Synthesis

Bateman Gradients in Hermaphrodites: An Extended Approach to Quantify Sexual Selection

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ABSTRACT: Sexual selection is often quantified using Bateman gradients, which represent sex-specific regression slopes of reproductive success on mating success and thus describe the expected fitness returns from mating more often. Although the analytical framework for Bateman gradients aimed at covering all sexual systems, empirical studies are biased toward separate-sex organisms, probably because important characteristics of other systems remain incompletely treated. Our synthesis complements the existing Bateman gradient approach with three essential reproductive features of simultaneous hermaphrodites. First, mating in one sex may affect fitness via the opposite sex, for example, through energetic trade-offs. We integrate cross-sex selection effects and show how they help characterizing sexually mutualistic versus antagonistic selection. Second, male and female mating successes may be correlated, complicating the interpretation of Bateman gradients. We show how to quantify the impact of this correlation on sexual selection and propose a principal component analysis on male and female mating success to facilitate interpretation. Third, self-fertilization is accounted for by adding selfed progeny as a separate category of reproductive success to analyses of Bateman gradients. Finally, using a worked example from the snail *Biomphalaria glabrata*, we illustrate how the extended analytical framework can enhance our understanding of sexual selection in hermaphroditic animals and plants.

Keywords: mating success, reciprocal sperm exchange, reproductive success, selfing, sex allocation, sexual antagonism.

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Introduction

Quantitative analyses of sexual selection have been strongly influenced by Bateman's (1948) seminal work on *Drosophila melanogaster*. He found that male fitness increases more strongly with mating success than female fitness and triggered the development of quantitative measures of sexual selection within formal selection theory (Crow 1958; Wade 1979; Wade and Arnold 1980; Lande and Arnold 1983; Arnold 1994; Arnold and Duvall 1994; Andersson and Iwasa 1996). Our synthesis is driven by the observation that empirical evaluations of these measures are strikingly biased toward organisms with separate sexes (called gonochorists hereafter; recent overviews in Jones et al. 2005; Snyder and Gowaty 2007; Brown et al. 2009; Hunt et al. 2009) but remain strongly underrepresented in simultaneously hermaphroditic animals (called hermaphrodites hereafter). We begin by briefly introducing the Bateman gradient approach and its existing framework for hermaphrodites. Next, we propose three conceptual extensions that appear essential to more comprehensively capture sexual selection in hermaphrodites. We finally apply this extended analytical framework to empirical data and outline how it can inform a long-standing debate about sex role preferences in hermaphrodites.

Bateman Gradients in Gonochorists

Three different measures are central to the Bateman gradient approach (details in Arnold 1994; Jones 2009; for

Table 1: Abbreviations and definitions used throughout the text

Abbreviation	Definition
β	Slope of a linear regression, used to define the (sexual) selection gradients
β_{ss}	General notation for a sexual selection gradient ($=$ Bateman gradient)
β_m, β_f	Sexual selection gradients for males and females in gonochorists
β_{mm}, β_{ff}	Sexual selection gradients for male and female function in hermaphrodites (i.e., the change in RS_m with MS_m and in RS_f with MS_f, respectively)
β_{mf}, β_{fm}	Sexual selection gradients in hermaphrodites that show cross-sex effects (i.e., the change in RS_m with MS_f and in RS_f with MS_m, respectively)
I	Standardized variance in relative reproductive success; "opportunity for selection"
I_m, I_f	Respective I values for males and females
I_s	Standardized variance in relative mating success; "opportunity for sexual selection"
I_{sm}, I_{sf}	Respective I_s values for males and females
MS	Mating success
MS_m, MS_f	Male and female MS
RS	Reproductive success
RS_m, RS_f	Male and female RS

abbreviations and definitions, see table 1): (1) variance in relative reproductive success standardized by its squared mean (I), (2) variance in relative mating success standardized by its squared mean (I_s), and (3) the slope of a linear regression of reproductive success on mating success (β_{ss}), the so-called Bateman gradient (fig. 1).

The first two measures reflect opportunities or upper limits rather than actual (sexual) selection. I and I_s can vary due to processes other than (sexual) selection, and the resulting limitations for their informative value in studies of sexual selection have been discussed extensively elsewhere (Wade 1979; Clutton-Brock 1983; Sutherland 1985; Koenig and Albano 1986; Downhower et al. 1987; Grafen 1987; Hubbell and Johnson 1987; Kokko et al. 1999; Fairbairn and Wilby 2001; Shuster and Wade 2003; Jones 2009; Croshaw 2010; Klug et al. 2010; Wade and Shuster 2010). We therefore follow others (Arnold 1994; Arnold and Duvall 1994) in focusing on Bateman gradients (also called sexual selection gradients) as more direct measures of sexual selection.

In gonochorists, Bateman gradients represent the slope of a linear regression of sex-specific reproductive success (RS) on sex-specific mating success (MS):

$$RS_m = \beta_m MS_m + const + \varepsilon, \quad (1a)$$

$$RS_f = \beta_f MS_f + const + \varepsilon, \quad (1b)$$

where const defines the intercept. The regression slopes β_m and β_f (for males and females, respectively) reveal how variation in MS_m or MS_f contributes to differential RS_m or RS_f (fig. 1). Put differently, Bateman gradients capture the average reward (in terms of additional progeny) of being more successful in mate searching, courtship, precopulatory competition, mating, or sperm competition (depend-

ing on how mating success is measured, which we discuss below). ε represents the regression residuals, capturing variation in fitness due to sources other than mating success.

Bateman gradients are often seen to characterize the overall intensity of sexual selection, where a sex difference
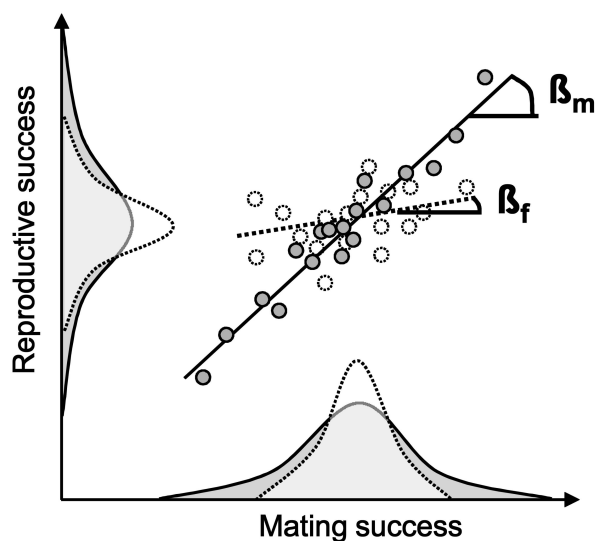

Figure 1: Arbitrary data representing individual measurements of reproductive success (RS) and mating success (MS) that are combined into male (m) and female (f) Bateman gradients (β). The distributions of RS and MS often tend to be broader for males (*gray with solid lines*) than for females (*white with dotted lines*), which manifests in a sex difference in the corresponding standardized variances I and I_s. The Bateman gradient—that is, the regression slope of RS on MS—indicates which sex obtains (on average) higher fitness returns from mating more often. β can become negative if mating depresses fitness.

in sexual selection is indicated by significantly different slopes. This interpretation is based on a path analytic view of selection (Arnold 1994; Arnold and Duvall 1994), which decomposes total selection into sexual and natural selection (such as viability or fecundity selection). Only those paths that connect to fitness via mating success are considered sexually selected. Even though this stringent view is challenged by recent pleas for broader definitions of sexual selection (reviewed in Jennions and Kokko 2010), we maintain it for the purpose of this synthesis.

