Resource variation generates positive correlations between pre- and post-copulatory sexually selected traits

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Lay summary

To produce offspring, males must win a mate and successfully fertilize an egg, both of which require energy. This leads to the expectation that species whose males invest more into winning mates invest less into egg fertilization and vice versa. We show, however, that reproductive investment is often not an either-or proposition. An increase in the amount of energy invested into reproduction often results in additional investment into both winning mates and fertilizing eggs.

Abstract Male fertilization success depends on investment in both pre- and post-copulatory sexually selected traits, and considerable attention has recently been paid to quantifying the strength and direction of covariance between pre- and post-copulatory trait expression. Here, building upon previous sperm competition models, we theoretically investigate how variation in total investment into fertilization success, as well as differences in the form of pre-copulatory competition, influence the correlation between pre- and post-copulatory traits across species. We found that whenever species differ in the total investment into fertilization, optimal partitioning of investment typically generates positive correlations between sexual traits and this prediction holds when competition is between multiple males or between just two males . This contrasts with the general expectation of a negative correlation based on the trade-off between investment in pre- and post-copulatory traits at the level of an individual. Nonetheless, negative correlations do arise under some conditions, notably when total investment into fertilization is similar across species, but species differ in the form of pre-copulatory male-male competition. These results imply that the assessment of underlying trade-offs between pre- and post-copulatory trait investment requires an evaluation of how overall investment into total fertilization success varies across species.

Keywords acquisition, allocation, contest competition, life-history trade-offs, scramble competition, sperm competition

Introduction

Male fertilization success, that is the number of offspring sired by a male, depends on pre-copulatory traits that influence mating success, such as ornaments and armaments, as well as post-copulatory traits that influence success in fertilizing ova when in competition with ejaculates from rival males (Parker 1998; Kvarnemo and Simmons 2013; Devigili et al. 2015). Theoretical models of sperm competition assume a trade-off between investment in pre- and post-copulatory sexually selected traits such that increased investment into pre-copulatory traits decreases investment in post-copulatory traits, and vice versa (Parker 1990; Parker 1998; Parker and Pizzari 2010; Parker et al. 2013). Such trade-offs are expected because producing and maintaining weapons and ornaments, as well as ejaculate traits, can be energetically expensive (Dewsbury 1982; Olsson et al. 1997; Emlen 2001; Hayward and Gillooly 2011). However, empirical studies of pre- and post-copulatory trait covariance have reported both positive and negative correlations, as well as a lack of correlation, between traits at both the intra- and inter-specific level (reviewed in Mautz et al. 2013; Lüpold et al. 2014; Simmons et al. 2017). Attempts to explain these inconsistent results focus on a range of additional life-history, ecological, and mating system variables; for example, positive correlations are frequently discussed in the context of resource variation (Lüpold et al. 2014; Buzatto et al. 2015; Simmons et al. 2017; Supriya et al. 2018). However, how such variation in resource availability might influence sexual trait covariance has yet to be explored theoretically. More generally, there has been a call for studies that provide a predictive framework for understanding how extrinsic factors modify the strength and direction of the correlation between pre- and post-copulatory sexual traits (Evans and Garcia-Gonzalez 2016).

The impact of resource variation on pre- and post-copulatory trait covariance is generally framed within the context of the model of van Noordwijk and de Jong (1986), who noted how differences in individual quality can result in positive correlations between life-history traits across individuals, even if the traits trade-off at the within-individual level. They introduced the terms acquisition i.e. amount of total resources available to individuals, and allocation, i.e. partitioning of resources between life-history components. Importantly, these models predict that when variance in acquisition is large with respect to variance in allocation, components of fitness covary positively, for example, richer individuals own larger houses and more expensive cars; but when variance in acquisition is relatively small, components of fitness covary negatively, for example, within a given fixed income class those who spend less on houses are able to spend more on a car (Van Noordwijk and de Jong 1986). Thus, given assumptions about how resource investment translates to fitness, one can model the expected negative covariance between components, and hence the variance in acquisition required to turn an association between two components of fitness from negative to positive (Price et al. 1993).

