

# Evolution of risk-taking during conspicuous mating displays

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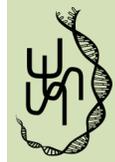
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In many species, males possess conspicuous characteristics to attract females. These traits often attract predators as well, and males thus may have to balance the conspicuousness of their signals in relation to the prevailing predation risk. Here we develop a theoretical model of optimal signaling and risk-taking behavior for males differing in the attractiveness of their signals. All else being equal, more attractive males should behave more cautiously. Yet this prediction may drastically change if males differ in any additional characteristic, especially if basal mortality rate or signaling costs are higher or if the vulnerability to predators is lower for attractive males. A key insight from our model is that male competition will create a positive feedback so that selection on male risk-taking strategies is acting in opposite directions. If selection acts on one male type to behave more cautiously, this will strengthen selection on males of the other types to take higher risks and vice versa. Our results further demonstrate that the asset-protection principle, which states that individuals with higher future expectations should behave more cautiously, may often be violated. We also offer an alternative to the handicap principle explaining the often found positive association between male ornamentation and viability: attractive males may simply behave more cautiously.

**KEY WORDS:** Adaptive dynamics, asset protection, boldness, personality, phenotypic plasticity, sexual selection, state-dependent selection.

Male traits favored by female choice often involve an elevated predation risk to its bearer (Ryan et al. 1982; Godin and McDonough 2003; Stuart-Fox et al. 2003; Lindström et al. 2006; Woods et al. 2007; Hernandez-Jimenez and Rios-Cardenas 2012). Extravagant ornaments and conspicuous displays may not only impress females but also attract the attention of predators (Magnhagen 1991; Zuk and Kolluru 1998; Kotiaho 2001). The strength of sexual selection is thus counterbalanced by natural selection and this viability cost of attractive signals is a fundamental underlying assumption in most models of the coevolution of male sexual ornaments and female preferences (Kuijper et al. 2012). Changes in predation risk are thus expected to have considerable effects on the expression of conspicuous sexually selected traits (Kotiaho 2001 and references therein), either due to directional selection or phenotypic plasticity. For instance, Endler's studies on Trinidadian guppies have convincingly shown that natural selection due to predation risk have changed the intensity of the conspicuous

male color patterns in natural populations (Endler 1980, 1983). However, changes in predation risk should also affect short-term behavioral decisions. If males perceive the presence of predators, one would expect them to behave more cautiously and reduce the conspicuousness of their display (Sih 1988; Lima and Dill 1990; Forsgren and Magnhagen 1993; Godin 1995; Fuller and Berglund 1996; Bertram et al. 2004; Simon 2007). This is indeed often the case: crickets that are disturbed stop singing for a while (Hedrick 2000), wax moths that hear an approaching bat will immediately stop calling (Greenfield and Baker 2003; Cordes et al. 2013), sticklebacks reduce courtship activity in the presence of predators (Candolin 1997), and male guppies court less conspicuously under intense predation risk (Endler 1987). However, males should at some point regain their previous display intensity. Indeed, males that quickly restart their courtship display (or do not reduce or interrupt their display at all) will benefit both from the extended time that they can be perceived by females and also from



the absence of competition from more careful rivals—of course at the cost of an increased predation risk. These contrasting selection pressures should lead to the evolution of an optimal level of risk taking during courtship where the benefit-to-cost ratio is maximized, very much analogously to how the fundamental trade-off between foraging and vigilance/escape time is expected to shape optimal foraging behavior under predation risk (Godin and Smith 1988; McNamara and Houston 1992; Houston et al. 1993; Dukas and Kamil 2000; Jones and Godin 2010).

Nonetheless, populations do not consist of identical individuals, but rather of different individuals with varying levels of risk-taking propensity (Sih et al. 2004; Réale et al. 2007). We may ask: which individual characteristics should influence a male's willingness to take great risks to attain matings? For instance, if some males have higher viability or for some other reason are better able to escape predator attacks than others, we may also expect such males to behave more boldly (e.g., DeWitt et al. 1999; López et al. 2005; Lindström et al. 2006; Fowler-Finn and Hebets 2011; Pascual and Senar 2014). Also, if males for other reasons differ in their survival probability and chances of future reproduction, this will likely affect their incentive to take risks (Clark 1994). Males with very low prospects of future reproduction may be expected to increase their effort in current reproduction reflecting terminal investment, even at the cost of still higher mortality (Polak and Starmer 1998; Candolin 2000; Nielsen and Holman 2012). Conversely, if males are expected to live long and have high expected future reproductive success they are expected to behave cautiously to protect this asset (Clark 1994; see also Wolf et al. 2007).

Another potentially important factor is males' intrinsic attractiveness. If males differ in the likelihood that females will choose them as mates, this will also affect both the cost and benefit of risk taking. Yet, the precise effect is difficult to intuitively predict. Everything else being equal, attractive males will have a higher reproductive value. This should select for cautiousness in accordance with the asset protection principle described above (Clark 1994). On the other hand, the immediate payoff from their riskiness, that is, the probability that they will actually be chosen by a female, will be higher for attractive males. In other words, although attractive males would have more to lose, they also potentially have more to win by taking risks. Intriguingly, the few empirical examples at hand show some contrasting results. When crickets are disturbed, for instance, attractive males take longer to emerge from their hiding place and resume singing than less-attractive males (Hedrick 2000). Ornamented wolf spiders court more cautiously under predation risk than males without conspicuous ornamentation (Fowler-Finn and Hebets 2011). In contrast, male wax moths with more attractive signals are more likely to disregard the danger of approaching foraging bats than males with unattractive signals, as they recommence singing sooner than

less-attractive males or do not pause at all (Cordes et al. 2014). These contrasting results in addition to the scarcity of any distinct theoretical predictions inspired us to develop a theoretical model. The aim was to provide clear predictions of evolutionarily stable risk-taking strategies for males differing in attractiveness. In addition, we examined how these predictions might change if we additionally assume different mortality rates of attractive and unattractive males in different situations (i.e., related or unrelated to ornamentation and courtship).

## The Model

We assume an “infinite island” population comprising many discrete patches (or “leks”) with continuous and overlapping generations. Mate competition occurs between all males within each subpopulation but not between individuals from different patches. We further assume that there are two different male types in the population—highly attractive and less-attractive males, with an attractiveness score  $\alpha_A$  and  $\alpha_a$ , respectively (see Table 1 for a list of all model parameters and variables). Because attractiveness is a relative measure, it will suffice to set the attractiveness of unattractive males to  $\alpha_a = 1$  and  $\alpha_A$  would then signify the relative attractiveness of attractive males compared to this. We will consequently do this in the subsequent analysis but keep the full notation ( $\alpha_A$  and  $\alpha_a$ ) in the model derivation. We further assume that the proportion of attractive males at birth is a fixed value ( $p_A$ ). Please note that this is not the same as the proportion of attractive males in the population ( $\hat{p}_A$ ), as this will be affected by differential mortality of attractive and unattractive males. Most crucially, this will be affected by their risk-taking behavior.

When males are signaling to attract females, there is a probability ( $q$ ) that a predator will be nearby and locate males. We assume that males can perceive whether a predator is present or not. If males perceive a predator's presence, they can either continue signaling (risky) or stop calling (cautious). The proportion of time spent signaling when predators are present (i.e., “risky signaling”) is the evolving trait ( $R$ ). This can be different depending on whether the male is attractive ( $R_A$ ) or unattractive ( $R_a$ ).

