Biological Sciences, Virginia Tech, 2125 Derring Hall, Blacksburg, VA 24061, USA, ^cDepartment of Biology, University of Missouri—St. Louis, One University Blvd, St. Louis, MO, 63121, USA

Bateman's principle, which states that male reproductive success should increase with multiple mating, whereas female reproductive success should not, has long been used to explain sex differences in behavior. The statistical relationship between mating success and reproductive success, or Bateman gradient, has been proposed as a way to quantify sex differences in sexual selection. We used a long-term data set on the distribution of paternity in the socially monogamous dark-eyed junco to examine the effect of multiple mating on lifetime reproductive success and to determine the relative contributions of within-pair and extra-pair mating. Both sexes exhibited a strong positive Bateman gradient, even when the number of breeding years was accounted for. Although theory suggests that this pattern indicates a strong potential for sexual selection in both sexes, we argue that the interpretation of strong Bateman gradients, particularly in females, has many potential complications. We discuss several alternative explanations for our results, none of which requires sexual selection acting on female traits, including targeting of inherently fecund females by males seeking extra-pair mates and increased power to detect extra-pair offspring as family size increases. Because neither of these explanations requires that increased mating success causes increased reproductive success, we conclude that using Bateman gradients to measure the potential for sexual selection may be misleading for some mating systems and life histories, such as the iteroparous social monogamy found in juncos. *Key words*: Bateman gradient, extra-pair mating, mating success, multiple mating, reproductive success, sexual selection. [*Behav Ecol*]

INTRODUCTION

The idea that males are eager to seek multiple mates, whereas females are resistant and prefer to mate with only a single male, has been a pervasive notion since Darwin (1859) published his theory of sexual selection. However, this idea was first discussed in quantitative terms by Bateman (1948) in a landmark paper relating sex differences in mate acquisition to offspring production in *Drosophila*. Bateman's results generated three main predictions regarding sexual selection (Arnold 1994): males should display greater variance than females in both 1) offspring number and 2) number of mates, and 3) the correlation between number of mates and number of offspring should be stronger in males than in females (Bateman 1948). The term "Bateman's principle," which was originally limited to the first of Bateman's proposals (Williams 1975), has since been used to refer to any or all of Bateman's three predictions (Dewsbury 2005), whereas the term "Bateman gradient" refers specifically to the statistical relationship between mating success (number of mates with which an individual produces offspring) and reproductive success described in (3), above (Arnold and Duvall 1994; Andersson and Iwasa 1996; Jones et al. 2002).

Although theorists have attempted to formalize the relationships among Bateman's principles and the evolution of sex differences (e.g., Wade and Arnold 1980; Arnold and Wade 1984; Arnold and Duvall 1994; Shuster and Wade 2003) and others have addressed potential conceptual problems in the application of Bateman's ideas (Gowaty 1997; Parker and Tang-Martinez 2005; Klug et al. 2010; Krakauer et al. 2011), empirical tests of Bateman's predictions have been rare until relatively recently (Tang-Martinez 2010).

A number of studies testing Bateman's first principle, that variance in reproductive success should be greater in males than in females, have confirmed its applicability to a variety of species (Clutton-Brock 1988; Le Boeuf and Reiter 1988; McLain 1991; Oring et al. 1991; Jones et al. 2002). However, a number of other studies from an equally broad taxonomic distribution have found that males and females do not differ in variance in reproductive success, including studies from birds (Scott 1988; Marti 1997; Weatherhead and Boag 1997; Thomas and Coulson 1998; Webster et al. 2001; Jensen et al. 2004), mammals (Ribble 1992; Topping and Millar 1998; Bartmann and Gerlach 2001), and invertebrates (Hafernik and Garrison 1986). In some cases, variance in offspring number was actually greater among females than males, including in meadow voles *Microtus pennsylvanicus* (Sheridan and Tamarin 1988), song sparrows *Melospiza melodia* (Smith 1988), and a variety of species with nonbreeding alloparents (Hauber and Lacey 2005). Determining the factors that contribute to variance in reproductive success in both sexes, and thus to the potential strength of selection, remains a major

Address correspondence to N.M. Gerlach. E-mail: nmgerlac@indiana.edu

Received 12 August 2011; revised 2 March 2012; accepted 27 March 2012.

challenge for behavioral ecologists and evolutionary biologists (e.g., Jones et al. 2000; Webster et al. 2007).

Bateman's third principle, that the relationship between mating success and offspring number should be strong and positive in males but not in females, has received mixed support. It has been supported by studies in taxa as diverse as moths (Bezzerides et al. 2008), water striders (Ronkainen et al. 2010), spiders (Maklakov and Lubin 2004), Columbian ground squirrels (Murie 1995), adders (Capula and Luiselli 1994), crayfish (Yue et al. 2010), and rough-skinned newts (Jones 2009). However, the universal applicability of Bateman's principle has been called into question by an increasing number of empirical studies. Indeed, even in some of Bateman's own replicates, females showed a positive relationship between mate number and offspring production, although with a shallower slope than males (Bateman 1948; Snyder and Gowaty 2007). A positive relationship between multiple mating and reproductive success has also been demonstrated in females of a variety of species across a wide taxonomic range (Table 1).

Despite increasing evidence of the prevalence of multiple mating by females (Ridley 1988; Griffith et al. 2002; Isvaran and Clutton-Brock 2007; Uller and Olsson 2008), a generalized version of Bateman's third principle—that females do not benefit directly from such matings—still holds sway in many areas of behavioral research. This is particularly true with respect to extra-pair mating, the term used to refer to multiple mating in species in which individuals form pair bonds to rear offspring but also copulate with individuals other than their pair-bonded partner. Most reviews of the subject have concluded that extra-pair mating rarely leads to increased individual reproductive success for the female, often by implicitly or explicitly citing Bateman's third principle as rationale, and that the benefits of extra-pair mating for females must arise primarily from indirect benefits such as greater offspring quality or numbers of grand-offspring (Westneat et al. 1990; Kempenaers and Dhondt 1993; Jennions and Petrie 2000; Griffith et al. 2002) although tests of this hypothesis have yielded mixed support (Akçay and Roughgarden 2007; but see Gerlach et al. 2012).

In this study, we examine whether extra-pair mating results in direct fitness benefits by examining the relationships among mating success, reproductive success, and extra-pair behavior in both female and male dark-eyed juncos (*Junco hyemalis*), a North American songbird. Juncos are a mildly sexually dimorphic and socially monogamous sparrow, with appreciable rates of extra-pair offspring (EPO) production (~27% of offspring; this study). A previous study of this species that reported a positive relationship between mate number and offspring number in both sexes was based on only two years of data (Ketterson et al. 1998), leaving a number of important questions unanswered. This report 1) considers field data from an additional 16 years and an additional 391 females; 2) measures lifetime rather than annual reproductive success and considers the effects of breeding tenure on the Bateman gradient; and 3) explicitly considers the effects of within-pair vs. extra-pair mating success on offspring production in both males and females.

MATERIALS AND METHODS

Field methods

This study was conducted on a population of free-living juncos breeding at and around Mountain Lake Biological Station in Giles Co., Virginia (Chandler et al. 1994). This population has been monitored during the breeding seasons continuously since 1983. Data reported in this study are from 1990 to 2007. During each year's adult census (typically 15 April–15 May), juncos were individually color banded, measured, and checked for age, sex, and reproductive

Table 1

Species with a positive relationship between mate number and reproductive success in females

