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Sexually selected traits evolve positive allometry when some matings occur irrespective of the trait

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Positive allometry of secondary sexual traits (whereby larger individuals have disproportionally larger traits than smaller individuals) has been called one of the most pervasive and poorly understood regularities in the study of animal form and function. Its widespread occurrence is in contrast with theoretical predictions that it should evolve only under rather special circumstances. Using a combination of mathematical modeling and simulations, here we show that positive allometry is predicted to evolve under much broader conditions than previously recognized. This result hinges on the assumption that mating success is not necessarily zero for males with the lowest trait values: for example, a male who lacks horns or antlers might still be able to copulate if encountering an unguarded female. We predict the strongest positive allometry when males typically (but not always) compete in large groups, and when trait differences decisively determine the outcome of competitive interactions.

11   Static allometry describes the scaling of body parts in relation to the whole, when comparing individuals

12   of the same species and ontogenetic stage. Based on the slope of a log–log regression of focal trait size

13   on body size, proportional scaling ("isometry", with a regression slope of 1.0) is distinguished from cases

14   where larger individuals have disproportionally larger ("positive allometry", slope > 1.0) or smaller

15   ("negative allometry", slope <1.0) traits. Striking secondary sexual traits such as ornaments or weapons

16   usually exhibit positive allometry (Huxley 1932; Gould 1974; Petrie 1988; Kodric-Brown et al. 2006; but

17   see Cuervo and Møller 2001 for a counterexample). For the most part these are 'dedicated' sexual traits

18   with no function other than enhancing mating success (Bonduriansky 2007). By contrast, non-sexual

19   traits, and traits with both sexual and non-sexual functions, usually show isometry or negative allometry

20   (Bertalanffy and Pirozynski 1952; Bonduriansky 2007; this also allows interpretation of structures of

21   extinct organisms; for the consequent view that pterosaur crests were sexually selected, see Tomkins et

22   al. 2010). An association between sexual selection and positive allometry has also been found in

23   comparative studies on stalk-eyed flies (Baker and Wilkinson 2001; Voje and Hansen 2013), earwigs

24   (Simmons and Tomkins 1996), and stag beetles (Knell et al. 2004). Various scenarios have been

25   proposed to explain the adaptive value of such patterns in a context of competitor assessment (Petrie

26   1988) or mate choice (Green 1992).

27   However, when evaluating such verbal arguments in the context of a formal model, Bonduriansky and

28   Day (2003) found surprisingly restrictive conditions for the evolution of positive allometry. The only

29   fitness function identified by Bonduriansky and Day (2003) as selecting for positive allometry was one

30   where viability increased with body size in a saturating manner, such that larger individuals, having less

31   scope for increasing their viability further, invested more in the sexual trait instead. In this context,

32   Bonduriansky and Day (2003) defined viability as "the probability of survival to the mating period",

33   which indeed has little scope for further increase once it reaches high levels, but which seems only

34   appropriate for semelparous species with a brief mating period. Although the argument can be

35   generalised by re-defining viability as expected lifespan (which is also consistent with Bonduriansky and

36   Day's mathematical formulation), there then appears to be no general reason why larger individuals

37   should be intrinsically less able to increase their lifespan. Thus, the prevalence of positive allometries

38   still appears enigmatic.

39   At a proximate level, Emlen et al. (2012) have recently proposed that this pattern may often arise from

40   growth processes involving the insulin signalling pathway: based on a study of rhinoceros beetles, they

41   suggested that positively allometric trait expression reflects heightened responsiveness of developing

3

42   trait tissue with respect to growth-stimulating physiological correlates of nutrition and overall body

43   growth. While mechanistically convincing, this hypothesis does not eliminate the need for an ultimate

44   explanation, since selection could be expected to modify this mechanism if the resulting trait sizes were

45   maladaptive for their bearers. For example, modifier genes could elevate the tissue-specific baseline

46   expression of genes involved in trait development (such as the *doublesex* gene in the taurus beetle;

47   Kijimoto et al. 2012), whose expression is currently conditioned on nutritional state. The observation

48   that positive allometry exists not only in species with continuous trait variation, but also in species with

49   discrete morphs, also hints that this pattern may have an adaptive basis, rather than being a mere by-

50   product of general growth processes (Tomkins et al. 2005).

