Altered sex-specific mortality and female mating success: ecological effects and evolutionary responses

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Abstract. Theory predicts that males and females should often join the mating pool at different times (sexual dimorphism in timing of emergence [SDT]) as the degree of SDT affects female mating success. We utilize an analytical model to explore (1) how important SDT is for female mating success, (2) how mating success might change if either sex's mortality (abruptly) increases, and (3) to what degree evolutionary responses in SDT may be able to mitigate the consequences of such mortality increase. Increasing male pre-mating mortality has a non-linear effect on the fraction of females mated: The effect is initially weak, but at some critical level a further increase in male mortality has a stronger effect than a similar increase in female mortality. Such a change is expected to impose selection for reduced SDT. Increasing mortality during the mating season has always a stronger effect on female mating success if the mortality affects the sex that emerges first. This bias results from the fact that enhancing mortality of the earlier emerging sex reduces female–male encounter rates. However, an evolutionary response in SDT may effectively mitigate such consequences. Further, if considered independently for females and males, the predicted evolutionary response in SDT could be quite dissimilar. The difference between female and male evolutionary response in SDT leads to marked differences in the fraction of fertilized females under certain conditions. Our model may provide general guidelines for improving harvesting of populations, conservation management of rare species under altered environmental conditions, or maintaining long-term efficiency of pest-control measures.

Key words: evolutionary response; mating success; reproductive asynchrony; sex-specific mortality; sexual dimorphism in timing.

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INTRODUCTION

A shared attribute of (rapidly) changing environmental conditions—often a consequence of human interference—is the intended or unintended impact on population dynamics (Shea 1998). Depending on target or reason of interference, we may be interested in understanding means either to mitigate its negative effects on populations (e.g., in the case of conservation or harvesting) or to maximize effects (e.g., in the case of pest control). For a proper understanding, it is primarily important (and often sufficient) to evaluate the mechanisms that affect female number and reproductive success. Nonetheless, assuming that males would more or less be irrelevant for population growth is not always justified (Rankin and Kokko 2007). For example, in butterflies—and particularly among moths—relevant fractions of females may remain unmated

because they fail to find a mating partner (Rhainds 2010); these females will not contribute to the next generation and this will obviously affect growth of populations.

In insects, birds, or fish, a sexual difference in emergence or arrival in the mating pool is frequent, usually referred to as "reproductive asynchrony" or "sexual dimorphism in timing of emergence" (SDT). For semelparous (reproduction once in a lifetime) species, SDT is known to have an effect on the fraction of females that successfully mate (Wiklund and Fagerström 1977, Zonneveld and Metz 1991, Morbey 2002, Kokko et al. 2006, Larsen et al. 2012, Degen et al. 2015), and that SDT can indeed increase the fraction of females that mate. This funding is of general relevance as nearly all annual animals, many insects, some Coleoidea, and a few vertebrates such as fish (e.g., pacific salmon, freshwater eels, and capelin, which are all examples of important commercial target species) and mammals (only in a few didelphid and dasyurid) are semelparous species (Cole 1954, Braithwaite and Lee 1979, Cortez et al. 1995, Murphy and Rodhouse 1999, Gjøsæter et al. 2002). However, the work of Calabrese and Fagan (2004) and Calabrese et al. (2008) shows that the level of SDT that maximizes female mating success also depends on population density—at low density encounters may become so unlikely that any level of reproductive asynchrony would reduce the mating success of females and thus population growth. Matters are further complicated by the fact that the evolutionary perspectives of females and males in this matter are similar but not necessarily identical (Zonneveld and Metz 1991, Degen et al. 2015); the level of SDT is an evolutionarily stable strategy (ESS) (1) for females if it minimizes the risk of mating failure—waiting cost hypothesis —and (2) for males if an invasive male with a different mean time of emergence or arrival achieves less access to mating partners—mate opportunity hypothesis (Zonneveld and Metz 1991, Morbey and Ydenberg 2001).

However, the discrepancy between the females' and males' perspective on the evolutionarily stable level of SDT and the resulting conflict of interest has previously been supposed to be small (review: Morbey 2013). This statement is based on the results of studies that assume equal mortality rates for females and males (Fagerström and Wiklund 1982, Zonneveld and Metz 1991). In a previous study, we modified the model of Zonneveld and Metz (1991) to account for divergent, sex-specific mortality rates during the mating season (Degen et al. 2015). With this approach, we demonstrated for polygynous and seasonal mating systems that protandry (males emerging before females) is generally more likely to evolve but protogyny may evolve if female survival during the mating season is considerably larger than male survival; in this case, a conflict of interest between females and males over the level SDT may become substantial (Degen et al. 2015).