Here, we extend these concepts of acquisition and allocation to correlations of species mean values to theoretically examine male investment into pre and post-copulatory sexually selected traits. Importantly, variance in acquisition or the amount of resources invested into fertilizations can vary considerably across species; males of some species are under selection to invest more heavily into gaining fertilizations than males of other species. This variation may arise due to differences in the operational sex ratio or breeding density (Emlen and Oring 1977; Janicke and Morrow 2018) or variation in the distribution and abundance of resources in the breeding season. For example, in polygynous systems, males classically invest a great deal into post-copulatory fertilization success, whereas in monogamous ones, males invest more into raising offspring (Requena and Alonzo 2017). In turn, acquisition variation is expected to generate a positive covariance between two subcomponents of fertilization success (e.g. pre- and post-copulatory episodes of selection), counteracting the negative covariance resulting from a trade-off induced by energetic constraints.

In this paper, we used specific fitness functions (i.e. models that determine how allocation translates to fitness), including those developed by Parker et al. (2013), to ask how much variation in investment into total fertilization success is required to shift across-species correlations from negative to positive. We find it is surprisingly little. Indeed, in the simplest case, *any* variation in total investment generates a perfect positive correlation across species. This is contrary to the general sentiment that when components of fitness strongly trade-off, they should be negatively correlated across species. We consider the consequences of these results for recent tests of evolutionary trade-offs between pre- and post-copulatory sexual selection, as well as more generally.

Model 1: Modelling resource variation using linear fitness functions

We first consider models of resource allocation where a male's success in both pre- and post-copulatory competition increases linearly with his investment (e.g. Parker and Ball 2005). Following Parker et al. (2013), we symbolize total male investment into obtaining fertilizations as *R* (i.e. acquisition). *R* can reflect any unit of energy or resource, the exact definition of which can be difficult to pin down (Metcalf 2016). However, given that we are examining how variation in *R* affects allocation to pre- and post-copulatory investment, it is the relative values of *R*, and not the absolute values, that are of importance. For example, males of a species with $R = 10$ are investing twice the total energy budget for fertilization as males of a species with $R = 5$, and half as much as males of a species with $R = 20$. We set *k* to be the proportion invested into pre-copulatory sexually selected traits and hence $(1-k)$ is the proportion invested into post-copulatory sexually selected traits. As in most other models of sperm competition, fitness, *w*, is the product of the probability of mating, w_m, and the probability of a fertilization given a mating, $w_{f//m}$, both of which are assumed to contribute independently. Given these conditions:

$$w_m = akR \quad [1a]$$

$$w_{f/m} = b(1-k)R \quad [1b],$$

where *a* and *b* are positive constants that determine returns on investment to fitness in relation to expenditure on pre- and post-copulatory competition, respectively. We follow Parker et al. (2013) in calling *a* the mate competition loading coefficient, which determines the extent to which investment in pre-copulatory competition translates into mating success (i.e. the payoff on investment). Similarly, *b* determines the extent to which investment in post-copulatory competition translates into success at fertilizing ova. Differentiating the product of equations (1a) and (1b) with respect to k and setting the result equal to 0, shows that male reproductive fitness is maximized at $k = 0.5$, independent of R, a and b. Thus, a species in which males invest more into achieving fertilizations should invest any additional resources equally into both pre- and post-copulatory sexually selected traits. Consequently, any interspecific variation in allocation into fertilization success leads to a perfect positive correlation between pre- and post-copulatory trait investment across species (Fig. 1).