Species	Citation
Invertebrates	
Nematodes (<i>Caenorhabditis</i> spp.)	(Diaz et al. 2010)
Promethea moth (<i>Callosamia promethea</i>)	(Morton 2009)
Leaf beetle (<i>Chrysochus cobaltinus</i>)	(Schwartz and Peterson 2006)
Katydid (<i>Conocephalus nigropleurum</i>)	(Lorch et al. 2008)
Pseudoscorpion (<i>Cordylochernes scorpioides</i>)	(Newcomer et al. 1999)
Fly (<i>Drosophila simulans</i>)	(Taylor et al. 2008)
Polychaete worm (<i>Galeolaria caespitosa</i>)	(McLeod and Marshall 1990)
Cricket (<i>Gryllus bimaculatus</i>)	(Tregenza and Wedell 1998)
Sea urchin (<i>Heliocidaris erythrogramma</i>)	(Evans and Marshall 2005)
Moth (<i>Helicoverpa armigera</i>)	(Hou and Sheng 1999)
Redback spider (<i>Latrodectus hasselti</i>)	(Andrade and Kasumovic 2005)
Fireflies (<i>Photinus</i> spp.)	(Lewis et al. 2004)
Seed beetle (<i>Stator limbatus</i>)	(Moya-Larano and Fox 2006)
Sea urchins (<i>Strongylocentrotus</i> spp.)	(Leviton 2005)
Grain beetle (<i>Tenebrio molitor</i>)	(Worden and Parker 2001)
Red flour beetle (<i>Tribolium castaneum</i>)	(Pai et al. 2005)
Arctiid moth (<i>Utethisa ornatix</i>)	(LaMunyon 1997)
Birds	
Tengmalm's owls (<i>Aegolius junereus</i>)	(Korpimäki et al. 2011)
Northern flicker (<i>Colaptes auratus</i>)	(Wiebe and Kempenaers 2009)
Dark-eyed junco (<i>Junco hyemalis</i>)	(Ketterson et al. 1998; this study)
Brown headed cowbird (<i>Molothrus ater</i>)	(Woolfenden et al. 2002)
Fish	
Cichlid (<i>Neolamprologus pulcher</i>)	(Dierkes et al. 2008)
Guppy (<i>Poecilia reticulata</i>)	(Becher and Magurran 2004; Evans and Magurran 2000; Neff et al. 2008)
Atlantic salmon (<i>Salmo salar</i>)	(Garant et al. 2001)
Brown trout (<i>Salmo trutta</i>)	(Serbezov et al. 2010)
Amphibians	
Small-mouthed salamander (<i>Ambystoma texanum</i>)	(Gopurenko et al. 2007)
Tiger salamander (<i>Ambystoma t. tigrinum</i>)	(Williams and DeWoody 2009)
Foam-nesting treefrog (<i>Chiromantis xerampelina</i>)	(Byrne and Whiting 2008)
Montandon's newt (<i>Triturus montandoni</i>)	(Osikowski and Rafinski 2001)
Reptiles	
Black ratsnake (<i>Elaphe obsoleta</i>)	(Blouin-Demers et al. 2005)
Leopard gecko (<i>Eublepharis macularius</i>)	(LaDage et al. 2008)
Sand lizard (<i>Lacerta agilis</i>)	(Olsson et al. 1994)
Common lizard (<i>Lacerta vivipara</i>)	(Eizaguirre et al. 2007)
Water python (<i>Liasis fuscus</i>)	(Madsen et al. 2005)
Adder (<i>Vipera berus</i>)	(Madsen et al. 1992)
Mammals	
Agile antechinus (<i>Antechinus agilis</i>)	(Kraaijeveld-Smit et al. 2002)
Gunnison's prairie dog (<i>Cynomys gunnisoni</i>)	(Hoogland 1998)
Yellow-toothed cavy (<i>Galea musteloides</i>)	(Keil and Sachser 1998)
Yellow-pine chipmunk (<i>Tamias amoenus</i>)	(Schulte-Hostedde et al. 2004)

condition (Reed et al. 2006). Beginning in 1990, all adults also had a small blood sample drawn via wing vein puncture for later DNA analysis (Ketterson et al. 1998).

During each breeding season, we located nests throughout the study area. The female and the social male associated with each nest were identified by behavioral observations of marked birds. Six days after hatching (day 6), nestlings were individually banded and blood samples were drawn for DNA analysis. We continued to monitor nests until the offspring left the nest on day 11–12 post-hatching. Only offspring seen on or after nest-leaving day were considered to have successfully fledged. Juncos in our population re-nest throughout the breeding season (late April–early August) and can produce 2–3 successful broods during this time (Nolan et al. 2002).

Genotyping and paternity analyses

Blood samples were stored in Longmire's solution, a lysis buffer, between collection and later analysis (Longmire et al. 1988). All samples were extracted using a standard phenol–chloroform procedure and then genotyped either by minisatellites (1990–1996) or by microsatellites (1997–2007) (for microsatellite details, see Gerlach et al. 2012). Nestling paternity for individuals prior to 1997 was determined by band-sharing analyses (Raouf et al. 1997). For nestlings from 1997–2007, paternity was assigned using the program CERVUS (Marshall et al. 1998; Kalinowski et al. 2007). Conspecific brood parasitism is extremely rare in the junco; only one nestling out of 2182 sampled offspring did not match the female associated with its nest (Ketterson et al. 1998; this study).

Of the 2182 sampled offspring, 1563 were determined to be sired by their social father (within-pair offspring, WPO), and 585 were sired by an extra-pair male (EPO). The remaining 34 nestlings were assigned a genetic sire but could not be classified as either WPO or EPO because their social father was not identified in the field. For 142 of the 585 EPO, either band-sharing analyses or CERVUS eliminated the social father as a putative genetic sire (indicating the nestling was an EPO), but these methods were unable to assign a genetic sire (indicating the true sire was not among the sampled males). In cases in which there was more than one “excluded but unassigned” offspring in a brood, we used the program COLONY (Jones and Wang 2010) to estimate full and half-siblings among nestlings with known maternity, and thus the minimum number of sires that contributed to the brood.

Quantifying offspring and mate numbers

To obtain the most comparable measures of offspring numbers for males and females, we considered only those offspring for which we had at least partial information about their genetic paternity ($n = 2182$) and only those adults that could be associated with these offspring ($n = 436$ females/435 males). Thus, every female in our sample produced at least one genotyped offspring, and every male in our sample was either the social father or the genetic sire of at least one offspring. By limiting our sample in this way, we avoided falsely inflating female reproductive success relative to that of males and were able to examine both apparent and actual reproductive success for the males in our sample. As a consequence of this sampling technique, the numbers presented represent minimum values for each parent's total number of offspring. Similarly, because we excluded females and most males with zero reproductive success, our estimates of variance in these measures are almost certainly underestimates of the true level of variance in the population at large (Shuster 2009).

This sampling method may affect estimates of mate number as well; uncounted offspring sired off the study site by a male in our sample also represent an uncounted mate for that male. For females, mating with a male from off the study site would produce an offspring that was known to be an EPO, but for which no genetic sire could be assigned. We were able to partially address this issue by using the sibship analyses in the program COLONY (Jones and Wang 2010) to estimate the number of unknown sires. For broods in which neither sire identity nor sire number could be determined (i.e., broods prior to 1997 for which microsatellite genotypes were unavailable), all “excluded but unassigned” offspring were conservatively considered to have had a single sire. Thus, the number of mates acquired by both males and females is also a minimum estimate of the true value. For all analyses of mating success, only genetic mates were considered; social partners with which an individual never produced offspring were not included as part of that individual's number of mates. In this study, we used the mean annual number of mates for each individual as its measure of mating success; using total lifetime number of mates instead did not affect the significance of the relationships between mating success and reproductive success in any of our analyses.

Breeding years

Number of sampled breeding years indicates the number of years between 1990 and 2007 in which an adult was known to be present on our study site, and so equals the number of years in which they could have potentially contributed to the sample of genotyped offspring. For the majority of birds sampled (391M/400F), this was equivalent to longevity (Table 2); 80 birds (44M/36F) had at least 1 breeding year (average = 2.0 years) either before or after our sampling period of 1990–2007.

Statistics

As part of an ongoing study, during some years some individuals in our population were implanted with exogenous testosterone (males: 1994–2000; females: 2001–2002 and 2005–2007). As testosterone affects extra-pair behavior in male juncos (Raouf et al. 1997; Reed et al. 2006) and nest success in female juncos (O'Neal et al. 2008), we accounted for these implants by calculating a score (“% T years”) that represents the number of years an individual was implanted with testosterone divided by the number of years they were present in our sample. Although this technique does not account for every potential effect of testosterone manipulations (e.g., number of implanted neighbors influencing mating success), it does address the individual contributions of implanted individuals to the Bateman gradient. Further, the slopes of Bateman gradients for years in which implants were given are comparable to years in which they were not (Supplementary Figure S1).

Male and female mean mating and reproductive success were compared using *t*-tests, and male and female variances in mating and reproductive success were compared using Levene's *F*-test. Bateman gradients were calculated using a generalized linear model (GLM) with a Poisson error distribution, including number of mates, number of sampled breeding years, and % T years as covariates. Each model was run for the sexes separately, and then with the sexes combined, with sex added to the model as a fixed factor, and the interaction terms sex \times number of mates, sex \times breeding years, and sex \times % T years included in the model, but removed if they were not significant (Engqvist 2005).