Sex-specific Bateman gradients elegantly capture all the possible combinations of sexual selection on the two sexes (Arnold 1994; Jones 2009). The sex with the steeper Bateman gradient experiences stronger selection to increase MS, whereas the other sex benefits less from additional matings or may even suffer if RS declines with MS. Note that Bateman gradients inform us exclusively about the operation of sexual selection (Arnold and Duvall 1994) in an "all else being equal" fashion. They do not capture how the effort for obtaining additional matings trades off with other life-history components (Jennions and Kokko 2010), nor do they show responses to selection (Wade and Arnold 1980). Neither aspect is within the scope of this synthesis.

Bateman Gradients in Hermaphrodites

While analyses of sexual selection have historically focused on gonochorists, there is growing awareness for an important role of sexual selection in simultaneous hermaphrodites (Charnov 1979; Queller 1983; Morgan 1994; Willson 1994; Baur 1998; Michiels 1998; Delph and Ashman 2006; Leonard 2006; Bedhomme et al. 2009). With both sexes (and their associated traits) united in a single body, hermaphrodites offer exciting perspectives to study how sexual selection affects traits such as resource allocation to male and female function (sex allocation: Charnov 1982; Schärer 2009; Schärer and Janicke 2009), the expression of copulatory roles (Charnov 1979; Anthes et al. 2006), or the rate of self-fertilization (Goodwillie et al. 2005; Jarne and Auld 2006). Moreover, while earlier theoretical work suggested that runaway sexual selection may be restricted in hermaphrodites because both male and female fitness are depressed by the cost of male displays (Morgan 1994), recent theoretical models (B. Kuijper, L. Schärer, and I. Pen, unpublished manuscript) and evidence for correlated evolution of exaggerated male and female traits (Koene and Schulenburg 2005; Beese et al. 2006; Anthes et al. 2008) point to the opposite. Placing all these mechanisms in a quantitative context opens novel perspectives for our understanding of sexual selection, both in hermaphrodites and in general.

The assessment of Bateman gradients in hermaphrodites has some tradition in plants, revealing some cases where floral morphology is subject to sexually antagonistic selection (reviewed in Ashman and Morgan 2004; Delph and Ashman 2006). Only a single study to date has explicitly calculated the variance measures underlying the calculation of Bateman gradients for a hermaphroditic animal (Lorenzi and Sella 2008), finding larger variation in female than in male reproductive success under promiscuity.

The paucity of attempts to quantify sexual selection in hermaphroditic animals is surprising, given that the initial formulation of Bateman gradients explicitly envisioned their universal application (Arnold 1994; Arnold and Duvall 1994). One drawback of these formulations is that some facets that are central to hermaphrodite reproduction were not explicitly treated. In this synthesis, we thus complement and extend Arnold's (1994) framework with three central aspects that will enable a more comprehensive treatment of sexual selection in hermaphrodites. In "Cross-Sex Effects in Hermaphrodite Bateman Gradients," we discuss the relevance and analytical treatment of cross-sex interactions between male and female sex functions. In "Mating Success, Mating Modes, and Bateman Gradients," we outline how reciprocal mating can lead to collinearity between predictor variables and suggest an analysis based on principal components to aid the interpretation of the resultant Bateman gradients. In "Selfing and the Calculation of Bateman Gradients," we discuss the role of self-fertilization in sexual selection and incorporate selfed offspring into the calculation of Bateman gradients.

Cross-Sex Effects in Hermaphrodite Bateman Gradients

Generalizing Bateman gradients to hermaphrodites requires recognizing that each individual yields two measures of MS (MS_m and MS_f for male and female function, respectively) and two measures of RS (RS_m and RS_f; table 1). Male and female measurements are thus inherently nonindependent. As a solution, Arnold (1994) suggested performing multiple regression analyses, where MS and RS through the alternative sex functions are added as covariates (with coefficients a and b, respectively) to equations (1) and thus held constant; that is,

$$RS_m = \beta_m MS_m + a_m MS_f + b_m RS_f + const + \varepsilon_m, \quad (2a)$$

$$RS_f = \beta_f MS_f + a_f MS_m + b_f RS_m + const + \varepsilon_f. \quad (2b)$$

This approach successfully treats nonindependence of male and female measurements but suffers from two weaknesses. First, adding RS in the other sex function to the model merges predictor and response variables. Therefore, we propose a covariance-based approach that solves this issue. Second, Arnold (1994) added MS in the other sex function only as a statistical control, not to explicitly study

the interaction between male and female components of fitness. We prefer to consider these cross-sex effects as central biologically relevant parameters, rather than as a statistical nuisance, when studying sexual selection in hermaphrodites. In doing so, Bateman gradients inform us not only about how male and female reproductive success vary with their corresponding mating success but also about whether and how these traits interfere with, or reinforce, each other (fig. 2).

Starting from equations (2a) and (2b), we remove RS as a predictor variable and replace the covariate coefficients a and b by terms that explicitly reflect the underlying cross-sex effects (note that the latter does not modify the analytical procedure or outcome per se but rather highlights our change in perspective to consider cross-sex terms a central informative result):

$$RS_m = \beta_{mm}MS_m + \beta_{mf}MS_f + \text{const} + \varepsilon_m, \quad (3a)$$

$$RS_f = \beta_{ff}MS_f + \beta_{fm}MS_m + \text{const} + \varepsilon_f. \quad (3b)$$

The within-sex gradients (β_{mm} and β_{ff}) in these equations are equivalent to those introduced for gonochorists (eqq. [1]). For example, β_{ff} (in eq. [3b]) is the partial regression of RS_f on MS_f while holding MS_m constant. The

hermaphrodite-specific cross-sex coefficient β_{fm} captures how RS_f varies with MS_m. For example, if male copulations are energetically costly and reduce egg output, MS_m diminishes RS_f and β_{fm} becomes negative. Setting the cross-sex terms to 0 simplifies equations (3) to the special case applicable to gonochorists (eqq. [1]). Several novel research questions arise in relation to the cross-sex terms: How important are cross-sex interaction terms quantitatively compared with within-sex terms? What is the prevalence of sexually mutualistic selection (within-sex and cross-sex terms of equal sign) versus sexually antagonistic selection (opposite signs; see example in fig. 3)? Do the cross-sex terms reinforce or decrease the difference in sexual selection between the sexes? These fundamental questions have not yet been addressed empirically but are crucial to understanding the role of cross-sex effects for sexual selection in hermaphrodites.