51   Our present work provides new theoretical insights based on the basic (but surprisingly

52   underappreciated) premise that sexual traits help males elevate their mating success above a baseline,

53   but this baseline is not necessarily zero. Biological justification for assuming non-zero baseline success

54   comes e.g. from species where the effect of trait size on mating success has been studied

55   experimentally (wing size in *Drosophila*; Ewing 1964), or where naturally occurring mutants that have

56   lost a sexual trait have been documented to have substantial success (field crickets; Zuk et al. 2006). We

57   address the adaptive basis of positive allometry in two ways. First, we present a model that predicts

58   positive allometry under the assumption of non-zero baseline mating success. We expose the logic of

59   this result, extending its generality to a wide range of fitness functions. Second, taking into account the

60   game-theoretic consideration that the adaptive value of a trait depends on traits expressed by other

61   population members, we use individual-based simulations to study how allometry evolves under more

62   explicit assumptions about the mode of competition.

63   **Mathematical model**

64   We seek the optimal expression of a secondary sexual trait (henceforth, 'trait'). We measure body size x

65   and trait size y in the same units of mass. Trait mass is included in body mass, so there is no trade-off

66   between x and y. Rather, we take body mass to reflect available resources that can be allocated

67   between trait and viability, leading to a trade-off as often considered in 'costly signalling' models of

68   sexual selection (e.g., Getty 2006). A proportion u of resources is allocated to the trait, defining trait size

69   as $y = ux$ ($0 \le u \le 1$). We let mating success M increase with trait size according to the function $M=c+y^{p}$,

70   where c denotes baseline success in the absence of the trait, and p is a parameter controlling the shape

71   of the function. We assume that allocation to the trait reduces viability V according to the function $V=1-$

72   *u*. Interpreting mating success as an offspring production rate and viability as expected lifespan, fitness

73   is given by $W = MV$.

74   Using standard calculus, we identify the optimal allocation $u*$ that maximises W. The dependence of $u*$

75   on body size *x* then reveals the predicted allometric pattern: when $u*$ increases with *x*, larger individuals

76   invest a higher proportion of their resources in the trait, i.e. we have found positive allometry. For

77   example, assuming a linear increase (*p* = 1) of mating success with trait size, we obtain

78    $$u* = \frac{x - c}{2x}$$

79   This yields isometry for *c* = 0 and positive allometry for *c*>0 (noting that neither *c* nor *x* can be negative).

80   Similarly, for a quadratic increase (*p* = 2) of mating success with trait size, we obtain

81    $$u* = \left(\frac{x}{3} + \frac{\sqrt{x^2 - 3c}}{3} \right) \Big/ x,$$

82   which again yields isometry for *c*=0, and positive allometry for *c*>0.

83   At this point it is worth pointing out a connection with Bonduriansky and Day's (2003) model. By

84   substituting $c + y^p$ for *M*, our fitness function becomes $W = (c + y^p)V$, which is as a generalisation of a

85   fitness function considered in Bonduriansky and Day's example 4. Interestingly, if Bonduriansky and

86   Day's implicit assumption of *c*=0 is modified into *c*>0 in their example, their corresponding prediction of

87   isometry changes into positive allometry. Thus, despite differences in the underlying models, both agree

88   about the role of *c* > 0 for the evolution of positive allometry.

89   Some of the assumptions of the specific model above, such as a linear decline in viability with decreasing

90   allocation ($V = 1 - u$), could be rightfully criticized as being quite restrictive. We therefore now take a step

91   back from these specific assumptions in order to explore the generality of the result. In general, if fitness

92   is the product of two life-history dimensions (in this case, reproductive rate *M* and lifespan *V*), the

93   fitness gain from increasing each of these dimensions by a given amount is proportional to the current

94   value of the other dimension. This point can be illustrated by envisioning fitness as the area of a

95   rectangle, as shown in figure 1. The fitness gain from investing in a given dimension *i* is also proportional

96   to the increment rate f_i, which measures how steeply *i* increases as a function of the corresponding

97   investment. If there is a trade-off between *M* and *V*, the optimal strategy (assuming non-zero

98 investment in the trait) will balance the marginal fitness gains from investing along each dimension,

99 leading to the condition:

100 $$M \cdot f_V = V \cdot f_M \qquad (1)$$

101 By rearranging and making explicit that the increment rates f_i may be functions of the respective

102 investments, we obtain

103 $$\frac{M}{f_M(xu^*)} = \frac{V}{f_V(x(1-u^*))} \qquad (2).$$

104 Insofar as M and V that are caused by investments, they can in part be represented as integrals of all

105 increments up to the current investment, i.e. up to xu^* (for the trait) or $x(1-u^*)$ (for viability):

106 $$M = c + \int_0^{xu^*} f_M(k)dk = c + F_M(xu^*), \quad V = \int_0^{x(1-u^*)} f_V(k)dk = F_V(x(1-u^*))$$

107 where c is the baseline reproductive rate at zero investment, and F_i, is the anti-derivative of f_i.

108 Substituting into eq. (2), we obtain the implicit solution

109 $$\frac{F_M(xu^*)+c}{f_M(xu^*)} = \frac{F_V(x(1-u^*))}{f_V(x(1-u^*))} \qquad (3),$$

110 from which we can draw fairly general conclusions. Whenever increment functions are expressible in the

111 form $f_i(k)=ak^p$ (where $a > 0$ and $p \geq 0$), the ratio $F_i(k)/f_i(k)$ can be written as $k/(1+p)$. Given that k is a

112 product that is always proportional to x in our model, it follows that the ratio $F_i(k)/f_i(k)$, too, is

113 proportional to x. The proportionality with x on both sides of eq. (3) allows us to conclude that the

114 optimal allocation u^* will not depend on body size x as long as $c = 0$ (i.e., zero-trait males never mate)

115 and all fitness effects are expressible as products of power functions (with $p \geq 0$).

116 What happens if some matings occur irrespective of trait sizes? This is captured by the model as $c > 0$.

117 Now, increasing x while keeping u^* constant increases the LHS less than the RHS in equation (3).

118 Therefore, to keep satisfying (3) in the face of increasing x, u^* has to increase too: this direction is based

119 on noting that F_M/f_M increases with u^*, whereas F_V/f_V decreases with u^*. Thus, $c > 0$ predicts a positive

120 correlation between x and u^*, i.e. positive allometry.

121 By similar reasoning we can also recover Bondurianský & Day's (2003) result that a saturating viability

122 function can lead to positive allometry even when $c = 0$. To make their point in the current framework,

123 let us assume that viability is a saturating function with limiting value $\lim_{x(1-u)\to\infty} V(x(1-u)) = V_{\max}$. Now if

124 we increase x for a given level of u^* so that V approaches $V_{\max}$, the corresponding increment rate f_V must

125 approach zero while F_V remains positive. It follows that, for large-bodied individuals (high x), the ratio

126 F_V/f_V on the RHS of eq. (3) increases without bounds, while the LHS remains simply proportional to x

127 (assuming a power function for mating success, and $c = 0$). This means that a compensatory increase in

128 u^* is required to keep the equation satisfied in the face of increasing x, predicting positive allometry.

129 **Simulations**

130 Individual-based simulations are a powerful way to explore the robustness and general applicability of

131 analytical predictions, as several restrictive assumptions can be relaxed with ease (Kuijper et al. 2012).

132 We simulate a population of N females and N males that reproduce in discrete, non-overlapping

133 generations (using Matlab R2011b; code available upon request). Males are randomly assigned to one of

134 s environmentally determined, evenly spaced size classes between size $x=1/s$ and $x=1$. Each individual

135 carries s haploid loci whose allelic values u_x ($0 < u_x < 1$) encode size-specific allocation strategies that are

136 expressed only in males of the appropriate size. Individual trait size $y = u_x x$ and viability $V=1-u_x$ depend

137 on resource allocation as in the mathematical model above. However, in this discrete-generation

138 context, we now interpret V as a probability of being present when matings occur, noting that this is

139 similar in effect to our previous interpretation of V as lifespan: in either case, the important feature is

140 that V predicts a male's expected number of mating opportunities. As detailed in the section 'mating'

141 below, a proportion q of all matings are uncontested in the sense that they fall to a random male

142 irrespective of trait size, while the remaining matings are subject to trait-related competition between n

143 males at a time. Competition can be envisaged either as contest competition or as female choice, in

144 which case females inspect n males before choosing to mate with one of them. Note that the proportion

145 q of uncontested matings replaces the abstract baseline success c of our above models. We additionally

146 introduce a parameter β to control the decisiveness of the trait as a determinant of mating success

147 *within* a competitive group of n males.