We here adopt an adaptive dynamics approach, in which the traits (conditional risk-taking behavior) are evolving in a population that is at its dynamical equilibrium. In short, we assume a population where almost all individuals have the same strategy values, that is, the resident strategies  $\hat{R}_A$  and  $\hat{R}_a$ , respectively. Yet these traits will in its turn affect male mortality and thus the number of attractive and unattractive males in the population ( $n_A, n_a$ ). We now assume that ecological processes occur at a faster time scale than evolutionary processes, so that following changes in  $\hat{R}_A$  and  $\hat{R}_a$ , the population will have reached its equilibrium density

**Table 1.** Definition of variables and parameters used.

$\alpha_i$	Male attractiveness
$R_i$	Male risky behavior—propensity to signal when predators are present
$\mu_{b,i}$	Male basal mortality rate
$\mu_{s,i}$	Additional male mortality rate during signaling
$\mu_{p,i}$	Additional male mortality rate during signaling with predator present
$f$	Proportion of time females may be nearby perceiving the signal
$q$	Proportion of time predators will be nearby perceiving the signal
$\rho$	Subpopulation birth rate (affecting subpopulation size)
$p_i$	Frequency of each male type
$n_i$	Number of each male type in subpopulation

The subscript  $i$  indicates that these are modeled as male type specific.

( $\hat{n}_A, \hat{n}_a$ ) before any further changes in males' risk-taking behavior occur.

We thus first have to come up with an expression for the changes in population density of type  $i$  males depending on their probability to take risks:

$$\frac{dn_i}{dt} = \rho \cdot p_i - \left( \underbrace{((1-f) + fq(1-\hat{R}_i))}_{\text{time silent}} \mu_{b,i} + \underbrace{f(1-q)}_{\text{time safe singing}} (\mu_{b,i} + \mu_{s,i}) + \underbrace{fq\hat{R}_i}_{\text{time risky singing}} (\mu_{b,i} + \mu_{s,i} + \mu_{p,i}) \right) n_i. \tag{1}$$

For simplicity we have here assumed age-independent mortality, yet the specific mortality rate may be different depending on whether males are signaling or not and whether they signal when there is an immediate predation risk or not. This is reflected in the different mortality rates  $\mu_{b,i}$ ,  $\mu_{s,i}$ , and  $\mu_{p,i}$ . In the expression above we have also introduced the parameter  $f$ , the proportion of total time females may be nearby and able to perceive the male signal. Thus  $(1-f) + fq(1-\hat{R}_i)$  will on average be the time portion in which a type  $i$  male will be silent, either because no females are nearby or because an additional predator will be present and the male chooses not to take any risk. During this time male mortality rate will equal  $\mu_{b,i}$ , which represents basal mortality rate. If females are present and no predators around ( $f[1-q]$  of the time), it will be safe for males to signal. Yet this signal may, for instance, be energetically costly, which will increase mortality rate by the factor  $\mu_{s,i}$ . Finally, if females and predators are present and the male shows risky behavior (on average

$fq\hat{R}_i$  of the time), there will be an additional predation risk  $\mu_{p,i}$ . The index  $i$  indicates that all these mortality rates can be modeled as male type specific. The “influx” of new individuals will be given by the expression  $\rho \cdot p_i$ , where the parameter  $\rho$  reflects the birth rate of the (sub)population. For simplicity, we assume this to be independent of male density. Thus, in principle we assume that female fecundity is not male or sperm limited. Setting  $\frac{dn_i}{dt} = 0$ , we can express the equilibrium densities of each male type as:

$$\hat{n}_i = \frac{\rho p_i}{\mu_{b,i} + \mu_{s,i} f(1-q) + \hat{R}_i f q (\mu_{s,i} + \mu_{p,i})}. \tag{2}$$

Next we will look at the fitness of males following different risk-taking strategies. Male lifetime reproductive success will be the product of average longevity ( $\lambda$ ) and mating rate ( $v$ ). Assuming age-independent mortality, male longevity will be exponentially distributed. Thus for a type  $i$  male with risk-taking  $R_i$ , the expected lifetime will equal the reciprocal of the mortality rate, that is,  $\lambda_i = \frac{1}{\mu_{b,i} + \mu_{s,i} f(1-q) + R_i f q (\mu_{s,i} + \mu_{p,i})}$ . For mating rate, we have assumed that for any given situation where a female is present and mate searching, the probability of mating success will be given by the focal male's attractiveness in relation to that of all males signaling, that is,  $v = \frac{\alpha}{\alpha + \sum_i \tilde{n}_i \alpha_i}$ . Here  $\tilde{n}_i$  refers to the number of males actually signaling, which will be different from  $\hat{n}_i$ . This is a special case of Tullock's contest success function, which has been widely applied in evolutionary biology for similar questions (see, e.g., Fawcett et al. 2011; Gavrillets 2012). Using this function, we implicitly assume that copulation duration and male recovery time (“time out,” see, e.g., Kokko and Jennions 2008) is negligible so that obtaining current matings does not influence the probability of obtaining future matings. With this additional assumption we can express a type  $i$  male's mating rate as:

$$v_i = f \left( \sum_{j,k} \text{Poi}(j | \hat{n}_A) \cdot \text{Poi}(k | \hat{n}_a) \cdot ((1-q) \cdot \varphi + q R_A \cdot \gamma) \right), \tag{3}$$

where  $\varphi = \frac{\alpha_i}{\alpha_i + j\alpha_A + k\alpha_a}$  is the probability of mating when all males are signaling, and  $\gamma = \sum_{j'=0}^j \sum_{k'=0}^k \text{Bin}(j' | j \cdot \hat{R}_A) \text{Bin}(k' | k \cdot \hat{R}_a) \frac{\alpha_i}{\alpha_i + j'\alpha_A + k'\alpha_a}$  is the probability of mating when only risk-taking males are signaling. In equation (3) the expression  $\text{Poi}(j | \hat{n}_A) \cdot \text{Poi}(k | \hat{n}_a)$  specify the (Poisson distributed) probability that a subpopulation will consist of exactly  $j$  attractive and  $k$  unattractive males. In case there is no predator around, this will also be the number of males signaling (provided they assess females to be near). However, if a predator is present, the expression  $\text{Bin}(j' | j \cdot \hat{R}_A) \text{Bin}(k' | k \cdot \hat{R}_a)$  gives the (binomially distributed) probability that at any given time exactly  $j'$  and  $k'$  of these will actually be signaling.

Male fitness is given by his lifetime reproductive success  $w_i = \lambda_i \cdot v_i$ . Potentially, the ESS's  $\{R_a^*, R_A^*\}$  will be found by solving the following equation system:

$$\begin{cases} \left. \frac{\partial}{\partial R_A} w_A (R_A, \hat{R}_A | \hat{R}_a, \hat{n}_A, \hat{n}_a) \right|_{R_A = \hat{R}_A = R_A^*} = 0 \\ \left. \frac{\partial}{\partial R_a} w_a (R_a, \hat{R}_a | \hat{R}_A, \hat{n}_A, \hat{n}_a) \right|_{R_a = \hat{R}_a = R_a^*} = 0 \end{cases}$$

However, interior solutions (i.e.,  $0 < R_i^* < 1$ , for all  $i$ ) were rarely found. Instead, we must focus on potential boundary solutions (i.e., one or both equilibrium solutions are  $R_i^* = 0$  and/or  $R_j^* = 1$ , for details and analyses see Appendix 1). Furthermore, it was not possible to find analytical solutions to this system. Still, it is straightforward to find numerical solutions for given values of the different parameters. Yet, the equation describing mating rate (eq. (3)) is an infinite (convergent) series. We therefore approximated equation (3), substituting the values of  $[j, k]$  and  $[j', k']$  with the expected mean values ( $[\hat{n}_A, \hat{n}_a]$  and  $[\hat{R}_A \cdot \hat{n}_A, \hat{R}_a \cdot \hat{n}_a]$ , respectively), using a third-order Taylor approximation (see Appendix 2), which takes both variance and skewness of the distribution into account. We numerically evaluated convergence and evolutionary stability for all solutions.