Equations (3a) and (3b) remain unsatisfying in that we relate the two response variables (RS_m and RS_f) independently to the same set of predictor variables (MS_m and MS_f). This is not a statistical problem per se, because the regression for each trait remains unbiased. From a biological perspective, however, we explicitly seek to understand sexual selection under the constraints imposed on
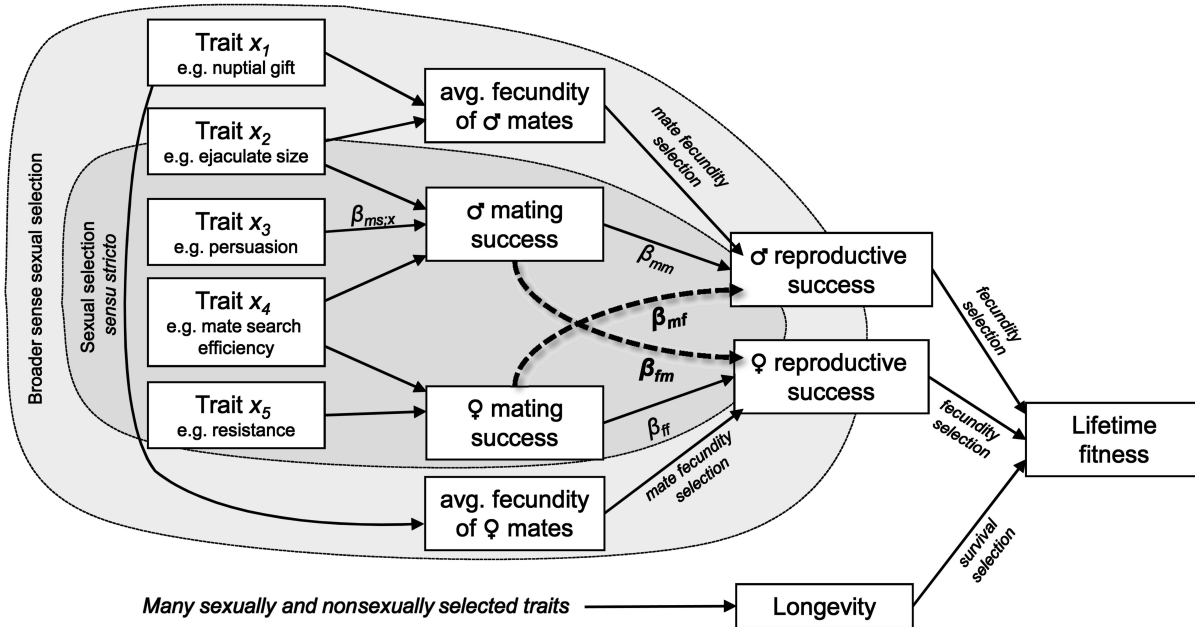

Figure 2: Path diagram of selection illustrating how cross-sex terms (*dashed arrows*) complement the analysis of Bateman gradients in hermaphrodites (modified from Arnold 1994; Arnold and Duvall 1994; abbreviations in table 1). Following these authors, we base our framework on a rather narrow definition of sexual selection (*dark gray*), noting that many researchers favor broader views (*light gray*). The diagram also illustrates how Bateman gradients complement analyses of sexual selection on specific traits x. Total sexual selection on x_i ($\beta_{ss;x}$) is the Bateman gradient times the regression slope that relates trait variation to mating success ($\beta_{ms;x}$). Formal details of such analyses have been developed elsewhere (Lande and Arnold 1983; Morgan 1992) and are not further considered here.
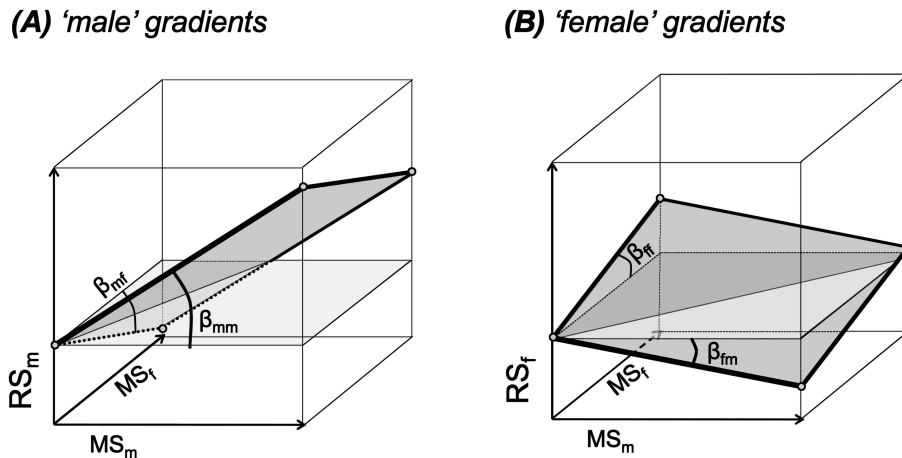
(A) 'male' gradients

(B) 'female' gradients

Figure 3: Arbitrary example illustrating the interactive nature of Bateman gradients in hermaphrodites. Male reproductive success (RS_m; *A*) and female reproductive success (RS_f; *B*) are represented as partial regression planes on male and female mating success (MS_m and MS_f). The graphs exemplify positive Bateman gradients for each sex (β_{mm} and $\beta_{ff} > 0$) that are reduced by some costs of matings via the other sex function (β_{mf} and $\beta_{fm} < 0$). The overall Bateman gradient is steeper for the male function ($\beta_{mm} > \beta_{ff}$), but male RS is depressed more strongly through female matings than vice versa ($\beta_{mf} < \beta_{fm}$).

RS_m and RS_f by sex allocation trade-offs or budget effects (Schärer 2009). In addition to the separate analyses for each sex, we thus need to understand how the within- and cross-sex effects contribute to covariance between RS_m and RS_f. Hence, instead of adding opposite-sex fitness as covariates as in equations (2a) and (2b), we propose to expand the covariances between the expressions of RS_m and RS_f in equations (3a) and (3b) to obtain

$$\text{Cov}(RS_m, RS_f) =$$
$$\text{Cov}(\beta_{mm}MS_m + \beta_{mf}MS_f + \varepsilon_m, \beta_{fm}MS_m + \beta_{ff}MS_f + \varepsilon_f) \quad (4)$$
$$= \text{Cov}(\beta_{mm}MS_m + \beta_{mf}MS_f, \beta_{fm}MS_m + \beta_{ff}MS_f) + \text{Cov}(\varepsilon_m, \varepsilon_f).$$

Note that the covariances between residuals (ε) and predictors (MS) have been omitted because they are 0 by definition. We now expand the left-hand covariance term to obtain

$$\text{Cov}(RS_m, RS_f) =$$
$$\beta_{mm}\beta_{fm}\text{Var}(MS_m) + \beta_{mf}\beta_{ff}\text{Var}(MS_f) \quad (5)$$
$$+ (\beta_{mm}\beta_{ff} + \beta_{mf}\beta_{fm})\text{Cov}(MS_m, MS_f) + \text{Cov}(\varepsilon_f, \varepsilon_m).$$

These terms identify the types of sexual or nonsexual selection that contribute to covariation between RS_m and RS_f. Specifically, the first two terms represent the combined effect of MS in one sex role on RS via both sexes. Each term becomes negative when the direct and cross-sex effects have opposite signs (fig. 3), for example, when mating

in the male role reduces egg output, yielding $\beta_{fm} < 0$. Negative terms thus identify sexually antagonistic selection. The terms are positive when direct and cross-sex gradients have equal signs, representing sexually mutualistic selection. The third term is the component of covariance between RS_m and RS_f due to covariance between MS_m and MS_f. It shows whether (positive or negative) covariance in male and female mating success has a shared effect on covariance in fitness. The last term describes the covariance between the unexplained parts of RS_m and RS_f, that is, variation that is not linked to MS. This residual variation is unlinked to sexual selection sensu stricto (fig. 2) but may be under other forms of selection. For example, this term may capture the effects of individual variation in survival, which increases positive covariance between male and female reproductive success. Likewise, effects of postcopulatory selection that are not captured by the underlying definition of mating success ("How Definitions of Mating Success Affect Bateman Gradients") will enter this term. The decomposition can further reveal whether the absence of covariance between RS_m and RS_f results from a balance between sexual and nonsexual selection. The worked example in "Bateman Gradients in Hermaphrodites: A Worked Example" further exemplifies the interpretation of this decomposition of covariances.