148 Each iteration of the simulation proceeds through the following stages:

149   *Mating.* Each female is assigned to mate with one or more males. For each of (1–*q*)*N* females, *n*

150   potential mates (competitors) are randomly sampled from the population, with individual sampling

151   probabilities proportional to *V*. Competitive success between these males is then determined based on

152   trait size according to the Tullock function (a standard method in economics and evolutionary biology;

153   Gavrilets, 2012; Tullock, 1980), such that the *i*th male has probability $y_i^\beta \Big/ \sum_{j=1}^{n} y_j^\beta$ of siring any given

154   offspring produced by the focal female. Here, the parameter $\beta > 0$ measures the decisiveness of trait

155   differences in controlling success, with $\beta > 1$ describing situations where the best competitors

156   disproportionally dominate the competition. The remaining *qN* females each mate with one male

157   sampled randomly from the population, again with sampling probabilities proportional to *V*.

158   *Reproduction.* Each female has 2 sons and 2 daughters, each of which receives a set of alleles from its

159   parents by unlinked Mendelian inheritance. Alleles mutate with independent probability *μ*, such that

160   new allelic values are drawn from a bounded (between 0 and 1) normal distribution centered around

161   the previous value, with standard deviation *σ*. Each male is assigned to a randomly chosen size class,

162   such that different alleles are exposed to selection over generations. The next generation is formed by

163   randomly sampling *N* offspring of each sex. The remaining offspring are discarded.

164   In the final time step of each simulated population, we calculate the allometric slope *b* from the

165   regression of log(*y*) on log(*x*). Results show arithmetic means across 800 replicate simulations. Each

166   replicate ran for 1000 generations, by which time an evolutionary equilibrium had been reached.

167   The results confirm the intuition that a 'baseline' mating success, achievable for males of any

168   phenotype, should select for positive allometry, but with some interesting details. Allometric slopes

169   evolved to be steepest at an intermediate frequency of uncontested matings. They also became steeper

170   when competitive interactions involved more males at a time and when, within these competitive

171   groups, traits were decisive predictors of mating success (Figure 2). These results are understandable

172   once realizing that the central result, that positive allometry is found when males should gain some

173   fitness even if their traits are poor, cannot be extrapolated to the extreme: totally randomly determined

174   mating success (achievable by setting *q* to its logical maximum of 1, or alternatively *n* to its minimum of

175   1) would obviously not select for positive allometry but for the absence of traits. Mean trait size indeed

176   evolved to higher values when uncontested matings were rare (low *q*), when competitive interactions

177 involved more males at a time (high *n*), and when trait differences decisively determined the outcome of

178 competitive interactions (high β) (Figure 3).

Discussion

180 Our models show that positive allometry in secondary sexual traits evolves easily if a male's expected

181 baseline mating success in the absence of the trait is greater than zero. There are many possible reasons

182 why this may be so. Males may occasionally be simply in the right place at the right time, when

183 competitors are absent and a female requires sperm (Wedell et al. 2002; Rhainds 2010). Females may

184 also vary in their preferences (Jennions and Petrie 1997), which is important in the current context as it

185 often implies that some matings will occur in a more random fashion than others. For example, females

186 in better condition are often documented to be choosier (Cotton et al. 2006), or some females are

187 forced to make more hurried mate choice decisions than others; in either case, from the male

188 perspective, some matings are more contested than others (e.g. buff-breasted sandpiper females mate

189 both on leks and outside them, Lanctot et al. 1997).

190 Similar arguments apply to mating systems characterised mainly by male-male competition. In these

191 systems, too, a male may sometimes find himself with a female and no other males nearby, while at

192 other times secondary sexual traits such as weaponry determine mating success. Females may even

193 benefit from mating with males with smaller sexual traits, if the underlying genes are subject to intra-

194 locus sexual conflict (e.g., Harano et al. 2010). Another possible reason for non-zero baseline mating

195 success is the existence of alternative male reproductive tactics, some of which may be independent of

196 trait size or may even be hindered by large traits (Oliveira et al. 2008).

