

Sexual Conflict and the Tragedy of the Commons

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Submitted April 7, 2010; Accepted January 2, 2011; Electronically published May 3, 2011

ABSTRACT: It is widely understood that the costs and benefits of mating can affect the fecundity and survival of individuals. Sexual conflict may have profound consequences for populations as a result of the negative effects it causes males and females to have on one another's fitness. Here we present a model describing the evolution of sexual conflict, in which males inflict a direct cost on female fitness. We show that these costs can drive the entire population to extinction. To males, females are an essential but finite resource over which they have to compete. Population extinction owing to sexual conflict can therefore be seen as an evolutionary tragedy of the commons. Our model shows that a positive feedback between harassment and the operational sex ratio is responsible for the demise of females and, thus, for population extinction. We further show that the evolution of female resistance to counter harassment can prevent a tragedy of the commons. Our findings not only demonstrate that sexual conflict can drive a population to extinction but also highlight how simple mechanisms, such as harassment costs to males and females and the coevolution between harassment and resistance, can help avert a tragedy of the commons caused by sexual conflict.

Keywords: adaptive dynamics, population dynamics, coevolution, social evolution, evolutionary suicide.

Introduction

Sexual reproduction is widely considered an evolutionary mystery, because it involves a twofold cost. This cost is a result of anisogamy and is due to the production of males halving the population growth rate (West et al. 1999; Agrawal 2006). Under anisogamy, one of the sexes evolves to produce small gametes that contribute virtually no resources to the zygote. The shift from investing in few gametes to producing numerous gametes (which is a specialty of the male sex) represents escalating competition between males. The cost of sex arises only when males

shift resource use away from offspring provisioning, and it is thus often remarked that the twofold cost of sex is more appropriately referred to as the cost of male production (Maynard Smith 1978; Jennions and Kokko 2010).

This twofold cost is key to understanding the evolution of sexual reproduction, but it also has other consequences. For males, females form the limiting resource. Numerous male traits, such as sperm competition, have evolved as a consequence of competition among males, which can lead to male gametes vastly outnumbering female gametes or to investment in weaponry (Emlen 2008). Such scenarios can lead to a tragedy of the commons, since behaviors are favored that are advantageous to individuals but detrimental to the group or population as a whole (Hardin 1968; Rankin et al. 2007*b*). Sexual conflict over mating is a tragedy of the commons whenever male-male competition reduces the availability of females (or their gametes) for all males, for example, via elevated female mortality (Le Galliard et al. 2005; Rankin and Kokko 2006). Given the increasing emphasis in the evolutionary literature on understanding the demographic consequences of group-detrimental behaviors using the framework of the tragedy of the commons (e.g., Rankin et al. 2007*b*; Frank 2010), it is surprising that sexual conflict has not featured more strongly in such work; so far, we have virtually no theoretical background for understanding the potentially negative population-level consequences of male behaviors toward females.

If male behavior harms female reproduction, the cost of sex can be larger than twofold. Studies of sexual conflict have documented numerous examples of reproductive costs (Chapman et al. 2003; Arnqvist and Rowe 2005). Extreme cases include toxic seminal fluids that appear to harm females as a form of collateral damage (Chapman et al. 1995; Wigby and Chapman 2005), as well as male mating behaviors that physically damage females (Le Galliard et al. 2005). Milder cases, which nevertheless can

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increase the cost of sex, include size dimorphisms that force mothers to invest more energy into male offspring (Rankin and Kokko 2007). Also, sexual harassment of females by males has been shown to impose costs on females—in terms of reduced fecundity or survival—in a number of systems (e.g., Réale et al. 1996; Crudgington and Siva-Jothy 2000; Shine et al. 2000, 2001; Maklakov et al. 2006; Rönn et al. 2006, 2007; Godsen and Svensson 2009). A recent study of water striders demonstrated that while aggressive males had an advantage in local competition for mates, this had a negative impact on their fitness when considered across a wider metapopulation as a result of the harm they imposed on females (Eldakar et al. 2009).

The population-level consequences of sexual conflict, albeit rarely documented, can be severe (Kokko and Brooks 2003; Le Galliard et al. 2005; Valero et al. 2008) but typically depend on both the population density and the sex ratio. For example, in the common lizard *Lacerta vivipara*, males harm females by inflicting mating scars and damaging the skin on the backs of females (Le Galliard et al. 2005). Male-biased populations of these lizards have been shown to exhibit higher female mortality than female-biased populations, owing to a higher level of harassment of females by males (Le Galliard et al. 2005). The harm induced by male lizards was predicted to drive populations to extinction within 40 years, if they started out with a male bias (Le Galliard et al. 2005). This highlights that the tragedy does not have to stop at a 50% reduction in population growth rate, which would be predicted if the cost of sex were always precisely twofold. Instead, individually selected adaptations can lead to detrimental effects up to the point at which a whole population or species is driven to extinction (Matsuda and Abrams 1994a, 1994b; Boots and Sasaki 2003; Parvinen 2005; Rankin and López-Sepulcre 2005; Rankin et al. 2010).

Given that sexual conflict among animals is widespread (Arnqvist and Rowe 2005), the population-level cost of sex could often be greater than twofold. If sexual conflict elevates female mortality and becomes more severe when populations are male biased, what prevents sexual conflict from regularly driving populations to extinction? We investigate two potential mechanisms that may avert a tragedy of the commons: (1) costs to males of harassing females (since such direct costs are known to prevent a tragedy of the commons in other situations; Rankin et al. 2007b) and (2) joint evolution between male harassment and female resistance (Arnqvist and Rowe 2002; Rönn et al. 2007). We do this by building a model based on adaptive dynamics theory that separately treats the evolution of phenotypic traits in males and females and does not make any specific assumptions about the underlying genetic sys-

tem, such as diploidy or additive genetics. To evaluate the robustness of our results and to see how they might be influenced by explicit genetic assumptions, we further analyze a corresponding individual-based model. We show that costs of harassment and the underlying population ecology are key determinants of whether populations can be driven to extinction by sexual conflict.

Model and Results

Evolving Traits

We examine the evolution of male harassment of females and of female resistance to male-induced harm, both of which are sex specific. Males express a harassment level y that improves male mating success but reduces survival for males as well as females. We denote the corresponding costs g and h for males and females, respectively. Such costs may be of very unequal magnitude for the harasser and the target of harassment. Females express a level of resistance x ($0 \leq x \leq 1$) that improves their survival but simultaneously reduces their fecundity by a factor $p(x)$ ($0 \leq p(x) \leq 1$). A description of the variables and parameters used in the model is given in table 1.

Population Dynamics

Since our model links trait evolution to its demographic consequences, we must specify population dynamics explicitly. To do this, we assume that the population dynamics of males and females unfold in continuous time. Male density is denoted M and female density F . We assume that reproduction takes negligible time, so all males and

Table 1: Model variables and parameters

Variables and parameters	Description
M	Density of males
F	Density of females
y', y	Level of male harassment for a mutant (y') and a resident (y)
x', x	Level of female resistance for a mutant (x') and a resident (x)
r	Primary sex ratio (proportion of males)
b	Intrinsic birth rate
μ	Scale of density-dependent death rate
c	Cost to males of investing in harassment
k	Cost to females of experiencing harassment
u	Shape of returns to males from investing in harassment
a	Cost to females of resisting harassment
d	Efficiency of female resistance in reducing the costs of male harassment

females can mate at any time, and the operational sex ratio (OSR) is the same as the adult sex ratio. Females have an intrinsic birth rate b and produce males with probability r and females with probability $1 - r$ (if $r = 1/2$, the primary sex ratio is even).

