

Resolving the tragedy of the commons: the feedback between intraspecific conflict and population density

D. J. RANKIN

Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Science, University of Helsinki, Finland

Keywords:

density-dependent benefits;
extinction;
public goods;
tragedy of the commons.

Abstract

Competition and conflict among individuals can favour exploitative strategies that undermine the common good. Theory suggests that this can lead to a tragedy of the commons and ultimately population extinction, a phenomenon known as evolutionary suicide. Here, I present a model of the evolutionary tragedy of the commons that explicitly considers the population dynamics where individuals invest in individually costly competitive traits. In the simplest form, this supports the notion that selection for high levels of conflict can cause evolutionary suicide. However, as competition comes with survival and fecundity costs, a feedback between the investment in competition and population density can act to reduce the level of conflict and prevent the population from going extinct. This suggests that the interaction between population ecology and the evolution of competition and conflict among individuals may be an important mechanism in resolving the level of competition and conflict among individuals.

Introduction

Determining why individuals do not evolve to exploit the common good has long been a central theme of social evolution (Leigh, 1977; Frank, 1995; Keller, 1999; Foster, 2004). The tragedy of the commons, used to illustrate the idea, states that if individuals compete selfishly over a common resource, overexploitation will always occur (Hardin, 1968). Classical models of the tragedy of the commons assume that individuals that over-exploit a common resource will gain the benefit, but that the cost will be paid by other members of the population.

A tragedy of the commons may sometimes occur if the actors also pay an individual cost (Dawkins & Krebs, 1979). For example, in intraspecific contests, if individuals evolve traits such as armaments, which are costly to express, then they may be favoured due to the benefit they provide relative to other members of the population. If such a trait is able to spread, having a high relative fitness but a low absolute fitness, then the resulting population density will be reduced (Dieckmann &

Ferrière, 2004). This may be seen as a tragedy of the commons, as it is individual conflict and selfishness which ultimately results in higher costs for all individuals involved.

Recent theory has revealed that genes expressing extreme traits may invade and, in some cases, cause the population to go extinct, a phenomenon known as evolutionary suicide (Matsuda & Abrams, 1994; Ferrière, 2000; Dieckmann & Ferrière, 2004; Rankin & López-Sepulcre, 2005). Despite the fact that extinctions are very difficult to observe, some evidence suggesting that evolution may result in extinction comes from the social bacterium *Myxococcus xanthus*. In this bacterium, individuals develop co-operatively to form complex fruiting structures, where individuals in the fruiting body are released as spores to form new colonies (Fiegna & Velicer, 2003). One should expect that strains which 'cheated' and were more likely to become spores would have a selective advantage over wild-type strains. Artificially selecting for such strains showed that these cheaters could invade wild-type populations, and that this could result in the overall extinction of the population (Fiegna & Velicer, 2003).

Much research has focused on how the tragedy of the commons may be resolved. Factors such as high relatedness in social groups (Wenseleers & Ratnieks, 2004), diminishing returns (Foster, 2004), policing in insect

Correspondence: Daniel J. Rankin, Laboratory of Evolutionary and Ecological Dynamics, Department of Biological and Environmental Science, PO Box 65 (Viikinkaari 1), FIN-00014 Helsinki, Finland.
Tel.: + 358 9 1915 7866; fax: +358 9 1915 7694;
e-mail: daniel.rankin@helsinki.fi

societies (Ratnieks & Wenseleers, 2005) or pleiotropy (Foster *et al.*, 2004) may all act to constrain the evolution of harmful traits, and thus reduce the potential for a tragedy of the commons to arise in such populations.

A less explored factor which could prevent a tragedy of the commons is the number of individuals interacting in the population (e.g. Suzuki & Akiyama, 2005; Kokko & Rankin, 2006). For example, at low population densities, one should expect lower encounter rates and more *per capita* resources, which may result in less intense conflicts. As conflict is likely to affect both fecundity and survival, this should inevitably have an effect on population density. We should therefore expect a feedback between density and conflict, which may act to resolve a tragedy that might have occurred in the absence of such a feedback (Kokko & Rankin, 2006).