Table 2
Means and variances of reproductive success and mating success in male and female dark-eyed juncos

	Females			Males			<i>t</i> -test			<i>F</i> -test	
	Mean \pm SE	<i>n</i>	$I_{females}$	Mean \pm SE	<i>n</i>	I_{males}	<i>t</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>P</i>
Previous study											
No. of offspring											
Total	3.73	45	0.513	3.26	50	0.721					ns
No. of mates	1.16	45	0.373	1.02	50	0.670					ns
This study											
No. of sampled yrs	2.01 \pm 0.06	436		2.476 \pm 0.07	435		-5.128	841.8	<0.001	19.004	<0.001
No. of offspring											
Total	4.98 \pm 0.19	436	0.644	4.64 \pm 0.22	435	0.949	1.184	855.8	0.237	9.727	0.002
At fledging	3.10 \pm 0.16	436	1.137	2.89 \pm 0.16	435	1.364	0.934	869	0.351	0.907	0.341
No. of EP mates	1.35 \pm 0.03	436	0.170	1.04 \pm 0.02	435	0.241	8.587	863.0	<0.001	34.206	<0.001
No. of EPO											
Total	1.33 \pm 0.10	436	2.312	1.00 \pm 0.09	435	3.475	2.435	864.6	0.015	7.961	0.005
At fledging	0.82 \pm 0.07	436	3.307	0.63 \pm 0.07	435	5.076	1.904	867.3	0.057	7.108	0.008
No. of EP mates	0.48 \pm 0.03	436	1.782	0.29 \pm 0.02	435	2.253	5.134	765.4	<0.001	73.646	<0.001
No. of WPO											
Total	3.57 \pm 0.16	436	0.874	3.59 \pm 0.17	435	0.975	-0.104	869	0.917	2.895	0.089
At fledging	2.25 \pm 0.13	436	1.502	2.25 \pm 0.13	435	1.543	-0.027	869	0.978	0.329	0.567
No. of WP mates	0.84 \pm 0.02	436	0.186	0.74 \pm 0.02	435	0.326	3.857	849.7	<0.001	36.906	<0.001

Number of mates are measured as mean annual mating success. $I_{females}$ and I_{males} are calculated as the relative variance, i.e., variance divided by the mean squared. The *t*-test compares male and female mean values; the *F*-test compares male and female variances. Historical data (referred to in Table as "previous study") are from Ketterson et al. (1998). Bold values are significant at $P < 0.05$.

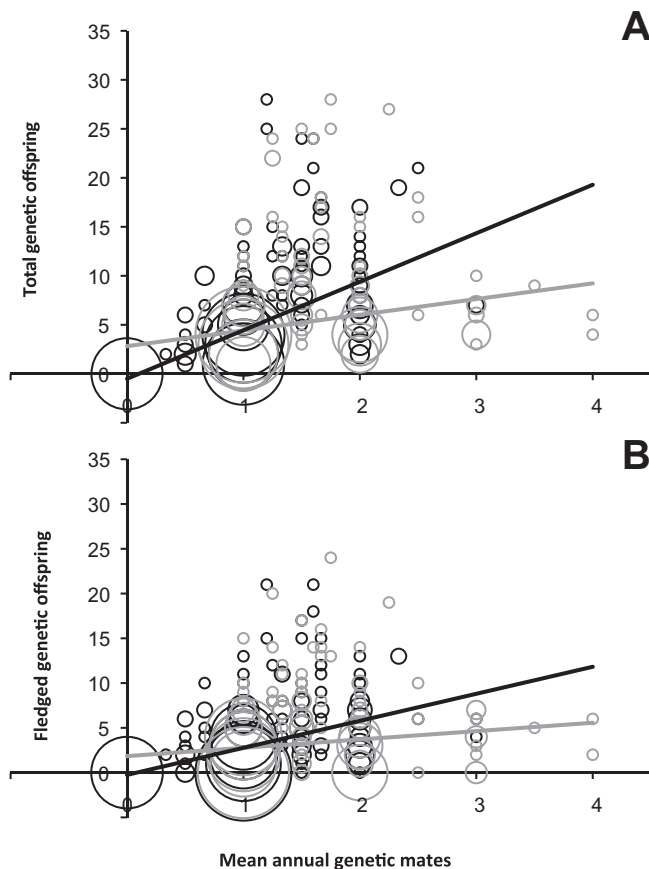


Figure 1
Bateman gradients for male (black) and female (gray) juncos, depicting the relationship between the mean number of annual genetic mates and the lifetime number of offspring (A) at genotyping and (B) at fledging. The diameter of the circle represents the number of individuals at that point, with the smallest circles in each graph representing one individual.

RESULTS

General distribution of paternity

Of 2182 offspring for which we had at least partial knowledge of their genetic relationships (paternity and/or sibships), 1563 were WPO and 585 were EPO (27% EPO). A total of 436 females produced the 2173 offspring of known maternity (4.98 offspring/female). Regarding males, 401 social males were associated with 2163 offspring (5.39 apparent offspring/social father), and 390 males sired the 2019 offspring that had identifiable genetic fathers (5.18 offspring/genetic sire). Although the sets of social males and genetic sires were mostly overlapping, there were some EP sires without a known social mate and some social males that did not sire any genetic offspring, such that our data set included 435 males in total.

Opportunity for selection

As expected based on the adult sex ratio, the sexes did not differ significantly in mean total number of offspring, mean number of WPO, or mean number of any type of offspring at fledging (Table 2). Females had significantly higher mean annual total and extra-pair mating success, as well as higher numbers of EPO than did males (Table 2), although this is likely due to the fact that in our sample, females but not males could produce offspring with extra-pair partners of unknown identity. Females also had significantly greater mean annual within-pair mating success than males (Table 2); the mean lifetime number of within-pair mates is the same for both sexes (1.02 ± 0.03 in females, 1.02 ± 0.04 in males), so this difference in mean annual success may reflect the fact that males in our sample had significantly longer life spans than females.

Variances for males were significantly greater than variances for females in number of total offspring, number of EPO both overall and at fledging, and mean annual number of within-pair and extra-pair mates. Males and females did not differ significantly in any other variance component (Table 2).

However, because we restricted our sample to only those adults that produced at least one genotyped offspring, the true difference in variances between the sexes will likely depend on the number of individuals with zero reproductive success in each sex.

Bateman gradients—overall

Both the annual number of genetic mates and the number of sampled breeding years strongly predicted the number of offspring surviving to day 6 in both sexes (Table 3, Figure 1A). When the sexes were considered together, there was a significant interaction of sex and number of genetic mates such that greater mating success increased reproductive success more in males than in females, and a significant interaction between sex and the number of sampled breeding years such that a longer breeding tenure increased reproductive success more in females than in males (Table 3).

Many offspring were lost to predators between day 6 and the age of nest-leaving (fledging), so the mean number of genotyped young at fledging was smaller, but the relationships between mating success and reproductive success remained significant when the number of fledged offspring was considered as the measure of reproductive success (Table 3; Figure 1B). Similarly, the number of breeding years was again a significant predictor of the number of fledglings in both sexes, and mating success had a stronger effect on reproductive success in males than in females, whereas number of breeding years had a stronger effect on reproductive success in females than in males (Table 3).

Bateman gradients—EP vs. WP mating

When an individual's overall annual mating success was partitioned into extra-pair and within-pair mates, both of these variables significantly predicted total reproductive success in both sexes, with number of within-pair mates having the stronger effect on total offspring number. Again, number of breeding years also significantly predicted reproductive success in both sexes. When the sexes were considered together, there was a significant interaction effect of sex and both

within-pair and extra-pair mating success, with males having a greater slope than females for both measures (Table 4).

In both males and females, both extra-pair mating success and the number of breeding years significantly predicted the number of EPO produced. When the sexes were considered together, there was a significant interaction effect between sex and extra-pair mating success such that increased extra-pair mating success had a larger effect on EPO production in males than in females (Table 4; Figure 2A). However, there was no interaction of sex and the number of breeding years, indicating that the number of breeding years affects EPO production similarly in males and females (Table 4).

Although the number of within-pair mates significantly predicted the number of WPO produced by both males and females, there was no interaction of sex and mating success, indicating that increased within-pair mating success had a similar effect on WPO production in both males and females (Table 4; Figure 2B). As in analyses of total reproductive success, the number of breeding years predicted WPO production in both sexes, but had a larger effect in females (Table 4).

