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Smallegange, I.M.; Johansson, J.

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Life-History Differences Favor Evolution of Male Dimorphism in Competitive Games

Isabel M. Smallegange^{1,*} and Jacob Johansson²

1. Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94084, 1090 GB Amsterdam, The Netherlands;
2. Department of Biology, Theoretical Population Ecology and Evolution Group, Ecology Building, Lund University, SE-22362 Lund, Sweden

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ABSTRACT: Many species exhibit two discrete male morphs: fighters and sneakers. Fighters are large and possess weapons but may mature slowly. Sneakers are small and have no weapons but can sneak matings and may mature quickly to start mating earlier in life than fighters. However, how differences in competitive ability and life history interact to determine male morph coexistence has not yet been investigated within a single framework. Here we integrate demography and game theory into a two-sex population model to study the evolution of strategies that result in the coexistence of fighters and sneakers. We incorporate differences in maturation time between the morphs and use a mating-probability matrix analogous to the classic hawk-dove game. Using adaptive dynamics, we show that male dimorphism evolves more easily in our model than in classic game theory approaches. Our results also revealed an interaction between life-history differences and sneaker competitiveness, which shows that demography and competitive games should be treated as interlinked mechanisms to understand the evolution of male dimorphism. Applying our approach to empirical data on bulb mites (*Rhizoglyphus robini*), coho salmon (*Oncorhynchus kisutch*), and bullhorned dung beetles (*Onthophagus taurus*) indicates that observed occurrences of male dimorphism are in general agreement with model predictions.

Keywords: alternative reproductive phenotypes, environmental threshold model, evolutionarily stable strategy (ESS), polymorphism, threshold trait, two-sex population model.

Introduction

In many species, males compete vigorously among each other for access to females (Andersson 1994). As a result of strong male-male competition, evolution may give rise to alternative reproductive tactics (ARTs) within the male sex of a species. Male ARTs are found in many taxa, and if ARTs are composed of different phenotypes, males typically belong to one of two alternative morphs: fighters or sneakers (Oliveira et al. 2008). Fighters are large and pos-

sess morphological structures that are used as weapons in male-male competition, whereas sneakers are smaller, lack (large) weapons, and adopt a sneaker strategy to gain access to females. In salmonid fishes, for example, sneakers spawn surreptitiously (Gross 1991), whereas in horned dung beetles, sneakers find females by circumventing and bypassing fighters that guard tunnel entrances containing a breeding female (Moczek and Emlen 2000).

The majority of male dimorphisms are controlled by a conditional strategy (Tomkins and Hazel 2007; Oliveira et al. 2008). The environmental threshold (ET) model is currently at the forefront as a means to understand the evolution of conditional strategies (Tomkins and Hazel 2007; Buoro et al. 2012). The model was conceptualized more than 30 years ago (Hazel 1977; Hazel et al. 1982) and formalized mathematically in 1990 and 2004 (Hazel et al. 1990, 2004). The model can take into account frequency-dependent selection and can be used to model both the trajectory and the outcome of selection on a conditional strategy (Hazel et al. 2004). Its results are almost identical to those of an earlier model on the conditional strategy (Lively 1986), but unlike the latter model, the ET model uses quantitative genetic theory (Hazel et al. 1990, 2004). The ET model is based on the premise that male morph expression depends on whether or not an individual reaches a critical threshold, or switch point, during ontogeny. This threshold is assumed to be under polygenic control and is influenced by a cue such as body size or hormone level. If an individual reaches the threshold, then it develops into a fighter; otherwise, it develops into a sneaker.

Apart from differences in competitive ability, another prominent difference between fighters and sneakers is that sneakers can have a shorter maturation time than fighters (Gross 1991; Oliveira et al. 2008; Smallegange 2011a). This difference can be striking: in salmonid fishes, sneakers (jacks) return to the breeding grounds at least one breeding season earlier than fighters (hooknoses) born in the same

* Corresponding author; e-mail: i.smallegange@uva.nl.

cohort (Gross 1991). The growth rate of populations of male dimorphic species can be critically influenced by the demographic rates, including maturation rate, of alternative male morphs (Caswell and Weeks 1986). For example, by maturing early, sneakers not only avoid the extra mortality risk associated with prolonged development, but crucially, they can mate earlier in life than slow-maturing fighters. A higher proportion of sneaker males in a population can therefore reduce generation time and thereby increase the population growth rate (Caswell 2001). Earlier maturation and opportunity to mate, coupled with the fact that the mating successes of sneakers and fighters differ (Oliveira et al. 2008), also mean that a change in the proportion of sneakers likely affects mean lifetime reproductive success and thereby, again, population growth rate (Caswell 2001). Note that both inferences on how the proportion of sneaker males can affect population growth rate assume that populations have overlapping generations (reproduction can be discrete or continuous; Caswell 2001). Differences in maturation time between male morphs are not considered in the ET model, but given their links to per capita population growth rates and thereby to the differential capacities of competing strategies to invade or persist in invasions (McGill and Brown 2007), it is very likely that they affect the evolutionary outcome of male-male competition.