Model 2: Modelling resource variation using non-linear fitness functions

Male mating success does not always increase linearly with investment (Hosken and House 2011). For example, in the case of contest competition between males, many males may not receive any matings despite their investment into pre-copulatory sexually selected traits and thus variance in male mating success is highly skewed (e.g. Dubuc et al. 2014). Therefore, as a next step, we modeled covariance between pre- and post-copulatory traits using nonlinear fitness functions. Parker et al. (2013) recently introduced a model incorporating variation in the form of pre-copulatory male-male competition (i.e. from direct contest to scramble competition), and showed how relative investment between pre- and post-copulatory traits varies with (1) the level of sperm competition, (2) the payoff per unit of investment in pre-copulatory traits (termed the "mate competition loading"), and (3) the number of males competing for each mating. In these models benefits depend on the form of pre-copulatory male-male competition and may increase either asymptotically or exponentially (Fig. 2). We extend Parker et al.'s (2013) models by also allowing R (i.e. total male investment into fertilization success) to vary. We assume that the average number of matings per male is two (n = 2) and the population is at equal sex ratio, so average number of ejaculates received by a female is also two (N = 2). However, we obtained similar results using different values of N (e.g. N = 1.5, 5 and 10; data not shown) reflecting variation in the level of sperm competition faced by males.

Following Parker et al. (2013), we compared the effects of male-male (contest) competition with that of mate searching (scramble competition). In contest competition, pre-copulatory competition for matings is typically between two or a few males (see Fig. 2a for fitness functions under contest competition), with a high degree of female monopolization leading to a strong skew in male mating success. As per Parker et al. (2013), we model dyadic contest competition (hereafter simply referred to as contest competition). Specifically, for contests between two males, the number of matings, n, obtained by a mutant male investing kR resources into mate attraction is (eqn 7 of Parker et al. (2013) substituting T and $\hat{T}$ with kR and $\widehat{kR}$ respectively) :

$$n = 2\hat{n} \frac{1}{1+(\widehat{kR}/kR)^{a}} \qquad [2a].$$

Here, k is the proportion invested into pre-copulatory traits and $\hat{n}$ is the average number of matings per male. In these models, the fitness benefit gained by a mutant male by altering his investment into mate attraction depends upon the investment strategy of other males in the population, i.e. benefits are frequency dependent, with $\widehat{kR}$ denoting the average male investment into pre-copulatory traits (equivalent to $\hat{T}$ in Parker et al. (2013)). Because investment is written in arbitrary units, we can set $\widehat{kR}$ equal to 1 (R is now measured in units of $\widehat{kR}$) so that:

$$n = 2\hat{n}\,\frac{1}{1+(1\,/kR)^{a}} \qquad [2b].$$

In models of scramble competition, an infinite number of males effectively compete for each copulation and the ability of males to monopolize females tends to be low. Following Parker et al. (2013), we model scramble competition as $M \to \infty$, and mating success increases with effort spent in acquiring matings (see Fig. 2b for fitness functions under scramble competition), such that the number of matings, n, obtained by a mutant male is (eqn 8 of Parker et al. (2013):

$$n = \hat{n}\,(kR)^{a} \qquad [2c].$$

As before, a denotes the ‘mate competition loading’ term or the payoff on investment into pre-copulatory competition (i.e. the extent to which investment in pre-copulatory competition translates into mating success), k is the proportion invested into pre-copulatory traits, and $\hat{n}$ is the average number of matings per male. Here again, we substituted T and $\hat{T}$ with kR and $\widehat{kR}$ respectively and set $\widehat{kR}$ equal to 1.

With respect to post-copulatory investment, the value of a mating for a male is the fraction of matings that result in a fertilization, v. Here, we use the intensity model of sperm competition in which all males receive on average the same number of matings (i.e. n = 2), and following Parker et al. (2013) define the average value of a mating as:

$$v = \frac{(1-k)R}{(1-k)R+(N-1)} \qquad [2d]$$

where N is the mean number of ejaculates received by a female and k is again the proportion invested into pre-copulatory traits (see Fig. 2c for fitness function for fertilization success given sperm competition). Here, we substituted (1-k) R for s the male's ejaculate size and $\widehat{(1-k)}R$ for $\hat{s}$ which is the average population-level ejaculate size for a male and set $\widehat{(1-k)}R$ equal to 1. We used the intensity model in which all females mate with N males where $N \geq 2$, and not the alternative risk model where females either mate once per clutch with a probability 1- q or twice with the probability q. We chose the intensity model because both of these models perform similarly within the risk range (i.e. between N = 1 and 2) and the intensity model is more broadly applicable (Parker and Ball 2005; Parker et al. 2013).