To capture the assumed demographic consequences of the traits x and y as described above, we consider the following population dynamics of male and female densities:

$$\frac{dF}{dt} = (1 - r)p(x)bF - h(x, y, M, F)F - l(M, F)F \quad (1a)$$

$$\frac{dM}{dt} = rp(x)bF - g(y)M - l(M, F)M. \quad (1b)$$

In these equations, density-dependent mortality is represented by the function $l(M, F)$. For simplicity, we assume logistic density dependence, such that $l(M, F)$ increases linearly with population density, $l(M, F) = \mu(M + F)$, where the parameter μ scales the density-dependent mortality. In keeping with adaptive dynamics theory, we assume a homogeneous population such that all males and females (except for the occasional rare mutant) have the same trait values x and y , respectively (we later relax this assumption in an individual-based model).

We assume that a male's investment y in harassment imposes a cost on the male by elevating his mortality in proportion to y . We describe this by the function $g(y) = cy$, where c scales these costs to males. Similarly, male harassment increases female mortality, which is described by the function $h(x, y, M, F)$. We derive our examples below using the function $h(x, y, M, F) = (1 - dx)yM/F$, which implies that the harassment costs experienced by females decrease with female resistance and increase as males become more common relative to females. The first effect is described by $1 - dx$, where d scales the efficiency of female resistance. Since h cannot be negative, we assume that $0 \leq d \leq 1$ (implying that $0 \leq 1 - dx \leq 1$). The second effect is described by kyM/F , where k scales how strongly harassment increases female mortality. Since female resistance x may impose a cost on females, we assume that female fecundity is reduced by the factor $p(x) = 1 - ax$, where a scales a female's cost of investing in resistance ($0 \leq a \leq 1$). This fecundity cost can be large, as in the case of bedbugs developing a harder outer shell (Reinhardt et al. 2003), or small, as in the case of females kicking to avoid copulation in the seed beetle *Callosobruchus maculatus* (Edvardsson and Tregenza 2005).

Extinction Threshold

There are three equilibria of the dynamics described by equations (1): the first is the extinction equilibrium at

$\hat{M} = 0$ and $\hat{F} = 0$, whereas male and female densities are positive at the other two equilibria. Calculating the Jacobian matrix of equations (1) and determining its eigenvalues, we see that only one of the two nonextinction equilibria is stable, and we therefore focus on this equilibrium in the following analyses. Examining the eigenvalues of the Jacobian matrix at $\hat{M} = 0$ and $\hat{F} = 0$ yields a threshold condition for the levels of male harassment y that cause extinction:

$$y \geq y_{\text{ext}} = \frac{bp(x) \frac{2\sqrt{rk(1-dx)[rk(1-dx) - c(1-r)]} + 2rk(1-dx) - c(1-r)}{c^2}}{c^2}. \quad (2)$$

For $r > c/[c + k(1 - dx)]$, the extinction threshold y_{ext} is real and positive, and for $x = 0$, it simplifies to

$$y_{\text{ext}} = b \frac{2\sqrt{rk[rk - c(1-r)]} + 2rk - c(1-r)}{c^2}.$$

We note in passing that had we assumed density-dependent harassment, $h(x, y, M, F) = (1 - dx)kyM$, instead of frequency-dependent harassment, $h(x, y, M, F) = (1 - dx)kyM/F$, deterministic extinction would not be possible. This finding is consistent with analogous results for parasite-mediated extinction, where it has been shown that deterministic extinction can occur only under frequency-dependent transmission and not under density-dependent transmission (e.g., Boots and Sasaki 2003; Rankin et al. 2010).

Evolution of Male Harassment

We now investigate whether evolution drives the harassment level y above the extinction threshold y_{ext} . For our first model, we use adaptive dynamics theory (Metz et al. 1992, 1996; Dieckmann and Law 1996; Dieckmann 1997; Geritz et al. 1998; Mesz ena et al. 2001; Dieckmann and Metz 2006) to account for the eco-evolutionary feedback between the population dynamics and the evolution of our two evolving traits. As such, our analysis assumes that ecological and evolutionary timescales are sufficiently separated (so that the densities of males and females rapidly reach equilibrium). We do not distinguish between genotypes and phenotypes, and the terms "mutants" and "residents" refer to individuals with rare or prevalent trait values, respectively. Since our results in equations (3)–(10) are based on selection gradients, equivalent results could be derived if we had instead followed the quantitative genetics method of Lande (1976; Iwasa et al. 1991), with uncorrelated traits and small additive genetic variances.

We assume that harassment at level y provides a male with an absolute mating benefit $f(y)$. However, since mat-

ing opportunities are limited by the availability of females, a male's mating success must be evaluated relative to that of all other males; this implies that selection on y is frequency dependent, since a male's mating success depends not only on his own $f(y)$ but also on the $f(y)$ of other males. In a first step of analysis, we assume that females possess no resistance (i.e., $x = 0$, and thus $p(x) = 1$). The invasion fitness (Metz et al. 1992) of a mutant male with trait value y' in a population dominated by the resident trait values x and y is given by the mutant's per capita growth rate when rare:

$$\lambda_M(y', x, y) = rb \frac{\hat{F} f(y')}{\hat{M} f(y)} - g(y') - l(\hat{M}, \hat{F}). \quad (3)$$

The factor $f(y')/f(y)$ represents the relative benefits of mating to a male investing y' in harassment. In a homogeneous population (where $y' = y$), this term equals 1. We derive our examples below using the function $f(y) = y^u$, so the shape of the dependence of the mating benefit $f(y)$ on the harassment level y is determined by u . If $u > 1$, the benefits of harassment are accelerating, while if $u < 1$, these benefits are decelerating.

The selection gradient for the male harassment level y is

$$s_M(x, y) = \left. \frac{\partial \lambda_M(y', x, y)}{\partial y'} \right|_{y'=y} = \frac{bru \hat{F}}{y \hat{M}} - c. \quad (4)$$

The selection pressure on y vanishes at the evolutionarily singular strategy y^* , which is thus obtained by solving the equation $s_M(y^*) = 0$:

$$y^* = bu \frac{c(1-r) - kru}{c^2(1-u)}. \quad (5)$$

If the singular strategy $y = y^*$ satisfies inequality (2), the evolution of harassment causes population extinction through sexual conflict when $y \geq y_{\text{ext}}$. Such selection-driven extinction is known as evolutionary suicide (Ferrière 2000; Dieckmann and Ferrière 2004; Parvinen 2005; Rankin and López-Sepulcre 2005). Figure 1 shows an example of the evolutionary dynamics of male harassment, including its effect on male and female densities. The evolutionary dynamics of y are determined by the equation $dy/dt = \delta s_M(y)$, where δ is a small number that scales the speed of evolution (Lande 1976; Hofbauer and Sigmund 1990; Iwasa et al. 1991; had we used the canonical equation of adaptive dynamics [Dieckmann and Law 1996], the right-hand side would also contain \hat{F}). Figure 1A and 1B show a case in which the population persists despite the evolutionary aggravation of sexual conflict. Here the number of females exceeds the number of males, but the population is not driven to extinction, since the per capita

harassment experienced by females remains mild despite the high level of harassment imposed by each male. In contrast, figure 1C and 1D show a case in which the population is driven to extinction. Here the level of male harassment remains relatively low, but since the population contains many more males than females, the positive feedback between the declining fraction of females and the increasing harassment they experience causes extinction.