In any case, we can expect that the level of SDT is adapted to the typical ("natural") conditions and population densities that occurred in the past. Currently, many populations are dramatically influenced by human activities, however, and populations may thus exist under conditions different from those under which SDT evolved. It is important to bear in mind that altered environmental conditions can affect mortality rates in the period ahead of the mating season or mortality during the mating season; obviously combined effects are also conceivable. The former occurs, for example, by enhancing larval mortality in insects and the latter, for example, by pheromone traps used to control pest species (review: Cardé 1995, Witzgall et al. 2010). Further, mortality may in the simplest case just be random with respect to gender—but in many cases, added mortality risks may predominately and sometimes even exclusively affect one sex. Examples include the male-biased attraction of moth to artificial light at night (Altermatt et al. 2009, Truxa and Fiedler 2012, Degen et al. 2016), sex-specific consequences of global warming (Martins et al. 2012), sex-specific pest control (Witzgall et al. 2010), or harvesting that affects one sex more than the other (Hilborn and Walters 1992). Consequently, it is important to understand how far the prevailing ("natural") level of SDT contributes to and possibly enhances population decline under altered conditions; how such effects depend on the life stage they affect, as this has important effects on population regulation (Ratikainen et al. 2008); and how SDT might possibly evolve in the future and potentially mitigate the effects of changed mortality.

Previous studies have already investigated how altered environmental conditions and modified population density might affect mating or reproductive success of females (Calabrese and

Fagan 2004, Robinet et al. 2007, Calabrese et al. 2008, Larsen et al. 2012), but these studies did not specify to what extent such effects would be caused by a possible maladaptation of SDT to new environmental conditions.

In this study, we want to investigate how maladapted SDT contributes to female mating failures and therefore to population decline, and how SDT might change when adapting to new conditions. More specifically, we will take into account that altered conditions do not necessarily affect the survival of both sexes similarly, nor affect different life stages equally: For simplicity and sake of argument, we will take a look at the two most extreme assumptions of such human interference, that is, that the added mortality occurs either only before ("pre-mating") or during the mating season. To investigate these questions, we modified a previously developed model (Degen et al. 2015) reflecting the semelparous lifestyle in such a way that it accounts for different mortality rates before (and during) the mating season. The model correspondingly assumes (1) that any individual only participates in a single mating season; (2) that females mate only once or die unmated, whereas males are capable of multiple matings; (3) that each mating contributes equally to reproductive success; and (4) that mating does not reduce the male's chance for future matings. As females do not compete (over mating opportunities), finding the evolutionarily stable level of SDT from their perspective, that is, the SDT maximizing the fraction of fertilized females, is a simple optimization problem, whereas for males that do compete over mating opportunities, frequency-dependent selection mandates an invasion analysis.

Materials and Methods

The primary target of our analysis is understanding how rapid (anthropogenically induced) changes either in pre-mating mortality or in mortality during the mating season would affect female mating success and population dynamics and how such changes might affect evolution of SDT. To evaluate this, we first model the population dynamics of mate-seeking individuals during the season and derive the evolutionarily stable level of SDT under "natural conditions," that is, before anthropogenic effects commence.

The temporal development of male and female population densities during a reproductive season can be described by two differential equations that have been introduced and thoroughly evaluated by Zonneveld and Metz (1991) and Degen et al. (2015). The model describes the temporal sequence of female and male emergence and the resulting probability that females will mate and reproduce before dying. Accordingly, the relative densities of virgin females $V(T)$ and males $M(T)$ increase at any moment due to the emergence of new individuals and decline due to mortality and—in the case of virgin females—due to the transition of virgin females that mate successfully into the "class" of mated females. For large populations of females and males—where stochastic effects and extinction can be ignored—the temporal dynamics in abundance can be described by the equations

$$\frac{\partial M(T)}{\partial T} = \psi \varrho_m g(T; \tau) - \lambda_m M(T) \tag{1}$$

$$\frac{\partial V(T)}{\partial T} = (1 - \psi)\varrho_f g(T; 0) - (\lambda_f + \varphi M(T))V(T). \tag{2}$$

We assume that emergence of females and males follows a probability density function $g(T, \mu)$ that is similar in shape for females and males but offset by the mean difference in emergence timing τ—τ is the measure of SDT in the population. The sex-ratio at birth (e.g., at egg-laying) is determined by the fraction of males (ψ) and females ($1 - \psi$). Changes in pre-mating season survival are accounted for by additional sex-specific mortality factors (ϱ_m and ϱ_f); if these are different between sexes, they alter the sex-ratio at emergence compared to that at birth. Note that this sex-ratio is not identical with the "operational sex-ratio" at any specific moment during the mating season.