Mating Success, Mating Modes, and Bateman Gradients

In "Cross-Sex Effects in Hermaphrodite Bateman Gradients," we outlined how cross-sex selection and noninde-

pendence of male and female RS can be incorporated when analyzing Bateman gradients in hermaphrodites. Here we treat another important issue mentioned by Arnold (1994), namely, that reciprocal gamete transfer between mates (meaning that both partners assume both sexual roles) increases collinearity between our predictor variables, male and female MS. Being widespread in hermaphrodites (Charnov 1979; Michiels 1998), reciprocal mating restricts the degree to which MS_m and MS_f can vary independently. To assess possible effects of covariation in male and female MS on Bateman gradients, we first outline alternative definitions of mating success, then discuss how these distinctions may affect the degree to which male and female MS are collinear, and finally propose a modified analytical approach for data sets with strong predictor collinearity.

How Definitions of Mating Success Affect Bateman Gradients

Even within our rather narrow definition of sexual selection (fig. 2), the biological interpretation of Bateman gradients varies depending on how exactly we define and quantify mating success. We discuss the consequences of using three different measures of MS that follow the tradition of basing Bateman gradients on counts of the number of (actual or genetic) mates (Bateman 1948; Arnold and Duvall 1994; terminology according to Shuster and Wade 2003). These three measures of MS encompass the result of sexual selection up to different selection episodes between mate searching and fertilization (table 2), accumulating the effects of sexually selected traits up to this particular episode.

Mate-number promiscuity (table 2, stage a) counts the number of different individuals with which a focal individual has copulated and thus captures the maximum number of partners with which the focal could share offspring. Mating-number promiscuity (table 2, stage b) refers to the total number of copulations of a focal individual, meaning that consecutive matings with the same partner are counted multiply. To some extent, this may reflect differential sperm amounts donated and received in multiple inseminations, even though decreasing ejaculate sizes and diminishing returns for multiple inseminations are not taken into account. Genetic mate-number promiscuity (table 2, stage c) counts the number of individuals that actually bear the progeny of a focal male or that sire the offspring of a focal female. Hence, only copulations that lead to successful fertilization are considered.

The first two measures directly relate to copulation as a central target of sexual selection (e.g., Bjork and Pitnick 2006) and are close to Darwin's original definition (Darwin 1871; see also Wade and Shuster 2005). On the downside, the derived Bateman gradients fail to capture variation in RS that is caused by sexually selected traits with postcopulatory effects, such as ejaculate size, seminal fluid components, sperm motility, or cryptic female choice (Parker 1970; Thornhill 1983; Birkhead and Pizzari 2002). Genetic mate-number promiscuity is more directly related to fertilization as a final step in sexual selection than the simple counts of mating partners (Arnold and Wade 1984) and thus also captures those postcopulatory processes that determine whether a given sire-dam combination achieves any successful fertilization. Given its original usage by Bateman (1948) and implementation into the analytical framework by Arnold (1994), genetic mate-number promiscuity is the most frequently used measure in Bateman gradient analyses (recently, e.g., Jones et al. 2004, 2005;

Table 2: Effects of alternative measures of mating success on the meaning of derived Bateman gradients

Multiplicative components of fitness (W)	Stage	Potential sexually selected traits
Precopulatory:		
Encountered mates per day	a	Locating and reaching conspecifics (e.g., mobility, activity, pheromones)
Copulations per encountered mate	b	Achieving or avoiding copulations (e.g., choice, combat, display, coercion, genital morphology)
Postcopulatory:		
Fertilizations per copulation	c	Successful fertilization (e.g., sperm quality and quantity, seminal fluids, cryptic choice, guarding)
Postzygotic:		
Hatchlings per zygote		Genetic compatibility, selective abortion, egg provisioning, etc.
Juveniles per hatchling		Monopolization of maternal provisioning, maternal and paternal (genetic) effects
Adults per juvenile		Maternal and paternal (genetic) effects

Note: Mate-number promiscuity (stage a), mating-number promiscuity (stage b), and genetic mate-number promiscuity (stage c) encompass sexual selection up to different consecutive selection episodes (exemplified as multiplicative fitness components in the left column) and thus capture only those sexually selected traits (right column) that acted up to this episode. Depending on the chosen measure, Bateman gradients thus reflect the expected fitness returns from seeking and securing novel mates (a), copulating more often with familiar or novel partners (b), or successfully fertilizing more different partners (c).
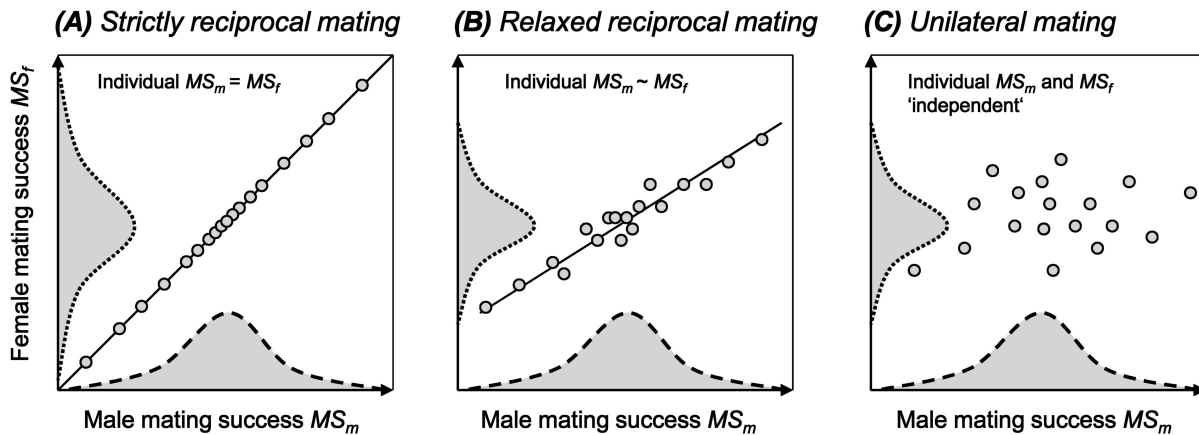
Figure 4: Arbitrary examples illustrating how hermaphrodite mating modes can generate collinearity between male and female mating success (MS). When MS is defined at the level of copulations, individual MS_m and MS_f (and the variances of their underlying data distributions) will be identical in systems with strictly reciprocal mating (*A*). The link between MS_m and MS_f (and their population variances) becomes weaker when reciprocal mating is not obligatory (*B*). In systems with unilateral matings (*C*), MS_m and MS_f are no longer mechanically connected. Depending on circumstances, they may thus show positive, neutral (as plotted here), or negative covariance.