By replacing the y in inequality (2) for $x = 0$ with $y = y^*$ according to equation (5), we see that harassment evolution causes extinction, if

$$u > 1, \quad (6)$$

$$1 \geq r \geq \frac{c}{c+k}.$$

Interestingly, this condition is independent of both the intrinsic birth rate b and the scale μ of the density-dependent death rate. Inequality (6) shows that accelerating returns to males from investing in harassment ($u > 1$) are needed for evolutionary suicide to occur. It also shows that the potential for evolutionary suicide critically depends on the costs of male harassment both to males from expressing the trait (c) and to females from male-induced harm (k). If the ratio of male costs to female costs, $c/(c+k)$, is less than the primary sex ratio r , then evolutionary suicide occurs, whereas if this ratio exceeds r , the population can persist. For an even primary sex ratio, $r = 1/2$, the condition $r > c/(c+k)$ simplifies to $k > c$, so the harm inflicted on females must exceed the cost males pay for harassment.

We can understand these results by considering the effect of harassment on the relative densities of males and females. For $u > 1$, the evolution of harassment may continue to accelerate, increasingly affecting the population densities of males and females. If $r > c/(c+k)$, females suffer from more harassment-related mortality than males, which leads to greater harassment per female, since there are more males than females. This further increases female mortality, until the population is driven to extinction. In contrast, if $r < c/(c+k)$, males suffer from more harassment-related mortality than females, which decreases male density and thus further reduces the per capita level of harassment females experience.

These findings are confirmed by figure 2, which shows how the evolutionarily singular level of harassment (fig. 2A) and the male and female density (fig. 2B) vary with the costs of harassment to males. We see that the population is driven to extinction for $c < k$. Low costs to males result in high levels of harassment and thus extinction. High costs to males enable population persistence but decrease the density of males through their effect on male fitness. It is also interesting to observe that the greater the

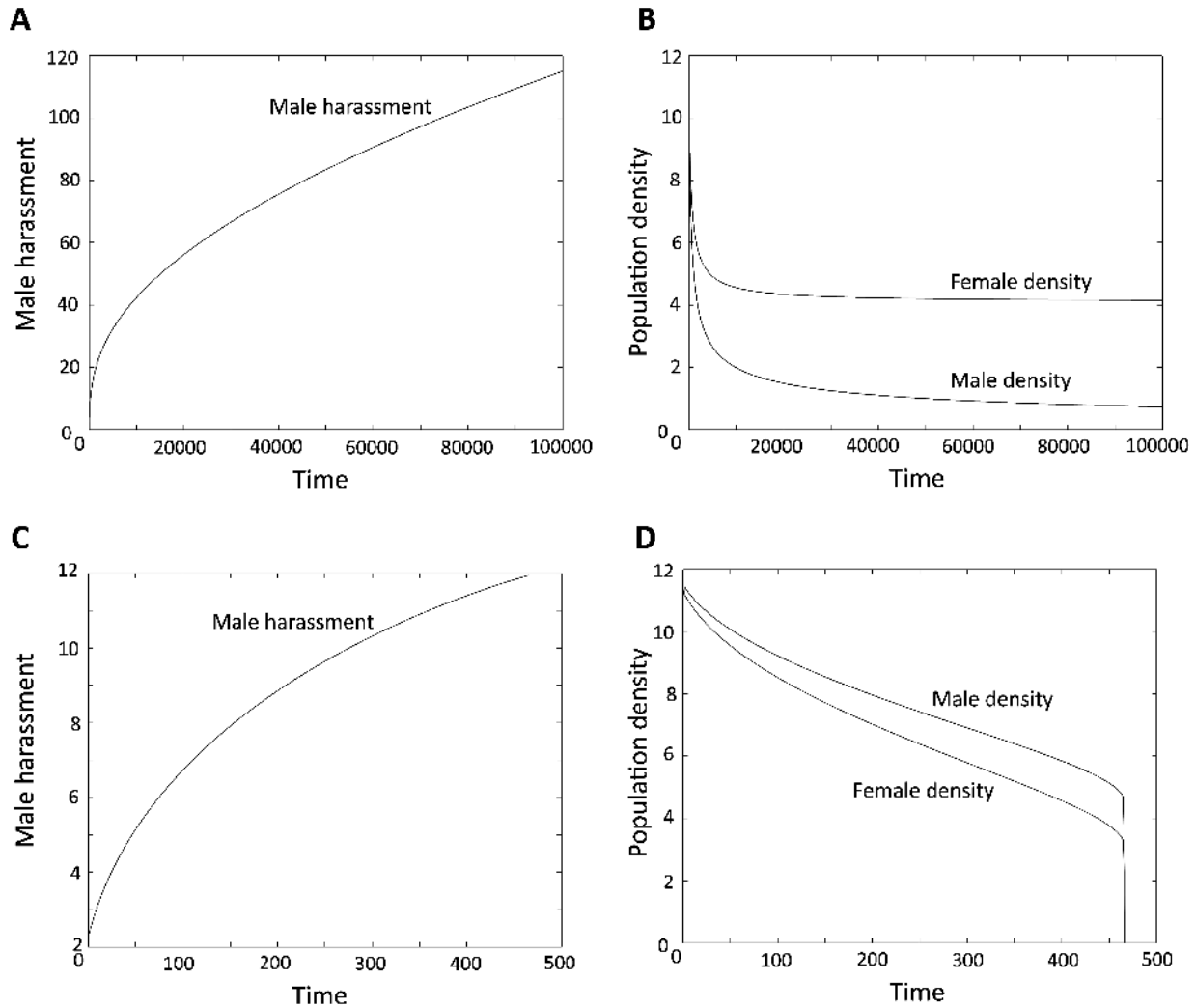


Figure 1: Evolution of male harassment (A, C) and implications for the population densities of males and females (B, D) in the analytical model. A and B show a case without selection-driven extinction ($c = 1.2$), whereas C and D show a case with evolutionary suicide ($c = 0.8$). Other parameters: $r = 1/2$, $b = 50$, $\mu = 1$, $k = 1$, $u = 1.01$, $a = 1$, $d = 0$, $x = 0$, and $\delta = 0.01$.

cost of harassment to males, the greater the density of females. This effect arises through a feedback between male density and the costs to males: if harassment increases male mortality, the lower resulting density of males creates conditions that are more favorable to females. Under an even primary sex ratio, the more females reproduce, the more even the OSR will be, and this in turn further reduces the harm inflicted on females.