Following emergence, virgin female and males are continuously removed due to sex-specific mortality rates that affect survival in the mating period (λ_f and λ_m, respectively, second terms in Eqs. 1, 2. In addition, the pool of virgin females is also reduced by successful mating; matings occur with encounter rate φ. Females mate only once and reproduce immediately after fertilization, whereas males are capable of multiple mating (polygynous mating system); whole population

reproductive output is thus determined by the term $\varphi M(T)V(T)$ integrated over the whole season.

We assume—similar to Zonneveld and Metz (1991) and Degen et al. (2015)—that the probability of emergence at a given time (T) of males and females follows a logistic function with mean value μ.

$$g(T; \mu) = \frac{e^{T+\mu}}{(1 + e^{T+\mu})^2} \tag{3}$$

Without loss of generality, we can choose $\mu_f = 0$ for the mean time of female emergence. As in Zonneveld and Metz (1991) and Degen et al. (2015), real time t is transformed to a "scaled time" $T = t/\beta$ indicating that temporal variables are measured in units of variance of the emergence probability distribution. The model version here extends the approach of Degen et al. (2015) by accounting for additional pre-reproductive and sex-specific mortality risks by factors $1 - \varrho_m$ and $1 - \varrho_f$.

The dynamics of male and female densities can be calculated by numerical integration of Eqs. 1, 2 (for details see Zonneveld and Metz 1991, Degen et al. 2015). From the females' perspective, mating and thus reproductive success ($H(\tau)$) depend on the level of SDT (τ) in a population—natural selection should tune τ to maximize success as has been studied in detail by Zonneveld and Metz (1991) and Degen et al. (2015).

$$\max_{\tau \in \mathbb{R}} H(\tau) = \int_{-\infty}^{\infty} \frac{\varphi}{\psi \varrho_m} M(T, \tau) V(T, \tau) dT \tag{4}$$

From the males' perspective, the optimal SDT should instead maximize the number of matings. The optimal SDT (τ) is obviously frequency-dependent as males compete for matings and can be determined by an adaptive dynamics approach: We have to analyze the total number of matings $\bar{H}(\bar{\tau}, \tau)$ achieved by rare mutant males (emerging on average $\bar{\tau}$ time units ahead or later depending on sign of $\bar{\tau}$) within a resident population with scaled SDT (τ). Zonneveld and Metz (1991) and Degen et al. (2015) have already presented a step-by-step procedure to optimize $\bar{H}(\bar{\tau}, \tau)$ for a given set of parameter, we just refer to these publications for further details. The approach is not complicated or changed by the addition of a pre-mating mortality that was not included in our original model, that is,

$$\bar{H}(\bar{\tau}, \tau) = \int_{-\infty}^{\infty} \frac{\varphi}{\psi \varrho_m} M(T, \bar{\tau}) V(T, \tau) dT. \tag{5}$$

A resident strategy τ is an ESS if any choice of $\bar{\tau}$ results in less or equal reproductive success for the invasive males than for the residents. As already outlined in the introduction, the evolutionarily stable level of SDT is often nearly identical as seen from the perspective of females and males; under some conditions—especially if female mortality in the mating season is considerably lower than that of males—the two evolutionarily stable strategies can deviate substantially, however (Degen et al. 2015). Applying these methods, we will first identify—for a given parameter setting—the evolutionarily stable level of SDT to define reproductive performance under the "original (natural)" situation as reference. This will then be compared to the reproductive performance emerging in scenarios with deviating ecological conditions, that is, with altered mortality rates either before or during the mating season.

In fact, it can easily be shown that

$$\bar{H}(\bar{\tau}, \tau, \varphi) = \frac{\varrho_f}{\varrho_m} \bar{E}(\bar{\tau}, \tau, \varrho_m \varphi) \tag{6}$$

with $\bar{E}(\bar{\tau}, \tau, \varrho_m \varphi)$, the corresponding fitness function from Degen et al. (2015). In other words, $\bar{H}(\bar{\tau}, \tau, \varphi)$ changes in accordance with the sex-ratio at emergence and the absolute number of males emerging.