Mills et al. 2007; Levitan 2008). It is also convenient because it spares the effort of observing mating behavior, since both mating success and reproductive success are inferred from genetic markers. Nevertheless, we consider the usage of this measure problematic, because it merges pre- and postcopulatory components of sexual selection and thus partially confounds predictor (MS) and response (RS) variables. Each mating scored for genetic MS is automatically associated with at least one additional offspring, inherently biasing the regression of RS on MS. Moreover, since we are looking at successful fertilizations rather than copulations, a sampling artifact gives more weight to more fecund females (Ketterson et al. 1997), because the probability that a given female bears at least one progeny of a given male increases with female fecundity. Hence, even if all females in a population mated exactly *n* times, the likelihood of detecting multiple sires would increase with brood size, generating a positive Bateman gradient that does not reflect any sexual selection.

A reasonable solution to the outlined problems may be to use multiple measures of MS. This permits one to partition the relationship between MS and RS, as well as the (potentially opposing) effects of focal traits, between successive pre- and postcopulatory episodes of sexual selection and thus provides a more fine-scale understanding of sexual selection.

Mating Success and Mating Modes in Hermaphrodites

Why does the underlying definition of mating success determine the degree to which our two predictor variables,

MS_m and MS_f, become collinear? The likelihood of collinearity increases the more closely the definition of mating success relates to actual copulations. This effect is particularly strong in hermaphrodites that engage in reciprocal (both partners assume both mating roles) rather than unilateral (one partner acting in the male mating role, the other in the female role) copulations. In what follows, we focus on a copulation-related definition of MS, but note that effects of mating mode may also carry over to genetic definitions of MS.

In systems with strictly reciprocal mating, individuals always copulate in both roles, leading to identical values of MS_m and MS_f within individuals and thus to identical population variances in MS_m and MS_f (fig. 4*A*). This occurs where conditionally bidirectional behavior (Anthes et al. 2005) or morphological restrictions on copulatory position and genital interlock (e.g., some nudibranchs, earthworms, flatworms) enforce reciprocal copulation. Independent optimization of MS_f and MS_m is then restricted, and selection can target only overall individual MS. Hence, in equations (3a) and (3b), RS_m and RS_f are now both regressed on the same predictor variable ($MS_m = MS_f$).

An intermediate situation (relaxed reciprocal mating) arises where bidirectional gamete exchange is not morphologically or behaviorally enforced but where animals vary in their overall propensity to copulate or tend to alternate mating roles between successive copulations (e.g., Sella and Lorenzi 2000; Anthes and Michiels 2007; Facon et al. 2008). MS_m and MS_f will then generally be positively correlated (fig. 4*B*), but their population variances can diverge when some individuals bias their mating strategy to either male

or female sex function. The other extreme is reached with a strictly unilateral mating mode. As in gonochorists, MS_m and MS_f can now vary independently and remain bound only by their population means (fig. 4C). Individuals may even specialize in the male or female mating role in response to, for example, body size (Ohbayashi-Hodoki et al. 2004) or age (Hermann et al. 2009), possibly leading to negative correlations between MS_m and MS_f.

Hermaphrodite mating modes can thus strongly affect the degree to which MS_m and MS_f are collinear, implying that mating modes may affect the action and efficiency of sexual selection. For example, one may expect precopulatory sexual selection to be particularly strong in hermaphrodites that can independently optimize MS_m and MS_f, whereas the focus may shift to postcopulatory selection in systems with strictly reciprocal mating (Charnov 1979).

Collinear Mating Success and Principal Components

The analytical problem with collinearity between MS_m and MS_f when calculating Bateman gradients is that it makes the multiple regression slope estimates statistically fragile (Mitchell-Olds and Shaw 1987), because an overestimation of one slope necessarily leads to an underestimation of the other. In data sets with collinear predictors, MS_m and MS_f should thus be replaced with their (per definition uncorrelated) principal components. The formal details of the underlying principal component analyses (PCA), the mathematical link between the PCA-based regression coefficients and those given in equations (3a) and (3b), and the consequences for the decomposition of covariance components (eq. [5]) are given in appendix A in the online edition of the *American Naturalist*.

An important benefit of a PCA approach is that it aids the biological interpretation of Bateman gradients when MS_m and MS_f are collinear in that it changes the biological meaning of the resulting regression coefficients. The PCA can be performed either on raw mating success values (i.e., on the variance-covariance matrix of MS_m and MS_f) or on standardized values (i.e., on the corresponding correlation matrix). In both cases, one PC axis (PC_1) is proportional to the sum of (raw or standardized) MS_m and MS_f (i.e., the position along the regression lines in fig. 4) and thus captures overall mating activity (see app. A). Hence, coefficients for the regression of RS on PC_1 ($\beta_{m_{PC_1}}$ and $\beta_{f_{PC_1}}$ for RS_m and RS_f, respectively) show how RS varies with overall mating activity. This relationship cannot be attributed to either sex. Hence, if collinearity is strong (i.e., PC_1 represents the major axis), the corresponding data set may not allow disentangling sexual selection via male and female function separately.

The other PC axis (PC_2) captures the difference between MS_m and MS_f within individuals (i.e., the orthogonal residuals in fig. 4) and thus represents the sexual bias in mating activity (see app. A). PC_2 becomes the major axis in systems where individuals differ little in overall mating activity but vary in how strongly they specialize on copulations in the male or female sexual role. Coefficients for the regression of RS on PC_2 ($\beta_{m_{PC_2}}$ and $\beta_{f_{PC_2}}$) indicate how substituting a mating in one sex function by a mating in the other sex function affects fitness. This information is the prime added value of the PCA approach relative to analyses of Bateman gradients based on the original values of MS_m and MS_f. We may intuitively expect $\beta_{m_{PC_2}}$ and $\beta_{f_{PC_2}}$ to be opposite in sign, meaning that a female bias in mating activity tends to increase female fitness but to depress male fitness (and vice versa). Our worked example in "Bateman Gradients in Hermaphrodites: A Worked Example," with indications for the opposite pattern, highlights the need for broad empirical evaluation.

The value of the PCA approach will depend on characteristics of the specific data set and the research questions. Coefficients based on the original MS measurements show the gain in fitness from engaging in one additional mating through one sex function while holding mating success in the other sex function constant. When MS_m and MS_f are strongly correlated, individuals rarely have such an option. The PCA-based regression coefficients capture such situations more intuitively, showing the gain in fitness from substituting a mating in one sex function by a mating in the other sex function. This also transfers into the modified covariance decomposition (eq. [A5] in app. A), which then clearly highlights how overall variation in mating activity on the one hand and specialization into the male or female sex on the other hand contribute to the covariance between male and female RS.

Selfing and the Calculation of Bateman Gradients

A third phenomenon to consider when calculating Bateman gradients in simultaneous hermaphrodites is self-fertilization (Jarne and Charlesworth 1993). Selfing is widespread across the animal kingdom, and selfing rates cover the full range between obligate outcrossing and obligate selfing (Tsitrone et al. 2003; Jarne and Auld 2006). Self-fertilization has strong implications for sexual selection, which is typically seen to act between (not within) individuals. Analyses of sexual selection in hermaphrodites therefore require a framework that explicitly incorporates selfing.