To find optimal investment into pre- and post-copulatory traits, we solved for the maximum of the product of equations 2b and 2d (for contest competition) and of 2c and 2d (for scramble competition) for various values of a and R as a function of k using the *"optimize"* function in the R package 'stats' (R Core Team 2014). We found that across a wide range of parameter space, correlations between investment into pre- and post-copulatory traits are positive, although not generally equal to one. Specifically, positive correlations are always present when R varies and the form of pre-copulatory male-male competition is held fixed (i.e. solid and dashed lines, Figs 3a-c). Moreover, for a fixed value of R, investment into post-copulatory traits is always higher for contest competitors (solid line) than scramble competitors (dashed line), who have more to gain by increasing investment into post-copulatory traits that secure fertilizations. The difference between contest competitors and scramble competitors is most evident when the mate loading coefficient, *a*, is high (Fig. 3c).

More generally, we found that positive correlations are inevitable if *R* varies and the form of pre-copulatory competition is invariable, whereas negative correlations are inevitable if the form of pre-copulatory competition varies and *R* is fixed (Fig. 3). Importantly, this leads to a rich realm of possibilities in the strength and direction of the correlation in empirical data. For example, consider two species, one of which is investing R = 10 total units, and the other, R = 20 total units, and a high mate loading coefficient (see e.g. Fig. 3c). While variation in R should generally result in a positive correlation between pre- and post-copulatory investment, if the investor of 20 units is a scramble competitor (far right point on dashed line in Fig. 3c) and the investor of 10 units a contest competitor, pre- and post-copulatory investment will be negatively correlated.

Next, in order to evaluate the relative impact of variation in resource investment and the form of pre-copulatory male-male competition (denoted by the number of males competing for a mating, *M*) on trait covariance, we explored the effect of simultaneous variation in both *R* and *M*. We utilized the common equation for pre-copulatory benefits, derived from equation [6] of (Parker et al. 2013), so that:

$$n = M\hat{n}\,\frac{1}{1+(M-1)(1/kR)^{a}} \qquad [3]$$

Here, varying the value of *M* implies moving from a dyadic contest competition scenario ($M = 2$) to scramble ($M \rightarrow \infty$) competition in an infinite population. We maximized the product of equations 2d and 3 with respect to *k*, fixing *a* = 3. We specified variation in values of *R* and *M* using random number generators from a uniform distribution over the following intervals: *R* varies between 100:105, 100:150, 100:200, 100:250 and 100:300; *M* varies between 2:3, 2:5, 2:10, 2:100 and 2:1000 (Fig. 4). We calculated the correlation between investment in pre- and post-copulatory traits for 1000 random values of *R* and *M* for each pairwise combination of the intervals in *R* and *M*. We allowed for an up to threefold difference across species in the amount of total resources invested by males in gaining fertilizations (i.e. *R* varied from 100-300) and included variation in the total number of males competing for each mating opportunity ranging from dyadic contest (here defined as *M* = 2) to scramble (here defined as *M* = 1000) competition. We plotted the average values from the correlation between *M* and *R* for each of the 1000 iterations after running it through a lowess smoother. All analyses were done in the R statistical package (R Core Team 2014) and plotted with the R package 'lattice' (Sarkar 2008).

These analyses show that positive correlations between investment in pre- and post-copulatory traits are more widely predicted than negative ones (Fig. 4a). Negative correlations arise only when there is less than two-fold variation in resources invested coupled with substantial variation in the number of males competing for a mating opportunity (Fig. 4b). We found similar results when we used different values of *a* (*a* = 1 or 5; see Figs. S1 & S2), though negative correlations between pre- and post-copulatory traits were slightly more prevalent when *a* was lower (i.e. *a* = 1, Fig S1). Nonetheless positive correlations still dominated the parameter space, regardless of the value of *a*, and negative correlations were still found only when there was low variation in *R* (Fig. S1 & S2).