RESULTS AND DISCUSSION

Ecological consequences of added pre-mating mortality

We will first consider a scenario where some added mortality factor reduces the number of individuals emerging or arriving in the breeding area. Such factors could be habitat disturbance, pest control or, for example, harvesting of salmon (Morbey 2000) that remove individuals from the population ahead of the mating season. We will show the consequences of such mortality risks for the number of females that will mate successfully scaled to the number of females originally emerging; the number of females mating and reproducing in turn determines the population size in the next generation. Note that this fraction corresponds directly to the total number

of matings achieved by males. To explore the immediate effect of such added pre-mating mortality risk, we assume that timing of emergence is adapted to the initial ("natural") conditions where such added risk did not occur. We thus use the methods described above to identify the evolutionary level of SDT (τ) under natural conditions from the females' and males' perspective. Intuitively and trivially, results demonstrate that removal of females has (initially) a stronger effect on the proportion of females fertilized than the removal of males; in a polygynous mating system as assumed here, the loss of some males can easily be compensated for by other males (Fig. 1). Further, and equally trivial, we recognize that the effect of added female mortality is strictly linear. This must be so as the mating probability for a virgin female ($\varphi M(T)$) at a given moment (T) is not affected by the number of females that emerge (see Eq. 2).

In contrast, selectively killing males would initially have little effect on the number of females that will reproduce successfully. However, if males become too rare, females face an increasing risk of
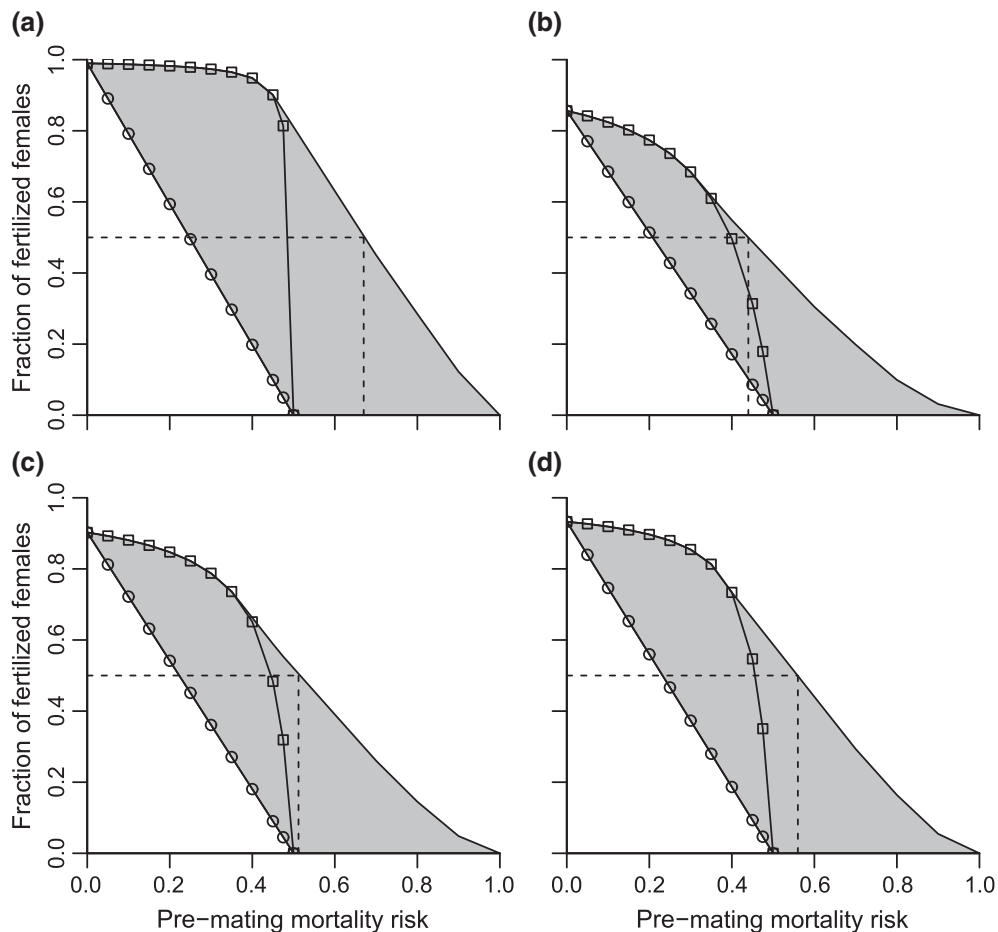

Fig. 1. Fraction of females successfully mating (scaled to the number emerging) as a function of added pre-mating mortality risk. Circles mark scenarios where mortality affects females only, and squares indicate scenarios where only male mortality is changed. The shaded area envelops all outcomes for scenarios combining female and male mortality. The hatched lines indicate the maximum total harvest rate that was possible under the constraint that 50% of the females emerging in the population must mate for the population to persist. (a) Male and female mortality rates are equal ($\lambda = 0.1$), encounter rate $\varphi = 30$. (b) Male and female mortality rates are equal ($\lambda = 0.1$), encounter rate $\varphi = 2$. (c) Female mortality rate during breeding season $\lambda_f = 1$, male mortality $\lambda_m = 0.1$, encounter rate $\varphi = 30$. (d) Female mortality rate $\lambda_f = 0.1$, male mortality $\lambda_m = 1$, encounter rate $\varphi = 30$.