Arnold (1994) proposed to include the self and selfed offspring into the tabulations of MS and RS, respectively. This approach is unsatisfactory, however, because the treatment of self-gametes in the context of sexual selection is all but straightforward. The mechanisms for selfing and

successful cross-fertilization are not necessarily equivalent and may interfere with each other. Moreover, selfed offspring may often be of inferior quality compared with outcrossed offspring because of inbreeding depression (Charlesworth and Charlesworth 1987; Jarne et al. 1991). We therefore propose to, where feasible, cleanly separate selfed and outcrossed offspring in quantifications of sexual selection. This is achieved by treating selfed offspring (RS_s) as a distinct third fitness category next to the outcrossed maternal and paternal offspring (RS_f and RS_m). RS_s is then twice the number of selfed offspring to adequately account for the number of gene copies as the fitness currency. Mating success retains its previous meaning and counts the number of nonself mates. We thus maintain the Bateman gradients defined in equations (3a) and (3b) for outcrossed offspring but add a third equation that exclusively includes the offspring sired through selfing:

$$RS_s = \beta_{sm}MS_m + \beta_{sf}MS_f + \text{const} + \varepsilon_s. \quad (3c)$$

The regression coefficients indicate how matings in the male or female role affect the number of selfed offspring (β_{sm} and β_{sf}, respectively). We intuitively expect both terms to be negative: β_{sm} will be negative if male gametes are limiting and thus gametes used for outcrossing subtract from those available for selfing (pollen discounting; Lloyd 1992). β_{sf} will be negative when there is ovule or egg discounting, for example, because females preferentially outcross their eggs as long as allosperm are available (Tsitrone et al. 2003). Real values may vary with selfing rate, the efficiency of self-fertilization, and inbreeding depression, calling for empirical evaluation in systems with differential selfing strategies.

The covariance between selfed offspring and either maternal or paternal outcrossed offspring can be decomposed equivalently to equations (5); for example,

$$\text{Cov}(RS_s, RS_f) =$$
$$\beta_{sm}\beta_{fm}\text{Var}(MS_m) + \beta_{sf}\beta_{ff}\text{Var}(MS_f) \quad (5a)$$
$$+ (\beta_{sm}\beta_{ff} + \beta_{fm}\beta_{sf})\text{Cov}(MS_m, MS_f) + \text{Cov}(\varepsilon_f, \varepsilon_s).$$

The first two terms show how the covariance between selfed and maternal outcrossed offspring is affected by the contributions of MS_m and MS_f, respectively. The third term reflects the effect of the correlation between MS_m and MS_f. The last term captures residual variance. Imagine, for example, a preferential outcrosser without sperm discounting, negligible effects of male matings on female fitness, and compensation for occasional failure to find a mate by self-fertilization. The resulting negative $\text{Cov}(RS_s, RS_f)$ is then primarily captured by $\beta_{sf}\beta_{ff}\text{Var}(MS_f)$, illustrating the

fact that low MS_f reduces the production of outcrossed maternal offspring ($\beta_{ff} > 0$) and triggers selfing ($\beta_{sf} < 0$).

It will be revealing to compare Bateman gradients and the underlying covariance components of nonselfers with selfers that follow alternative strategies. Delayed selfers preferentially outcross and typically self-fertilize only to compensate for a lack of sperm receipt (Tsitrone et al. 2003). This strategy should generate steep negative gradients for selfed offspring (eq. [3c]) because those disproportionally occur in the low-MS categories in both sex functions. In systems with prior selfing (e.g., Tian-Bi et al. 2008), equation (3c) may reveal shallower or even flat Bateman gradients. Here, inbreeding depression must be largely purged, and selfing is maintained even after repeated copulations. In such systems, selfing may thus serve as a strategy in mate choice and sperm competition (Lloyd 1979; Lüscher and Milinski 2003) rather than as a compensatory mechanism, and the value of selfing in this context could be quantified using the extended Bateman gradient approach outlined here. In this context, measuring RS_s at consecutive developmental stages provides quantifications of sexual selection that are more or less affected by inbreeding depression. By comparing Bateman gradients obtained using RS based on fertilized eggs or seeds with those obtained using RS based on later stages (hatchlings, seedlings, or juveniles), one can estimate how inbreeding depression modifies the selection pressures on mating as a male or as a female.

Bateman Gradients in Hermaphrodites: A Worked Example

To exemplify the analysis of hermaphrodite Bateman gradients outlined above, here we present a data set from the freshwater snail *Biomphalaria glabrata*. *Biomphalaria glabrata* is a primarily outcrossing hermaphrodite (Mavarez et al. 2002) that copulates frequently in the field and laboratory (Vernon and Taylor 1996; Rupp and Woolhouse 1999). Copulations are easy to observe and allow distinguishing unilateral male, unilateral female, and reciprocal copulations (Trigwell et al. 1997). Mating is typically unilateral, and mating roles tend to be exchanged after successful mating, conforming to "relaxed reciprocal mating," as discussed above. Snails lay multiple transparent egg masses per week, each containing ~15–30 eggs (Pimentel 1957; Jarne et al. 1993). Because of inbreeding depression, offspring are typically outcrossed when allosperm are available, but snails readily self-fertilize when sexually isolated (Vianey-Liaud 1976; Vianey-Liaud et al. 1989).

Our data contain information on mating and reproductive success for 30 replicate focal snails under a promiscuous mating regime (details on data collection in app. B in the online edition of the *American Naturalist*; fig. 5).
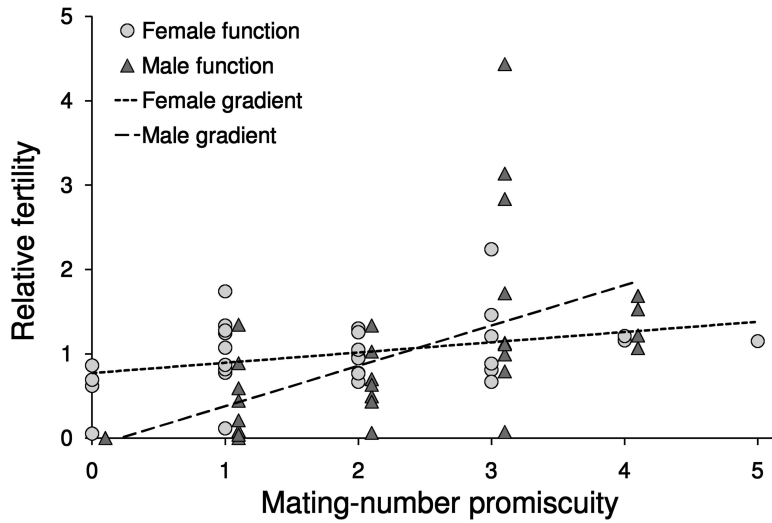
Figure 5: Sample data set and within-sex Bateman gradients for 30 focal *Biomphalaria glabrata* snails (for details, see main text and app. B in the online edition of the *American Naturalist*).