## Results

### RISK-TAKING BEHAVIOR OF ALL MALES

One of the most influential parameters affecting a male's propensity to signal during predation risk is obviously the predators' effectiveness in causing male predator-related mortality rate ( $\mu_p$ ) during courtship events. At very low values of  $\mu_p$  all males should always signal when a predator is present and at very high values males should never signal when a predator is present. All results are thus presented in relation to different levels of predation risk. Yet in our model, there are also several parameters that influence the general propensity to take courtship-related risk, but which are not related to different male types. Most importantly, increasing values of  $q$  (predation pressure) will increase overall risk taking (see Fig. 1A). Furthermore, the more often females will be around (increasing  $f$ ), the less risky males should behave (see Fig. 1B). Finally, risk taking should increase with increasing values of the subpopulation birth rate  $\rho$  (see Fig. 1C). Everything else being equal, this parameter will determine the number of males and thus the intensity of sexual competition in each patch.

In addition to differences in attractiveness, the resulting evolutionarily stable risk-taking strategies of males will primarily depend on the different mortality rates  $\mu_{x,i}$ . We here present results from a few selected typical scenarios.

### SCENARIO 1: EVERYTHING ELSE BEING EQUAL

( $\mu_{b,a} = \mu_{b,A}, \mu_{s,a} = \mu_{s,A}, \mu_{p,a} = \mu_{p,A}$ )

Here, the only difference between males is that they differ in attractiveness. The main result is quite straightforward: for any parameter combination  $R_A^* \leq R_a^*$ . Thus, under these assumptions unattractive males are always predicted to be equally or more bold than attractive males (Fig. 1). Under a wide range of parameter values describing mortality rate due to signaling-related mortality rate, this effect is rather large. Attractive males should seldom or never take any risks, whereas at the same time less-attractive males should often or always take risks. Intriguingly, even a very small difference in male attractiveness is predicted to generate these large differences (Fig. 1D).

### SCENARIO 2: RISK-INDEPENDENT MORTALITY RATES

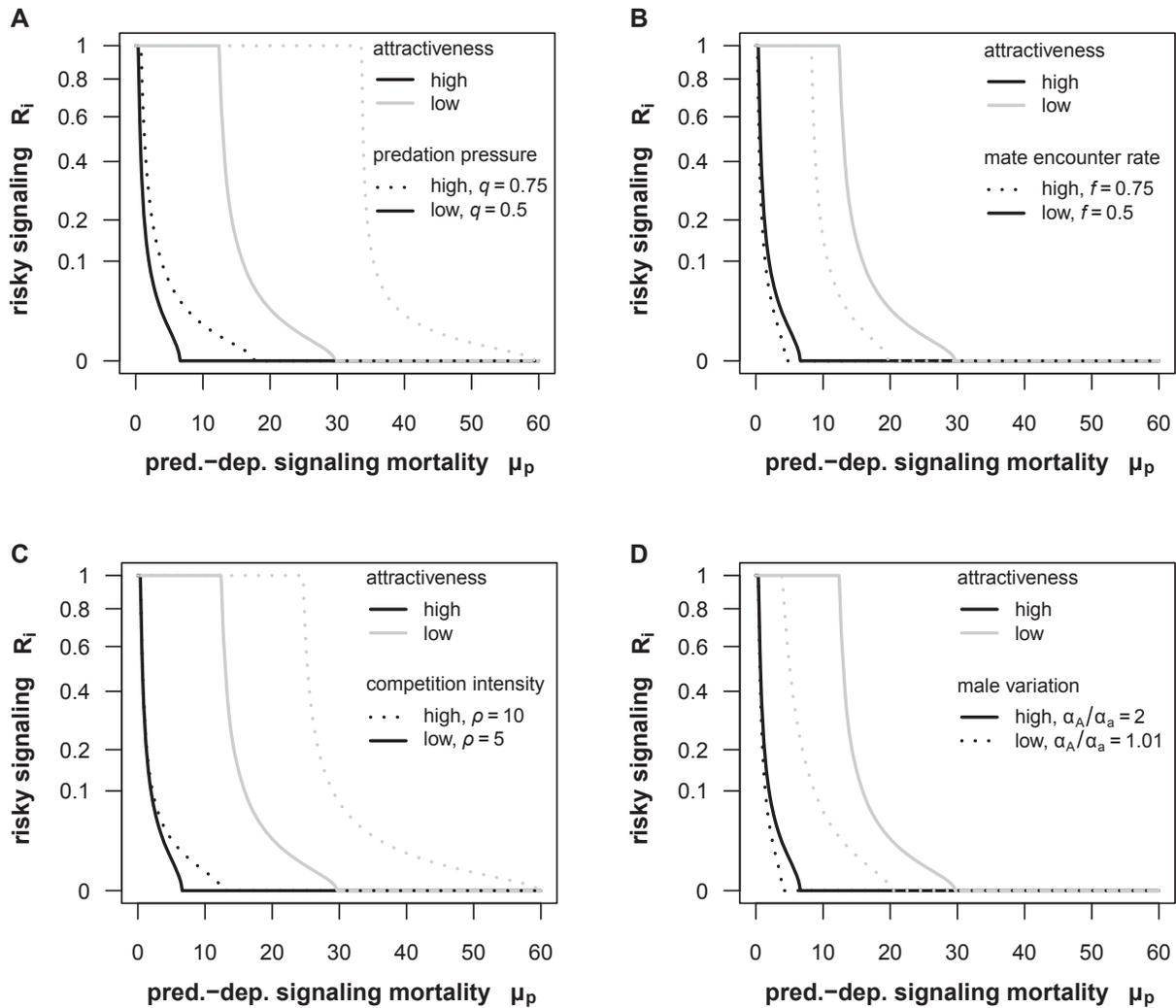
DIFFER ( $\mu_{b,a} \neq \mu_{b,A}$  AND/OR  $\mu_{s,a} \neq \mu_{s,A}, \mu_{p,a} = \mu_{p,A}$ )

As noted above, it was generally difficult to generate any exact analytical solutions to this system. Yet there is one noticeable exception to this: when considering the predation-related mortality rate at which type  $i$  individuals should switch from always taking risks to sometimes being careful given that type  $j$  individuals always take risks, one can show (see Appendix 3) that this will equal

$$\tilde{\mu}_{p,i} (R_i^* = 1 | \hat{R}_j = 1) = \frac{\mu_{b,i}}{f(1-q)}. \quad (4)$$

Thus, if individuals differ in basal mortality rate, those with the lowest background mortality are expected to be more careful at the lowest levels of signaling-dependent predation rate (see Fig. 2), irrespective of differences in attractiveness (or differences in signaling costs  $\mu_{s,i}$ ). If attractive males also have lower basal mortality rate than unattractive males, the effects of the differences in attractiveness and basal mortality rate will act in concert and  $R_A^* \leq R_a^*$  for any parameter combination.