Evolution of Female Resistance

In a second step of analysis, we can now look at the evolution of female resistance x ($0 \leq x \leq 1$) to male harassment. Following the assumptions described previously, the

invasion fitness of a mutant female investing x' in a resident population investing x is

$$\lambda_F(x', x, y) = (1 - r)p(x')b - h(x', y, \hat{M}, \hat{F}) - l(\hat{M}, \hat{F}). \quad (7)$$

From equation (7), the selection gradient for x is thus given by

$$s_F(x, y) = \left. \frac{\partial \lambda_F(x', x, y)}{\partial x'} \right|_{x'=x} = dk y \frac{\hat{M}}{\hat{F}} - ab(1 - r). \quad (8)$$

We can study the coevolution of male harassment and female resistance by examining the male and female se-

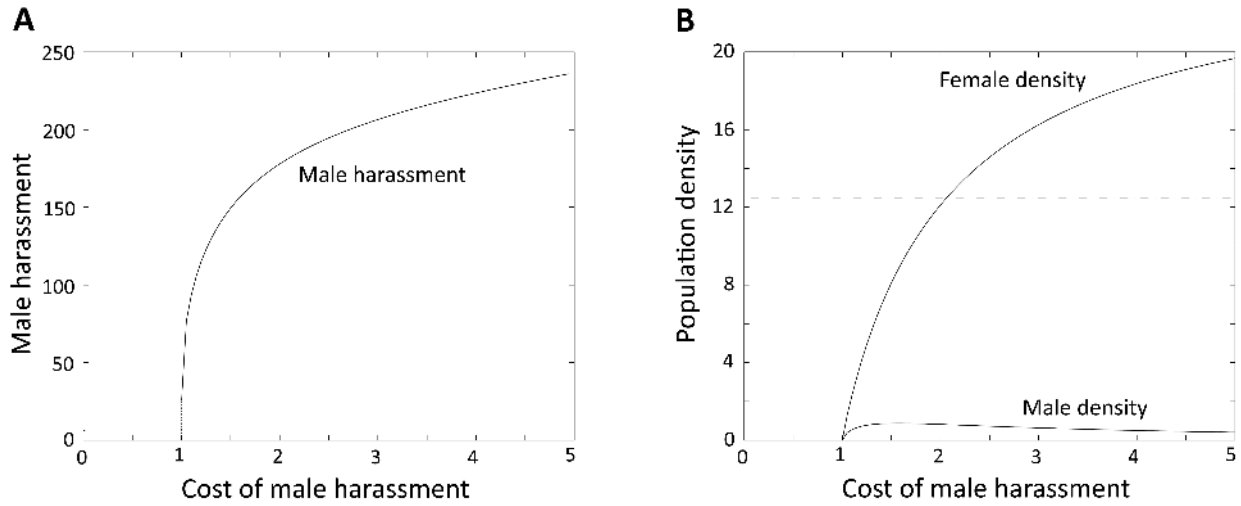


Figure 2: Influence of harassment cost to males on the evolutionary equilibrium of male harassment (A) and the resultant equilibrium densities of males and females (B) in the analytical model. The dashed line shows the equilibrium density of males and females in the absence of male harassment ($y = 0$) and female resistance ($x = 0$). Parameters: $r = 1/2$, $b = 50$, $\mu = 1$, $k = 1$, $u = 1.01$, $a = 1$, $d = 0$, and $x = 0$.

lection gradients in equations (4) and (8). An example of the joint evolutionary dynamics of male harassment and female resistance, $d(x, y)/dt = \delta(s_F(x, y), s_M(x, y))$, is given in figure 3. Solving this for $d(x^*, y^*)/dt = 0$ gives us the evolutionarily singular levels of female resistance x^* and male harassment y^* :

$$x^* = \frac{1}{a} - \frac{c(1-r)}{dkru}, \tag{9a}$$

$$y^* = \frac{bu(d-a)(1-r)}{cd(1-u)}. \tag{9b}$$

We can now use the threshold in inequality (2) to determine where evolution toward x^* and y^* imply population extinction. If we assume that the benefits of resistance are greater than the costs (i.e., $a > d$), sexual conflict drives the population to extinction if

$$u > 1, \tag{10}$$

$$1 \geq r > \frac{ac(1-u)}{ac + dku - au(c+k)}.$$

In other words, greater values of a or k —or smaller values of c —will result in evolutionary suicide. As for the case of male harassment evolving in the absence of female resistance, more male-biased primary sex ratios (greater values of r) or more accelerating harassment benefits (greater values of u) will increase the extinction risk resulting from sexual conflict.

Our results make intuitive sense, since if $u > 1$, runaway

selection for greater levels of sexual conflict may occur. If harassment is costly to males, this can prevent the OSR from becoming more biased; these costs prevent harassment from evolving toward the extinction threshold, not only because they directly hamper the evolution of strong (and thus costly) harassment but also because the costs to males manifest themselves as increases in male mortality. The reduction in male density resulting from the greater costs to males obviously limits the dangerous increase in the OSR. The opposite is true if the male-induced harm to females increases with k , since this magnifies the OSR bias.

Figure 4 shows how the evolution of female resistance depends on the cost to males of investing in harassment. We see that female resistance is favored at intermediate levels of the cost to males. If this cost is small, males evolve to be very harmful to females, so it does not pay to females to invest in resistance (Lee and Hays 2004). At the other extreme, high costs to males disfavor male harassment and thus reduce the need for resistance. It is in the intermediate range that female resistance is evolutionarily favored. Figure 4 shows that the evolution of female resistance can rescue the population from extinction in a significant part of the range $0 \leq c \leq k$, which we had previously shown to lead to population extinction in the absence of female resistance.

Individual-Based Model

To check the robustness of results and relax the simplifying assumptions made in the analyses above, we now examine

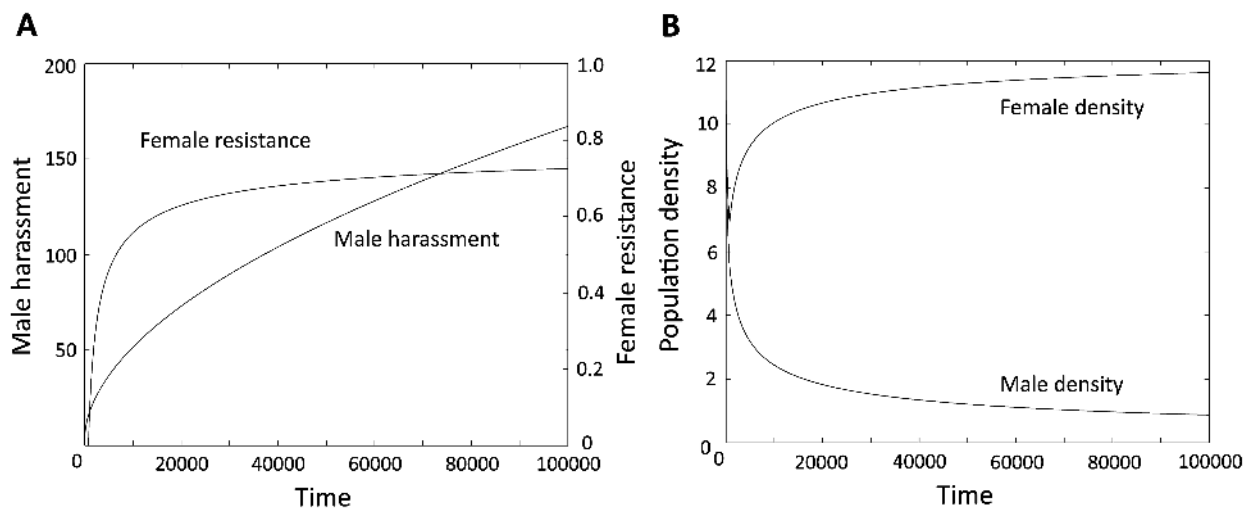


Figure 3: Coevolution of male harassment and female resistance (A) and implications for the population densities of males and females (B) in the analytical model. Parameters: $r = 1/2$, $b = 50$, $\mu = 1$, $u = 1.01$, $k = 1$, $a = 1/2$, $d = 1$, $c = 0.8$, and $\delta = 0.01$.