We find that the variance in RS is significantly higher for the male ($I_m = 1.03$) than for the female ($I_f = 0.18$) sexual function (Levene's test: $F_{1,58} = 7.74$, $P = .0073$), indicating that the opportunity for selection on the male function exceeds that on the female function. No such effect is detectable for the opportunity for sexual selection ($I_{sm} = 1.27$, $I_{sf} = 1.64$; $F_{1,58} = 0.11$, $P = .73$; note that this is likely due to restrictions on mating in the underlying experiment; app. B). As outlined above, variance measures alone are difficult to interpret, and we continue by calculating the Bateman gradients. Using the simple within-sex regressions (eqq. [1]), we find that RS_m and RS_f both increase significantly with sex-specific mating success, and this effect is stronger in the male function (table 3; fig. 5). The more comprehensive analysis including cross-sex terms (eqq. [3]) confirms this pattern but further reveals that RS_m and RS_f may also increase with matings in the opposite sex role (β_{mf} and β_{fm} are positive; table 3). (Note that these effects do not reach statistical significance in our preliminary data set, which we here present for illustrative purposes, not for rigorous statistical analysis.) Hence, mating success in *B. glabrata* may be under sexually mutualistic rather than antagonistic selection.

For the subsequent decomposition of the observed positive covariance between RS_m and RS_f (table 4), we follow the steps outlined in "Cross-Sex Effects in Hermaphrodite Bateman Gradients." We find that the values for the effect of MS on RS via both sexes are positive (table 4). Hence, mating more frequently in either sex function increases the covariance between male and female fitness, which supports the notion that selection on mating success is

sexually mutualistic. In addition, MS_m seems to capture more of the total covariance in fitness than MS_f, indicating that RS_m and RS_f correlate positively mostly because mating in the male role enhances both fitness components. The next term shows whether some of the covariance between RS_m and RS_f is due to covariance between MS_m and MS_f. We find that this term explains a sizable portion of the total fitness covariance (table 4), implying that collinearity between MS_m and MS_f has strong effects on both male and female fitness. Finally, the error term describing covariation that is not linked to MS and therefore inde-

Table 3: Regression coefficients for the *Biomphalaria glabrata* sample data set obtained with the alternative methods for calculating Bateman gradients

Analysis/component	Regression coefficient β	Comparison of slopes	
		t	P
Simple regression (eqq. [1]):			
Male (m)	.479*	−2.390	.020
Female (f)	.121*		
Multiple regression (eqq. [3]):[a]			
mm	.375**	−2.250	.028
ff	.053		
mf	.143	−1.49	.143
fm	.120		

Note: For details, see appendix B in the online edition of the *American Naturalist*.

[a] Includes cross-sex effects.

* $P < .05$.

** $P < .1$.

Table 4: Decomposition of variance components based on a sample data set from *Biomphalaria glabrata*

Source data and term	Value
Original MS:	
$\mathrm{Cov}(\mathrm{RS_m}, \mathrm{RS_f})$	.093
$\beta_{\mathrm{mm}}\beta_{\mathrm{fm}}\mathrm{Var}(\mathrm{MS_m})$	.057
$\beta_{\mathrm{mf}}\beta_{\mathrm{ff}}\mathrm{Var}(\mathrm{MS_f})$	.012
$(\beta_{\mathrm{mm}}\beta_{\mathrm{ff}} + \beta_{\mathrm{mf}}\beta_{\mathrm{fm}})\mathrm{Cov}(\mathrm{MS_m}, \mathrm{MS_f})$	.034
$\mathrm{Cov}(\varepsilon_{\mathrm{f}}, \varepsilon_{\mathrm{m}})$	−.011
Principal components of MS:	
$\mathrm{Cov}(\mathrm{RS_m}, \mathrm{RS_f})$	.093
$\beta_{\mathrm{m_{PC_1}}}\beta_{\mathrm{f_{PC_1}}}\mathrm{Var}(\mathrm{PC_1})$	.098
$\beta_{\mathrm{m_{PC_2}}}\beta_{\mathrm{f_{PC_2}}}\mathrm{Var}(\mathrm{PC_2})$	.006
$(\beta_{\mathrm{m_{PC_1}}}\beta_{\mathrm{f_{PC_2}}} + \beta_{\mathrm{m_{PC_2}}}\beta_{\mathrm{f_{PC_1}}})\mathrm{Cov}(\mathrm{PC_1}, \mathrm{PC_2})$	.000
$\mathrm{Cov}(\varepsilon_{\mathrm{f}}, \varepsilon_{\mathrm{m}})$	−.011

Note: For details, see appendix B in the online edition of the *American Naturalist*. The top half shows the covariance components as given in equation (5), whereas in the bottom half, $\mathrm{MS_m}$ and $\mathrm{MS_f}$ are replaced by their principal components ($\mathrm{PC_1}$, $\mathrm{PC_2}$), following equation (A5) in appendix A in the online edition of the *American Naturalist*.

pendent of mating is comparably small and of opposite sign to the covariance in RS (table 4). This suggests that fitness covariance in this data set is primarily due to variation in MS.

Next we show that we benefit from replacing the collinear measures of $\mathrm{MS_m}$ and $\mathrm{MS_f}$ (Pearson $r = 0.64$, $P < .0001$) by their principle components. The PCA approach first confirms that, within our experimental paradigm, individuals differed primarily in their overall mating activity ($\mathrm{PC_1}$ captures 82% of the total variance in MS) and much less in their sex bias in mating activity ($\mathrm{PC_2}$; table 5). The PCA approach (coefficients in table 5) indicates that frequent mating in general benefits male fitness more than female fitness ($\beta_{\mathrm{m_{PC_1}}} > \beta_{\mathrm{f_{PC_1}}}$). As a logical consequence, biasing mating activity in favor of male matings is clearly beneficial to male fitness and has little effect on female fitness ($\beta_{\mathrm{m_{PC_2}}} > \beta_{\mathrm{f_{PC_2}}}$, even though not statistically significant). A likely reason is that maternal fitness hardly declines even at very low $\mathrm{MS_f}$, where offspring can be produced by selfing (fig. 5). As a major insight, the PCA approach shows that individuals are selected not only to increase overall mating frequency but also, when possible, to bias mating activity in favor of the male role. Given unilateral copulations, this suggests that *B. glabrata* individuals may face conflicts over the preferable male role during mating.

The PCA-based decomposition of fitness covariance (table 4, bottom) explicitly shows that elevated overall mating activity increases both $\mathrm{RS_m}$ and $\mathrm{RS_f}$. The sex bias in individual mating activity contributes only a minor portion to fitness covariance. This value being positive confirms our interpretation that mating in either sex function is not detrimental to fitness through the other sex.

Perspectives

Earlier work by Arnold (1994) and Arnold and Duvall (1994) established the conceptual foundations for the analysis and interpretation of Bateman gradients in hermaphrodites. Building on their framework, our synthesis incorporates three important aspects of reproduction in hermaphrodites that remained insufficiently treated: (1) cross-sex interactions between male and female function to elucidate how hermaphroditism affects the strength and direction of sexual selection, (2) explicit solutions for the treatment of biological and statistical nonindependence between individual sex-specific measurements, and (3) an implementation of selfing into the framework for Bateman gradients.

Even though we have focused on copulating simultaneous hermaphrodites, our extensions can be adopted for other hermaphroditic systems, including external fertilizers, broadcast spawners, or wind- and animal-pollinated monoecious plants. For applications to plants, it will be useful to reconsider the definition of mating success. While our article has been guided by a view of physically interacting individuals, "mating" in plants needs to be connected with actual pollination events (such as the number of pollinator visits that transfer pollen of a given paternal plant or the number of pollen donors used in an artificial pollination). Beyond this, a logical next step would accommodate sexually polymorphic systems, such as gynodioecy (females co-occurring with hermaphrodites; Delph et al. 2007), androdioecy (males co-occurring with hermaphrodites; Pannell 2002; Weeks et al. 2006), or aphally (where some individuals lack a copulatory organ; Doums et al. 1998). Equations (3a) and (3b) then require extension to include pure males, pure females, or aphallic individuals, respectively. This would allow studying the interaction of concurrent selection on hermaphrodites and pure sex individuals.