However, if attractive males have higher basal mortality rate than unattractive males ( $\mu_{b,A} > \mu_{b,a}$ ), for instance because the potential to produce attractive signals pleiotropically affects male resting metabolic rate (see, e.g., Reinhold 1999), the predictions become considerably more complex. Then, if signaling-dependent predation costs are relatively low (low  $\mu_{p,i}$ ), attractive males should be bolder than less-attractive males (Fig. 2). Yet this effect may drastically change at higher values of  $\mu_p$ . If differences in basal mortality rate— $\mu_b$ —are not too high, there will be a point at which unattractive males should switch from being more careful to being bolder than attractive males (Fig. 2A–C). Under certain circumstances, there is even an area with two stable equilibria: high values of  $R_A^*$  in combination with low values of  $R_a^*$ , and vice versa (Fig. 2B, C). In this case, the resulting prediction will to some extent also depend on the evolutionary history of the



**Figure 1.** Results illustrating the effect of predator effectiveness ( $\mu_p$ ) and (A) the intensity of predation ( $q$ ), (B) the frequency of mating opportunities ( $f$ ), (C) the intensity of mate competition ( $\rho$ ), and (D) male attractiveness variation on the evolutionarily stable risk-taking behavior of attractive (black lines) and unattractive males (gray lines), respectively. Unless otherwise stated, the following parameter values were used throughout:  $\mu_{b,A} = \mu_{b,a} = 0.1$ ;  $\mu_{s,A} = \mu_{s,a} = 0.1$ ;  $p_A = 0.5$ ;  $f = 0.5$ ;  $q = 0.5$ ;  $\rho = 5$ ;  $\alpha_A/\alpha_a = 2$ .

system. If the present conditions gradually evolved from circumstances in which signaling-related predation rate was relatively high, one would expect attractive males to behave more carefully than unattractive males. In contrast, if previous conditions involved low values of  $\mu_p$ , one would expect attractive males to be bolder than unattractive males.

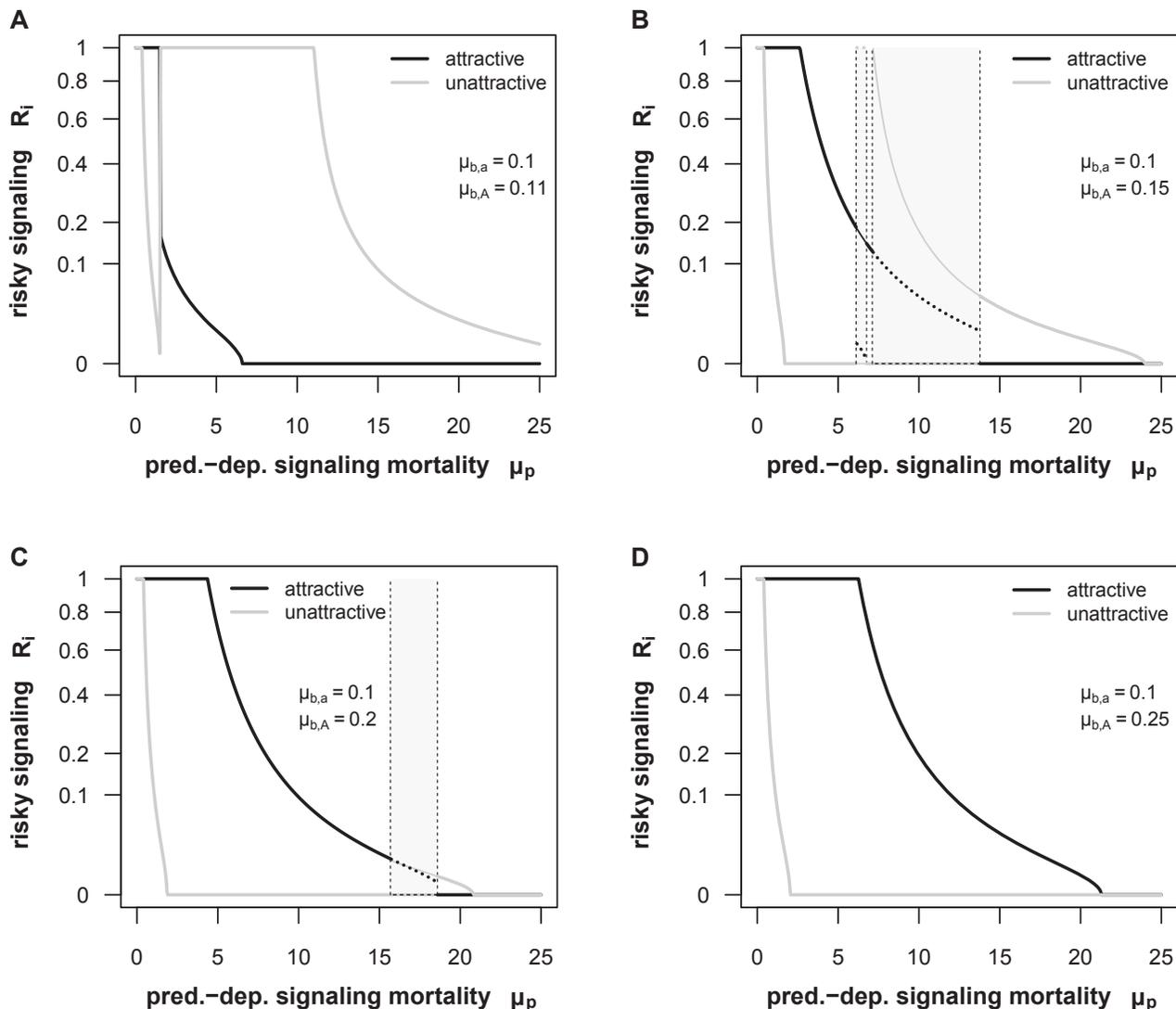
The predictions when males differ in predator-unrelated signaling costs ( $\mu_{s,A} \neq \mu_{s,a}$ ) are similar to those mentioned above regarding differences in basal mortality rate. Yet the effect of  $\mu_s$  is less “dominant” than the effect of  $\mu_b$ , apparently because males continuously face basal mortality costs, whereas signaling costs are only encountered occasionally. Thus, for even minute differences in  $\mu_b$  between males, it is possible to find values for  $\mu_p$  at which males with the highest basal mortality rate should behave the boldest irrespective of differences in any other characteris-

tic (see, e.g., Fig. 2A). For signaling costs, the differences need to be large enough to override other differences (cf. Fig. 3A, B). Thus if signaling costs are higher for attractive than for unattractive males ( $\mu_{s,A} > \mu_{s,a}$ ), attractive males should potentially be the bolder male type, at least at low levels of predator-related courtship costs (Fig. 3). At higher levels of  $\mu_p$  this effect is again expected to reverse, except if differences in signaling costs are much larger than differences in attractiveness. Again, areas with multiple equilibria are possible under certain circumstances (Fig. 3C, D).

### SCENARIO 3: MALES FACE DIFFERENT RISKS

( $\mu_{b,a} = \mu_{b,A}$ ,  $\mu_{s,a} = \mu_{s,A}$ ,  $\mu_{p,a} \neq \mu_{p,A}$ )

Differences in predation risk during courtship between male types are expected to affect different males’ propensity to signal under