DISCUSSION

Although Bateman's assertion that multiple mating should not lead to increased offspring production by females has until relatively recently been widely accepted in behavioral ecology, empirical tests to support this prediction have been surprisingly rare (Tang-Martinez 2010). In this study, we have shown that both male and female dark-eyed juncos vary in the number of mates with which they produced offspring and that this variation strongly predicts reproductive success in both sexes. This confirms the findings of a previous study in this species (Ketterson et al. 1998) and extends its perspective from annual to lifetime reproductive success; even when the number of active breeding years was taken into account, both sexes had significant positive Bateman gradients. These results suggest that multiple mating appears to have direct fitness benefits in both sexes. For males, this matches findings from many other species, and the causal mechanisms by which this pattern likely arises are well established (Trivers 1972; Westneat et al. 1990; Webster et al. 1995). As we discuss below, however, the relationship between mating

Table 3
Bateman gradients in dark-eyed juncos: reproductive success and overall mating success

Factor		Both Sexes, <i>n</i> = 871			Females, <i>n</i> = 436			Males, <i>n</i> = 435		
		β	Wald X^2	<i>P</i>	β	Wald X^2	<i>P</i>	β	Wald X^2	<i>P</i>
Total offspring	Intercept	-0.332	23.452	<0.001	0.384	33.679	<0.001	-0.338	24.058	<0.001
	Mean annual mates	0.863	409.990	<0.001	0.246	43.779	<0.001	0.865	410.146	<0.001
	No. of sampled years	0.498	735.427	<0.001	0.597	850.543	<0.001	0.497	729.772	<0.001
	% T years	-0.095	3.088	0.079	-0.167	3.017	0.082	-0.060	0.845	0.358
	Sex	0.713	56.335	<0.001						
	Sex × Mean annual mates	-0.616	119.024	<0.001						
	Sex × Sampled years	0.097	12.670	<0.001						
Sex × % T years	Removed									
Fledged offspring	Intercept	-0.801	84.313	<0.001	-0.133	2.484	0.115	-0.801	84.313	<0.001
	Mean annual mates	0.836	236.312	<0.001	0.213	19.408	<0.001	0.836	236.312	<0.001
	No. of sampled years	0.516	498.433	<0.001	0.663	676.529	<0.001	0.516	498.433	<0.001
	% T years	-0.148	3.024	0.082	-0.692	20.959	<0.001	-0.148	3.024	0.082
	Sex	0.667	30.204	<0.001						
	Sex × Mean annual mates	-0.623	73.444	<0.001						
	Sex × Sampled years	0.147	18.136	<0.001						
Sex × % T years	-0.554	9.844	0.002							

Bold values are significant at $P < 0.05$. β s given are for a GLM with a Poisson error distribution. For analyses with sexes combined, β s are for male = 0 and female = 1.

Table 4

Bateman gradients in dark-eyed juncos: reproductive success and within-pair (WP) and extra-pair (EP) mating success

Factor	Both sexes, $n = 871$			Females, $n = 436$			Males, $n = 435$			
	β	Wald X^2	P	β	Wald X^2	P	β	Wald X^2	P	
Total offspring	Intercept	-0.543	46.141	<0.001	0.336	17.537	<0.001	-0.543	46.194	<0.001
	Mean annual EP mates	0.708	205.439	<0.001	0.204	32.602	<0.001	0.709	204.764	<0.001
	Mean annual WP mates	1.198	294.517	<0.001	0.343	22.881	<0.001	1.197	294.053	<0.001
	No. of sampled years	0.495	742.299	<0.001	0.590	821.023	<0.001	0.495	738.540	<0.001
	% T years	-0.120	4.892	0.027	-0.136	1.961	0.161	-0.113	2.962	0.085
	Sex	0.877	60.619	<0.001						
	Sex \times EP mates	-0.504	68.625	<0.001						
	Sex \times WP mates	-0.853	72.928	<0.001						
Sex \times sampled years	0.094	11.936	0.001							
EP offspring	Intercept	-2.348	425.577	<0.001	-1.576	237.412	<0.001	-2.391	300.762	<0.001
	Mean annual EP mates	2.069	576.982	<0.001	1.144	631.612	<0.001	2.066	549.950	<0.001
	No. of sampled years	0.657	563.900	<0.001	0.630	261.132	<0.001	0.686	300.816	<0.001
	% T years	0.021	0.034	0.855	0.155	0.961	0.327	-0.117	0.484	0.487
	Sex	0.731	43.172	<0.001						
	Sex \times EP mates	-0.921	91.151	<0.001						
	Sex \times sampled yrs	Removed								
WP offspring	Intercept	-0.998	159.844	<0.001	-1.141	102.340	<0.001	-1.026	116.183	<0.001
	Mean annual WP mates	1.645	672.335	<0.001	1.608	262.421	<0.001	1.675	399.402	<0.001
	No. of sampled years	0.514	642.730	<0.001	0.617	657.365	<0.001	0.514	641.354	<0.001
	% T years	-0.156	6.422	0.011	-0.128	1.048	0.306	-0.172	5.711	0.017
	Sex	-0.180	6.804	0.009						
	Sex \times WP mates	Removed								
	Sex \times sampled years	0.104	11.151	0.001						

Bold values are significant at $P < 0.05$. β s given are for a GLM with a Poisson error distribution. For analyses with sexes combined, β s are for male = 0 and female = 1. Sex \times % T years was included in each model, but was not significant and was therefore removed from the final analyses.

success and offspring production need not be causal in either sex, and particularly for females, a positive Bateman gradient may arise through other means than sexual selection.

What do Bateman gradients say about selection in juncos?

The similar variances in mate numbers and the strong positive slopes of the Bateman gradients for male and female juncos suggest that both sexes have the potential to experience similarly strong sexual selection. These variances include only individuals that bred successfully; including nonbreeding individuals would likely increase the variance in both mating success and reproductive success. However, although a positive Bateman gradient allows us to estimate an upper limit of the strength of sexual selection experienced by a population (Arnold and Duvall 1994), it does not by itself predict the actual strength of sexual selection in that population as measured by the causal relationships between particular phenotypes and mating success. Such relationships may be estimated using phenotypic sexual selection gradients (Lande and Arnold 1983), which are often much weaker in females than in males (for juncos, see McGlothlin et al. 2005). Even if variance in mating success could be attributed to phenotypic variance in both sexes, the traits that predict high mating success may be different in males and females. Thus, even very similar Bateman gradients may arise from very different patterns of selection in the two sexes and may give rise to very different evolutionary responses. Determining which phenotypic traits underlie the variance in mating success in each sex is a major goal of empirical research in sexual selection (Bro-Jørgensen 2011; Rosvall 2011).

One obvious phenotype that could increase mating success in both males and females is a behavioral propensity to engage in extra-pair mating. In both sexes of the junco, we found that both extra-pair and within-pair mating success were related to increased reproductive success. However, the

slope of the Bateman gradient on the number of within-pair mates was greater in both sexes than the slope of the Bateman gradient on the number of extra-pair mates, suggesting that within-pair mating contributes more to total fitness than does extra-pair mating. A similar pattern has been reported in male house wrens (*Troglodytes aedon*), a species in which males may gain additional broods either sequentially with the same social mate or simultaneously via polygynous mating (Poirier et al. 2004; Whittingham and Dunn 2005).

The greater effect of within-pair vs. extra-pair mating on reproductive success in juncos indicates that producing broods with multiple sequential social mates, rather than extra-pair mating, is most related to increased offspring production. This suggests that acquiring and breeding with multiple social mates during a breeding season, either by facultative mate switching or via the ability to acquire a replacement mate following mate desertion or death, may be an important component of reproductive success in both sexes.

Probability of detection

A Bateman gradient with a positive slope may indicate a statistical artifact rather than a biological signature of sexual selection. Rare events are more likely to be detected in a larger sample; thus, multiple matings are more likely to be detected for individuals with greater numbers of offspring (Burley and Parker 1998). Most Bateman gradients based on data from natural populations (including ours) do not use mating success per se, but rather the number of successfully fertilized females (for males) or the number of males that successfully fertilized an egg (for females) as detected from the surviving offspring (Dewsbury 2005). Thus, the data points used to estimate these gradients necessarily have a lower limit of $y = x$; e.g., it is impossible to detect 6 mates for an individual that produced only 4 offspring. This lower bound tends to bias gradients