197 Finally, sexual selection can also occur simply via the ability of males to locate females (e.g. Jennions et

198 al. 2012). Although not directly addressed in our simulation, this scenario is still covered by our

199 analytical argument. Again, a positive (albeit perhaps low) mate encounter rate is then expected even if

200 a male only moves for naturally selected reasons (e.g. foraging). Consequently, adaptations that

201 enhance a male's ability to find females — such as olfactory sensitivities of male moths, or locomotory

202 performance — also fall into the category of traits for which positive allometry is expected, although

203 measuring the trait size might prove challenging in these cases.

204 How does our model relate to previous theory? In an exercise of theoretical reverse-engineering, Kodric-

205 Brown et al. (2006) showed how the assumption that a given allometric pattern is optimal can be

206   mathematically rephrased in terms of the optimality of underlying growth decisions during ontogeny.

207   Their model did not, however, investigate whether selection would favour one or another sign of the

208   allometric relationship. They conclude that positive allometries are the inevitable result of differential

209   allocation to structures that enhance mating success, but this appears to rest on the assertion that "*by*

210   *definition* [emphasis added], exaggerated structures exhibit positive allometries". This raises the

211   question of whether, if one had arbitrarily made the opposite definition, one could have derived an

212   incorrect prediction that sexual selection favours 'non-exaggerated structures' with negative

213   allometries. Our present model addresses the gap in this argument, by letting the sign of the

214   relationship evolve, which allows a first test of the explanatory power of any evolutionary argument:

215   does it produce the pattern that prevails in nature, if alternatives are in principle allowed as well.

216   In this context, the important precursor for our work is Bonduriansky and Day's (2003) model that

217   includes an explicit account of growth trajectories. Although their model only rarely produced positive

218   allometry, this difference proves rather superficial: our analysis shows that including a nonzero baseline

219   mating success for males would easily produce positive allometry in their model too.

220   It is important to note that a positive baseline expectation for male mating success for all males does

221   not translate into an empirical prediction that all males in a specific sample must mate at least once. The

222   actual distribution of matings will heavily depend on the operational sex ratio. Consider, for example,

223   three males competing for two females. Even if all have some chance of succeeding, it is not possible (if

224   females only mate with one male each), for all males to secure a mating. It is consequently a

225   considerable empirical challenge to verify our assumption that small traits do not completely preclude

226   mating success: the expected distribution of matings under $c = 0$ and a small positive value of c can look

227   very similar. Indirect tests may prove easier: our model makes several predictions regarding the strength

228   of the allometric relationship. Currently, we are not aware of datasets suited to testing our prediction

229   that the relationship is at its steepest when a substantial proportion of matings are uncontested (the

230   sire is determined through random processes) but, as a whole, there remains a reliable relationship

231   between trait size and mating success. Additionally, to clarify empirically to what extent observed trait

232   sizes are optimal for males of different sizes, experimental manipulation of growth patterns (e.g., Emlen

233   et al. 2012; Kijimoto et al. 2012), combined with measurements of lifetime reproductive success (e.g.,

234   Rodriguez-Munoz et al. 2010) would be extremely valuable.

235 To drive home the intuitive message of our model, we conclude with an analogy that compares mating

236 competition with competitive sports. It is a conspicuous fact that professional athletes, despite

237 presumably being much more talented at their discipline than the average person, also invest a lot more

238 time and energy in improving their skill. One reason for this is that the rewards of improvement are

239 greatest for potential champions, for whom this can make the difference between becoming actual

240 champions or not. Compared to this, recreational athletes invest a lot less, presumably because skill

241 improvement does not make as big a difference to them. The point of this analogy is to provide a sense

242 of why those individuals with the best a priori chances of winning should also invest most in doing so.

243 Note that this argument works only if individual who don't excel at competing can obtain alternative

244 rewards, namely from a regular job (in the sport context), or in terms of baseline mating success (in the

245 sexual selection context).