Despite the importance of life-history differences in male dimorphisms, these differences have also been left out in game-theoretic approaches to studying the evolution of male dimorphism (e.g., Maynard Smith 1982; Tanaka et al. 2009). Classic game-theoretical models predict that male dimorphism occurs when the costs of fighting to fighters are higher than the reward (hawk-dove game; Maynard Smith 1982), and this condition is relaxed to a certain extent when sneakers adopt a sneaker strategy (Tanaka et al. 2009). However, it is unclear how life histories and competitive games interact to shape variation in the incidence of male dimorphism. In order to shed light on this question, we investigate within a single framework how differences in maturation rate (which we take to be inversely proportional to maturation time) and competitive ability between fighters and sneakers affect the evolution of male dimorphism. We adopt the following three-step integrative approach. First, we model a stylized life cycle of a male dimorphic species. We use a density-dependent, two-sex population model to derive the demographic rates of adult females, fighters, sneakers, and the offspring they produce, zygotes. The proportion of zygotes that develop into fighters is denoted β ; thus, $0 < \beta < 1$ represents male dimorphism. We adopt a general approach where we assume that β is affected by natural selection but leave open the exact interpretation of the underlying mechanisms. The parameter β could, for ex-

ample, be determined by the threshold that determines male morph development in a conditional strategy (Tomkins and Hazel 2007). Given a certain regime of environmental variability, the lower the threshold, the more fighters are produced and the higher is β . A second possibility is to interpret β as intermediate between 0 and 1 as a strategy of alternative phenotype production by which parents impose a conditional strategy on their male offspring (Maynard Smith 1982, p. 73). Finally, an intermediate β could be viewed as the probability with which an individual switches its phenotype, that is, a probabilistic mixed strategy *sensu* Gross (1996; see “Discussion”). In our model, fighters and sneakers compete for mating opportunities, and the probability of successfully gaining access to females depends on a male’s own morph and the morph of its opponent. Because our model also includes differences in maturation rate between the two male morphs, which carry over to affect survival and fertility, our approach adds a demographic perspective to previous models based on game theory (Maynard Smith 1982; Tomkins and Hazel 2007) and adds a game-theoretical element to previous demographic models (Hutchings and Myers 1994). For our second step, we use adaptive dynamics to study evolution in the two-sex population model. Specifically, we investigate how the evolutionarily stable strategy (ESS; Maynard Smith and Price 1973) of β depends on (i) the strength of male-male competition, (ii) the costs to fighters of fighting, (iii) the benefit to sneakers of sneaking access to females, and (iv) the difference between sneakers and fighters in maturation rate. Third, we apply our approach to empirical data and use the results from steps one and two to investigate whether the model can explain the male dimorphism of three species that are commonly used as model systems to study male morph coexistence: the bulb mite (*Rhizoglyphus robini*), coho salmon (*Oncorhynchus kisutch*), and the bullhorned dung beetle (*Onthophagus taurus*).

Material and Methods

Two-Sex Population Model

Our stylized life cycle includes four discrete stage classes (fig. 1): zygotes, females, fighters, and sneakers, hereafter indexed z , x , f , and s , respectively. Their population densities are denoted n_i ($i = z, x, f, s$). Zygotes are undifferentiated with respect to sex or male morph. The proportion of zygotes that develops into males equals ρ , and the proportion of males that develops into fighters equals β . The rate at which zygotes of a certain class grow—that is, mature—into the adult stage is denoted G_i ($i = x, f, s$). Hence, the rate at which zygotes enter the female, fighter, and sneaker adult stages equals, respectively, $(1 - \rho) G_z$,

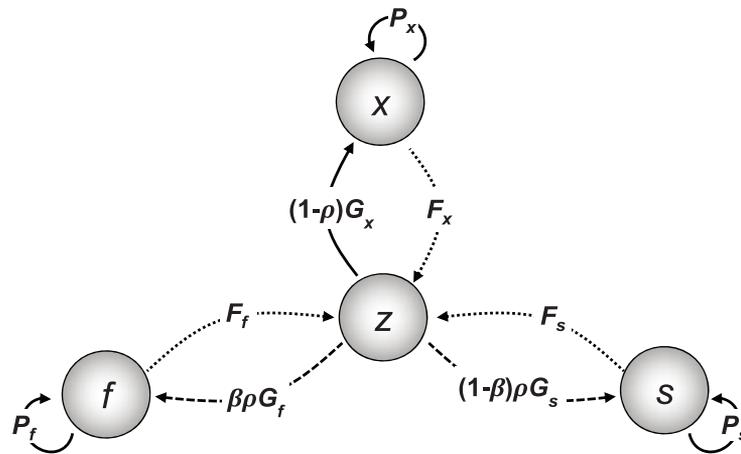


Figure 1: Stylized life cycle of a male dimorphic species. Females (x), fighters (f), and sneakers (s) produce zygotes (z) at rates F_i ($i = x, f, s$). Zygotes develop into females, fighters, or sneakers at rates that are set by the sex ratio (ρ) and male morph ratio (β). Terms P_i and G_i denote survival and maturation rates, respectively. As in all matrix population models, demographic rates are controlled by processes such as growth, survival, and fertility (solid lines denote rates that are controlled only by demography), but in our model, male maturation rates are additionally controlled by evolution (of β ; dashed lines), and fertility rates are additionally controlled by male-male competition (dotted lines).

$\rho\beta G_f$, and $\rho(1 - \beta) G_s$ (fig. 1). The rate of surviving and staying in the adult stage class equals P_i ($i = x, f, s$) (fig. 1). For simplicity, we assume that zygotes develop into adults within one time step so that $P_z = 0$.