Discussion

Here, we theoretically examined how variation in both total resources invested in fertilization (i.e. the sum of pre- and post-copulatory trait investment) and the form of pre-copulatory male-male competition influences the strength and direction of covariance between pre- and post-copulatory sexual traits. Using specific fitness functions developed for sperm competition theory, we quantitatively predict when life-history traits that trade-off within species result in positive correlations across species in the context of sexual selection and relative investment in male sexual traits. We show that even a 1.5-fold difference between species in the amount of resources invested into total fertilization success generally results in positive correlations between pre- and post-copulatory trait investments across species. Moreover, we find that correlations between pre- and post-copulatory traits are expected to be positive under both contest and scramble competition, and only become negative under limited conditions. That is, when inter-specific variation in resource allocation to total fertilization success is low and the form of pre-copulatory competition varies across species (i.e. species vary in the average number of males competing for each mating along a continuum from dyadic contest competition to scramble competition) (Fig. 4).

Comparative studies in a range of taxa have frequently reported a positive correlation between the expression of pre- and post-copulatory traits (Wedell 1993; Dunn et al. 2001; Greig and Pruett-Jones 2009; Lüpold et al. 2014; Simmons and Fitzpatrick 2016; Supriya et al. 2018). Most notably, Lüpold et al. (2014) evaluated the correlation between testes size (a measure of post-copulatory investment) and either weaponry or sexual size dimorphism (a measure of pre-copulatory investment) in 10 taxa and found mostly positive correlations between testes size and weaponry (5/5 taxa examined) and testes size and sexual size dimorphism (5/9 taxa examined). In that study, four of the taxa (4/10) were classified as having an invariant mating system (i.e., all species were considered either monopolizing or non-monopolizing species) and these taxa were generally associated with the largest positive correlations between pre- and post-copulatory trait investment. Assuming species with female monopolization approximate contest competitors and species exhibiting low or no female monopolization are often scramble competitors, these empirical findings are generally consistent with our model results. The major exception was the Acanthocephala (also known as the thorny-headed worms) which showed a negative correlation between sexual size dimorphism and testes size despite all species being classified as able to monopolize females. Lüpold et al. (2014) classified all acanthocephalans this way because males appear to fight over access to females and use copulatory plugs, which presumably prevent copulations from rival males and restrict the potential for multiple mating. However, we suggest that it is plausible that the mating system of acanthocephalans may actually be more variable than assumed by Lupold et al. (2014). This is because it is unknown if copulatory plugs are a universal feature of the Acanthocephala and, even when present, they may not prevent multiple mating by females (Amin et al. 2011). Additionally, considerable inter-specific variation in the degree of female bias in the adult sex ratio (Poulin 1997) suggests that the ability of males to monopolize females is likely to be variable across species. As such, we suggest that a variable mating system, and thus variation in the form of pre-copulatory competition, might explain the weak (c.f. Voordouw 2001) negative relationship observed in the Acanthocephala.

More generally, large variation in the number of males competing for a mating may explain the negative correlations between pre- and post-copulatory traits in a range of taxa (Lüpold et al. 2014; Kahrl et al. 2016). For example, in a study of pinnipeds, approximately two-thirds of the species were classified as contest competitors (n=19 with harems) and one-third of the species were classified as showing variation in the number of males competing for a mating (n=14 without harems), and across all species there was a negative relationship between sexual size dimorphism and relative testes size (Fitzpatrick et al. 2012; Lüpold et al. 2014). Lüpold et al. (2014) noted that the degree of female monopolization is a major determinant of the among species correlation between pre- and post-copulatory trait expression. Our results build on this and suggest that the correlation is affected by the extent to which the number of males competing for each mating varies across species and, even more importantly, by variation among species in the total amount of resources invested into acquiring fertilizations.