The scarcity of empirical studies demonstrating evolutionary suicide suggests that not only should we ask whether population-level extinction can occur as a result of individual conflict, but also which factors may act to reduce the level of conflict. Here, I present a model looking at a population-wide tragedy of the commons, where individuals compete selfishly for a resource by investing in aggressive behaviour. I incorporate a feedback, between population density and the benefit gained from investing in competition, to investigate what role such a feedback could play in resolving the level of conflict, and preventing the tragedy of the commons.

Model

Population dynamics

The model describes a population in which individuals compete over a resource by investing in reproductive competition (*sensu* Foster, 2004). The amount that individuals can invest in competition is defined as z . We can assume that the amount of benefit an individual gains from investing in competition will be relative to what other members of the population do; an individual will only gain a benefit if it invests more in competition than the population on average (Frank, 1995, 1998; Foster, 2004). This competition can be over an arbitrary resource, and such competition may apply to various conflicts where individuals engage in competition over factors such as space, territories or mates. Similarly such competition can apply to situations where individuals choose not to invest in a common resource, like a co-operative trait such as sentinel behaviour (where a low z would indicate co-operation).

The benefit individuals gain from investing in competition is measured in terms of the contribution their genes make to the next generation, relative to other individuals. The benefit gained will also depend on the density of the population, and can be described by the function $f(z_i, \bar{z}, N)$, where z_i is the amount that individual i invests in competition, \bar{z} is the mean investment across

the population and N is the population density. We use a function where $f(z_i, \bar{z}, N) = 1$ when $z_i = \bar{z}$, as the benefit gained from investing in z_i is relative to \bar{z} .

We shall also assume that investing in z imposes a cost, in terms of an increased mortality risk, which is defined by the function $g(z)$. This cost could be due to reduced survival due to allocating resources to competition, the cost of armaments used in fighting (e.g. Emlen, 2001) or extra predation risk because of the strategy (e.g. Jakobsson *et al.*, 1995; Dunn *et al.*, 2004).

When looking at growth at the population level, we shall take the average *per capita* benefits and costs of investing in competition across all individuals within the population. We can write the growth rate of N as:

$$\dot{N} = \bar{f}(\mathbf{z}, \bar{z}, N)bN - \bar{g}(\mathbf{z})N - l(N)N \quad (1)$$

where \mathbf{z} represents a vector of all phenotypes of z in the population, b is the birth rate and the function $l(N)$ represents density-dependent mortality. In the absence of an invading mutant we shall assume a homogenous population, such that all strategies in the population are the same, so we can therefore assume that the function $\bar{f}(\mathbf{z}, \bar{z}, N) = f(z, \bar{z}, N) = 1$ and $\bar{g}(\mathbf{z}) = g(\bar{z})$. The population dynamics can then be written as $\dot{N} = bN - g(\bar{z})N - l(N)N$.

Invasion analysis

Now, we imagine a mutant which has a strategy z' . We wish to investigate the conditions under which such a strategy can invade a population with individuals expressing the phenotype \bar{z} . If we assume that the mutant is rare, and that it will not be able to have a discernible influence on the resource, we can assume that the costs it experiences will only be those costs of expressing the trait.

Assuming ecological equilibrium of the resident population, the fitness of an individual bearing the strategy z' is $w' = bf(z', \bar{z}, \hat{N}) - g(z') - l(\hat{N})$. While there are a number of functions we could use to describe how mortality changes with density, here we assume that the *per capita* mortality increases linearly with density, such that $l(N) = \mu N$, where μ scales this mortality. Using this, and solving eqn (1) to find \hat{N} , the equilibrium population density, we can simplify this equation to become:

$$w' = bf(z', \bar{z}, \hat{N}) - b + g(\bar{z}) - g(z') \quad (2)$$

If all members of the population behave the same, the chance of any given individual contributing to the next generation will be equal. If a mutant individual invests slightly more in competition, they will produce more offspring than other individuals in the population. However, such an investment will come at a cost, which is represented by the last term on the right hand side.