Reproduction is described by fertility functions F_i ($i = x, f, s$) (fig. 1) composed of offspring production by females and the competitive interactions between fighters and sneakers, both of which are density and frequency dependent. We assume that the fertility functions depend on the number of births, $B_{x,j}$, that result from matings between females and males of morph j (Caswell 2001, p. 583). The female fertility function equals

$$F_x = \frac{1}{2n_x} \sum B_{x,j} = \frac{B_{x,s} + B_{x,f}}{2n_x}, \quad (1)$$

and the fertility function of a male of morph j equals

$$F_j = \frac{1}{2n_j} B_{x,j}. \quad (2)$$

In these functions, $B_{x,j}$ is assumed to depend on the clutch size k produced per mating (Caswell 2001, p. 584), the number of males of morph j that a female encounters per time step, $e_{x,j}$, and the probability that encounters between females and males of morph j result in successful matings, $p_{x,j}$:

$$B_{x,j} = kp_{x,j}e_{x,j}. \quad (3)$$

Density regulation occurs through clutch size, which is assumed to decrease with the density of females according to the function

$$k = \frac{k_0}{1 + n_x}, \quad (4)$$

where k_0 is the clutch size produced in the absence of competition. Note that we assume that clutch size is independent of the morph of a female's mate. We assume that a female encounters males of morph j at a rate that is proportional to the fraction of that type of male in the population: $n_j / \sum n_i$ (conforming to a law of mass action; see, e.g., Fredrickson 1971; Ruxton et al. 1992). We let e_0 denote the number of individuals (of any type) encountered by a focal individual per time step, and thus we have

$$e_{x,j} = e_0 \frac{n_x n_j}{\sum n_i} = e_0 \frac{n_x n_j}{n_x + n_s + n_f}. \quad (5)$$

Note that $e_{x,j}$ is proportional to the harmonic-mean birth function if there is only one male morph (Caswell and Weeks 1986). The probability that encounters between females and males of morph j result in successful matings, $p_{x,j}$, depends on the strength of male-male competition c_m . If $c_m = 0$, then there is no competition over breeding females and $p_{x,j}$ equals 1; if $c_m = 1$, then matings are preceded by competition between two males. For simplicity, we disregard the possibility that more than two males interact simultaneously. If $0 < c_m \leq 1$, then $p_{x,j}$ depends on the morph i of the opponent and the relative frequency of males of morph i in the population. This relative frequency is given by $n_i / (n_s + n_f)$. The matrix \mathbf{M} gives the probabilities that males of morph j (rows) gain

Table 1: Definitions of the demographic rates and parameters of the two-sex population model

Rate/parameter	Definition
β	Proportion of fighters in the male population
C	Fighter's costs defined as a reduced probability of gaining access to females
c_m	Strength of male-male competition
ε	Probability of sneaking successfully when opponents are fighters
e_0	No. individuals (of any type) encountered by a focal individual per time step
F_i	Reproduction rate of adults in stage class i
G_i	Maturation rate of zygotes of stage class i into the adult stage class i
k_0	Clutch size produced per mating in the absence of density dependence
P_i	Survival rate of adults in stage class i
ρ	Sex ratio
V	Probability of accessing a female in the absence of costs

Note: The subscript i denotes females (x), fighters (f), and sneakers (s).

access to the female when in competition with males of morph i (columns):

$$\mathbf{M} = \begin{bmatrix} m_{ff} & m_{fs} \\ m_{sf} & m_{ss} \end{bmatrix} = \begin{bmatrix} (V - C)/2 & V - \varepsilon \\ \varepsilon & V/2 \end{bmatrix}.$$

The above notation is similar to the classic hawk-dove game (Maynard Smith 1982), but note that our matrix entries are probabilities, which are bound between 0 and 1. Here V can be interpreted as the probability of accessing the female in the absence of costs. Under ideal conditions, $V = 1$. Two sneakers that interact suffer no costs and therefore have a probability $V/2$ of accessing the female. If two fighters interact, their probability of accessing the female equals $(V - C)/2$, where C represents a cost in the form of a reduction in the probability of gaining access to females. This means that a proportion C of these matings is unsuccessful, for example, because males are injured during the contest or because females are no longer present when a contest terminates. Fighters can defeat sneakers easily, but sneakers can sneak to gain access to females. In interactions between fighters and sneakers, sneakers gain access to the female with probability ε , and fighters gain access to the female with probability $V - \varepsilon$. The parameter ε is therefore the sneaker's advantage and poses a small cost to the fighters (note that ε is similar to the parameter G in the hooknose-jack payoff matrix of Tanaka et al. 2009). In experimental or field studies, ε can be measured as the probability that sneakers are able to mate successfully when competing with fighters for access to females (e.g., Hutchings and Myers 1988; Hunt and Simons 2001). Although, in theory, ε can be both 0 and 1 as it is a probability and therefore bounded by 0 and 1, in reality, the probability of sneakers mating successfully is low so that ε is low but not (very close to) 0. We assume that $\varepsilon < V$. Putting it all together, this gives

$$p_{x,j} = 1 - c_m + c_m \left(\frac{n_f}{n_s + n_f} m_{jf} + \frac{n_s}{n_s + n_f} m_{js} \right). \quad (6)$$

The resulting population projection matrix includes all demographic rates (i.e., survival, growth, and reproduction rates) of the four stage classes and takes the form

$$\mathbf{A} = \begin{bmatrix} 0 & F_x & F_f & F_s \\ (1 - \rho)G_x & P_x & 0 & 0 \\ \beta\rho G_f & 0 & P_f & 0 \\ (1 - \beta)\rho G_s & 0 & 0 & P_s \end{bmatrix}. \quad (7)$$

Our two-sex population model is then defined by $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$, where \mathbf{n}_t is the population vector at time t , and \mathbf{A}_t is the projection matrix at time t defined by the current population vector. Definitions of all demographic rates and parameters are provided in table 1.