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312

313   Figure legends

314   Figure 1. Fitness can be interpreted graphically as the area of a rectangle with dimensions $M \times V$. In
315   the special case depicted here, where each dimension can be increased at a constant and equal cost
316   ($f_V=f_M$), the optimal allocation strategy prescribes that the rectangle be a square. If reproductive rate is
317   proportional to the size of a secondary sexual trait, and if a non-zero baseline reproductive rate *c* applies
318   in the absence of the trait, then resource allocation (represented by dashed lines) should be biased
319   towards lifespan, but less so if the resource budget is large (compare total number of dashes, and their
320   contribution to each dimension, from left to right panel). If the resource budget reflects body size, this
321   predicts positive allometry.

322   Figure 2. Allometry at evolutionary equilibrium, as a function of the frequency of uncontested matings,
323   *q*. Males compete in groups of *n*=2 (dash-dotted), *n*=4 (solid), *n*=8 (dashed) or *n*=16 (dotted). The
324   decisiveness of trait differences in controlling the outcome of competition increases from A (β=1) to B
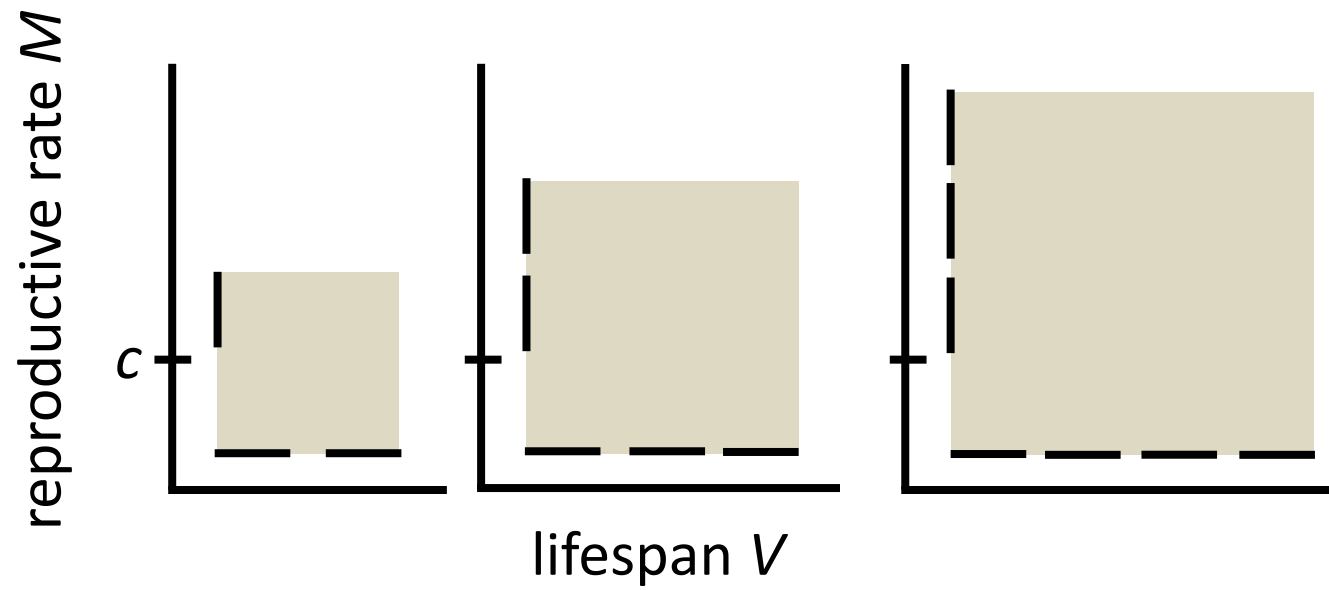325   (β=2) to C (β=4). Other parameter values: *N*=500; μ=0.02; σ=0.01, *s*=5.

326   Figure 3. Mean trait size at evolutionary equilibrium, as a function of the frequency of uncontested

327   matings, q. Males compete in groups of $n=2$ (dash-dotted), $n=4$ (solid), $n=8$ (dashed) or $n=16$ (dotted).