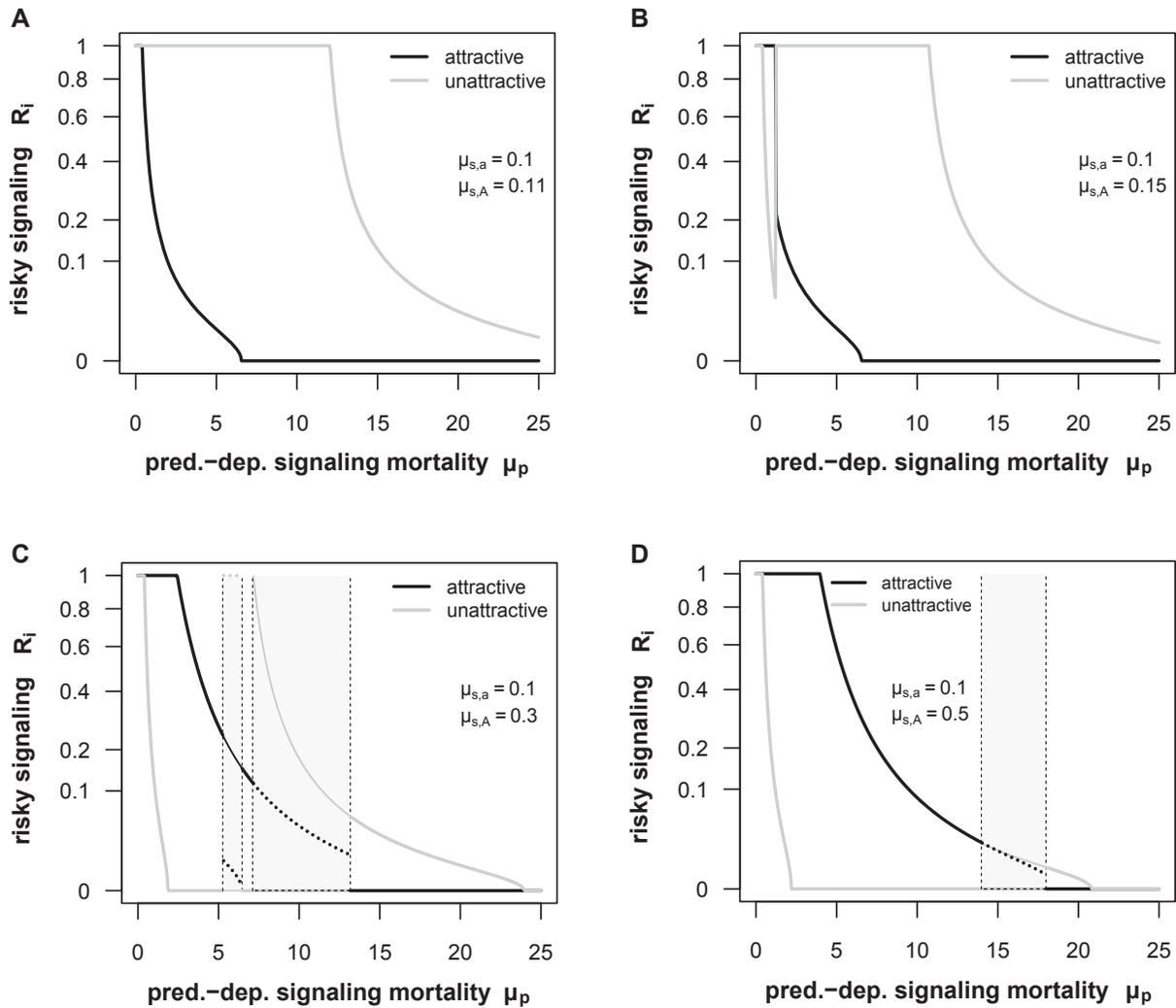
**Figure 2.** The effect of differences in basal mortality rate ( $\mu_b$ ) on the evolutionarily stable risk-taking behavior of attractive (black lines) and unattractive males (gray lines), respectively, under different levels of predator-dependent signaling mortality. The panels (A)–(D) signify increasing differences in male basal mortality rate ( $\mu_{b,A} - \mu_{b,a}$ ). The following parameter values were used throughout:  $\mu_{s,A} = \mu_{s,a} = 0.1$ ;  $p_A = 0.5$ ;  $f = 0.5$ ;  $q = 0.5$ ;  $\rho = 5$ ;  $\alpha_A/\alpha_a = 2$ . The shaded zones correspond to areas with two possible evolutionary equilibria. Here, matching line style (thin solid lines or thicker dotted lines) indicates matching pairs of  $\{R_A^*, R_a^*\}$  values.

predation risk. The default expectation should be that males with higher values of  $\mu_p$  should also behave more cautiously. Thus, if more attractive males have higher predation costs when signaling (for instance because their signals are more conspicuous), the results are straightforward: they should always behave more cautiously (results not shown). However, if attractive males have lower predation cost when signaling (for instance due to higher viability and condition, i.e., the handicap principle, see Zahavi 1975), then the results become similar to the situation when basal mortality differs. At relative low values of predator-related signaling cost, males facing the highest predation risk should always behave more cautiously (Fig. 4A, see also eq. (4)). Yet as predation risk increases, this effect will potentially be outweighed by

differences in attractiveness, and the most attractive males should behave more cautiously, although the risk of predation is lower for those males (Fig. 4).

## Discussion

Here we report results from a model aiming to predict and provide explicit testable hypotheses regarding optimal risk-taking behavior for males that differ in attractiveness. We found that, all else being equal, more attractive males should signal more carefully in predator-exposed situations (Fig. 1). Yet, this prediction might change if either (1) attractive males face higher basal mortality rate, (2) signaling costs are higher for attractive males, or



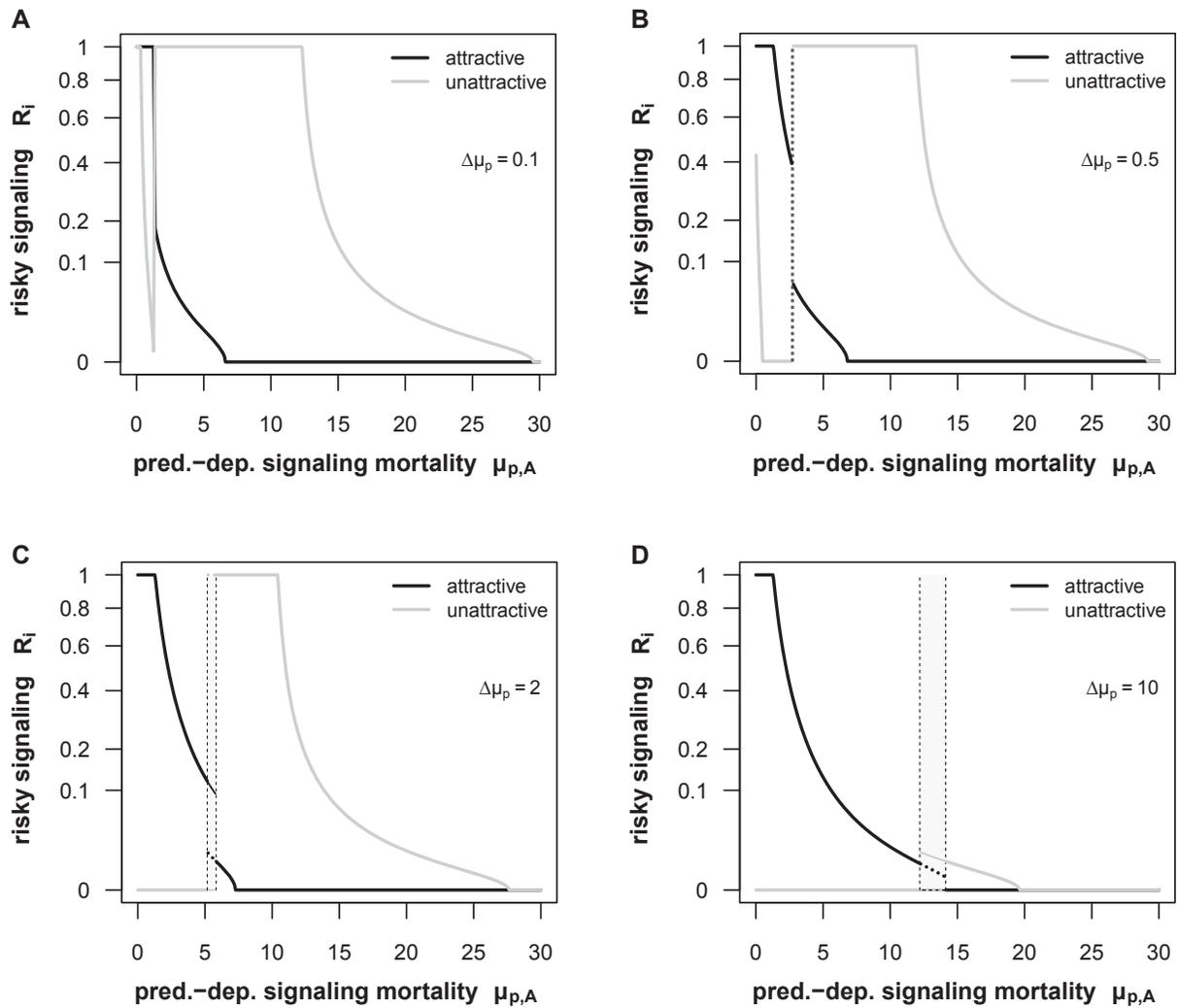
**Figure 3.** The effect of differences in signaling costs ( $\mu_s$ ) on the evolutionarily stable risk-taking behavior of attractive (black lines) and unattractive males (gray lines), respectively, under different levels of predator-dependent signaling mortality. The panels (A)–(D) signify increasing differences in male signaling costs ( $\mu_{s,A} - \mu_{s,a}$ ). The following parameter values were used throughout:  $\mu_{b,A} = \mu_{b,a} = 0.1$ ;  $\rho_A = 0.5$ ;  $\rho = 5$ ,  $q = 0.5$ ;  $f = 0.5$ ;  $\alpha_A/\alpha_a = 2$ . The shaded zones correspond to areas with two possible evolutionary equilibria. Here, matching line style (thin solid lines or thicker dotted lines) indicates matching pairs of  $\{R_A^*, R_a^*\}$  values.