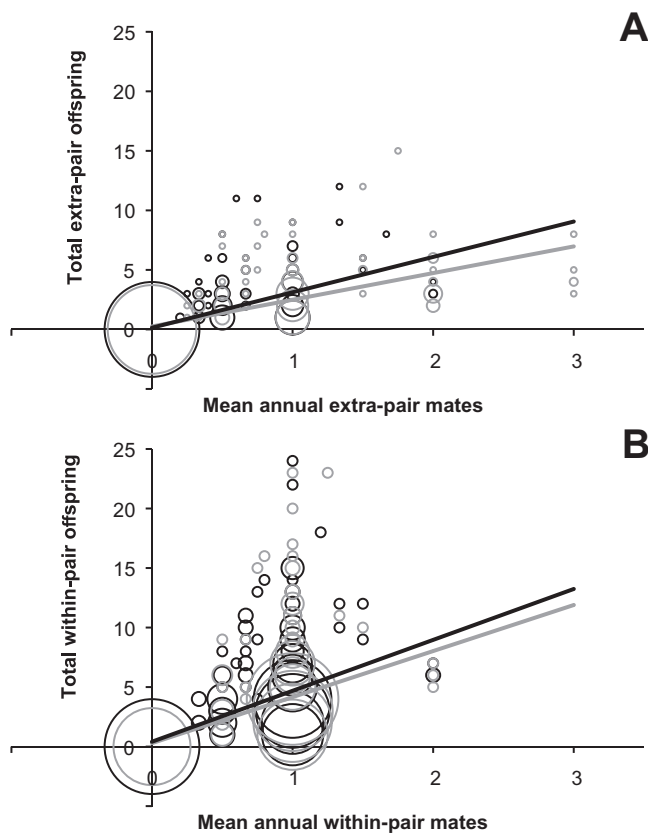


Figure 2
Bateman gradients for male (black) and female (gray) juncos displaying the relationship between mean annual mating success and lifetime offspring production, plotted separately for (A) extra-pair and (B) within-pair reproduction. The diameter of the circle represents the number of individuals at that point, with the smallest circles in each graph representing one individual. Because our data include only adults that produced at least one social or genetic offspring, the point at the origin represents those individuals that did not produce offspring of the specific type; for example, those individuals at the origin in (A) are those that produced only WPO.

upward, suggesting that positive gradients may arise via random processes. This issue of detectability is especially relevant in systems in which 1) gaining an additional mate is an event that occurs with relatively low frequency and/or 2) average fecundity, either lifetime or per breeding event, is low (Burley and Parker 1998).

Use of the slope of offspring number on realized mating success to assess the effect of selection on mating behavior without taking into account the problems of life history and detectability may result in an overestimation of the maximum strength of sexual selection. Although a typical Bateman gradient of offspring number on realized mate number would predict strong selection on mating frequency, a Bateman gradient of offspring number on the number of copulatory partners may be much shallower. Thus, if the pattern of increased reproductive success with increased mate number is driven primarily by the chance effects of detection rather than by additive genetic variation for actual mating frequency, a population may have a positive Bateman gradient but little potential for evolutionary response in mating behavior.

Problems of causality

Another persistent problem with the interpretation of Bateman gradients is the conflation of correlation and

causation. In studies—including this one—that use Bateman gradients to discuss the direction and force of sexual selection, the slope of the gradient is frequently described as “number of offspring gained for each additional mate” (e.g., Krakauer 2008), a phrasing that is certainly suggested by the standard orientation of the axes of mating success and reproductive success. However, the relationship created by reversing the axes has an equally valid causal interpretation: a positive slope would suggest that individuals have more mates because they have more offspring. The slope of this “inverse Bateman gradient” could be interpreted as “number of additional mates detected for each offspring sampled.” Although no such relationship between large broods and increased incidence of multiple mating was found across the mean values for viviparous species in a recent meta-analysis (Avise and Liu 2011), such a pattern may still hold within a single species. In fact, a positive relationship between offspring number and mate number can be generated by repeated subsampling of a single large brood (Panova et al. 2010), demonstrating that a positive Bateman gradient may sometimes have statistical but not biological significance. The fact that the relationship between mate number and offspring number may be probabilistic rather than predictive is particularly problematic for females. If selection is acting primarily on traits that affect fecundity rather than those that affect mating behavior, then the acquisition of multiple mates may be a passive effect of increasing offspring number, rather than its cause.

Therefore, although a positive covariance between offspring number and mate number indicates the potential for sexual selection on females (i.e., reproductive success as a function of mate number), selection may often be acting more strongly on traits that increase fecundity rather than mate number. Males have been shown to prefer females with traits that signal high fecundity in a variety of taxa, including insects (Bonduriansky 2001), fish (Herdman et al. 2004), and birds such as jungle fowl (Cornwallis and Birkhead 2007), zebra finches (Monaghan et al. 1996), and rock sparrows (Griggio et al. 2005). If this increased male preference correlates with increased likelihood of copulation/fertilization, then more fecund females will have greater numbers of realized mates, and thus females will tend to display a positive Bateman gradient. It is unclear whether male juncos display such a preference; if males were directing the majority of their courtship effort toward highly fecund females, then the females with the highest reproductive success should also have the highest percent of EPO, a pattern found in a previous study of the junco (Ketterson et al. 1998) but not in our larger data set ($r = 0.035$, $n = 429$, $P = 0.476$). However, as we have argued above, nonrandom mating by males is not necessary; higher fecundity may lead to a larger number of realized mates by chance as well.

One example of this interdependence of fecundity, female mating success, and positive Bateman gradients comes from northern water snakes (*Nerodia sipedon*). Prosser and colleagues (2002) found a strong positive Bateman gradient in female water snakes. However, when they accounted for female body size, the positive relationship between mating success and reproductive success disappeared. A positive correlation between female body size and offspring number is common in ectotherms (Vitt and Congdon 1978; Sargent et al. 1986; Shine 1992; Kraak and Bakker 1998). In the water snake, larger females also have more males that sire their clutches (Prosser et al. 2002), although whether this is due to active male choice on female size or an increased likelihood of detection of multiple sires with increased sample size is unclear. In cases such as this, although the Bateman gradient would indicate a strong potential for sexual selection, the increased mate numbers are most likely a result of increased female body size rather than its cause, and thus the actual

selection experienced by females is more properly classified as fecundity selection (Clutton-Brock 2009).

Life history

The extent to which a positive Bateman gradient reveals something about sexual selection may also depend in large part on the life history of the organism in question. In organisms in which females are semelparous and each large clutch of eggs is fertilized by an even mixture of sperm from all the males with which a female has mated, we would indeed predict that females should have shallow Bateman gradients. However, in iteroparous species, each clutch of eggs represents more offspring and a new chance to acquire more mates, which may lead to a positive association between mating success and reproductive success by random chance. In the extreme case, females sample from a large pool of males each time an egg needs to be fertilized. The more times a female samples, the more unique males she is likely to encounter, which is likely to lead to an even stronger positive Bateman gradient by random sampling. Thus, in iteroparous species, positive Bateman gradients in females may arise from a real biological phenomenon distinct from sexual selection: the need to mate anew each time an egg or a clutch is laid.

Extreme iteroparity may also tend to reduce Bateman gradients in males. If a female must acquire fresh sperm for each egg she produces, a male can no longer monopolize all of a female's offspring by mating with her once. As a consequence, males will likely face a tradeoff between mating with the same female repeatedly and searching for new females. In such a tradeoff, there may be multiple equivalent strategies. For example, if a single mating event tends to lead a single fertilized egg, it does not matter from a male's point of view whether he mates with the same female four times in a row or with four different females over the same time period. Although these two strategies have equivalent reproductive success, they have very different mating success, which creates variation in the relationship between these two variables, thus reducing the Bateman gradient. Although this example is highly simplified, the same general principle—that variation in male mating strategy may reduce the male Bateman gradient—should apply to real-world systems as well. When we consider life history, it should not be surprising for Bateman gradients to be similar in males and females, even in species with typical sex roles.

Although it is beyond the scope of the current paper to analyze in detail the life histories of the species in which females have positive Bateman gradients (Table 1), a few broad trends can be observed. In general, these species can be classified by their degree of iteroparity and their offspring output per reproductive event. In species in which females produce one (or a few) very large broods of offspring, such as many of the invertebrates and fish, a positive Bateman gradient may result from the increased detection probability of rare events. Species with several large broods may primarily be experiencing male preference for highly fecund females. On the other hand, highly iteroparous species, such as the junco, may show positive female Bateman gradients primarily due to the increased opportunity for re-sampling available males at each reproductive event. Although we do not have any direct evidence regarding sperm storage and usage in the junco, remating for each clutch of eggs is probably a necessity, and it is likely that females also often recopulate to fertilize each egg within a clutch (Nolan et al. 2002).

The effects of detection probability, fecundity selection, and iteroparous resampling, which are likely to interact and correlate with one another, may all contribute to positive Bateman gradients across species. The relative importance of

these factors within a species is probably dependent on that species' life-history characteristics. Teasing apart these effects should be a major goal of future research in the evolution of mating systems.

Why do females mate multiply?