328   The decisiveness of trait differences in controlling the outcome of competition increases from A (β =1)

329   to B (β =2) to C (β =4). Other parameter values: N=500; μ=0.02; σ=0.01, s=5.
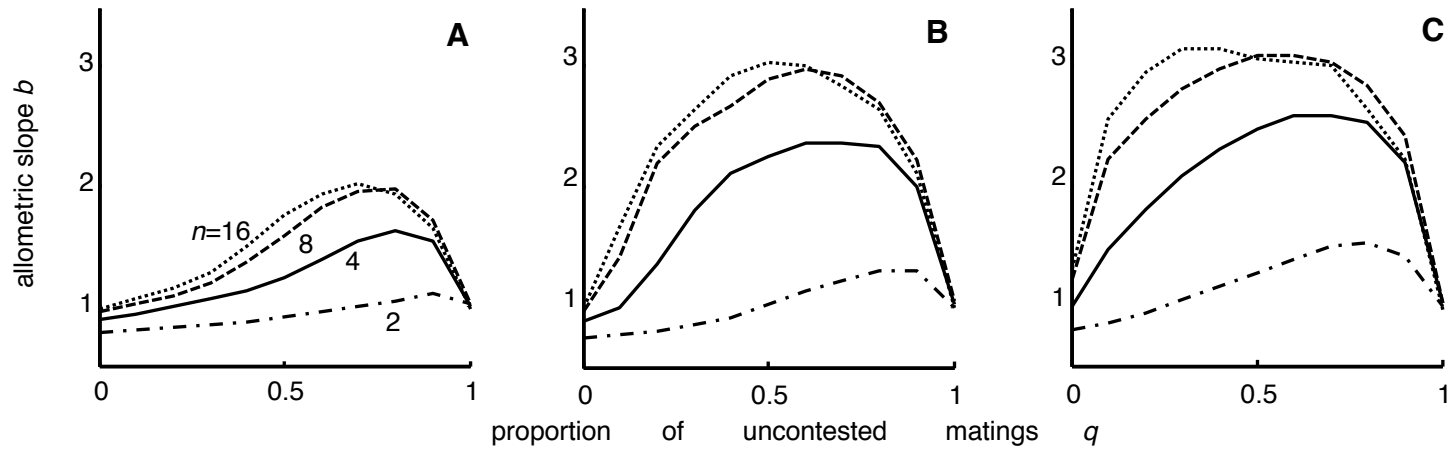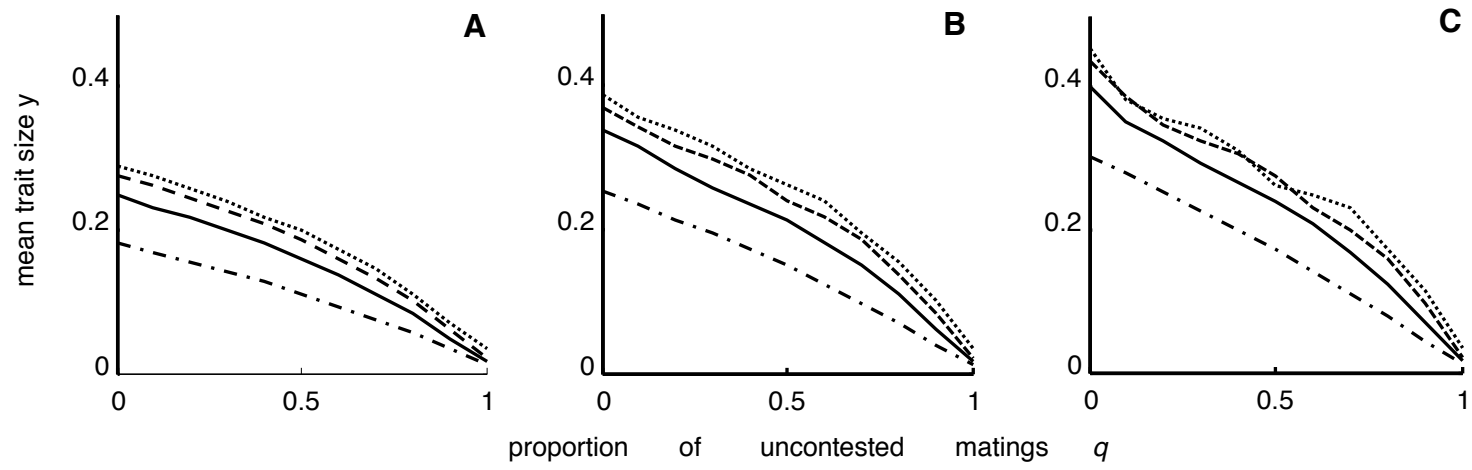
Figure 1

Figure 2

Figure 3