Evolutionary Dynamics

In order to find the evolutionarily stable strategy of β , β_{ESS} , we used the adaptive dynamics approach as outlined in Geritz et al. (1998). This approach assumes that there is a resident population with trait value β that is in a dynamical equilibrium when new mutants appear. Whether or not mutants with trait value β' are able to successfully invade the resident population depends on their initial population growth rate at the moment of invasion. Here this population growth rate, $W(\beta', \beta)$, is given by the dominant eigenvalue of the matrix \mathbf{A} of the invading population with trait value β' in the environment set by the resident population at equilibrium (cf. Kisdi 2002). The direction of evolutionary change is determined by the selection gradient, which is defined as the slope of $W(\beta', \beta)$ with regard to the variant trait at $\beta' = \beta$: $h(\beta) = \partial W(\beta', \beta) / \partial \beta' |_{\beta' = \beta}$. If the selection gradient is positive (negative), then a mutant with a slightly higher (lower) trait value will invade and replace the resident. In adaptive

dynamics as well as other approaches to studying gradual evolution, for example, quantitative genetics (Lande 1982; Abrams et al. 1993), candidate evolutionary endpoints are found where the selection gradient equals zero. If this point is furthermore resistant to invasions as well as an attractor for gradual evolution (convergence stable), then it can, following McGill and Brown (2007), be considered an ESS. Strategies for which the selection gradient vanishes in our model are convergent stable, but once adopted by the resident population, they are evolutionarily neutral, that is, they have the same fitness (here, population growth rate) as any variant strategy (eqq. [A13]–[A21]; eqq. [A1]–[A27] available in the online appendix). In the context of adaptive dynamics, such evolutionary neutrality represents a special limiting case between an ESS and an evolutionary branching point (cf. Geritz et al. 1998), and it has been shown that they can turn into an invasion-resistant strategy through only slight adjustments of the model structure (Dieckmann and Metz 2006). The implications of the emerging fitness equality are also well studied in the context of classic game theory (Bishop and Cannings 1978), as it is a common outcome of many classic matrix games, including the original hawk-dove game. In keeping with the original notation of Maynard Smith (1974), however, we refer to these endpoints as ESSs from this point forward. In “Results” below, we explore different scenarios to investigate how β_{ESS} depends on (i) the strength of male-male competition (c_m), (ii) the fighter’s costs (reduced probability of gaining access to females; C), (iii) the probability of sneaking successfully (ε), and (iv) the difference in maturation rate between fighters and sneakers (measured as the ratio G_f/G_s). For these cases, we assumed equal survival rates for the different adult classes, that is, $P_f = P_s = P$.

Male Dimorphism in Bulb Mites, Coho Salmon, and Bullhorned Dung Beetles

Using our approach, we investigated for which values of c_m , ε , and C there is an evolutionarily stable male dimorphism in bulb mites, coho salmon, and bullhorned dung beetles. Fighters in the bulb mite have a thickened and sharply terminated third pair of legs, which they can use to kill other males (Radwan et al. 2000). Sneaker bulb mites, which are called scramblers, are defenseless with unmodified legs (Smallegange 2011a). Fighter coho salmon are called hooknoses and have well-developed secondary sexual characters, including elongated jaws, which they use in fighting for access to females (Gross 1991). Sneaker coho salmon, or jacks, show little development of secondary sexual characters, are considerably smaller than hooknoses, and adopt a sneaker strategy to gain access to females (Gross 1991). In turn, fighter bullhorned dung beetle males (major males)

have large head horns that they use to fight for access to females, whereas the smaller sneaker bullhorned dung beetle males (minor males) are hornless and sneak copulations (Moczek and Emlen 2000). Importantly, in all three species, fighters have a longer maturation time (and, hence, lower maturation rate) than sneakers (Gross 1991; Hunt and Simmons 1997; Smallegange 2011a; table A1, available online), fulfilling a crucial assumption of our model. Furthermore, in all three species, male morph development depends on whether males reach a critical size threshold during ontogeny (Gross 1991; Moczek and Emlen 2000; Smallegange 2011a), which means that a conditional strategy best matches each male dimorphism. Both genetic and environmental factors may influence the position of the threshold within the body size distribution of males of each species (Koseki and Fleming 2006; Smallegange 2011a; Smallegange and Coulson 2011), suggesting that the underlying threshold for male morph expression is a polygenic trait, which matches the assumptions of the ET model (Tomkins and Hazel 2007). Note that although Smallegange and Coulson (2011) assumed, based on Radwan (1995), that the male dimorphism in the bulb mite is a genetic polymorphism, we now know that environmental conditions play a large role in male morph expression in the bulb mite dimorphism. Details on model parameterization for each species and on finding β_{ESS} can be found in the appendix. (All data used for model parameterization are taken from published studies, with references listed in table A1. Data underlying table A1 are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.81m7r> [Smallegange and Johansson 2014].)

Results

Evolution of Male Dimorphism

First, we derived the dynamic equilibrium of the resident population (eqq. [A1]–[A4]), after which we performed the evolutionary analysis. Next (eqq. [A5]–[A12]), we show that the sign of the selection gradient, and thus the direction of evolution of β , is controlled by a factor that we denote Q :

$$Q = (G_f - G_s)(1 - c_m) + \frac{c_m[\beta G_f^2(V - C)/2 + (1 - \beta)G_f G_s(V - \varepsilon) - (1 - \beta)G_s^2 V/2]}{\beta G_f + (1 - \beta)G_s}. \quad (8)$$

If Q is positive (negative) for all values of β in the interval between 0 and 1, then $\beta_{\text{ESS}} = 1$ ($\beta_{\text{ESS}} = 0$) and all males are fighters (sneakers). If $Q = 0$ for some value of β between 0 and 1, then it corresponds to an evolutionarily stable male dimorphism. Because the solution to $Q = 0$

is not immediately obvious, we study it for different scenarios of increasing biological complexity.