(3) attractive males are less vulnerable to predation. Then attractive males may be predicted to behave more boldly especially if predator-related mortality rate is relatively low (see Figs. 2–4). These contrasting predictions may also be reflected in some of the inconsistencies found between empirical studies of these phenomena (Hedrick 2000; Fowler-Finn and Hebets 2011; Cordes et al. 2014). Possibly these discrepancies can be explained by differences between species regarding the costs males pay to be attractive.

The mating system prototype we had in mind when designing the model was a “lek”-like situation, in which males produce conspicuous signals to increase their attractiveness to females. Yet, the model results are also applicable to a number of different situations. For example, the conspicuous signal need not

necessarily be a flexible trait, such as an acoustic courtship call. It can equally well represent a fixed ornament, such as an eye-catching coloration. Yet in this case the risk-taking behavior ( $R_i$ ) will rather be characterized by “time out of hiding refuge” or something equivalent. Our model is not even limited to situations where female choice is the main determinant of differential reproductive success. In fact, the parameters  $\alpha_A$  and  $\alpha_a$  may equally well illustrate male differences in fighting ability in male–male competition, and  $R_i$  will then also represent the propensity to compete for matings under situations of increased predation risk.

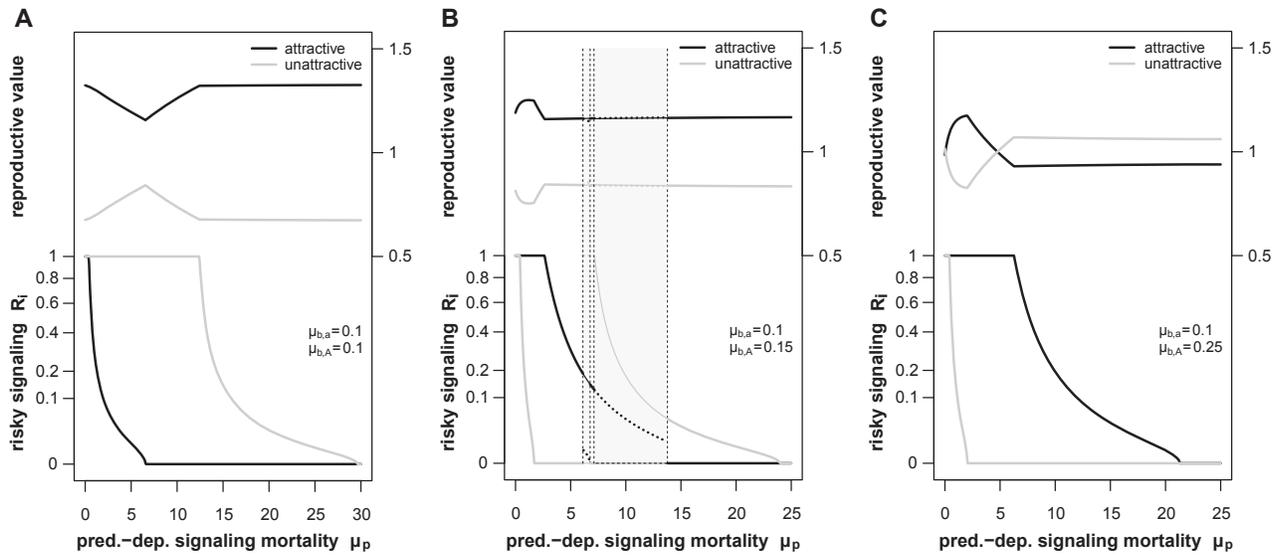
A general feature of our model results is that slightly different male types are predicted to show very distinct differences in risk-taking behavior. Typically, one male type should always take risks, whereas the other type should always behave with



**Figure 4.** The effect of differences in predator-dependent signaling mortality ( $\Delta\mu_p = \mu_{p,a} - \mu_{p,A}$ ) on the evolutionarily stable risk-taking behavior of attractive (black lines) and unattractive males (gray lines), respectively. The panels (A)–(D) signify increasing differences in the value of  $\Delta\mu_p$ . The difference in predator-dependent signaling mortality ( $\Delta\mu_p$ ) corresponds to the log odds ratio of the probability that an unattractive male is captured in relation to the probability of predation of an attractive male. A value of  $\ln 2 \approx 0.7$  thus corresponds to twice the odds of predation of an unattractive male compared to the odds of predation on an attractive male. The following parameter values were used throughout:  $\mu_{b,A} = \mu_{b,a} = 0.1$ ;  $\mu_{s,A} = \mu_{s,a} = 0.1$ ;  $p_A = 0.5$ ;  $\rho = 5$ ,  $q = 0.5$ ;  $f = 0.5$ ;  $\alpha_A/\alpha_a = 2$ . The shaded zones correspond to areas with two possible evolutionary equilibria. Here, matching line style (thin solid lines or thicker dotted lines) indicates matching pairs of  $\{R_A^*, R_a^*\}$  values.

caution. Intriguingly, this was the case, even with minute differences between males (Fig. 1D). In other words, small intrinsic differences can generate very large differences in optimal behavior. This is an interesting result regarding the recent attention given to the proximate and ultimate causes of personality differences (Sih et al. 2004; Stamps 2007; Careau et al. 2008; Biro and Stamps 2010; Dingemanse and Wolf 2010; Réale et al. 2010). It is generally well acknowledged that such differences can be upheld by inherent differences in “state” (see McNamara and Houston 1996; Dall et al. 2004; Wolf and Weissing 2010). Consequently, there has been a focus to link differences in personality traits, such as boldness and aggressiveness, to some inherent individual state

differences (e.g., Rands et al. 2003; Wolf et al. 2007; Houston 2010; Luttbegg and Sih 2010). The present model, which is also a model of state-dependent behavior, surprisingly demonstrates that the state differences needed to generate such personality differences may be difficult to disentangle from random noise, so that apparently identical individuals may behave very differently (e.g., Freund et al. 2013). The reason for this counterintuitive result is a positive feedback in combination with selection on the two male strategies in opposing directions. As selection acts on attractive males to behave less risky in predator-related situations, this will reinforce selection on unattractive males to take high risks. First, because attractive males take lower risks, competition will



**Figure 5.** The association between risk-taking behavior (bottom panel) and reproductive value (top panel) for males differing in attractiveness and mortality rate. The panels (A)–(C) signify increasing differences in male basal mortality rate ( $\mu_{b,A} - \mu_{b,a}$ ) and correspond to Figure 2A, B, D. The following parameter values were used throughout:  $\mu_{s,A} = \mu_{s,a} = 0.1$ ;  $p_A = 0.5$ ;  $\rho = 5$ ,  $q = 0.5$ ;  $f = 0.5$ ;  $\alpha_A/\alpha_a = 2$ . The shaded zones correspond to areas with two possible evolutionary equilibria. Here, matching line style (thin solid lines or thicker dotted lines) indicates matching pairs of  $\{R_A^*, R_a^*\}$  values. In populations with constant size and age-independent mortality, reproductive values remain constant during lifetime and their calculation (see, e.g., Stearns 1992) can be simplified to  $w_i = \lambda_i \cdot v_i$ .

be more relaxed in risky situations. Second, competition will be intensified in risk-free situations because attractive males will survive relatively better by taking lower risks. As a result, the relative benefit of taking risks will decrease for attractive males, as less-attractive males are still expected to signal at a high level during risky situations. This will reduce risk-taking behavior for attractive males even more, changing selection pressure on unattractive males to take further risks and so on.