Although we now have numerous examples of taxa in which females that mate multiply have increased reproductive success (see Table 1), there is still a lack of widespread acceptance of the idea that such promiscuity may be the result of direct selection on females (but see Rosvall 2011). This is perhaps due to the lack of any obvious and universal cause for why mating with multiple males would increase female reproductive success. Offspring production by females is believed to be limited primarily by available resources or time rather than by number of mates, particularly in species in which females invest more in individual offspring than do males (Trivers 1972). If females are limited by their access to nutrients, parental care, or viable sperm, then an extra-pair mating that provides these resources will indeed increase a female's reproductive success (Stacey 1982; Davies 1985; Ridley 1988; Fox 1993; Hunter et al. 1993; Sheldon 1994; Levitan and Petersen 1995; Reynolds 1996; Arnqvist and Nilsson 2000). However, in many species, females are not sperm limited, and extra-pair males do not provide any resources other than genetic material. In these cases, the mechanism that underlies any positive relationship between female mating success and offspring number is rarely clear.

In our population of dark-eyed juncos, there is certainly a strong relationship between female mate number and reproductive success; females that mate multiply have more offspring. However, referring to this phenomenon as a "direct benefit" of multiple mating may infer a degree of causality that is not supported empirically. The evidence that multiple mating directly causes female juncos to produce more offspring is scant at best. Rather, female juncos may vary intrinsically in their ability to produce and rear offspring in ways that are independent of the number of males with which they mate. The sources of such variation are as yet unknown but may include variation in heterozygosity, health, territory quality, nest site selection, or ability to defend against predators (Nagy and Holmes 2004; Clotfelter et al. 2007; Ortego et al. 2007; Goodenough et al. 2008). If these highly fecund females acquire more mates than less fecund females, either by active male mate choice for some trait that signals fecundity or as an effect of increased detection of rare events, then a positive Bateman gradient would emerge.

To conclude, Bateman gradients serve to describe the relationship between numbers of mates and reproductive success. When the relationship is positive in females, the gradients reveal situations in which females may benefit from multiple matings, but it is critical to recall that multiple mating may not be the cause of increased fitness, but rather a consequence of increased fecundity. Thus, mating behavior per se may not be the trait under selection, but rather an epiphenomenon of selection on other traits that lead to increased reproductive success in females. Although there are a number of clear cases of sexual selection acting directly on female traits (Rosvall 2011), positive Bateman gradients may arise from many other mechanisms. Future studies should exercise caution in interpreting such gradients as evidence for sexual selection in females and instead focus on the causal mechanisms that lead to this statistical pattern.

SUPPLEMENTARY MATERIAL

Supplementary Material can be found at <http://www.beheco.oxfordjournals.org/>.

FUNDING

This work was supported by the National Science Foundation (grant numbers BSR 91-114980, IBN 94-08061, IBN 97-28384, IBN 02-16091, BSC-05-19211, and IOS-0820055 to E.D.K., DDIG 0808051 to N.M.G., and DDIG 0508692 to J.W.M.).

Thanks to members of the E. Brodie III and Ketterson research groups and M. Webster for comments on the manuscript; M. Wade for helpful discussion; Mountain Lake Biological Station and the Mountain Lake Hotel for facilitating fieldwork on their properties; the Center for the Integrative Study of Animal Behavior for assistance in the laboratory; B. Harr for providing primers; E. Snajdr for help with data compilation; and the many people who contributed to collecting the long-term field data.

REFERENCES

- Akçay E, Roughgarden J. 2007. Extra-pair paternity in birds: review of the genetic benefits. *Evol Ecol Res.* 9:855–868.
- Andersson M, Iwasa Y. 1996. Sexual selection. *Trends Ecol Evol.* 11:53–58.
- Andrade MCB, Kasumovic MM. 2005. Terminal investment strategies and male mate choice: extreme tests of Bateman. *Integr Comp Biol.* 45:838–847.
- Arnold SJ. 1994. Bateman's principles and the measurement of sexual selection in plants and animals. *Am Nat.* 144:S126–S149.
- Arnold SJ, Duvall D. 1994. Animal mating systems: a synthesis based on selection theory. *Am Nat.* 143:317–348.
- Arnold SJ, Wade MJ. 1984. On the measurement of natural and sexual selection: theory. *Evolution.* 38:709–719.
- Armqvist G, Nilsson T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Anim Behav.* 60:145–164.
- Awise JC, Liu J-X. 2011. Multiple mating and its relationship to brood size in pregnant fishes versus pregnant mammals and other viviparous vertebrates. *P Natl Acad Sci USA.* 108:7091–7095.
- Bartmann S, Gerlach G. 2001. Multiple paternity and similar variance in reproductive success of male and female wood mice (*Apodemus sylvaticus*) housed in an enclosure. *Ethol.* 107:889–899.
- Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. *Heredity.* 2:349–368.
- Becher SA, Magurran AE. 2004. Multiple mating and reproductive skew in Trinidadian guppies. *Proc R Soc Biol.* 271:1009–1014.
- Bezzerides AL, Iyengar VK, Eisner T. 2008. Female promiscuity does not lead to increased fertility or fecundity in an arctiid moth (*Utetheisa ornatrix*). *J Insect Behav.* 21:213–221.
- Blouin-Demers G, Gibbs HL, Weatherhead PJ. 2005. Genetic evidence for sexual selection in black ratsnakes, *Elaphe obsoleta*. *Anim Behav.* 69:225–234.
- Bonduriansky R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol Rev.* 76:305–339.
- Bro-Jørgensen J. 2011. Intra- and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. *Evol Biol.* 38:28–41.
- Burley NT, Parker PG. 1998. Emerging themes and questions in the study of avian reproductive tactics. *Ornithol Monogr.* 49:1–20.
- Byrne PG, Whiting MJ. 2008. Simultaneous polyandry increases fertilization success in an African foam-nesting treefrog. *Anim Behav.* 76:1157–1164.
- Capula M, Luiselli L. 1994. Can female adders multiply? *Nature.* 369:528–528.
- Chandler CR, Ketterson ED, Nolan V Jr, Ziegenfus C. 1994. Effects of testosterone on spatial activity in free-ranging male dark-eyed juncos, *Junco hyemalis*. *Anim Behav.* 47:1445–1455.
- Clotfelter ED, Pedersen AB, Cranford JA, Ram N, Snajdr EA, Nolan V Jr, Ketterson ED. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia.* 154:493–503.
- Clutton-Brock TH. 1988. Reproductive success. In: Clutton-Brock TH, editor. *Reproductive success*. Chicago (IL): The University of Chicago Press; p. 472–485.
- Clutton-Brock T. 2009. Sexual selection in females. *Anim Behav.* 77:3–11.
- Cornwallis CK, Birkhead TR. 2007. Experimental evidence that female ornamentation increases the acquisition of sperm and signals fecundity. *Proc R Soc Biol.* 274:583–590.
- Darwin C. 1859. *On the origin of species by means of natural selection*. London: John Murray.
- Davies NB. 1985. Cooperation and conflict among dunlocks, *Prunella modularis*, in a variable mating system. *Anim Behav.* 33:628–648.
- Dewsbury DA. 2005. The Darwin-Bateman Paradigm in historical context. *Integr Comp Biol.* 45:831–837.
- Diaz SA, Haydon DT, Lindström J. 2010. Sperm-limited fecundity and polyandry-induced mortality in female nematodes *Caenorhabditis remanei*. *Biol J Linn Soc.* 99:362–369.
- Dierkes P, Taborsky M, Achmann R. 2008. Multiple paternity in the cooperatively breeding fish *Neolamprologus pulcher*. *Behav Ecol Sociobiol.* 62:1581–1589.
- Eizaguirre C, Laloï D, Massot M, Richard M, Federici P, Clobert J. 2007. Condition dependence of reproductive strategy and the benefits of polyandry in a viviparous lizard. *Proc R Soc Biol.* 274:425–430.
- Engqvist L. 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim Behav.* 70:967–971.
- Evans JP, Marshall DJ. 2005. Male-by-female interactions influence fertilization success and mediate the benefits of polyandry in the sea urchin *Heliocidaris erythrogramma*. *Evolution.* 59:106–112.
- Evans JP, Magurran AE. 2000. Multiple benefits of multiple mating in guppies. *P Natl Acad Sci USA.* 97:10074–10076.
- Fox CW. 1993. Multiple mating, lifetime fecundity and female mortality of the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Funct Eco.* 7:203–208.
- Garant D, Dodson JJ, Bernatchez L. 2001. A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *J Heredity.* 92:137–145.
- Gerlach NM, McGlothlin JW, Parker PG, Ketterson ED. 2012. Promiscuous mating produces offspring with higher lifetime fitness. *Proc Roy Soc Biol.* 279:860–866.
- Goodenough AE, Hart AG, Elliot SL. 2008. Variation in offspring quality with cavity orientation in the great tit. *Ethol Ecol Evol.* 20:375–389.
- Gopurenko D, Williams RN, DeWoody JA. 2007. Reproductive and mating success in the small-mouthed salamander (*Ambystoma texanum*) estimated via microsatellite parentage analysis. *Evol Biol.* 34:130–139.
- Gowaty PA. 1997. Principles of females' perspectives in avian behavioural ecology. *J Avian Biol.* 28:95–102.
- Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol Ecol.* 11:2195–2212.
- Griggio M, Valera F, Casas A, Pilastro A. 2005. Males prefer ornamented females: a field experiment of male choice in the rock sparrow. *Anim Behav.* 69:1243–1250.
- Hafernik JE Jr, Garrison RW. 1986. Mating success and survival rate in a population of damselflies: results at variance with theory? *Am Nat.* 128:353–365.
- Hauber ME, Lacey EA. 2005. Bateman's principle in cooperatively breeding vertebrates: the effects of non-breeding alloparents on variability in female and male reproductive success. *Integr Comp Biol.* 45:903–914.
- Herdman EJE, Kelly CD, Godin J-GJ. 2004. Male mate choice in the guppy (*Poecilia reticulata*): do males prefer larger females as mates? *Ethol.* 110:97–111.
- Hoogland JL. 1998. Why do female Gunnison's prairie dogs copulate with more than one male? *Anim Behav.* 55:351–359.
- Hou M, Sheng C. 1999. Fecundity and longevity of *Helicoverpa armigera* (Lepidoptera: Noctuidae): effects of multiple mating. *J Econ Entomol.* 92:569–573.
- Hunter FM, Petrie M, Otronen M, Birkhead T, Møller AP. 1993. Why do females copulate repeatedly with one male? *Trends Ecol Evol.* 8:21–26.
- Isvaran K, Clutton-Brock T. 2007. Ecological correlates of extra-group paternity in mammals. *Proc R Soc Biol.* 274:219–224.
- Jennions MD, Petrie M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biol Rev.* 75:21–64.
- Jensen H, Saether B-E, Ringsby TH, Tufto J, Griffith SC, Ellegren H. 2004. Lifetime reproductive success in relation to morphology in the house sparrow *Passer domesticus*. *J Anim Ecol.* 73:599–611.