In the simplest scenario, there is no male-male competition so that $c_m = 0$. Equation (8) then simplifies to

$$Q = G_f - G_s. \tag{9}$$

With a lower maturation rate (due to longer maturation time) for fighters compared to sneakers, we have $G_f < G_s$ and hence $Q < 0$. This means that at the endpoint of evolution, $\beta_{ESS} = 0$ and there are only sneakers.

Next, we consider two scenarios in which males always compete prior to mating so that $c_m = 1$. First, we assume equal maturation rates of fighters and sneakers ($G_f = G_s$), and the solution to $Q = 0$ (eq. [8]) occurs when (eqq. [A22], [A23])

$$\beta = \frac{V - 2\varepsilon}{C}. \tag{10}$$

According to equation (10), the ESS is intermediate ($0 < \beta_{ESS} < 1$) when

$$V - 2\varepsilon < C. \tag{11}$$

In this case, we therefore have coexistence either due to a sneaker advantage (large ε), high fighter costs (C), or a combination thereof. When there is no sneaker advantage ($\varepsilon = 0$), the condition for a male dimorphism in our model simplifies to that of the classic hawk-dove game (Maynard Smith 1982): $V < C$ (but note that in our model, V and C are probabilities, whereas in the hawk-dove game, V is the gain in fitness and C represents fitness costs).

In our second male-male competition scenario, we assume that fighters have a lower maturation rate than sneakers so that $G_f < G_s$. Then $Q = 0$ when (eq. [A24])

$$\beta = \frac{V(G_f/G_s) - V/2 - \varepsilon(G_f/G_s)}{V(G_f/G_s) - V/2 - (G_f/G_s)^2(V - C)/2}. \tag{12}$$

According to equation (12), an intermediate β_{ESS} ($0 < \beta_{ESS} < 1$) exists when (eq. [A25])

$$V - \frac{2\varepsilon}{G_f/G_s} < C. \tag{13}$$

This inequality summarizes how key parameters influence the evolution of male dimorphism in our model. Male dimorphism is favored when fighter's costs (C) are high and the sneaker advantage (ε) is strong (fig. 2), in which case the number on the left-hand side of equation (13) is low. In contrast, the ESS is a monomorphic fighter population when C and/or ε are low (fig. 2). A higher maturation rate of the sneaker morph ($G_s > G_f$) reduces the ratio G_f/G_s and therefore reduces the number on the left-hand side of equation (13), however. The consequences of this for the evolution of male dimorphism are that as

