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## Bateman Gradient

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## Synonyms

Sexual selection gradient

## Definition

The slope of a (usually simple, linear) regression
of the number of offspring on the number of
mates.

## Introduction

In 1948, the English geneticist Angus John Bateman
published a pioneering study of genetic parentage in
the fruit fly *Drosophila melanogaster* (Bateman
1948). Bateman set up small breeding populations
of flies and used visible mutations to determine the
mother and father of the resulting offspring. He then
used these data to address the question of why
competition for mates is usually stronger in males
than in females. Although some authors have criti-
cized empirical details of Bateman's study (e.g.,
Snyder and Gowaty 2007), his conceptual

framework has profoundly influenced modern sex-
ual selection theory.

When males and females occur in roughly
equal numbers – as they do in *D. melanogaster* –
the average number of offspring produced by
members of each sex must also be equal, because
each offspring has exactly one mother and one
father. Bateman showed, however, that the vari-
ance in offspring number was higher in males than
females. He attributed this result to two main
causes: (1) males were more variable than females
in the number of matings they achieved, and
(2) the correlation between offspring number and
the number of mates was stronger in males than in
females. This stronger relationship, Bateman
argued, arises from the fundamental sex differ-
ence in gamete size. Because sperm are smaller
and more numerous than eggs, female offspring
production is less strongly limited by fertilization
opportunities. Males should consequently experi-
ence stronger selection to increase their number of
mates, at least in species where their only contri-
bution to the next generation is their sperm.

Bateman's ideas lay largely dormant until the
renaissance of sexual selection theory in the
1970s, where they were revived in particular by
Trivers (1972). Bateman's observations and con-
clusions were integrated with formal selection
theory (Arnold and Duvall 1994; Jones 2009;
Henshaw et al. 2018), which led to more precise
quantitative definitions of Bateman's principles.
Perhaps the most important insight was that the
strength of sexual selection is related to the slope

of the relationship between reproductive success (number of offspring) and mating success (number of mates). Arnold and Duvall (1994) showed that this relationship could be quantified using a regression coefficient (Fig. 1), and they named this quantity the *sexual selection gradient*. Andersson and Iwasa (1996) later suggested the name *Bateman gradient* to distinguish it from other types of selection gradients.

## Definition

The Bateman gradient $\beta_{ss}$ quantifies the slope of the relationship between an individual's number of mates or matings (i.e., their mating success $M$) and their number of offspring (i.e., their reproductive success $R$). Most commonly, Bateman gradients are calculated as the slope of a simple linear regression of reproductive success on mating success (Arnold and Duvall 1994; Jones 2009; Henshaw et al. 2018: Fig. 1). Explicitly, this means that:

$$\beta_{ss} = \frac{\text{cov}(M,R)}{\text{var}(M)}$$

Bateman gradients are estimated separately for each sex, usually over a constrained time period such as a breeding season. They are best calculated using *relative* reproductive success, which is standardized by dividing each individual's reproductive success by the mean reproductive success of all individuals of the same sex (Jones 2009). In this case, the Bateman gradient can be interpreted as a linear selection gradient on mating success (Arnold and Duvall 1994). Some authors additionally recommend mean-standardizing mating success (Jones 2009).
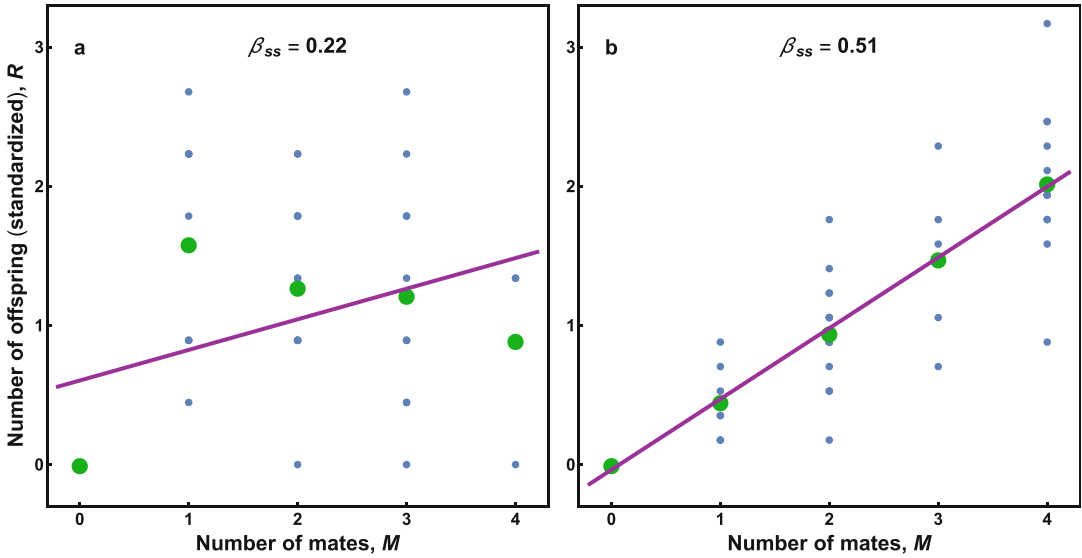
## Measurement and Interpretation

Three issues should be kept in mind when measuring and interpreting Bateman gradients. First, the most intuitive interpretation of a Bateman gradient is causal – how much would a typical individual's reproductive success increase if they were granted an extra mating? Despite this intuition, Bateman gradients are most often measured in freely mating populations, where mating and reproductive success covary naturally (Anthes et al. 2017). Such correlative studies are vulnerable to confounding factors that affect both mating and reproductive success, which complicates interpretations of the Bateman gradient. If potential confounders are identified and measured, then they can be included as covariates in the regression of reproductive success on mating success. The Bateman gradient can then be defined as a partial regression coefficient (Henshaw et al. 2018). Nonetheless, the potential for unmeasured confounders means that manipulative experiments are essential to pin down the causal relationship between mating and reproductive success (Anthes et al. 2017).