- Jones AG. 2009. On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution*. 63:1673–1684.
- Jones AG, Arguello JR, Arnold SJ. 2002. Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough-skinned newt. *Proc R Soc Biol*. 269:2533–2539.
- Jones AG, Rosenqvist G, Berglund A, Arnold SJ, Avise JC. 2000. The Bateman gradient and the cause of sexual selection in a sex-role-reversed pipefish. *Proc R Soc Biol*. 267:677–680.
- Jones OR, Wang J. 2010. COLONY: a program for parentage and sibship inference from multilocus genotype data. *Mol Ecol Resources*. 10:551–555.
- Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol*. 16:1099–1106.
- Keil A, Sachser N. 1998. Reproductive benefits from female promiscuous mating in a small mammal. *Ethol*. 104:897–903.
- Kempnaers B, Dhondt AA. 1993. Why do females engage in extra-pair copulations? A review of hypotheses and their predictions. *Belg J Zool*. 123:93–103.
- Ketterson ED, Parker PG, Raouf SA, Nolan V Jr, Ziegenfus C, Chandler CR. 1998. The relative impact of extra-pair fertilizations on variation in male and female reproductive success in dark-eyed juncos (*Junco hyemalis*). *Ornithol Monogr*. 49:81–101.
- Klug H, Heuschele J, Jennions MD, Kokko H. 2010. The mismeasurement of sexual selection. *J Evol Biol*. 23:447–462.
- Korpimäki E, Salo P, Valkama J. 2011. Sequential polyandry by brood desertion increases female fitness in a bird with obligatory biparental care. *Behav Ecol Sociobiol*. 65:1093–1102.
- Kraaijeveld-Smit FJL, Ward SJ, Temple-Smith PD. 2002. Multiple paternity in a field population of a small carnivorous marsupial, the agile antechinus, *Antechinus agilis*. *Behav Ecol Sociobiol*. 52:84–91.
- Kraak SBM, Bakker TCM. 1998. Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Anim Behav*. 56:859–866.
- Krakauer AH. 2008. Sexual selection and the genetic mating system of Wild Turkeys. *Condor*. 110:1–12.
- Krakauer AH, Webster MS, Duval EH, Jones AG, Shuster SM. 2011. The opportunity for sexual selection: not mismeasured, just misunderstood. *J Evol Biol*. 24:2064–2071.
- LaDage LD, Gutzke WHN, Simmons RA II, Ferkin MH. 2008. Multiple mating increases fecundity, fertility and relative clutch mass in the female leopard gecko (*Eublepharis macularius*). *Ethology*. 114:512–520.
- LaMunyon CW. 1997. Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. *Ecol Entomol*. 22:69–73.
- Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution*. 37:1210–1226.
- Le Boeuf BJ, Reiter J. 1988. Lifetime reproductive success in northern elephant seals. In: Clutton-Brock TH, editor. *Reproductive success*. Chicago (IL): The University of Chicago Press. p. 344–362.
- Leviton DR. 2005. The distribution of male and female reproductive success in a broadcast spawning marine invertebrate. *Integr Comp Biol*. 45:848–855.
- Leviton DR, Petersen C. 1995. Sperm limitation in the sea. *Trends Ecol Evol*. 10:228–231.
- Lewis SM, Cratsley CK, Rooney JA. 2004. Nuptial gifts and sexual selection in *Photinus* fireflies. *Integr Comp Biol*. 44:234–237.
- Longmire JL, Lewis AK, Brown NC, Buckingham JM, Clark LM, Jones MD, Meincke LJ, Meyne J, Ratliff RL, Ray FA, Wagner RP, Moyzis RK. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. *Genomics*. 2:14–24.
- Lorch PD, Bussière LF, Gwynne DT. 2008. Quantifying the potential for sexual dimorphism using upper limits on Bateman gradients. *Behaviour*. 145:1–24.
- Madsen T, Shine R, Loman J, Håkansson T. 1992. Why do female adders copulate so frequently? *Nature*. 355:440–441.
- Madsen T, Ujvari B, Olsson M, Shine R. 2005. Paternal alleles enhance female reproductive success in tropical pythons. *Mol Ecol*. 14:1783–1787.
- Maklakov AA, Lubin Y. 2004. Sexual conflict over mating in a spider: increased fecundity does not compensate for the costs of polyandry. *Evolution*. 58:1135–1140.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol*. 7:639–655.
- Marti CD. 1997. Lifetime reproductive success in barn owls near the limit of the species' range. *Auk*. 114:581–592.
- McGlothlin JW, Parker PG, Nolan V Jr, Ketterson ED. 2005. Correlational selection leads to genetic integration of body size and an attractive plumage trait in dark-eyed juncos. *Evolution*. 59:658–671.
- McLain DK. 1991. Components of variance in male lifetime copulatory and reproductive success in a seed bug. *Behav Ecol Sociobiol*. 29:121–126.
- McLeod L, Marshall DJ. 2009. Do genetic diversity effects drive the benefits associated with multiple mating? A test in a marine invertebrate. *PLoS ONE*. 4:e6347.
- Monaghan P, Metcalfe NB, Houston DC. 1996. Male finches selectively pair with fecund females. *Proc R Soc Biol*. 263:1183–1186.
- Morton ES. 2009. The function of multiple mating by female Prometheus moths, *Callosamia promethea* (Drury) (Lepidoptera: Saturniidae). *Am Midl Nat*. 162:7–18.
- Moya-Laraño J, Fox CW. 2006. Ejaculate size, second male size, and moderate polyandry increase female fecundity in a seed beetle. *Behav Ecol*. 17:940–946.
- Murie JO. 1995. Mating behavior of Columbian ground squirrels. I. Multiple mating by females and multiple paternity. *Can J Zool*. 73:1819–1826.
- Nagy LR, Holmes RT. 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important? *J Avian Biol*. 35:487–491.
- Neff BD, Pitcher TE, Ramnarine IW. 2008. Inter-population variation in multiple paternity and reproductive skew in the guppy. *Mol Ecol*. 17:2975–2984.
- Newcomer SD, Zeh JA, Zeh DW. 1999. Genetic benefits enhance the reproductive success of polyandrous females. *Proc Natl Acad Sci USA*. 96:10236–10241.
- Nolan V Jr, Ketterson ED, Cristol DA, Rogers CM, Clotfelter ED, Titus RC, Schoech SJ, Snajdr E. 2002. Dark-eyed junco (*Junco hyemalis*). In: Poole A, Gill F, editors. *The birds of North America*, No 716. Philadelphia (PA): The Birds of North America, Inc.
- O'Neal DM, Reichard DG, Pavilis K, Ketterson ED. 2008. Experimentally-elevated testosterone, female parental care, and reproductive success in a songbird, the dark-eyed junco (*Junco hyemalis*). *Horm Behav*. 54:571–578.
- Olsson M, Gullberg A, Tegelström H, Madsen T, Shine R. 1994. Can female adders multiply? *Reply*. *Nature*. 369:528.
- Oring LW, Colwell MA, Reed JM. 1991. Lifetime reproductive success in the spotted sandpiper (*Actitis macularis*): sex differences and variance components. *Behav Ecol Sociobiol*. 28:425–432.
- Ortego J, Calabuig G, Cordero PJ, Aparicio JM. 2007. Egg production and individual genetic diversity in lesser kestrels. *Mol Ecol*. 16:2383–2392.
- Osikowski A, Rafinski J. 2001. Multiple insemination increases reproductive success of female Montandon's newt (*Triturus montandoni*, Caudata, Salamandridae). *Behav Ecol Sociobiol*. 49:145–149.
- Pai A, Bennett L, Yan G. 2005. Female multiple mating for fertility assurance in red flour beetles (*Tribolium castaneum*). *Can J Zool*. 83:913–919.
- Panova M, Boström J, Hofving T, Areskoug T, Eriksson A, Mehlig B, Mäkinen T, André C, Johannesson K. 2010. Extreme female promiscuity in a non-social invertebrate species. *PLoS ONE*. 5:e9640.
- Parker PG, Tang-Martínez Z. 2005. Bateman gradients in field and laboratory studies: a cautionary tale. *Integr Comp Biol*. 45:895–902.
- Poirier NE, Whittingham LA, Dunn PO. 2004. Males achieve greater reproductive success through multiple broods than through extra-pair mating in house wrens. *Anim Behav*. 67:1109–1116.
- Prosser MR, Weatherhead PJ, Gibbs HL, Brown GP. 2002. Genetic analysis of the mating system and opportunity for sexual selection in northern water snakes (*Nerodia sipedon*). *Behav Ecol*. 13:800–807.
- Raouf SA, Parker PG, Ketterson ED, Nolan V Jr, Ziegenfus C. 1997. Testosterone affects reproductive success by influencing extra-pair fertilizations in male dark-eyed juncos (Aves: *Junco hyemalis*). *Proc R Soc Biol*. 264:1599–1603.