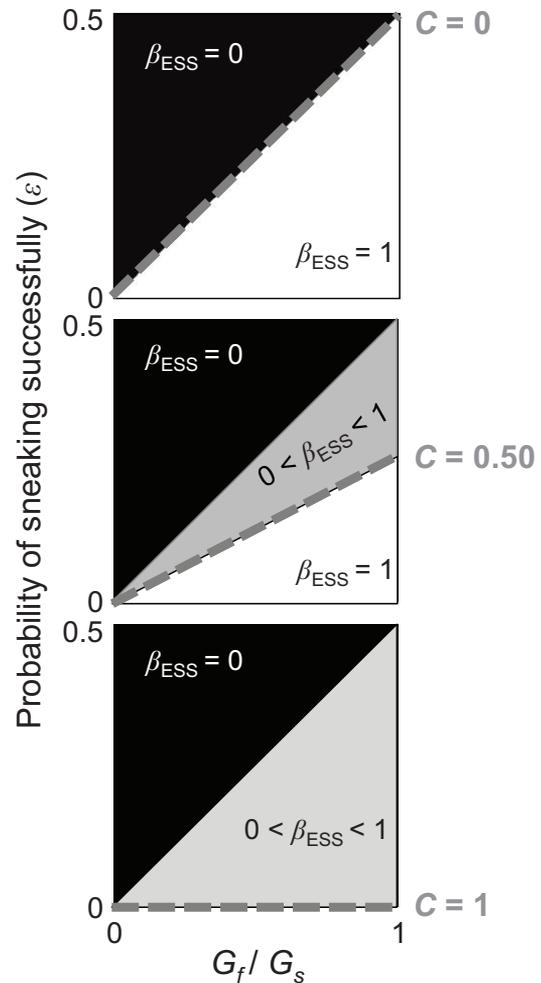


Figure 2: Effects of different maturation rates of fighters and sneakers on the evolutionary outcome of β . Plotted is the probability of sneaking successfully, ε , against G_f/G_s , the ratio of fighter to sneaker maturation rate. Above the diagonal, denoted by the black region, $V - 2\varepsilon/(G_f/G_s) < 0$ and $V G_f/G_s - V/2 - \varepsilon G_f/G_s < 0$ (see eqq. [12] and [13]), and the evolutionary endpoint is a male population consisting of only sneakers. In the gray and white regions, $V G_f/G_s - V/2 - \varepsilon G_f/G_s > 0$ (see eq. [12]). If at the same time $V - 2\varepsilon/(G_f/G_s) < C$ (eq. [13]), where C is the costs of fighting to fighters, male dimorphism is the evolutionary outcome. If, however, $V - 2\varepsilon/(G_f/G_s) > C$, then the evolutionary outcome is a male population comprising only fighters. Two examples are given in the middle and lower panels. The gray dashed lines in each panel denote where $V - 2\varepsilon/(G_f/G_s) = C$. In the middle panel, $C = 0.5$. Above this line (and below the diagonal), male dimorphism is the evolutionary outcome (gray region), and below this line, the evolutionary outcome is a male population of only fighters (white region). In the bottom panel, $C = 1$, and now the evolutionary outcome is either male dimorphism (gray region) or only sneakers (black region), depending on whether $V - 2\varepsilon/(G_f/G_s)$ is positive or negative. In all cases, $c_m = 1$ (strength of male-male competition) and $V = 1$ (probability of accessing a female in the absence of costs).

long as $C > 0$, male dimorphism occurs at lower values of ε as the ratio of G_f/G_s decreases (fig. 2). Furthermore, the ESS can also be a monomorphic sneaker population, and this is particularly likely to occur at low values of G_f/G_s (fig. 2). Overall, these results highlight that increased per capita population growth rates owing to a higher maturation rate of sneakers can favor the evolution of male dimorphism even in cases where C and/or ε are low. The inequality in equation (13) also shows that there is an interaction between differences in maturation rate (G_f/G_s) and the sneaker advantage (ε) since these factors occur as a quotient in this equation. Thus, male dimorphism is more likely to occur at low values of ε when the ratio G_f/G_s is low, whereas the effect of changing only one of these parameters is less when the other parameter is low. In contrast, the parameters C and V act independently from other parameters in the condition for an ESS of male dimorphism (eq. [13]). Note that, again, when there is no sneaker advantage ($\varepsilon = 0$), the condition for a male dimorphism simplifies to that of the classic hawk-dove game (Maynard Smith 1982). However, it is unlikely that ε equals 0 as sneakers are typically able to gain access to females to mate, although the probability of their succeeding at doing so is much lower than for fighters (Oliveira et al. 2008).

Empirical Test of the Model

We explored the evolution of male dimorphism in bulb mites, coho salmon, and bullhorned dung beetles in relation to the strength of male-male competition, c_m , and the probability of sneaking successfully, ε , for three values of the fighter's costs, C . In the bulb mite, regardless of the value of C , $\beta_{\text{ESS}} = 0$ for low values of c_m and high values of ε (fig. 3). Male dimorphism occurs ($0 < \beta_{\text{ESS}} < 1$) at higher values of c_m and lower values of ε : the higher the value of C , the larger is the parameter space for the occurrence of a male dimorphism (fig. 3). The results for coho salmon are similar, except that the parameter space where evolution favors male dimorphism is smaller than in the case of the bulb mite (fig. 3). In the bullhorned dung beetle, in contrast, the region of parameter space where male dimorphism is favored is much larger than in the coho salmon and the bulb mite (fig. 3). What is more, at higher values of C , male dimorphism is the most likely evolutionary outcome for the bullhorned dung beetle (fig. 3).

Discussion

The Role of Demography in the Evolution of Male Dimorphism

Demography is central to understanding phenotype evolution because survival and fertility can differ between

phenotypes, and this has consequences for population growth. Here we combined demography and game theory to investigate the evolution of male dimorphism. Our analysis revealed that male dimorphism is favored not only when the sneaker's advantage is high or when fighter costs are high but also when sneakers have a shorter maturation time and thereby higher maturation rate than fighters. This means that male dimorphism can evolve more easily in our model than in approaches based on classic game theory (Maynard Smith 1982; Tanaka et al. 2009), in which differences in maturation time are not taken into account. Our analysis also showed that the effect of life-history differences on the evolutionary outcome can be enhanced by a high sneaker's advantage (eq. [13]). This result underscores the fact that demography and competitive games should be treated as interlinked mechanisms to understand the evolution of male dimorphism, at least for species with overlapping generations. For male dimorphic species that have nonoverlapping generations (e.g., Dawson's burrowing bee [*Amegilla dawsoni*]; Alcock 1999), all individuals of the current generation, by definition, reach maturation before they are replaced by the next generation; maturation time is therefore independent of generation time. For those species, the population growth rate is determined by the per capita number of offspring produced (Stearns 1992). Thus, only if maturation times cause differences in reproductive output among male morphs will they influence the evolution of male dimorphism when generations are nonoverlapping.

In our approach to understanding the evolution of male dimorphism, we take into account demographic differences between the male morphs and incorporate a mechanistic mate competition model to arrive at the ESS of the proportion of fighter zygotes (β). The ET model ignores these aspects but specifies how male morph fitness varies with changing environmental conditions and also includes the genetic architecture of the threshold (and β ; Tomkins and Hazel 2007). Both the ET model and our approach increase our understanding of the evolution of male dimorphism. The logical next step would be to merge the two and consider a model that takes into account all aspects important for understanding the evolution of male dimorphism.