Previous theoretical models have implied that individuals with higher reproductive value should behave more cautiously than individuals with lower reproductive value (Clark 1994; Wolf et al. 2007). Our present model partly reinforces this conclusion. Everything else being equal, individuals with trait characteristics associated with higher future reproductive success (high attractiveness, low mortality) are expected to behave more cautiously. In this sense the results conform to the asset protection principle: “the larger an individual’s reproductive value (i.e., its asset), the more important it becomes that the asset be protected” (Clark 1994). However, this could only be verified here when variation in reproductive value is due to differences in one trait (i.e., based on “everything-else-being-equal-arguments,” see also Fig. 5A). With variation in more than one dimension, it is straightforward to disprove this principle. For instance, for many parameter values, multiple equilibria were possible (Figs. 2–4), thus either male type could be predicted to behave more risky. In this situation, linking riskiness to any particular characteristic such as reproductive values is of course futile (Fig. 5B). But also in other situations,

risk-taking behavior must not necessarily be linked to reproductive value in any foreseen pattern (Fig. 5B, C). Thus if attractive individuals are also the ones with the highest mortality, it is not at all guaranteed that the type with the highest reproductive value should behave most cautiously.

Our results are also related to a second important principle in behavioral and evolutionary ecology: the handicap principle (Zahavi 1975, 1977; Grafen 1990). A central idea behind the evolution of female preference for conspicuously ornamented males (despite the fact that such traits are likely to carry a mortality cost) is the notion that such males may potentially also be more viable. In other words, conspicuous and costly signals can reveal male viability and resistance to predators and parasites, as only viable males can afford to have such handicaps (see, e.g., Andersson 1982; Johnstone 1995). Hence, a female preference for such males may be beneficial and evolve (e.g., Iwasa et al. 1991). Yet simultaneously our model predicts that attractive males should behave more carefully, sometimes despite the fact that they would survive predator attacks better than unattractive males. In this situation, male status-dependent behavior will apparently counteract the evolution of any such indicator mechanism.

This further highlights the difficulty of determining the ultimate causes of differences in male behavior and survival, which is central to sexual selection theory. In some species, it has been reported that more ornamented males behave more cautiously under increased predation risk, and this has been interpreted as an adaptive reaction given that such males are likely to have more

conspicuous displays and thus cause increased predator attraction (Hedrick 2000; Fowler-Finn and Hebets 2011). Yet an alternative explanation is that such males behave more cautiously simply because they are more attractive to conspecific females. Hence, adaptive differential cautiousness may be driven by differences in  $\alpha_i$  rather than  $\mu_{p,i}$ . Similarly, if the expression of sexual ornaments is male quality-dependent (as predicted by the handicap principle, “good-genes,” or indicator mechanism) one may expect a positive association between ornamentation and male survival (see, e.g., Jennions et al. 2001), and studies demonstrating such a correlation are generally interpreted consistently with the idea that ornaments signal high quality (e.g., Alatalo et al. 1991; Hill 1991; Møller 1991; Kempenaers et al. 1992; Petrie 1992; Papeschi and Dessì-Fulgheri 2003). Yet, one must also consider that more ornamented males may simply survive better because they behave more cautiously in risky situations. To put it bluntly, ornamented males may not be more vigorous but simply behave more cowardly. Imagine that selection on male ornamentation is mainly driven by Fisherian mechanisms (see, e.g., Kuijper et al. 2012). In this case our model would predict that ornamented males should behave extremely cautiously (high  $\alpha_i$  in combination with high  $\mu_{p,i}$ ) potentially resulting in high survival. To control for such effects will be an additional challenge for studies testing the adaptive significance of female preferences for sexually extravagant males.

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## Appendix 1

### Equilibrium and Stability Conditions for System Boundary Solutions

There are four possible simple boundary solutions:

$I : \{R_a^* = 1, 0 < R_A^* < 1\}$ ;  $II : \{R_a^* = 0, 0 < R_A^* < 1\}$ ;  $III : \{0 < R_a^* < 1, R_A^* = 1\}$ ;  $IV : \{0 < R_a^* < 1, R_A^* = 0\}$ , satisfying:

$$I : \left\{ \begin{aligned} & \left. \frac{\partial}{\partial R_a} w_a (R_a, \hat{R}_a | \hat{n}_A, \hat{n}_a, R_A^*) \right|_{\hat{R}_a=1} > 0, \\ & \left. \frac{\partial}{\partial R_A} w_A (R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{R_A = \hat{R}_A = R_A^* \\ \hat{R}_a = 1}} = 0 \end{aligned} \right\}$$

$$II : \left\{ \begin{aligned} & \left. \frac{\partial}{\partial R_a} w_a (R_a, \hat{R}_a | \hat{n}_A, \hat{n}_a, R_A^*) \right|_{\hat{R}_a=0} < 0, \\ & \left. \frac{\partial}{\partial R_A} w_A (R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{R_A = \hat{R}_A = R_A^* \\ \hat{R}_a = 0}} = 0 \end{aligned} \right\}$$

$$III : \left\{ \begin{aligned} & \left. \frac{\partial}{\partial R_a} w_a (R_a, \hat{R}_a | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{R_a = \hat{R}_a = R_a^* \\ \hat{R}_A = 1}} = 0, \\ & \left. \frac{\partial}{\partial R_A} w_A (R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, R_A^*) \right|_{\hat{R}_A=1} > 0 \end{aligned} \right\}$$

$$IV : \left\{ \begin{aligned} & \left. \frac{\partial}{\partial R_a} w_a (R_a, \hat{R}_a | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{R_a = \hat{R}_a = R_a^* \\ \hat{R}_A = 0}} = 0, \\ & \left. \frac{\partial}{\partial R_A} w_A (R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, R_A^*) \right|_{\hat{R}_A=0} < 0 \end{aligned} \right\}.$$

For these to be locally convergent stable, the following condition must also be fulfilled:

$$\frac{d}{d\hat{R}_i} \left( \frac{\partial}{\partial R_i} w_i(R_i, \hat{R}_i | \hat{n}_i, \hat{n}_j, \hat{R}_j) \Big|_{R_i=\hat{R}_i, \hat{R}_j=\{0,1\}} \right)_{\hat{R}_i=R_i^*} < 0.$$

Furthermore, the condition for evolutionary stability is given by:

$$\frac{\partial^2}{\partial R_i^2} w_i(R_i, \hat{R}_i | \hat{n}_i, \hat{n}_j, \hat{R}_j) \Big|_{R_i=\hat{R}_i=R_i^*, \hat{R}_j=\{0,1\}} < 0.$$

In these expressions,  $i$  is the type for which the equality holds in the boundary solution, hence

$$\frac{\partial}{\partial R_i} w_i(R_i, \hat{R}_i | \hat{n}_i, \hat{n}_j, \hat{R}_j) \Big|_{R_i=\hat{R}_i=R_i^*, \hat{R}_j=\{0,1\}} = 0,$$

and  $j$  is the other type.