not finding a mating partner before dying—male mortality reduces the mating term in Eq. 2 as male number is reduced. We found that beyond a critical male mortality $(1 - \varrho_m^*)$, removal of further males from the population would have a proportionally stronger effect for the number of reproducing females than the removal of females themselves (Fig. 1). Formally, this must be so because both curves must ultimately reach the bottom line (no fertilized females) as the pre-mating mortality of the sex under investigation reaches 100%. The magnitude of $1 - \varrho_m^*$ depends on mortality rates during the mating season and encounter rate, that is, the parameters that define the females' difficulty in finding mating partners: If finding a mating partner is easy, for example, if mating season mortality (λ) is low and female–male encounter rate (φ) is high, we could indeed remove a large fraction of males before it becomes less damaging to remove females instead of males (e.g., ~90% of males; $\varphi = 30$ and $\lambda_f = \lambda_m = 0.1$; Fig. 1a). In contrast, if encounter rate (φ) is low or the mortality (λ) rate during the mating season is high, the value of males becomes larger and the critical mortality $1 - \varrho_m^*$ becomes smaller (e.g., ~70% of males; $\varphi = 2$ and $\lambda_f = \lambda_m = 1$; Fig. 1b). In a laboratory experiment with beetles, Snyder et al. (2014) found that harvesting had an effect on the population density when they harvested females only (66% of the females), but not when they harvested randomly or males only (66% of the males). They suggested, however, that continued removing of males could have an effect.

Scenarios where the added mortality is random with respect to sex provide very similar results to those with pure female mortality (results not shown): The fraction of females mated primarily and linearly depends on the fraction of individuals removed except if the pre-mating mortality risk becomes very large.

Ecological consequences of added mortality during the mating season

If we consider the effect of changing mortality during the mating season, we mostly find results just opposite to those described above: In the majority of scenarios, increasing male mortality has a stronger effect on the number of females mating successfully than a similar increase in female mortality (Fig. 2); the only exception occurs in scenarios where protogyny evolves under "natural conditions," that is, where long-lived females emerge ahead of males (Fig. 2b). Indeed, this result just points to the more general principle—increasing the mortality of the early-emerging sex typically has a much stronger effect on the fraction of females mating than increasing the mortality of the later emerging sex. Under natural conditions, selection tends to favor earlier emergence of the sex that survives better in the mating season
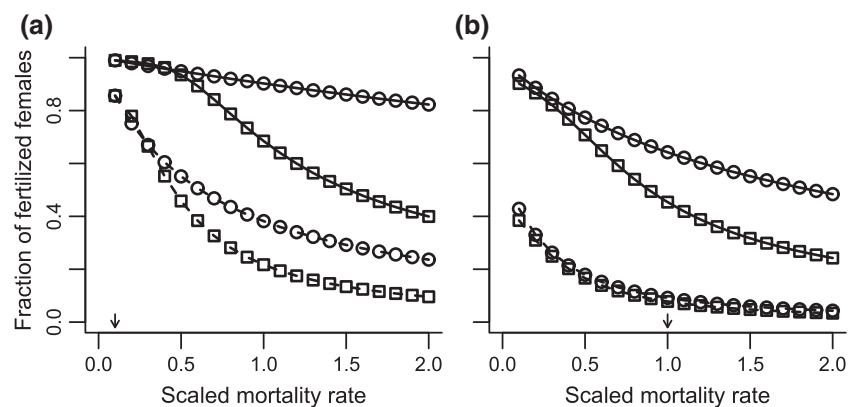

Fig. 2. Fraction of females successfully mating in response to changes in mortality rates during the mating season with sexual dimorphism in timing of emergence fixed to evolutionarily stable level for initial conditions (female perspective; see *Introduction*). Circles mark scenarios with increased female mortality and squares scenarios with increased male mortality rate. Solid lines indicate scenarios with high encounter rate ($\varphi = 30$) and hatched lines scenarios with low encounter rates ($\varphi = 2$). In all scenarios, only the mortality of one sex increases. In (a), the mortality of the sex which is not affected (arrow on the *x*-axis) is 0.1; in (b), it is 1.

(Degen et al. 2015). Abruptly increasing the mortality of just that sex would have the consequence that the two sexes will hardly encounter each other anymore so that the female average waiting time before successfully mating can increase greatly and consequently a large fraction of females may die unmated. Because in polygynous mating systems there is a fundamental bias toward earlier emergence of males, explained by the male competition for mating opportunities (Wiklund and Fagerström 1977, Zonneveld and Metz 1991, Degen et al. 2015), protandry is the more typical evolutionary outcome. It is this reason that increasing male mortality should typically have a stronger effect on the fraction of females that mate than increasing female mortality.