Influence of the Environment

We have been agnostic as to where in the life cycle the environment influences the threshold for male morph expression and hence the proportion of fighter zygotes, β . The first and most common case, which is assumed by the ET model, is that the environment influences whether individuals pass the threshold for male morph expression during ontogeny. In that case, β is composed of the pro-

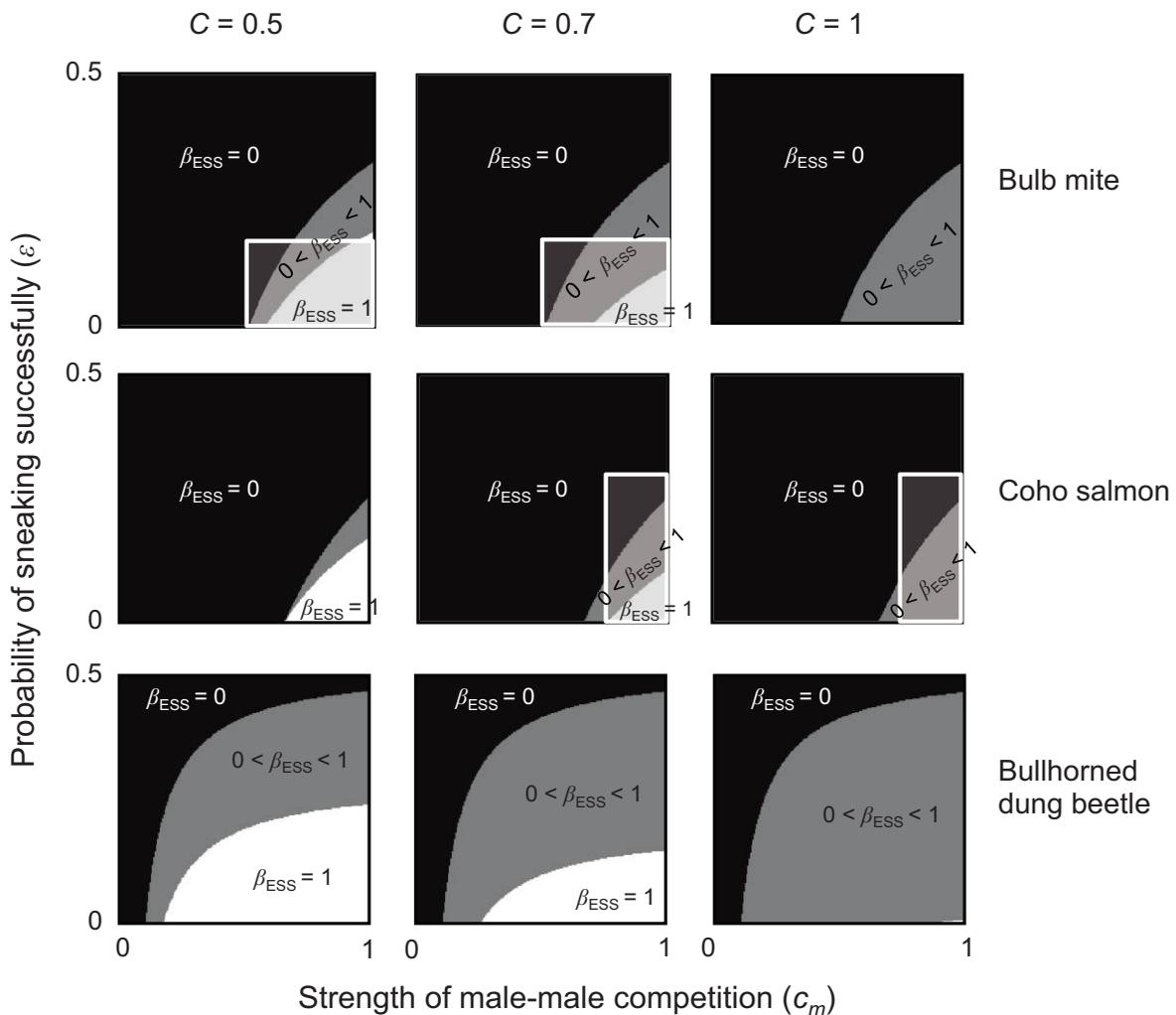


Figure 3: Male dimorphism in bulb mites, coho salmon, and bullhorned dung beetles. Plotted is the probability of sneaking successfully, ϵ , against the strength of male-male competition, c_m , for three different values of C , the fighter’s costs. Male dimorphism occurs in the gray region ($0 < \beta_{ESS} < 1$), whereas sneakers are produced only in the black region ($\beta_{ESS} = 0$) and fighters only in the white region ($\beta_{ESS} = 1$). For each species, the region of male dimorphism increases with increasing values of C . Boxes in panels indicate parameter space for estimated values of ϵ , c_m , and C (see “Discussion”). See online appendix for parameter values.

portion of fighters in the male population in a given, variable environment. Second, the environment could influence parental decisions to invest differentially into offspring so that some of an individual’s sons emerge as sneakers and the remainder as fighters. The parameter β then represents the proportion of fighter sons produced by an individual. Maynard Smith (1982) suggests such a scenario for species where parents provide their offspring with a brood mass that contains all the nutrition necessary for the offspring’s development (e.g., Dawson’s burrowing bee [Tomkins et al. 2001]). He hypothesizes that in those species, females can impose a conditional strategy on their sons by regulating the quantity of food supplies: males

provided with ample food develop into fighters, whereas individuals provided with limited food are unable to develop weapons and become sneakers. In this scenario, sneakers have their own fitness merits, at least from the point of view of their parents in terms of the number of grandchildren they have. This would explain why, even in the most favorable environments, evolution does not always lead to populations where all males are fighters (Smallegange 2011a). Third and finally, the influence of the environment could be greatest during the adult phase when individuals switch phenotype in a probabilistic manner. This switching probability is then represented by β . Gross (1996) termed this strategy a probabilistic mixed

strategy, but he found no empirical examples of this occurring in nature.