Table 5: Principal components of $\mathrm{MS_m}$ and $\mathrm{MS_f}$ and the resulting PCA-based Bateman gradients in our sample data set from *Biomphalaria glabrata*

	Principal components		Regression coefficients (eqq. [3])		Comparison of slopes	
	$\mathrm{PC_1}$	$\mathrm{PC_2}$	$\mathrm{PC_1}$	$\mathrm{PC_2}$	t	P
Loading:						
$\mathrm{MS_m}$	.634	.773	$\beta_{\mathrm{m_{PC_1}}}$	.348*	−2.010	.049
$\mathrm{MS_f}$	.773	−.634	$\beta_{\mathrm{f_{PC_1}}}$	.118*		
Eigenvalue	2.395	.511	$\beta_{\mathrm{m_{PC_2}}}$	.199	−.540	.589
Percent	82.4	17.6	$\beta_{\mathrm{f_{PC_2}}}$	.059		

Note: Same data as in table 4. Principal component calculations based on the covariance matrix.

* $P < .05$.

A second desirable development concerns the evolutionary dynamics of Bateman gradients, an aspect about which the static framework used here is silent. Morgan (1994) already established that hermaphroditism may constrain potential evolutionary trajectories, and empirically establishing these trajectories in response to variation in, for example, different mating modes will now be revealing.

Third, while the Bateman gradient approach ignores individual variation in offspring quality (or reproductive value), there is rising awareness that female MS often increases RS primarily through offspring quality or enhanced genetic diversity (Jennions and Petrie 2000; Simmons 2005; Sprenger et al. 2010) rather than through pure offspring numbers. It thus seems timely (though challenging) to develop approaches that complement quantifications of Bateman gradients with measures that disentangle sexually and nonsexually selected contributions to variation in offspring quality or survival (cf. Kirkpatrick and Lande 1989).

Our extensions to the Bateman gradient approach for hermaphrodites also offer novel perspectives on other phenomena of sexual selection. First, Bateman gradients may inform a long-standing debate about "preferred mating roles." While Charnov (1979) and many others since have argued that mating in hermaphrodites is primarily motivated by a desire to donate rather than receive sperm, the alternative view of a general preference for the female mating role has also been advocated (Leonard 2005, 2006, and references therein). Generally, hermaphrodites should prefer the mating role that offers higher benefit from additional matings (Anthes et al. 2006), and this can depend greatly on the recent mating history (Koene and Ter Maat 2005). The sex function with the higher expected benefit is easily identified using Bateman gradients. Whether this preference is actually exhibited then further depends on the effort or cost involved in achieving additional matings, an aspect about which Bateman gradients are silent (Jennions and Kokko 2010).

Furthermore, Bateman gradients could illustrate the interplay between preferred mating roles and sex allocation (Janicke and Schärer 2009; Schärer 2009). Given the Fisher condition (Fisher 1958; Houston and McNamara 2005), any bias in sex allocation automatically increases the returns per unit investment to the sex function with the lower resource allocation. Animals may thus preferably exhibit this sex function during mating (Schärer 2009), which could be tested by correlating Bateman gradients against sex allocation in a comparative context. Within populations, relatively male-biased individuals may instead be more competitive in the male function and therefore preferably copulate in that role (Janicke and Schärer 2009). This could be tested by manipulating sex allocation experimentally and studying the resulting Bateman gradients.

Finally, our reworked analytical treatment of Bateman gradients for hermaphrodites will aid future analyses of sexual selection on individual traits. A prime goal will be to establish which traits experience sexually mutualistic, antagonistic, or neutral selection (cf. Garefalaki et al. 2010) and to understand how alternative selection regimes vary with the ecological and social context (Ashman and Morgan 2004; Brown et al. 2009). Corresponding empirical analyses are already available for some hermaphroditic plants (Campbell 1989; Morgan and Conner 2001; Hodgins and Barrett 2008) but are still lacking for hermaphroditic animals. We hope that our synthesis stimulates research efforts into these directions.

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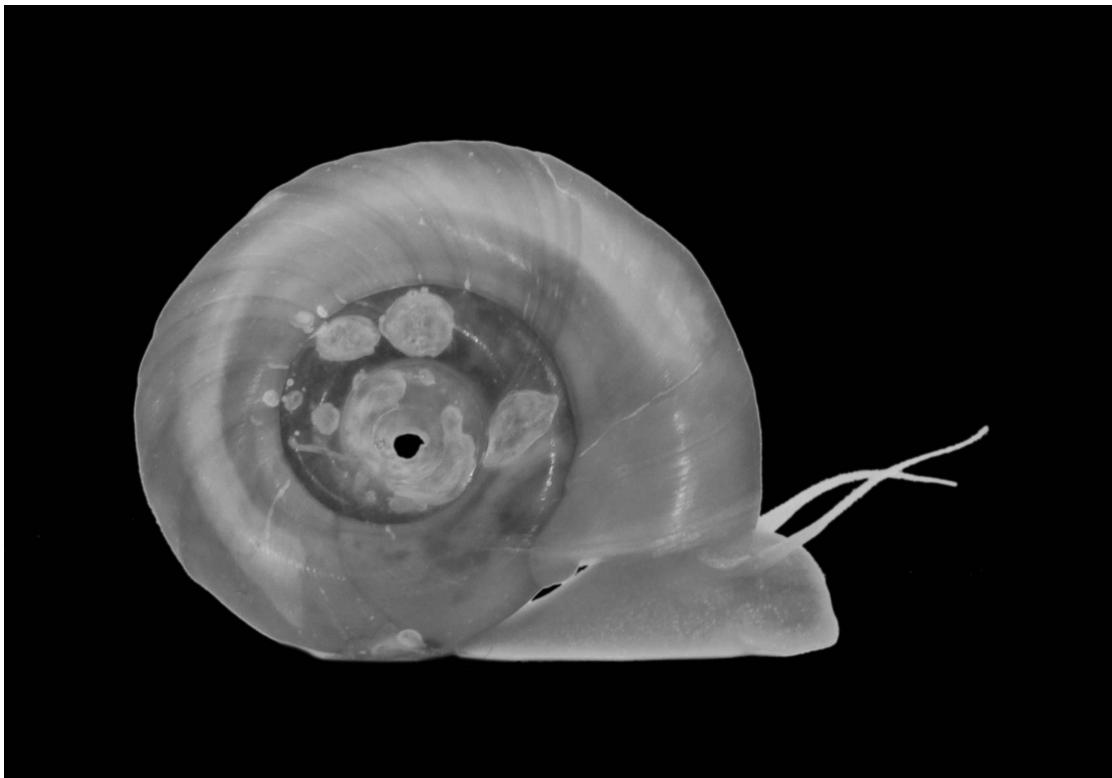
The hermaphroditic freshwater snail *Biomphalaria glabrata* can assume either sex role during copulation, but fitness benefits are highest when playing male. Image by Gregor Schulte and Nils Anthes.