A mutant will spread through the population if $w' > 0$. From eqn (2), we can investigate whether evolution will converge to an evolutionary singular strategy (the ESS –

see Appendix 1) and whether such an ESS will be stable (Geritz *et al.*, 1998).

The tragedy of the commons

In the loosest sense, the tragedy of the commons refers to a situation where competition between individuals results in both parties having a lower pay-off than if they had refrained from competing. However, as mentioned above, it can apply to more extreme situations where conflict between individuals causes the extinction of the whole population (Rankin & López-Sepulcre, 2005).

For evolution to result in extinction, the population must converge to an ESS that is not viable (i.e. it lies in a region where the population can no longer persist). Using the equilibrium population density \hat{N} to calculate which values of \bar{z} will cause the population to go extinct will allow us to investigate whether or not an ESS will be ecologically feasible (i.e. if that ESS will allow the population to persist).

Taking the model presented above, we assume the simple function $g(z) = cz^\beta$, representing the cost of investing in strategy z . The shape of the costs can easily be altered, where β changes the shape of the function, as shown in Fig. 1a. If $\beta < 1$, then the costs increase in a decelerating way with an increase z , while if $\beta > 1$ the costs increase in an accelerating way with z .

A simple function to describe the benefit gained from investing in competition is:

$$f(z', \bar{z}, \hat{N}) = \left(\frac{z'}{\bar{z}}\right)^\alpha$$

modified from Frank (1995), where $\alpha \geq 0$ scales the benefits gained from investing in competition. There is no benefit if $\alpha = 0$. Using these two cost and benefit functions, we can show that the population will converge to an ESS which is not viable (where it lies in a region

where the population cannot be sustained) if $\alpha \geq \beta$ (Appendix 1). In other words, the population will evolve itself extinct if the individual benefits gained from investing more in competition increase at a greater rate than the individual cost, allowing dangerously competitive traits to evolve.

However, the above function, used to describe the benefit gained from competing, is unrealistic as it allows for the case where the mutant's fitness depends on the resident strategy when the resident population has gone extinct. To incorporate the effect of density on the benefit gained from investing in competition we therefore need to extend the benefit function presented above. To do this, we use the function:

$$f(z', \bar{z}, \hat{N}) = \left(\frac{z'}{\bar{z}}\right)^{h(\hat{N})}$$

where $h(\hat{N})$ describes how the magnitude of the relative benefit changes with population density. The power is taken to scale the amount of benefit gained from competing, such that $f(z', \bar{z}, \hat{N}) = 1$ when $z' = \bar{z}$ (i.e. there is no relative benefit when individuals are the same). As there can be no relative benefit when there is no population to interact with, $h(\hat{N})$ must become zero when $\hat{N} = 0$.

When population density is low, there will be fewer encounters between individuals than when population density is large. As a result of this, we assume that the relative benefit from investing in competition should increase as population density increases, i.e. $h(\hat{N})$ must increase with population density. For the sake of simplicity we will use:

$$h(\hat{N}) = \frac{\alpha \hat{N}}{\hat{N} + \gamma}$$

in the examples in this study. Here γ varies the amount that the benefit is influenced by density (the intensity of density-dependence). As γ increases, the benefit gained