Effect of evolutionary response for mitigating mortality effects

Up to this moment, we have analyzed how a rapid change in either pre-mating mortality risk or mortality rates during the mating season would affect the number of females that mate and reproduce. A substantial and lasting deviation from original ("natural") conditions would, however, impose selective pressure to adjust SDT (τ) to new conditions because individuals with alternative emergence times may gain higher fitness.

Consequently, the level of SDT that originally evolved in a population may be adjusted, thus mitigating the effect of added mortality—a desirable effect in the case of harvesting or in threatened species, but an evolutionary response that might undermine efficiency in pest control.

To evaluate the effect of evolutionary adjustment in the level of SDT and separate the effect of elevated mortality as such from that of maladaptation in SDT, we thus compare the effect of elevated mortality assuming the ESS SDT from the original mortality values with those for an SDT that is an ESS under the altered conditions. Considering the case of increased mortality risk in the pre-mating season, we recognize that increased female mortality risk has no effect on the mating success of the females surviving and consequently has no effect on the evolutionarily stable level of SDT (Fig. 3a)—this must be so as pre-mating mortality $(1 - \varrho_f)$ does not affect the terms relevant for a virgin female's mating success in Eq. 4. This is different, however, if the added mortality affects males—in this case, adjustment of SDT is selected for with a shift toward more similar emergence timing of females and males. Especially for scenarios where the evolutionarily stable level of SDT is large—those with low male mortalities during
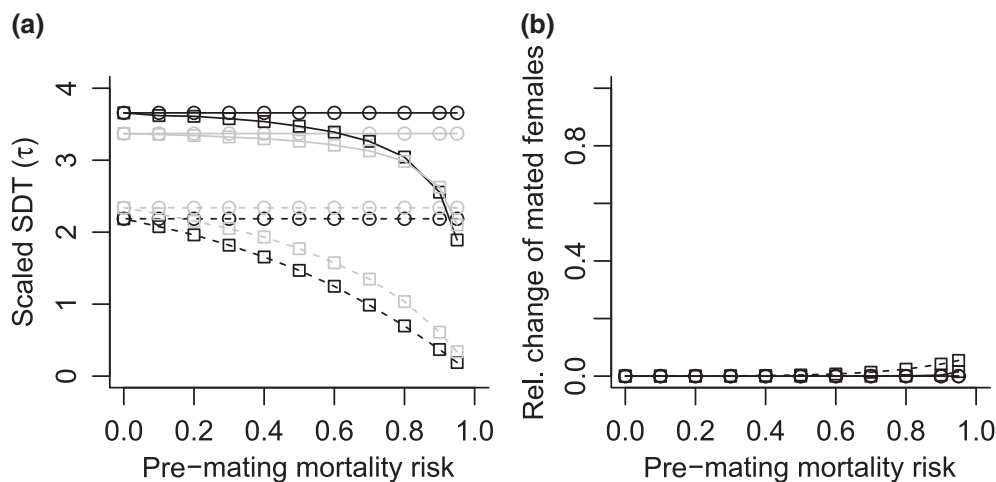

Fig. 3. (a) Evolutionarily stable level of sexual dimorphism in timing of emergence (SDT) from females' (black) and males' (gray) perspective for different added female (circles) and male (squares) pre-mating mortality risks (ϱ). (b) Relative change in the number of females mated resulting from an evolutionary adjustment of SDT from initial $\hat{\tau}$ to new conditions $\check{\tau}((H(\check{\tau}) - H(\hat{\tau}))/H(\hat{\tau}))$. Solid lines indicate scenarios with high encounter rate ($\varphi = 30$) and hatched lines scenarios with low encounter rates ($\varphi = 2$). Both male and female mortality rates during mating season are equal to 0.1. Added pre-mating mortality of sex not affected is fixed at $1 - \varrho = 0$.

the breeding season—an increased mortality risk in the pre-mating season could reduce the evolutionarily stable level of SDT substantially (Fig. 3a). However, such an adaptive response would have little effect on the fraction of females that reproduce successfully and would thus have little effect on the ecological impact of added pre-mating mortality (Fig. 3b). This result holds regardless of whether we assume that SDT evolves toward the females' or males' ESS.