Consistent with our results, a recent study of the frog *Crinia georgiana* shows a negative correlation between relative arm girth (a pre-copulatory sexually selected trait influencing the number of matings obtained) and testes size across populations (Dziminski et al. 2010; Parker et al. 2013). In this species, studies examining male fertilization success in relation to male density suggest this pattern may arise from density-dependent patterns of sexual selection acting on pre- and post-copulatory trait investment, with some populations more or less approximating conditions of contest competition and others approximating conditions of scramble competition and thus differing in allocation strategy (Buzatto et al. 2015; Buzatto et al. 2017). In this case then, these populations may approximate one of the negative slopes (grey contour lines) in Figure 3 where resource variation is less influential than variation in the form of pre-copulatory male-male competition. Another recent study recovered a trade-off between pre- and post-copulatory sexually selected traits using experimental manipulations in a crusader bug species (*Mictis profana*), but found a positive correlation between the traits in the natural population, which may be explained by variation in the amount of resources invested into fertilizations by different males (Somjee et al. 2018). Moreover, a study of three-spined sticklebacks (*Gasterosteus aculeatus*) found evidence for a negative correlation between investment in pre- and post-copulatory traits in food-restricted males, whereas a positive correlation was observed among males that were well-fed (Mehlis et al. 2015). Thus, empirical studies are beginning to show the importance of variation in both the number of males competing for a mating opportunity and resource investment on the correlation between pre- and post-copulatory trait expression at the intra-specific level. Our model shows that similar patterns would be expected across groups of closely related species.

In addition to both positive and negative correlations, studies have reported a lack of correlation between pre- and post-copulatory traits (Ferrandiz-Rovira et al. 2014;

Lüpold et al. 2015). Such a lack of correlation may arise if one or both traits under study are not reflective of total investment in either pre- or post-copulatory investment. Under these conditions, it is likely there would be considerable noise in the data and this would reduce or obscure any correlation. Such an effect would be particularly relevant when investment into the traits measured represents just a small fraction of the resources available for that fitness subcomponent, and this may be further confounded by trade-offs within each. For example, sperm size and sperm number trade off (Parker 1982; Immler et al. 2011), and as such it is unlikely that either of these traits alone reflects total post-copulatory investment. In addition, a lack of correlation may also arise if the species examined vary in mating system and resource availability such that a line fitted through the data points has a slope of zero (Fig. 3), which is perhaps most plausible when considering a small, taxonomically-restricted dataset.

In conclusion, we emphasize that empirical studies need to consider the potential contribution of variation in investment into major fitness components (here, total fertilization success) when measuring the relationship between fitness subcomponents. In the case of interacting episodes of pre- and post-copulatory sexual selection, consideration of the potential contribution of variation in total investment and energy availability is critical to our understanding of evolutionary trade-offs. As such we theoretically confirm the arguments of Simmons et al. (2017), who noted that consideration of additional life-history, ecological, and mating system variables is necessary when considering the strength and direction of correlations between pre- and post-copulatory sexually selected traits.

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Figure legends

Figure 1. Optimum pre- and post-copulatory investment (filled circles) for a given fixed level of total resources, *R*, invested into fertilization by a species, assuming linear fitness functions (eqns 1). For a taxon with fixed resource acquisition, *R*, allocation in pre- and post-copulatory trades-off according to the grey lines.

Figure 2. Illustrations of the fitness functions developed by Parker et al. (2013) in order to define returns on investment in pre-copulatory (a & b) and post-copulatory traits (c). (a) Pre-copulatory contest competition (Parker et al.'s (2013) eqn 7), here between two males, and (b) pre-copulatory scramble competition (Parker et al.'s (2013) eqn 8). For pre-copulatory competition, the "mate loading function", *a*, is a measure of the returns for investment. In all cases, each female is assumed to mate on average twice. (c) Sperm competition. There are two models: risk model, where some females mate twice and some once (solid line, here the proportion of females mating twice was set to 0.5), or the intensity model, where all females mate with N males and $N \geq 2$, here set to $N = 2$ (dashed line, all analyses in this paper use this model). No sperm precedence was allowed.

Figure 3. Effect of variation in the form of pre-copulatory male competition and resource investment on the relationship between pre- and post-copulatory investment (based on solutions to eqns (2)) for different values of the mate competition loading coefficient, *a*. Contest competition is given by the solid black line and scramble competition by the dashed line. When *R* is fixed, negative correlations are found across species as the form of pre-copulatory competition moves from scramble to contest (each gray line is a

contour of equal acquisition, R = 5, 10, 15, 20 with the size of the circle indicating the increase in acquisition).