In addition, there are four possible “corner” solutions  $\{R_a^*, R_A^*\} = \{0, 0\}; \{0, 1\}; \{1, 0\}; \{1, 1\}$  with the stability conditions:

$$\left\{ \begin{aligned} &\left. \frac{\partial}{\partial R_a} w_a(R_a, \hat{R}_a | \hat{n}_a, \hat{n}_A, \hat{R}_A) \right|_{\substack{R_a=\hat{R}_a=0 \\ \hat{R}_A=0}} < 0, \\ &\left. \frac{\partial}{\partial R_A} w_A(R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{\hat{R}_a=0 \\ R_A=\hat{R}_A=0}} < 0 \end{aligned} \right\},$$

$$\left\{ \begin{aligned} &\left. \frac{\partial}{\partial R_a} w_a(R_a, \hat{R}_a | \hat{n}_a, \hat{n}_A, \hat{R}_A) \right|_{\substack{R_a=\hat{R}_a=0 \\ \hat{R}_A=1}} < 0, \\ &\left. \frac{\partial}{\partial R_A} w_A(R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{\hat{R}_a=0 \\ R_A=\hat{R}_A=1}} > 0 \end{aligned} \right\},$$

$$\left\{ \begin{aligned} &\left. \frac{\partial}{\partial R_a} w_a(R_a, \hat{R}_a | \hat{n}_a, \hat{n}_A, \hat{R}_A) \right|_{\substack{R_a=\hat{R}_a=1 \\ \hat{R}_A=0}} > 0, \\ &\left. \frac{\partial}{\partial R_A} w_A(R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{\hat{R}_a=1 \\ R_A=\hat{R}_A=0}} > 0 \end{aligned} \right\}, \text{ and}$$

$$\left\{ \begin{aligned} &\left. \frac{\partial}{\partial R_a} w_a(R_a, \hat{R}_a | \hat{n}_a, \hat{n}_A, \hat{R}_A) \right|_{\substack{R_a=\hat{R}_a=1 \\ \hat{R}_A=1}} > 0, \\ &\left. \frac{\partial}{\partial R_A} w_A(R_A, \hat{R}_A | \hat{n}_A, \hat{n}_a, \hat{R}_a) \right|_{\substack{\hat{R}_a=1 \\ R_A=\hat{R}_A=1}} > 0 \end{aligned} \right\}, \text{ respectively.}$$

These are also simultaneously the conditions for convergence.

## Appendix 2

### Taylor Approximation of Average Mating Success

We assume that the number of males of type  $i$  calling in a patch under nonrisky and risky situations is a Poisson-distributed variable with mean  $\hat{n}_i$  and  $\hat{n}_i \cdot \hat{R}_i$ , respectively. This yields an

exact expression for average male mating success  $v_i$ , which is given in the main text, equation (3). Principally all terms in this function have the following structure:  $f\langle n_{i,k} \rangle = p_k \frac{\alpha_i}{\alpha_i + n_{i,k} \alpha_i + n_j \alpha_j}$ , where  $p_k$  is the probability that there will be exactly  $n_{i,k}$  males of type  $i$  signaling (given that there are  $n_j$   $j$  males). We can also express such terms as a Taylor approximation around the mean value  $\hat{n}_i$  (or  $\hat{n}_i \cdot \hat{R}_i$ ) as  $f\langle n_{i,k} \rangle = p_k (f(\hat{n}_i) + f'(\hat{n}_i)(n_{i,k} - \hat{n}_i) + \frac{1}{2} f''(\hat{n}_i)(n_{i,k} - \hat{n}_i)^2 + \frac{1}{3!} f'''(\hat{n}_i)(n_{i,k} - \hat{n}_i)^3 + \dots)$ . The average value  $\bar{f}$  can thus be expressed as  $\bar{f} = f(\hat{n}_i) + \frac{1}{2} f''(\hat{n}_i) \sum_k p_k (n_{i,k} - \hat{n}_i)^2 + \frac{1}{6} f'''(\hat{n}_i) \sum_k p_k (n_{i,k} - \hat{n}_i)^3 + \dots$  (because  $\sum_k p_k (n_{i,k} - \hat{n}_i) = 0$ ). Using the fact that for a Poisson distribution, the terms  $\sum_k p_k (n_{i,k} - \hat{n}_i)^2$  and  $\sum_k p_k (n_{i,k} - \hat{n}_i)^3$  both equal  $\hat{n}_i$ , and further making the reasonable assumption of no covariance between the number of  $i$  and  $j$  males in each patch, we get the following third-order approximation:

$$v_i \approx f \alpha_i [(1 - q) \omega + q R_i \psi]$$

$$\omega = \frac{1}{\alpha_i + \hat{n}_i \alpha_i + \hat{n}_j \alpha_j} + \frac{\hat{n}_A \alpha_A^2 + \hat{n}_a \alpha_a^2}{(\alpha_i + \hat{n}_A \alpha_A + \hat{n}_a \alpha_a)^3} - \frac{\hat{n}_A \alpha_A^3 + \hat{n}_a \alpha_a^3}{(\alpha_i + \hat{n}_A \alpha_A + \hat{n}_a \alpha_a)^4}$$

$$\psi = \frac{1}{\alpha_i + \hat{n}_A \hat{R}_A \alpha_A + \hat{n}_a \hat{R}_a \alpha_a} + \frac{\hat{n}_A \hat{R}_A \alpha_A^2 + \hat{n}_a \hat{R}_a \alpha_a^2}{(\alpha_i + \hat{n}_A \hat{R}_A \alpha_A + \hat{n}_a \hat{R}_a \alpha_a)^3} - \frac{\hat{n}_A \hat{R}_A \alpha_A^3 + \hat{n}_a \hat{R}_a \alpha_a^3}{(\alpha_i + \hat{n}_A \hat{R}_A \alpha_A + \hat{n}_a \hat{R}_a \alpha_a)^4}.$$

We further validated this approximation by comparing the result with results from the more computationally demanding method of summing up enough terms in equation (3) until the probability of more males in the patch (i.e.,  $Poi(j > N | \hat{n}_i)$ ) went below a certain threshold (in this case 0.001). This yielded qualitatively identical and quantitatively very similar results for those parameter combinations chosen.

## Appendix 3

### Proof of Equation (4)

To find the evolutionarily singular risk-taking strategy  $R_i^*$ , we first differentiate  $w(R_i, \hat{R}_i)$  with respect to  $R_i$  to get  $\lambda'_i \cdot v_i + \lambda_i \cdot v'_i$ . By observing that  $\lambda_i$  has the structure  $\lambda_i = \frac{1}{\alpha + \beta R_i}$ , we get the following condition for an ESS:

$$\frac{(\alpha + \beta R_i^*) v'_i - \beta v_i}{(\alpha + \beta R_i^*)^2} = 0 \quad \text{or simply} \quad (\alpha + \beta R_i^*) v'_i = \beta v_i.$$

If  $\hat{R}_i = \hat{R}_j = 1$ , we can considerably simplify things because then  $v'_i = q v_i$ . The ESS  $R_i^*$  will thus exactly equal one if  $(\alpha + \beta) q = \beta$ . We can now insert  $\alpha = \mu_{b,i} + \mu_{s,i} f(1 - q)$  and  $\beta = f q (\mu_{s,i} + \mu_{p,i})$ , and after some rearrangements we get  $\tilde{\mu}_{p,i} (R_i^* = 1 | \hat{R}_j = 1) = \frac{\mu_{b,i}}{f(1-q)}$ .