a genetically explicit individual-based model with diploid inheritance of harassment and resistance alleles. We consider one locus for harassment and one locus for resistance and assume free recombination between these loci. We also assume additive genetics and the absence of environmental variation, so an offspring's phenotype is the mid-parental value of the alleles inherited from the mother and the father. For example, the offspring's resistance is $x = (x_F + x_M)/2$, where x_M denotes the allelic value inherited from the mother and x_F the allelic value inherited from the father. Sexual reproduction involves segregation and recombination, and one of the parent's two homologous alleles is chosen at random to be inherited. Each individual thus possesses two harassment alleles and two resistance alleles. The harassment alleles are expressed only in males and the resistance alleles only in females. All other assumptions are as described above; in particular, we use the same functions to link phenotypes to per capita birth and death rates. Since populations in the individual-based model are finite, population dynamics are stochastic, and evolution is subject to genetic drift. Full details of the individual-based model are given in the appendix.

For $c < k$, and when harassment is not resisted by females, the population is driven to extinction as a result of harassment evolution (fig. 5A, 5B). Our assumption of an even primary sex ratio results in a vicious circle in which males become more abundant as harassment shortens female life span, diminishing female density and ultimately driving the population to extinction. Allowing female resistance and male harassment to coevolve (fig. 5C, 5D) can prevent extinction. The two examples in figure 5 reflect

a general pattern. When examining 25 model runs when costs to males were low ($c = 0.8$) and female resistance was not favored ($a = 1$ and $d = 0$), all 25 resulted in evolutionary suicide. When the costs to males were higher ($c = 1.2$), the population persisted in 23 out of the 25 considered replicate model runs, with an average final population size of 971.52 ± 82.7 (mean \pm SE) individuals. When females were allowed to evolve resistance (for $c = 0.8$, $a = 0.5$, and $d = 1$), persistence occurred in all 25 considered replicate model runs, with an average final population size of $1,770.6 \pm 17.5$ (mean \pm SE). All of these results are in good qualitative agreement with our analytical model.

Discussion

Here we have shown that the evolution of male harassment can result in the extinction of an entire population. In our model, the evolution of male harassment can lead to a vicious cycle in which fewer females survive while the mortality of the remaining females increases as a result of a high male to female ratio, until the population collapses. Our findings therefore confirm the results of Le Galliard et al. (2005). In particular, we have shown that an evolutionary tragedy of the commons can occur both in a simplified analytical model and in a genetically explicit individual-based model. While earlier studies based on simpler models have speculated that sexual conflict may cause population extinction (for a review, see Kokko and Brooks 2003), our model is, to our knowledge, the first

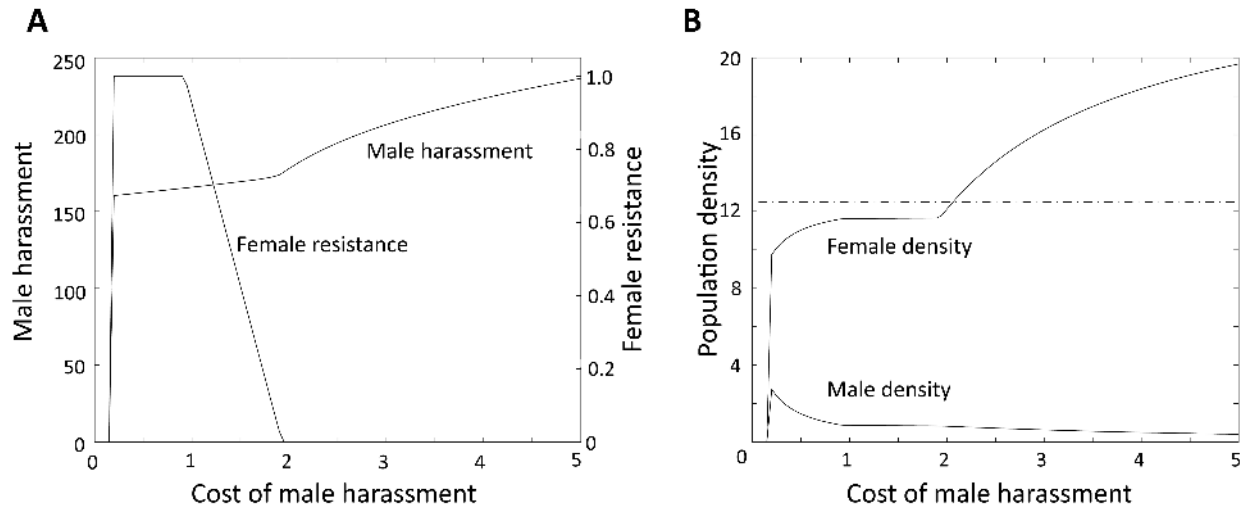


Figure 4: Influence of harassment cost to males on the evolutionary equilibrium of male harassment and female resistance (A) and the resultant equilibrium densities of males and females (B) in the analytical model. The dashed line shows the equilibrium density of males and females in the absence of male harassment ($\gamma = 0$) and female resistance ($x = 0$). Parameters: $r = 1/2$, $b = 50$, $\mu = 1$, $k = 1$, $u = 1.01$, $a = 1/2$, and $d = 1$.

to confirm this effect while being explicit about the underlying population dynamics.

Our analytical model highlights the importance of female-biased primary sex ratios as a mechanism that can limit the harm inflicted on females. However, a more important factor influencing extinction in our model is the ratio of male costs of harassment to male-induced harm to females. Under an even primary sex ratio, if investing in harassment is cheap for males and such harassment inflicts a large mortality cost on females, selection favors ever greater levels of harassment. Elevated female mortality creates a male-biased OSR, which intensifies harassment and feeds back to increase female mortality even further, until the population is driven to extinction. This is a fully expressed tragedy of the commons, since selection at no point turns to favor less harassing males as the shared resource (here the density of remaining females) diminishes.

The simplest way in which a tragedy of the commons can be averted is to make it costly for the exploiter (males) to exploit the resource (females), so harassing should be costly for males. Harassment is costly for males when competition among males and/or the pursuit of females for copulation implies higher mortality, increased predation risk, elevated energy requirements, or reduced time available for performing other functions. Thus, if a strong trade-off exists between the benefits males get from harassing, in terms of extra matings, and the costs of obtaining those matings, it will be advantageous for males to reduce harassment, which is likely to prevent extinction.

The extent to which harassment is costly will depend very much on the mating system, but our model predicts that a tragedy of the commons through sexual conflict is likely if harassment is cheap for males but costly to females.

An interesting result of our analysis is that if male costs of harassment exceed those inflicted on females, more male-induced harm actually increases population density, despite causing the sexual conflict to intensify. This occurs because conflict in this case elevates male mortality more than female mortality, and removing males can increase population growth via density dependence when males and females utilize the same resources (e.g., Wedekind 2002; Kokko and Brooks 2003; Rankin and Kokko 2007). In addition, the shape of the relationship between the benefits and costs of harassment to males could play a large role in promoting or inhibiting extinction. For example, decelerating costs to males might select for runaway evolution to greater levels of male harassment, thus favoring extinction, while accelerating costs are expected to have the opposite effect.