Figure 4. Predicted correlation between pre- and post-copulatory sexual traits as a function of variation in the number of males competing for each mating (M) and total investment (R). The correlation between pre- and post-copulatory investment (color bar on the right in (a) and Y-axis in (b)) is negative only when there is variation in M, combined with little variation in R. In these analyses, the mate loading coefficient (a) was set to 3. (a) Axis values give the interval from which randomly generated values were drawn; the lower value for the X axis interval in all cases is equal to 1. (b) X-axis reflects a move from dyadic contest competition (M = 2) to scramble competition (M = 1000) with intermediate values of M allowed to vary between the specified range and thus reflecting differences in mating system across species.

Figure 1.

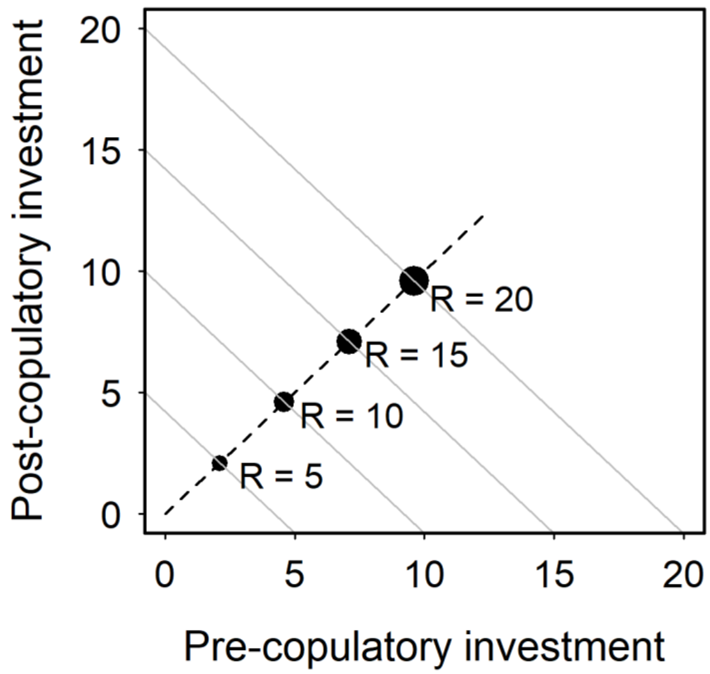

20
15
10
5
0
Post-copulatory investment
R = 20
R = 15
R = 10
R = 5
0
5
10
15
20
Pre-copulatory investment

Figure 2.

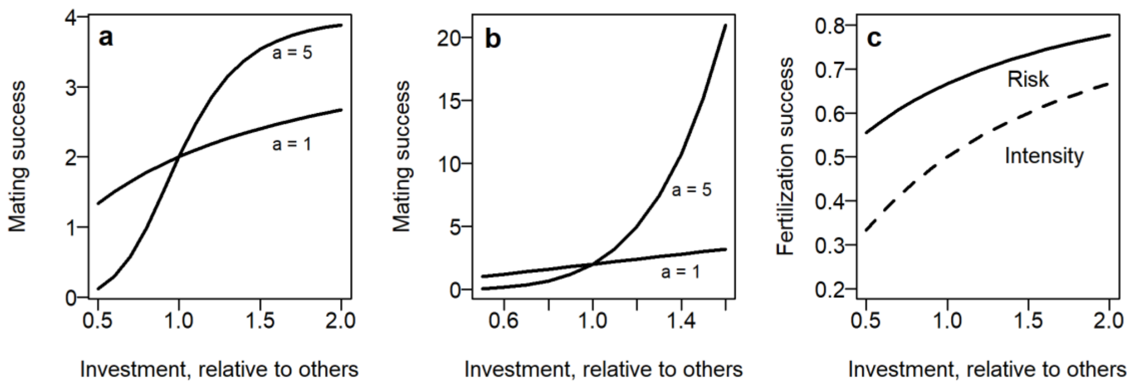

a
Mating success
a = 5
a = 1
Investment, relative to others
b
Mating success
a = 5
a = 1
Investment, relative to others
c
Fertilization success
Risk
Intensity
Investment, relative to others

Figure 3.