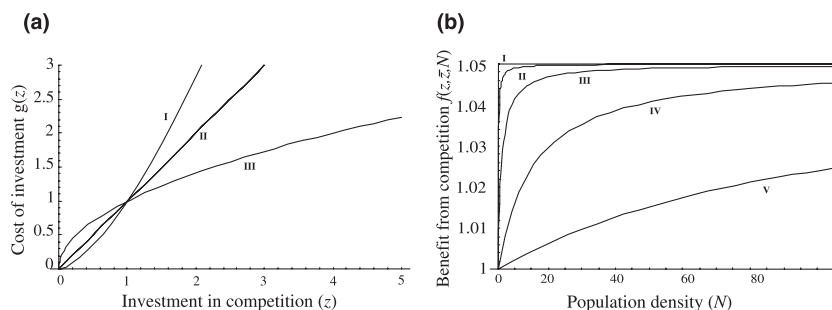


Fig. 1 Some assumptions of the model. Figure (a) shows the cost of investing in competition (z). The function used is $g(z) = cz^\beta$, where $c = 1$. Costs of competition can increase acceleratingly (I, $\beta = 1.5$), linearly (II, $\beta = 1$) or deceleratingly (III, $\beta = 0.5$). Figure (b) shows how the relative benefit gained from investing in competition changes with population density. Different strengths of density-dependent benefits are presented. All lines asymptote at 1.05. The function used is $f(z', \bar{z}, N) = \left(\frac{z'}{\bar{z}}\right)^{h(N)}$, where $h(N) = \frac{\alpha N}{N + \gamma}$, and the parameters used are $z'/\bar{z} = 1.05$ and $\alpha = 1$. The strength of density-dependence is (I) $\gamma = 0$, (II) $\gamma = 0.1$, (III) $\gamma = 1$, (IV) $\gamma = 10$, (V) $\gamma = 100$.

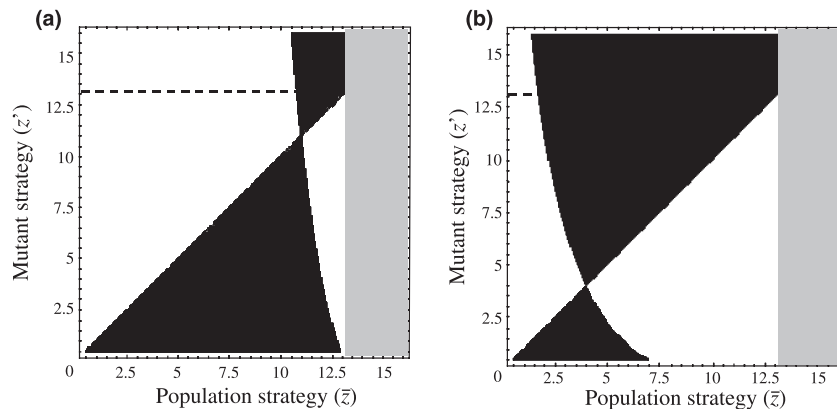


Fig. 2 Example pair-wise invasibility plots (PIPs) for the model. The x-axis shows the amount a resident strategy invests in competition, whereas the y-axis is the investment in competition by a mutant. White areas represent regions where the mutant can increase in density whereas black represents regions where the mutant will decrease in density. Evolution proceeds in small steps in the direction of the ESS, which is the point where the white and black areas intersect. The grey area represents the region where the population cannot persist and goes extinct. If a mutation arises which has a value greater than the dashed line, it will invade and drive the population extinct. The models are for weak density dependence (2a, $\gamma = 0.01$) and strong density dependence (2b, $\gamma = 100$) of the relative benefit gained from investing in competition. The other parameters in the figures are $b = 50$, $\alpha = 1$, $\mu = 1$, $c = 2$, $\beta = 1.5$.

from investing more in competition will depend increasingly on density, while if $\gamma = 0$ we have the same density-independent benefit function discussed above. This allows us to investigate the effect of varying intensities of density-dependence on the relative benefit gained from investing in competition. We can imagine that the benefit gained from investing in competition will start to tail off at higher densities, as the population becomes saturated. Figure 1b shows different shapes of the benefit function, with differing degrees of density-dependence. It can be seen that the relative benefit stabilizes at high densities.

Analyzing eqn (2) using the density-dependent benefit function shows that evolution will always converge to a viable, stable, ESS (see Appendix 1). This occurs under all conditions, and shows for this case that density-dependent benefits will prevent the population evolving itself extinct. Figure 2 shows two cases with differing degrees of density-dependence of the relative benefit of investing in competition. It can be seen that the ESS in Fig. 2a, where the relative benefit from investing in competition depends very little on density (low γ), is much closer to the extinction boundary than the ESS shown in Fig. 2b, which incorporates strong density-dependence of the benefit of investing in competition (high γ). The ESS analysis performed here (see Appendix 1) assumes small mutational steps. The area above the dotted line in Fig. 2 represents the region where a mutant which is capable of causing the population to go extinct will be able to invade. Whereas these figures show that γ will reduce the risk of extinction, by moving the ESS away from the extinction boundary, it can clearly be seen that extinction is still possible if mutations are much larger, with both weak and strong density-dependent benefits. How-