- Reed WL, Clark ME, Parker PG, Raouf SA, Arguedas N, Monk DS, Snajdr E, Nolan V Jr, Ketterson ED. 2006. Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. *Am Nat.* 167:667–683.
- Reynolds JD. 1996. Animal breeding systems. *Trends Ecol Evol.* 11:68–72.
- Ribble DO. 1992. Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. *J Anim Ecol.* 61:457–468.
- Ridley M. 1988. Mating frequency and fecundity in insects. *Biol Rev Camb Philos Soc.* 63:509–549.
- Ronkainen K, Kaitala A, Kivelä SM. 2010. Polyandry, multiple mating, and female fitness in a water strider *Aquarius paludum*. *Behav Ecol Sociobiol.* 64:657–664.
- Rosvall KA. 2011. Intrasexual competition among females: evidence for sexual selection? *Behav Ecol.* 22:1131–1140.
- Sargent RC, Gross MR, Van Den Berghe EP. 1986. Male mate choice in fishes. *Anim Behav.* 34:545–550.
- Schulte-Hostedde AI, Millar JS, Gibbs HL. 2004. Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. *Behav Ecol.* 15:351–356.
- Schwartz SK, Peterson MA. 2006. Strong material benefits and no longevity costs of multiple mating in an extremely polyandrous leaf beetle, *Chrysochus cobaltinus* (Coleoptera: Chrysomelidae). *Behav Ecol.* 17:1004–1010.
- Scott DK. 1988. Reproductive success in Bewick's swans. In: Clutton-Brock TH, editor. *Reproductive success*. Chicago (IL): The University of Chicago Press. p. 220–236.
- Serbezov D, Bernatchez L, Olsen EM, Vøllestad LA. 2010. Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. *Mol Ecol.* 19:3193–3205.
- Sheldon BC. 1994. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proc R Soc Biol.* 257:25–30.
- Sheridan M, Tamarin RH. 1988. Space use, longevity, and reproductive success in meadow voles. *Behav Ecol Sociobiol.* 22:85–90.
- Shine R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution.* 46:828–833.
- Shuster SM, Wade MJ. 2003. *Mating systems and strategies*. Princeton (NJ): Princeton University Press.
- Shuster SM. 2009. Sexual selection and mating systems. *P Natl Acad Sci USA.* 106:10009–10016.
- Smith JNM. 1988. Determinants of lifetime reproductive success in the song sparrow. In: Clutton-Brock TH, editor. *Reproductive success*. Chicago (IL): The University of Chicago Press. p. 154–172.
- Snyder BF, Gowaty PA. 2007. A reappraisal of Bateman's classic study of intrasexual selection. *Evolution.* 61:2457–2468.
- Stacey PB. 1982. Female promiscuity and male reproductive success in social birds and mammals. *Am Nat.* 120:51–64.
- Tang-Martínez Z. 2010. Bateman's principles: original experiment and modern data for and against. In: Breed MD, Moore J, editors. *Encyclopedia of animal behavior*. Oxford: Academic Press. p. 166–176.
- Taylor ML, Wigmore C, Hodgson DJ, Wedell N, Hosken DJ. 2008. Multiple mating increases female fitness in *Drosophila simulans*. *Anim Behav.* 76:963–970.
- Thomas CS, Coulson JC. 1998. Reproductive success of kittiwake gulls, *Rissa tridactyla*. In: Clutton-Brock TH, editor. *Reproductive success*. Chicago (IL): The University of Chicago Press. p. 251–262.
- Topping MG, Millar JS. 1998. Mating patterns and reproductive success in the bushy-tailed woodrat (*Neotoma cinerea*) as revealed by DNA fingerprinting. *Behav Ecol Sociobiol.* 43:115–124.
- Trengena T, Wedell N. 1998. Benefits of multiple mates in the cricket *Gryllus bimaculatus*. *Evolution.* 52:1726–1730.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. *Sexual selection and the descent of man, 1871–1971*. Chicago (IL): Aldine Publishing Company. p. 136–179.
- Uller T, Olsson M. 2008. Multiple paternity in reptiles: patterns and processes. *Mol Ecol.* 17:2566–2580.
- Vitt LJ, Congdon JD. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am Nat.* 112:595–608.
- Wade MJ, Arnold SJ. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. *Anim Behav.* 28:446–461.
- Weatherhead PJ, Boag PT. 1997. Genetic estimates of annual and lifetime reproductive success in male red-winged blackbirds. *Ecol.* 78:884–896.
- Webster MS, Chuang-Dobbs HC, Holmes RT. 2001. Microsatellite identification of extrapair sires in a socially monogamous warbler. *Behav Ecol.* 12:439–446.
- Webster MS, Pruett-Jones S, Westneat DF, Arnold SJ. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution.* 49:1147–1157.
- Webster MS, Tarvin KA, Tuttle EM, Pruett-Jones S. 2007. Promiscuity drives sexual selection in a socially monogamous bird. *Evolution.* 61:2205–2211.
- Westneat DF, Sherman PW, Morton ML. 1990. The ecology and evolution of extra-pair copulations in birds. In: Power DM, editor. *Current ornithology*. New York: Plenum Press. p. 331–369.
- Whittingham LA, Dunn PO. 2005. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. *Behav Ecol.* 16:138–144.
- Wiebe KL, Kempnaers B. 2009. The social and genetic mating system in flickers linked to partially reversed sex roles. *Behav Ecol.* 20:453–458.
- Williams G. 1975. *Sex and evolution*. Princeton (NJ): Princeton University Press.
- Williams RN, DeWoody JA. 2009. Reproductive success and sexual selection in wild eastern tiger salamanders (*Ambystoma t. tigrinum*). *Evol Biol.* 36:201–213.
- Woollfenden BE, Gibbs HL, Sealy SG. 2002. High opportunity for sexual selection in both sexes of an obligate brood parasitic bird, the brown-headed cowbird (*Molothrus ater*). *Behav Ecol Sociobiol.* 52:417–425.
- Worden BD, Parker PG. 2001. Polyandry in grain beetles, *Tenebrio molitor*, leads to greater reproductive success: material or genetic benefits? *Behav Ecol.* 12:761–767.
- Yue GH, Li JL, Wang CM, Xia JH, Wang GL, Feng JB. 2010. High prevalence of multiple paternity in the invasive crayfish species, *Procambarus clarkii*. *Int J Biol Sci.* 6:107–115.