Matters change considerably if added mortality affects survival rates during the mating season. In all scenarios, the mortality of one sex was fixed, while the mortality rate of the other sex was increased (Fig. 4). Expectedly, an increase in male mortality generally shifts the evolutionarily stable level of SDT in the direction of protogyny because protogyny is favored when females survive longer than males (Degen et al. 2015), whereas an increase in female mortality shifts the evolutionarily stable level of SDT in the opposite direction, that is, toward (increased) protandry. However, if initial survival of both sexes is high, increasing female mortality has a rather limited effect on the
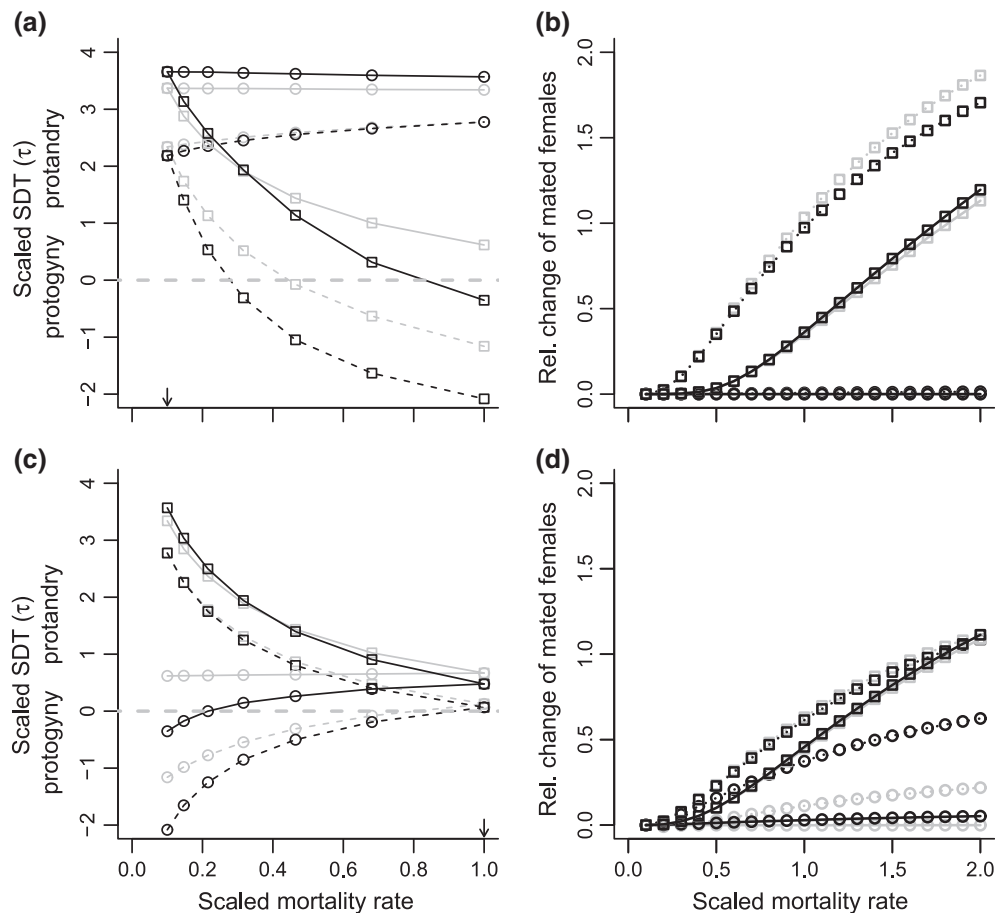

Fig. 4. Evolutionarily stable level of sexual dimorphism in timing of emergence (SDT) from females' (black) and males' (gray) perspective for different added female (circles) and male (squares) mortality risks during the mating season (λ; panels a and c). Relative change in the number of females mated resulting from an evolutionary adjustment of SDT from initial $\hat{\tau}$ to new conditions $\mathring{\tau}(H(\hat{\tau})/H(\hat{\tau}) - 1)$ (panels b and d). In all scenarios, only the mortality rate of one sex increases: Circles indicate scenarios with increased female and squares scenarios with increased male mortality rates. Scenarios with high encounter rate ($\varphi = 30$) are identified by solid lines and scenarios with low encounter rates ($\varphi = 2$) by hatched lines. In (a) and (b), the mortality rate of the sex which does not change (arrow on the x-axis) is 0.1, whereas in (c) and (d) it is 1.

evolutionary change in SDT. Also note that a change in mortality rates can affect the discrepancy between the females' and males' ESS. Common to all substantial deviations between the females' and males' ESS is that females prefer a SDT shifted more toward protogyny than males (Degen et al. 2015); that is, females would prefer to emerge earlier than the males would like them to do. Such discrepancy would, however, be relevant for the fraction of fertilized females only in scenarios with low encounter rates and high constant male mortality rate (Fig. 4d).