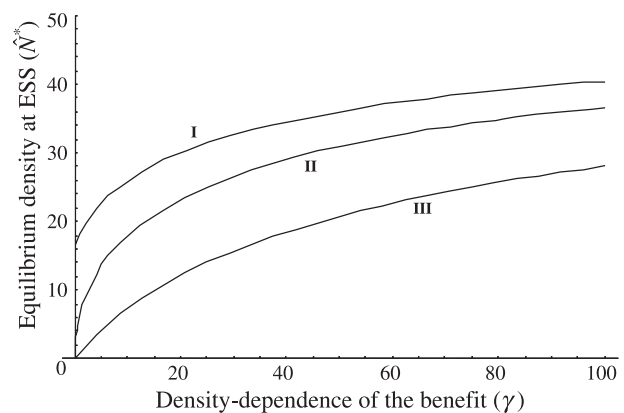


Fig. 3 Equilibrium population density when the population has reached an ESS, as a function of the strength of the density-dependence of the benefit gained from investing in competition (γ). Three curves are presented for accelerating (I, $\beta = 1.5$), linear (II, $\beta = 1$) and decelerating (III, $\beta = 0.5$) costs. The other parameters in the figure are $b = 50$, $\alpha = 1$, $\mu = 1$, $c = 2$.

ever, by comparing the pair-wise invisibility plots in Fig. 2, it can clearly be seen that larger (and dangerous) mutations will be more likely to invade if the density-dependence of the benefits are weak, rather than strong.

Analyzing how the strength of density-dependence (γ) influences the equilibrium population-density shows that increasing γ will always result in a higher overall equilibrium population density when the population is at an ESS (Appendix 2, Fig. 3). This suggests that density-dependent benefits of competition can potentially have a large effect in preventing the tragedy of the commons.

Discussion

There is no reason to assume that the benefits of investing in competition will be the same at low and high densities. The model here suggests that the intensity of competition should be different when there are fewer individuals to compete with, as opposed to more. In the complete absence of density-dependent benefits, the population will go extinct if the benefit of investing slightly more in competition increases at a rate greater than the individual cost. In other words, becoming more aggressively competitive will incur a slightly smaller cost relative to the benefit gained, favouring dangerously high competition. Such a situation could be possible where most of the cost is due to an initial investment in a morphology; e.g. investing in armaments could be large, but once in place the cost incurred from being slightly more aggressive than the norm would be fairly small.

Density seems to be a factor influencing the intensity of competition and conflict in a wide range of organisms. In the European earwig *Forficula auricularia*, where forceps are used in male-male competition, large-bodied 'macrolabic' male morphs with long forceps are favoured at high densities, while small-bodied 'brachylabic' male morphs with short forceps are favoured at low densities (Tomkins & Brown, 2004), despite the fact that macrolabic morphs are competitively superior (Radesäter & Halldórsdóttir, 1993; Forslund, 2000). It has been suggested that macrolabic morphs have a higher relative fitness in large populations, because of higher encounter rates and more fights, whereas the relative fitness of brachylabic morphs is higher at lower population densities (Tomkins & Brown, 2004). It is increasingly accepted that sexual selection and sexual conflict may influence population densities, even to the point of extinction (Kokko & Brooks, 2003). As a result, one would expect a feedback between the intensity of competition and the population density, which may act to prevent extinction in the absence of such a feedback (Kokko & Rankin, 2006).