Our model also does not explicitly include environmental cues involved in determining the threshold for male morph expression. In many species, body size is the predominant cue for male morph expression (Oliveira et al. 2008), and this is what we implicitly assumed in our model. In some species, however, population density is the most important cue, and high population density can suppress the fighter morph (Radwan 1995, 2001; note that male morph expression in the bulb mite and the bullhorned dung beetle is independent of population density [Radwan 1995; Buzatto et al. 2012], although to our knowledge, it is not known how population density affects male morph expression in coho salmon). Given these contrasting effects of population density on male morph expression and the fact that the role of population density in the evolution and maintenance of alternative reproductive tactics is likely underestimated (Kokko and Rankin 2006), future modeling efforts should aim to investigate the role of population density in the evolution of male dimorphism.

Applying the Model to Empirical Data

If life tables and empirical data on mating success are available, our model can be used to predict the occurrence of male dimorphism. Here we applied our model to three species, the bulb mite, coho salmon, and the bullhorned dung beetle, and in what follows we discuss whether our findings are biologically realistic. In the bulb mite, no precopulatory sneaker's advantage has been reported (Radwan 2009), although sneakers are occasionally able to displace fighters to gain access to females ($\hat{\epsilon}_{\min} = 0$; $\hat{\epsilon}_{\max} = 0.2$; Smallegange et al. 2012). Fighter bulb mites are competitively superior, but this means that the fighter's costs, in terms of being displaced from the mating position by another fighter, can be high ($\hat{C}_{\min} = 0.1$; $\hat{C}_{\max} = 0.7$; Smallegange et al. 2012). No exact figure on the strength of male-male competition in bulb mites exists. However, c_m is likely to be high ($\hat{c}_m > 0.5$), as during continuous behavioral observations, both fighters and sneakers tried repeatedly to prevent their opponent from accessing females (Smallegange et al. 2012). In light of these together, we find that male dimorphism in the bulb mite is evolutionarily stable at high C ($0.5 \leq C \leq 0.7$; fig. 3) and that, at very high C ($C = 0.7$), male dimorphism is more likely to evolve than male monomorphism, where the male population is composed of only fighters or only sneakers (fig. 3). In bulb mite populations that exist under conditions identical to those under which we measured, the model parameters are indeed composed of both fighters and sneakers (Smallegange 2011a). Competition between

males in male dimorphic salmonids such as coho salmon is very high ($\hat{c}_m \geq 0.8$), and since fighter males are able to kill their opponents, the costs of fighting for fighters is likely also high ($C \geq 0.7$; Gross 1991). We did not find estimates for the mating success of sneaker coho salmon. However, in two other salmonids, the mating success of sneakers when competing with fighters was estimated to be 0.20 ($\hat{\epsilon} = 0.20$) in *Oncorhynchus tshawytscha* (Berejikian et al. 2010) and to range from 0.05 to 0.30 in *Salmo salar* ($\hat{\epsilon}_{\min} = 0.05$; $\hat{\epsilon}_{\max} = 0.30$; Hutchings and Myers 1988). Again, we find that these parameter ranges overlap with the regions where we expect an evolutionarily stable male dimorphism in coho salmon (fig. 3). Finally, as in the bulb mite and coho salmon, male-male competition in the bullhorned dung beetle is intense (Moczek and Emlen 2000), but we were unable to find estimates for the costs of fighting to fighters and the benefit of sneaking to sneakers. Nevertheless, across the whole parameter space that we investigated, male morph coexistence was the most likely evolutionary outcome, particularly for higher costs of fighting to fighters (fig. 3). These results are rewarding and strengthen the applicability of our model. The realism of our model can be further increased by including physical costs of fighting (injury, death) and the influence of sire morph on clutch and egg sizes (cf. Smallegange 2011a) and by relaxing the assumption that competition always occurs between two males. Also, because sneakers and fighters can differ in other life-history traits such as longevity and survival rate (Radwan and Bogacz 2000; Munguía-Steyer et al. 2010) or not differ in maturation time but in their growth rate instead (Radwan et al. 2002), these should be considered in future work on the evolution of male dimorphism.

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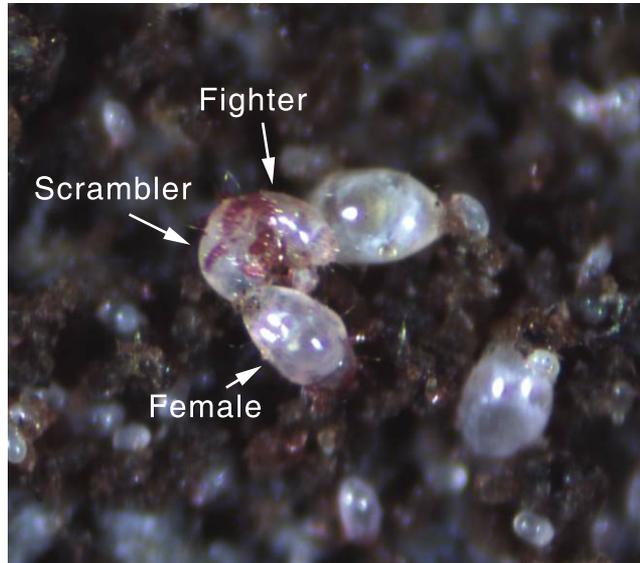
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Competition between fighter and scrambler (sneaker) male bulb mites (*Rhizoglyphus robini*). The scrambler male is mating with a female but is at the same time being attacked by a fighter male. Other mites of different life stages forage in the background. Photograph by Isabel Smallegange.