Coevolutionary dynamics occur under a wide range of circumstances, such as between predators and their prey and between parasites and their hosts (Dieckmann et al. 1995; van der Laan and Hogeweg 1995; Dieckmann and Law 1996; Gilchrist and Sasaki 2002), as well as between male harassment and female resistance (Arnqvist and Rowe 2002; Wigby and Chapman 2004; Rönn et al. 2007; Godsen and Svensson 2009). We have established conditions under which the coevolution of female resistance with male harassment can prevent extinction. Adaptations

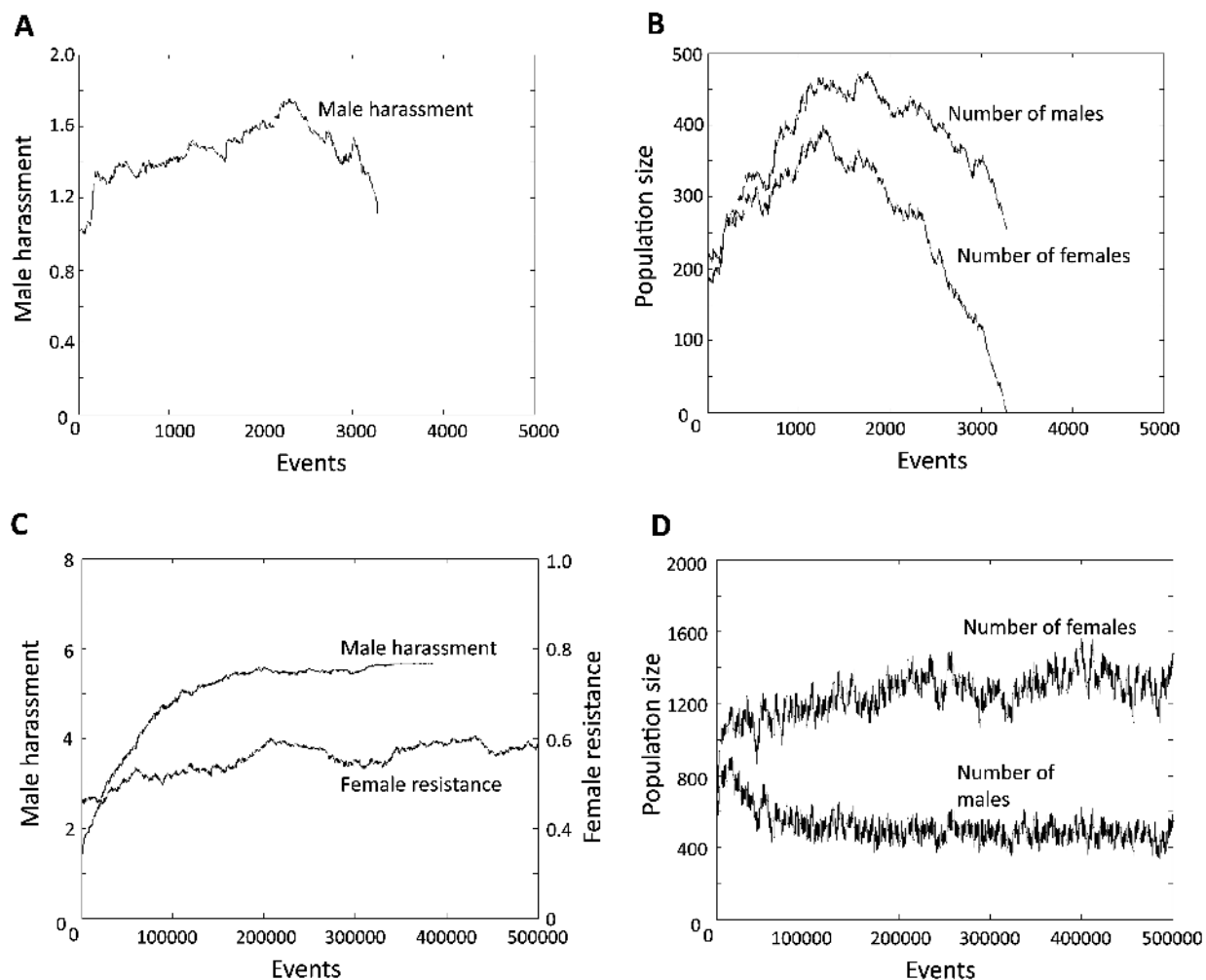


Figure 5: Evolution of male harassment (A, C) and implications for the population sizes of males and females (B, D) in two model runs of the individual-based model. In A and B, female resistance could not evolve ($x = 0$), whereas in C and D, it could coevolve together with male harassment ($a = 0.5$, $d = 1$). Other parameters: $r = 1/2$, $b = 20$, $\mu = 0.001$, $k = 1$, $u = 1.01$, and $c = 0.8$.

in females that counter harm caused by males result in less damage to females, thus increasing overall female fitness and a greater population density (fig. 4). Coevolutionary dynamics are influenced by the speed at which different traits can evolutionarily respond to changes in other traits (e.g., host-parasite dynamics are strongly influenced by the typically faster life cycles of the parasite). If the harming sex evolves faster than the harmed sex, extinction could occur under a wider range of circumstances than observed in our model. Conversely, if females can resist males by plastically reducing their mating rate (Lessells 2005), the harm to females is reduced, potentially preventing extinction.

Our models obviously do not consider all mechanisms that may conceivably prevent extinction through sexual

conflict. For instance, group structure can disfavor male harassment (Eldakar et al. 2009; Rankin 2011). Although we considered the feedback between sex-specific mortality and the per capita harassment experienced by females, our model has not explored all potential forms of feedback between demography and conflict. There are many other feedbacks that make selection a function of population characteristics such as density (Dieckmann and Metz 2006; Kokko and López-Sepulcre 2007), and such feedbacks can potentially resolve conflicts (Kokko and Rankin 2006; Rankin 2007; Knell 2009). However, since sexual selection on males can either intensify or relax with increasing density (Kokko and Rankin 2006; Klug et al. 2010), we based our model on the assumption of no change (the null case in the absence of any specific information) and instead fo-

cused on density-dependent shifts in the OSR. In nature, predicting even just the direction of such shifts is far from obvious. If conflict intensified at lower population densities (Kokko and Rankin 2006), this would increase the risk of evolutionary suicide. Any mechanism that favors male over female survival in low-density conditions (e.g., if males dominate females behaviorally during and after a population crash) could have this effect. On the other hand, there are conditions in which the mechanism we envisage to cause vicious circles will not apply as efficiently as we have assumed. OSRs can differ from primary sex ratios whether or not breeding is continuous, but any effects of male harassment are probably weaker with discrete generations than with overlapping generations (as modeled here), because in the former case each generation starts again with a roughly even primary sex ratio.