Whereas the idea of group size and population density as influencing co-operation and conflict has been implicit in a number of models of social conflict (Boyd & Richardson, 1988; Nowak *et al.*, 2004; Suzuki & Akiyama, 2005), these models have generally neglected the influence of these behavioural traits on the survival and fecundity of individuals. As shown in the present model, the strength of this feedback (here given by the strength of density-dependent benefits, γ) is likely to limit the level of competition, implying that the impact of competition on fecundity and survival will have an important influence on the level of conflict. Incorporating feedbacks between individual selection and an organism's influence on its environment (and demography) can often lead to different outcomes (e.g. Dieckmann & Metz, 2006), as demonstrated here by the fact that the population could evolve itself

extinct in the absence of density-dependent benefits (see Model).

How important are feedbacks?

While it is well known that behaviour can play a role in regulating population densities (e.g. Wolf, 1997; Mougeot *et al.*, 2003), there has been limited interest in the feedback between individual behaviour and population dynamics as a potential conflict-limiting mechanism, but there are a number of areas where such feedbacks are likely to be common. In territorial systems, for example, the intensity of conflicts over space will depend directly on the number of individuals that occupy a particular area, which in turn will influence the amount of space that is available (López-Sepulcre & Kokko, 2005).

Bacteriocins, which have a wide range of antimicrobial killing activity that is often limited to the same species (Riley & Wertz, 2002; Riley *et al.*, 2003), are produced by microbes as weapons against other members of the population. The cost of producing such proteins may come in the form of diverting resources from other cellular functions or ultimately in the death of the producing individual (Riley & Wertz, 2002). Whereas it is possible that within-group relatedness can influence the intensity of bacteriocin-mediated conflict (Gardner *et al.*, 2004), quorum sensing involving the density-dependent production of bacteriocins (Juhás *et al.*, 2005; van der Ploeg, 2005) could also act to reduce the intensity of competition (Travisano & Velicer, 2004). Such a reaction norm would act to reduce the level of conflict, and prevent a conflict-induced extinction by reducing the production of bacteriocins at low densities.

A potential feedback could occur between population density and conflict over sentinel effort (where not investing in sentinel effort would correspond to a high z in the model). While predation resulting from low vigilance could result in reduced population densities, individuals who do not invest in sentinel effort gain by being able to forage longer than their conspecifics (Bednekoff, 1997; Clutton-Brock *et al.*, 1999). The individual benefit of vigilance is larger at lower population densities (Clutton-Brock *et al.*, 1999; Wright *et al.*, 2001); sentinels often escape first, while if no-one is vigilant the individual-predation risk will be high (Bednekoff, 1997; Clutton-Brock *et al.*, 1999). Such a feedback could act to increase the sentinel effort, and may explain why individuals do not reduce their sentinel effort and destroy the common good provided by vigilance.

Model limitations

The model presented here functions as a phenomenological proof-of-principle, demonstrating that density-dependence can act as a potential conflict-resolving mechanism. The mechanism through which this works is not defined explicitly, and is merely assumed by the

functions used for both the costs and benefits of investing in competition (see Model and Fig. 1). The shape of the function describing how density influences the relative benefit gained from investing in competition could be very different to that shown in Fig. 1b. For example, one could imagine that the relative benefit increased linearly, or exponentially, with population density. However, it is likely that such shapes will act to strengthen the results presented here, in that they would render the benefit more sensitive to high population densities, which should reduce the level of conflict to an even greater extent than the function used here. As an additional point, it is worth noting that the feedback between individual behaviour and population density could be weakened by the fact that evolutionary change may sometimes occur on a similar time scale to ecological change (Hairston *et al.*, 2005).

The model also assumes a mean field structure, meaning that every individual has an equal chance of encountering any other individual. Population structure can influence the degree of relatedness between groups (e.g. Frank, 1995), and spatial structure has the effect of increasing the number of repeated interactions among individuals (Nowak & May, 1992; Killingback *et al.*, 1999), both of which could act as alternative conflict-limiting mechanisms.

Mutation rates

The analytical solution (see Appendix 1) rests on the questionable assumption that mutation occurs as small steps over evolutionary time (Dieckmann & Law, 1996; Barton & Polechová, 2005; Waxman & Gavrillets, 2005). However, the presented model allows us to see what would happen with greater mutational steps (Fig. 2). If large mutations occur, which represent a very strong level of investment in competition, and are able to invade, then the population will be driven to extinction. This occurs in all cases, regardless of whether or not the benefit gained from competition is density-dependent, but the region under which it occurs is greatly reduced with strong (Fig. 2b), compared to weak (Fig. 2a), density-dependent benefits.