Second, Bateman gradients condense the relationship between mating and reproductive success into a single number (the "slope"). However, such relationships are often not straight lines; rather, their steepness may vary with the number of matings. More generally, a *Bateman function* represents the average reproductive success of individuals with each integer number of matings (Fig. 1). For individuals with zero mating success, reproductive success is necessarily also zero, as no offspring can be conceived without mating. After the first mating, reproductive success may continue to increase, remain flat, or even decrease (e.g., if mating itself is dangerous or harmful), depending on a species' ecology and mating system (Anthes et al. 2017). Despite these nuances, the interpretation of Bateman gradients as selection gradients on mating success always holds, regardless of whether the Bateman function is linear or nonlinear.

Third, Bateman gradients are highly sensitive to technical issues affecting estimates of mating and reproductive success. In many studies, matings are not observed directly, but rather inferred by reconstructing the parentage of offspring. Only matings that lead to offspring are counted towards an individual's "mating success," which can lead to a spurious strengthening of the estimated relationship between mating and reproductive
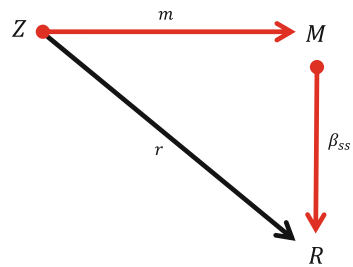
**Bateman Gradient, Fig. 1** Hypothetical relationships between an individual's number of mates $M$ and their number of offspring $R$, assuming that (**a**) additional mates after the first are detrimental to average offspring production, or (**b**) average offspring production increases linearly with the number of mates. Small blue circles represent individual mate and offspring numbers; large green circles represent the average offspring number of individuals with any given number of mates (i.e., the Bateman function); the purple line represents the simple linear regression of offspring number on mate number. The Bateman gradient $\beta_{ss}$ is the slope of this regression line. Offspring number has been standardized to have a mean value of one

success. Unsurprisingly, Bateman gradients based on genetic information alone are almost always higher than those based on observations of mating interactions (Anthes et al. 2017). Another issue is that when individuals are sampled from natural, open populations, mating and reproductive success are inevitably sampled incompletely for some individuals. This can lead to biased estimates of Bateman gradients. Statistical approaches exist to ameliorate such bias as long as certain assumptions are met (Jones 2015).

## The Strength of Sexual Selection

Sexual selection can be conceptualized as a type of natural selection that acts via causal pathways involving mating or fertilization success (Henshaw et al. 2018). Selection via mating success in particular is sometimes termed *pre-mating sexual selection* (Fig. 2). Using a path-analytic framework, the strength of pre-mating sexual



**Bateman Gradient, Fig. 2** Pre-mating sexual selection is any selection acting via causal pathways involving mating success $M$ (shown in red). Pre-mating sexual selection on an arbitrary trait $Z$ can be decomposed into two components: the mating differential $m$, which represents the relationship between the trait and mating success, and the Bateman gradient $\beta_{ss}$, which quantifies the relationship between mating success and reproductive success $R$. The variable $r$ represents any remaining selection acting on $Z$, other than pre-mating sexual selection

selection acting on a trait can be decomposed into two components, with one component representing the association between the trait and mating success and the other representing the

association between mating and reproductive success (Arnold and Duvall 1994; Jones 2009; Henshaw et al. 2018). One such decomposition is:

$$x = \beta_{ss}m$$

Here $x$ is the strength of sexual selection, $\beta_{ss}$ is the Bateman gradient (calculated as a simple or partial regression coefficient), and $m$ is the covariance between the trait and mating success (known as the *mating differential*). For traits that are standardized to have a variance of one, the strength of pre-mating sexual selection $x$ is limited in magnitude by:

$$|x| \leq |\beta_{ss}|\sqrt{\mathrm{var}\, M}$$

This upper bound, known as the *Jones index*, is informative even for traits that are not included in the analysis (Jones 2009; Henshaw et al. 2018). It is unbiased only if the estimate of $\beta_{ss}$ controls for all factors that confound the relationship between mating and reproductive success. The Jones index was highly correlated with the strength of pre-mating sexual selection in a simulation study (Henshaw et al. 2016).

## Sex Differences in the Bateman Gradient

In most animal species, males contribute only their sperm to the next generation. In such cases, Bateman gradients are invariably larger for males than for females (Janicke et al. 2016). However, large female Bateman gradients may occur for at least two reasons. First, if mate encounters are rare, then both males and females may often be mate-limited. Second, if males contribute substantial resources towards raising offspring, or provide nuptial gifts to their partners while mating, then female reproductive success may increase steeply with the number of mating partners (Trivers 1972). In rare cases, including several species in the pipefish family, paternal investment in offspring has led to female Bateman gradients exceeding their male counterparts (Janicke et al. 2016).

## Cross-References

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