Conclusions

Male harassment can increase female mortality (Arnqvist and Rowe 2005), and female mortality is often a strong determinant of equilibrium population densities (Rankin and Kokko 2007; Candolin and Heuschele 2008). Our model shows that through the vulnerability implied by this relationship, male harassment can cause a tragedy of the commons and even result in a population being driven to extinction. We have shown how this tragedy can be averted through the costs to males of investing in harassment and the coevolution of male harassment and female resistance. In addition, any individually selected trait that can result in local population extinction is subject to contravening selection at higher evolutionary levels (Rankin et al. 2007a). If sexual conflict frequently impairs a population's reproduction and viability, such higher-level selection may be an important factor limiting the intensities of male harassment we observe in nature.

Acknowledgments

We are grateful to B. Fischer, S. Geritz, E. Kisdi, and N. Michiels for insightful and engaging discussions. Two anonymous reviewers provided comments that greatly helped to improve the manuscript. H.K. and D.J.R. were funded by the Academy of Finland. D.J.R. is additionally funded by the Swiss National Science Foundation (grants PZ00P3-121800 and 31003A-125457) and a University of Zürich Forschungskredit grant. U.D. gratefully acknowledges support by the European Community's Sixth Framework Programme, the European Science Foundation, the Austrian Science Fund, the Austrian Ministry for Science and Research, and the Vienna Science and Technology Fund.

APPENDIX

Individual-Based Model

To test the robustness of our analytical model, we built an individual-based model to examine how our results are affected by introducing demographic stochasticity and an explicit genetic system, namely, diploid additive genetics. In our individual-based model, the population can have any distribution of trait values, and there is no assumption that all but one trait value should be rare. The model assumes diploid inheritance of harassment and resistance alleles at two freely recombining loci. An individual thus possesses two harassment alleles, one inherited from the father and the other from the mother. We further assume additive genetics (i.e., no dominance or epistasis), so the harassment trait is given by the arithmetic mean of the two harassment alleles. The harassment trait is expressed only in males; analogous rules apply to the resistance trait expressed only in females.

The individual-based model is initialized with a population of 400 individuals, randomly designated as either male or female. Each allele at each locus is drawn at random. To ensure sufficient variation in the traits, male harassment alleles (which can take any positive value) are drawn from a random exponential distribution with a mean of 1, while female resistance alleles (which can take values between 0 and 1) are drawn from a random uniform distribution between 0 and 1. Males express the harassment trait $y = (y_M + y_F)/2$, where y_M denotes the harassment allele inherited from the male and y_F the harassment allele inherited from the female. Females express the resistance trait $x = (x_M + x_F)/2$, where x_M denotes the resistance allele inherited from the male and x_F the resistance allele inherited from the female. For each trait, one of each parent's alleles is chosen at random to be inherited by the diploid offspring. We use the same functions to describe per capita birth and death rates as in the analytic model. The birth rate of a given female is thus given by $b(1 - ax)$ and the death rate of a given female by $(1 - dx)(k\bar{y}M/F) + \mu(M + F)$. We assume that all individuals mate sufficiently frequently, so females experience the same level of male harassment \bar{y} , given by the population average of all harassment traits y expressed by males. The death rate of a given male is given by $cy + \mu(M + F)$. We assume that the relative mating success of males is proportional to their mating ability y^u .

The model keeps track of birth and death events, which occur in continuous time. Each individual female has a unique birth rate and death rate, while males express death rates only. The next event that occurs in the population is chosen with a probability proportional to its rate. If the event is a death, the chosen individual is removed from

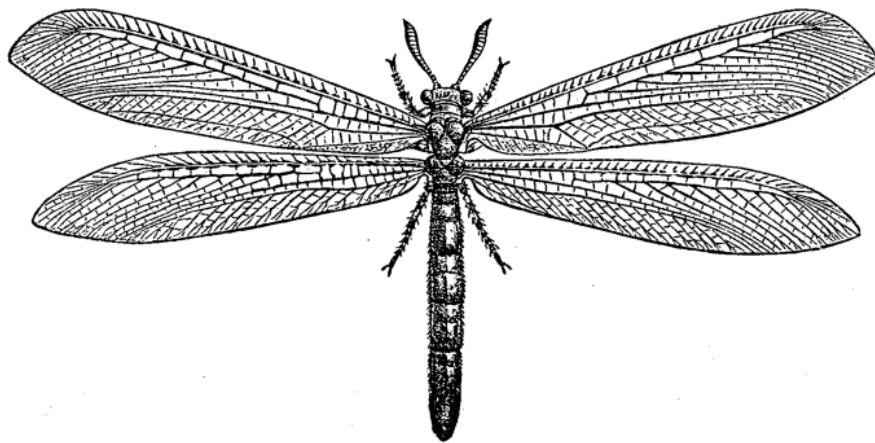
the population. If the event is a birth, a father is chosen with a probability proportional to his mating ability y^u and is mated with the chosen mother. The resultant offspring inherits one randomly chosen resistance allele and harassment allele from each parent. With probability r , the offspring is male, while with probability $1 - r$, it is female. The model is iterated for 500,000 events, or until the population is driven to extinction. The reported examples use parameter values $r = 1/2$, $b = 20$, $\mu = 0.001$, $k = 1$, and $u = 1.01$, and we change the cost c of male harassment and the cost a and benefit d of female resistance.