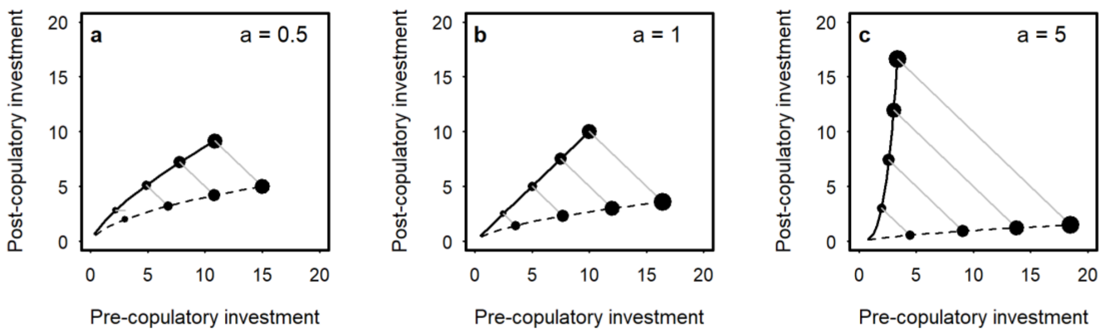
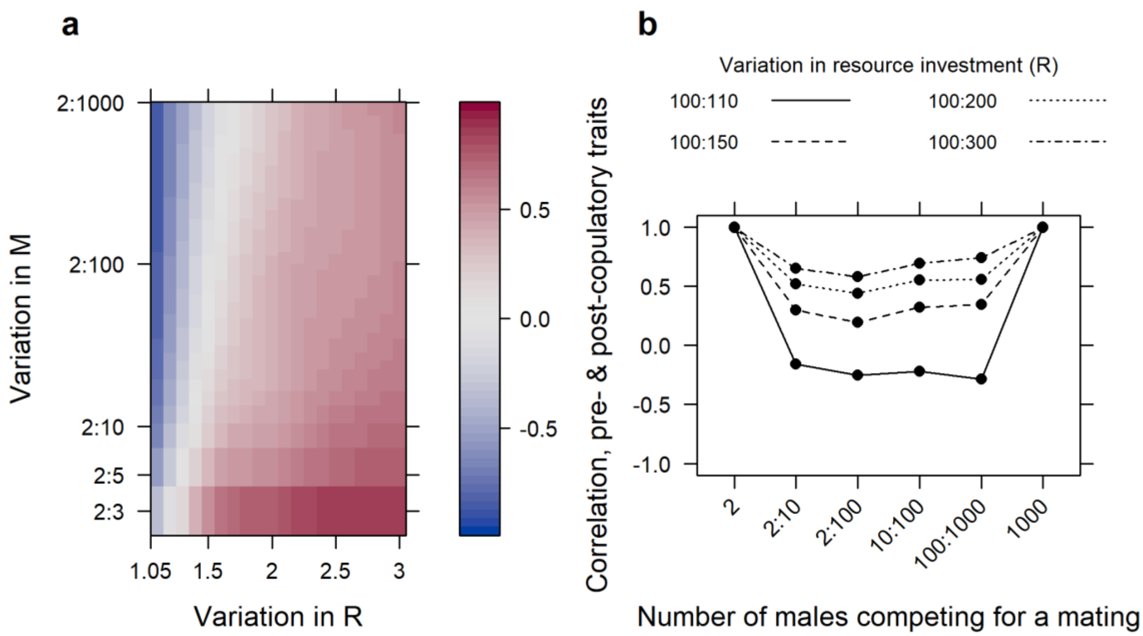

a
a = 0.5
b
a = 1
c
a = 5
Post-copulatory investment
Pre-copulatory investment
0
5
10
15
20

Figure 4.


a
2:1000
2:100
2:10
2:5
2:3
Variation in M
1.05
1.5
2
2.5
3
Variation in R
0.5
0.0
-0.5
b
Variation in resource investment (R)
100:110
100:200
100:150
100:300
1.0
0.5
0.0
-0.5
-1.0
Correlation, pre- & post-copulatory traits
2
2:10
2:100
10:100
100:1000
1000
Number of males competing for a mating