More importantly, we recognize that an adaptive response in SDT could substantially mitigate the effect of increased mortality rates (Fig. 4b, d). There we define "mitigation potential" by the relative change $((H(\tau) - H(\hat{\tau}))/H(\hat{\tau}))$ in the number of females mated ($H(\tau)$) resulting from an evolutionary adjustment of SDT (τ) from initial $\hat{\tau}$ to new conditions τ. For example, in scenarios with increased male mortality the relative change in the fraction of females that reproduce successfully ($H(\tau)$) could be 1.8—that is, female mating success is 2.8 times higher in adapted compared to non-adapted populations.

PRACTICAL IMPLICATIONS AND CONCLUSION

Our results may have practical implications in various fields of applied ecology. For example, encounter and mortality rate during the mating season define the mating success of females, and knowing these rates could allow optimizing harvesting strategies: Assuming that a population can be maintained if, for example, 50% (including a sensible safety margin) of females that emerge reproduce successfully, we can define the combination of male and female numbers to be removed that would maximize pre-mating harvesting without surpassing this margin (see example and gray-shaded areas in Fig. 1). Especially if females find mating partners easily (Fig. 1a), we could harvest in the non-reproductive season ~90% of males (ignoring possible genetic effects) in addition to ~45% of the females. This would allow for an overall harvesting rate of ~67%. In contrast, if mate finding is challenging (Fig. 1b), we could harvest ~70% of males in addition to ~17% of the females. This would allow for an overall harvesting rate of ~43%. Strategies completely focusing on harvesting males (below the

critical value!) would in this case already be near the optimal harvesting rate. More generally, our results caution against targeting the sex that emerges earlier in the breeding season especially if harvesting takes place in the mating season.

In the case of pest control implemented during the mating season, for example, when utilizing pheromone traps (mass trapping and "attract-and-kill"), measures often target males (review: Witzgall et al. 2010). Typically, a high proportion of males must be removed to produce a significant effect. It is known, however, that protandry improves the effect of removing males and that pheromones are increasingly efficient at low population densities (review: Witzgall et al. 2010). Our results demonstrate that under protandry—the more typical case among insects (Larsen et al. 2012)—male killing in the breeding season should indeed be more efficient in reducing the number of females reproducing than killing of virgin females (in similar numbers). In fact, the non-linear shape of curves in Fig. 2 suggests increasing returns with increasing efficiency of pest control!

Our results also show, however, that consequences of altered environmental conditions within the reproductive season could over time be diminished—sometimes even massively so—by an adaptive response. The mechanism outlined here is especially interesting as it is not due to declining efficiency of the control strategy per se (as is the case with evolution of resistance or tolerance (Georghiou 1972) but due to a change in general life history, that is, a change in timing of emergence. The potential for such evolutionary response should caution against light-handed and regular application of such pest management. Pest control limited to periods of severe pest outbreaks (i.e., integrated pest management) may preserve or at least prolong the efficiency of such control strategies (Furlong et al. 2011). Interestingly enough, an evolutionary response to altered environmental conditions affecting mortality in the pre-mating period would have little effect on the fraction of females fertilized. More generally, our results suggest that in pest control, measures affecting the early-emerging sex during the breeding season are always promising.

The potential for a (strong) mitigating effect of adaptation to new conditions may indeed be bad news for pest control but would be welcome in the context of harvesting or conservation. Light

pollution, for example, is a matter of great concern as artificial light sources attract flying insects in great numbers (Frank 1988, Eisenbeis and Hänel 2009), in moth often enough predominantly males (Altermatt et al. 2009, Truxa and Fiedler 2012, Degen et al. 2016). Over time, adaptation may possibly reduce the damage done by such "light traps" to populations. Indeed, just because artificial light is usually turned on and off in very predictable patterns—inducing a constant change of mortality rates—such adaptation may occur rather fast.

In insects, polygyny is the most common mating strategy, but it is far from being ubiquitous (Zonneveld 1992, Matthews and Matthews 2010). However, even if females were completely polyandric (i.e., readiness to mate is independent of the number of matings), protandry is an ESS if matings are weighted (e.g., mating virgin females is more valuable to males' reproductive success than mating non-virgin females). Consequently, as the degree of polyandry is probably low in most species, protandry is an ESS even if matings are unweighted Zonneveld (1992). Therefore, we believe that even though we restrict our discussion to monoandry, the ideas developed here are also relevant if females mate more than once in their life.

In summary, our model might explain differences in SDT between populations, for example, salmon (Morbey 2000), predict evolutionary response to changed environmental conditions, and may be useful in pointing out under which conditions sex-specific management strategies could be especially profitable, whether it is in the case of managing threatened populations, improving efficiency of pest control, or optimizing harvesting strategies.

Acknowledgments

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