Literature Cited

- Agrawal, A. F. 2006. Evolution of sex: why do organisms shuffle their genotypes? *Current Biology* 16:R696–R704.
- Arnqvist, G., and L. Rowe. 2002. Antagonistic coevolution between the sexes in a group of insects. *Nature* 415:787–789.
- . 2005. *Sexual conflict*. Princeton University Press, Princeton, NJ.
- Boots, M., and A. Sasaki. 2003. Parasite evolution and extinctions. *Ecology Letters* 6:176–182.
- Candolin, U., and J. Heuschele. 2008. Is sexual selection beneficial during adaptation to environmental change? *Trends in Ecology & Evolution* 23:446–452.
- Chapman, T., L. F. Liddle, J. M. Kalb, M. F. Wolfner, and L. Partridge. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* 373:241–244.
- Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. *Trends in Ecology & Evolution* 18:41–47.
- Crudgington, H. S., and M. T. Siva-Jothy. 2000. Genital damage, kicking and early death. *Nature* 407:855–856.
- Dieckmann, U. 1997. Can adaptive dynamics invade? *Trends in Ecology & Evolution* 12:128–131.
- Dieckmann, U., and R. Ferrière. 2004. Adaptive dynamics and evolving biodiversity. Pages 188–224 in R. Ferrière, U. Dieckmann, and D. Couvet, eds. *Evolutionary conservation biology*. Cambridge University Press, Cambridge.
- Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34:579–612.
- Dieckmann, U., and J. A. J. Metz. 2006. Surprising evolutionary predictions from enhanced ecological realism. *Theoretical Population Biology* 69:263–281.
- Dieckmann, U., P. Marrow, and R. Law. 1995. Evolutionary cycling in predator-prey interactions: population dynamics and the Red Queen. *Journal of Theoretical Biology* 176:91–102.
- Edvardsson, M., and T. Tregenza. 2005. Why do male *Callosobruchus maculatus* harm their mates? *Behavioral Ecology* 16:788–793.
- Eldakar, O. T., M. J. Dlugos, J. W. Pepper, and D. S. Wilson. 2009. Population structure mediates sexual conflict in water striders. *Science* 326:816.
- Emlen, D. J. 2008. The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics* 39:387–413.
- Ferrière, R. 2000. Adaptive responses to environmental threats: evolutionary suicide, insurance and rescue. *International Institute for Applied Systems Analysis, Laxenburg*.
- Frank, S. A. 2010. Demography and the tragedy of the commons. *Journal of Evolutionary Biology* 23:32–39.
- Geritz, S. A. H., É. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12:35–57.
- Gilchrist, M. A., and A. Sasaki. 2002. Modeling host-parasite coevolution: a nested approach based on mechanistic models. *Journal of Theoretical Biology* 218:289–308.
- Godsen, T. P., and E. I. Svensson. 2009. Density-dependent male mating harassment, female resistance, and male mimicry. *American Naturalist* 173:709–721.
- Hardin, G. 1968. The tragedy of the commons. *Science* 162:1243–1248.
- Hofbauer, J., and K. Sigmund. 1990. Adaptive dynamics and evolutionary stability. *Applied Mathematics Letters* 3:75–79.
- Iwasa, Y., A. Pomiankowski, and S. Nee. 1991. The evolution of costly mate preferences. II. The “handicap” principle. *Evolution* 45:1431–1442.
- Jennions, M. D., and H. Kokko. 2010. Sexual selection. Pages 343–364 in D. F. Westneat and C. W. Fox, eds. *Evolutionary behavioral ecology*. Oxford University Press, Oxford.
- Klug, H., J. Heuschele, M. D. Jennions, and H. Kokko. 2010. The mismeasurement of sexual selection. *Journal of Evolutionary Biology* 23:447–462.
- Knell, R. J. 2009. Population density and the evolution of male aggression. *Journal of Zoology (London)* 278:83–90.
- Kokko, H., and R. Brooks. 2003. Sexy to die for? sexual selection and the risk of extinction. *Annales Zoologici Fennici* 40:207–219.
- Kokko, H., and A. López-Sepulcre. 2007. The ecogenetic link between demography and evolution: can we bridge the gap between theory and data? *Ecology Letters* 10:773–782.
- Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:319–334.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- Lee, P. L. M., and G. C. Hays. 2004. Polyandry in a marine turtle: females make the best of a bad job. *Proceedings of the National Academy of Sciences of the USA* 101:6530–6535.
- Le Galliard, J. E., P. S. Fitze, R. Ferrière, and J. Clobert. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the USA* 102:18231–18236.
- Lessells, C. M. 2005. Why are males bad for females? models for the evolution of damaging male mating behavior. *American Naturalist* 165(suppl.):S46–S63.
- Maklakov, A. A., T. Bilde, and Y. Lubin. 2006. Inter-sexual combat and resource allocation into body parts in the spider, *Stegodyphus lineatus*. *Ecological Entomology* 31:564–567.
- Matsuda, H., and P. A. Abrams. 1994a. Runaway evolution to self-extinction under asymmetrical competition. *Evolution* 48:1764–1772.
- . 1994b. Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theoretical Population Biology* 45:76–91.
- Maynard Smith, J. 1978. *The evolution of sex*. Cambridge University Press, Cambridge.
- Meszéna, G., E. Kisdi, U. Dieckmann, S. A. H. Geritz, and J. A. J. Metz. 2001. Evolutionary optimisation models and matrix games

- in the unified perspective of adaptive dynamics. *Selection* 2:193–210.
- Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define fitness for general ecological scenarios? *Trends in Ecology & Evolution* 7:198–202.
- Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. van Heerwaarden. 1996. Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction. Pages 183–231 in S. J. van Strien and M. Verdun Lunel, eds. *Stochastic and spatial structures of dynamical systems*. North-Holland, Amsterdam.
- Parvinen, K. 2005. Evolutionary suicide. *Acta Biotheoretica* 53:241–264.
- Rankin, D. J. 2007. Resolving the tragedy of the commons: the feedback between population density and intraspecific conflict. *Journal of Evolutionary Biology* 20:173–180.
- . 2011. Kin selection and the evolution of sexual conflict. *Journal of Evolutionary Biology* 24:71–81.
- Rankin, D. J., and H. Kokko. 2006. Sex, death and tragedy. *Trends in Ecology & Evolution* 21:225–226.
- . 2007. Do males matter? the role of males in population dynamics. *Oikos* 116:335–348.
- Rankin, D. J., and A. López-Sepulcre. 2005. Can adaptation lead to extinction? *Oikos* 111:616–619.
- Rankin, D. J., A. López-Sepulcre, K. R. Foster, and H. Kokko. 2007a. Species-level selection reduces selfishness through competitive exclusion. *Journal of Evolutionary Biology* 20:1459–1468.
- Rankin, D. J., K. Bargum, and H. Kokko. 2007b. The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution* 22:643–651.
- Rankin, D. J., M. Bichsel, and A. Wagner. 2010. Mobile DNA can drive lineage extinction in prokaryotic populations. *Journal of Evolutionary Biology* 23:2422–2431.
- Réale, D., P. Boussès, and J. L. Chapuis. 1996. Female-biased mortality induced by male sexual harassment in a feral sheep population. *Canadian Journal of Zoology* 74:1812–1818.
- Reinhardt, K., R. Naylor, and M. T. Siva-Jothy. 2003. Reducing the cost of traumatic insemination: female bedbugs evolve a unique organ. *Proceedings of the Royal Society B: Biological Sciences* 270:2371–2375.
- Rönn, J., M. Katvala, and G. Arnqvist. 2006. The costs of mating and egg production in *Callosobruchus* seed beetles. *Animal Behaviour* 72:335–342.
- . 2007. Coevolution between harmful male genitalia and female resistance in seed beetles. *Proceedings of the National Academy of Sciences of the USA* 104:10921–10925.
- Shine, R., D. O’Conner, and R. T. Mason. 2000. Sexual conflict in the snake den. *Behavioral Ecology and Sociobiology* 48:392–401.
- Shine, R., M. P. LeMaster, I. T. Moore, M. M. Olsson, and R. T. Mason. 2001. Bumpus in the snake den: effects of sex, size, and body condition on mortality of red-sided garter snakes. *Evolution* 55:598–604.
- Valero, A., C. M. Garcia, and A. E. Magurran. 2008. Heterospecific harassment of native endangered fishes by invasive guppies in Mexico. *Biology Letters* 4:149–152.
- van der Laan, J. D., and P. Hogeweg. 1995. Predator-prey coevolution: interactions across different timescales. *Proceedings of the Royal Society B: Biological Sciences* 259:35–42.
- Wedekind, C. 2002. Manipulating sex ratios for conservation: short-term risks and long-term benefits. *Animal Conservation* 5:13–20.
- West, S. A., C. M. Lively, and A. F. Read. 1999. A pluralist approach to sex and recombination. *Journal of Evolutionary Biology* 12:1003–1012.
- Wigby, S., and T. Chapman. 2004. Female resistance to male harm evolves in response to manipulation of sexual conflict. *Evolution* 58:1028–1037.
- . 2005. Sex peptide causes mating costs in female *Drosophila melanogaster*. *Current Biology* 15:316–321.

Associate Editor: Suzanne H. Alonzo
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“While hunting spiders among the rocks on the hill north of Bartholomew’s pond in South Danvers, Mass., I unexpectedly found the pit of an ant-lion (*Myrmeleo immaculatus* De Geer) in a clear space under the shade of a large boulder.” From “The Ant Lion” by J. H. Emerton (*American Naturalist*, 1871, 4:705–708).