Small populations

As the population approaches extinction, the probability of mutations arising with phenotypes that invest a lot in competition will be small (Barton & Polechová, 2005). However, even if a population is not directly driven extinct, reducing the population size will increase the extinction risk. This may occur due to factors such as inbreeding (Saccheri *et al.*, 1998; Keller & Waller, 2002), mutational meltdown (where deleterious mutations become more likely to fixate, e.g. Lynch & Gabriel, 1990), Allee effects or demographic stochasticity (Stephens & Sutherland, 1999; Dennis, 2002; Drake &

Lodge, 2004; Saether & Engen, 2004). This study has shown that, if the benefits gained from competition are density-dependent, the impact on population density will be diminished, making the population less prone to the effects associated with small populations.

Conclusion

A number of behavioural studies have confirmed mechanisms such as coercion as a sufficient way of resolving conflict, which can thereby prevent the tragedy of the commons (Frank, 1995; Ratnieks & Wenseleers, 2005). The study presented here highlights another mechanism, where a simple feedback between selfish competition and population density can prevent tragedy without the need for external coercion. When the selective advantage of investing in competition decreases as a function of population density, not only will this decrease the level of conflict in the population, but it will also reduce the risk that such a conflict will drive the population extinct. The model here has shown that such density-dependent feedbacks could be important factors in reducing the intensity of conflicts we observe in nature.

Acknowledgments

I thank Katja Bargum, Kevin Foster, Katja Heubel, Hanna Kokko, Andrés López-Sepulcre and Amanda Thurman for discussions and comments on the manuscript. I also thank Ulf Dieckmann, Mike Fowler and Ace North for helpful discussions. This study was financed by the Academy of Finland (to Hanna Kokko).

References

- Barton, N.H. & Polechová, J. 2005. The limitations of adaptive dynamics as a model of evolution. *J. Evol. Biol.* **18**: 1186–1190.
- Bednekoff, P.A. 1997. Mutualism among safe, selfish sentinels: a dynamic game. *Am. Nat.* **150**: 373–392.
- Boyd, R. & Richardson, P.J. 1988. The evolution of reciprocity in sizable groups. *J. Theor. Biol.* **132**: 337–356.
- Clutton-Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S. & Manser, M. 1999. Selfish sentinels in cooperative mammals. *Science* **284**: 1640–1644.
- Dawkins, R. & Krebs, J.R. 1979. Arms races between and within species. *Proc. R. Soc. Lond. B.* **205**: 489–511.
- Dennis, B. 2002. Allee effects in stochastic populations. *Oikos* **96**: 389–401.
- Dieckmann, U. & Ferrière, R. 2004. Adaptive dynamics and evolving biodiversity. In: *Evolutionary Conservation Biology* (R. Ferrière, U. Dieckmann & D. Couvet, eds), pp. 188–224. Cambridge University Press, Cambridge.
- Dieckmann, U. & Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* **34**: 579–612.
- Dieckmann, U. & Metz, J.A.J. 2006. Surprising evolutionary predictions from enhanced ecological realism. *Theor. Pop. Biol.* **69**: 263–281.

- Drake, J.M. & Lodge, D.M. 2004. Effects of environmental variation on extinction and establishment. *Ecol. Lett.* **7**: 26–30.
- Dunn, M., Copelston, M. & Workman, L. 2004. Trade-offs and seasonal variation in territorial defence and predator evasion in the European Robin *Erithacus rubecula*. *Ibis* **146**: 77–84.
- Emlen, D.J. 2001. Costs and the diversification of exaggerated animal structures. *Science* **291**: 1534–1536.
- Ferrière, R. 2000. *Adaptive Responses to Environmental Threats: Evolutionary Suicide, Insurance and Rescue. Options 2000*, IIASA. Laxenbourg, Austria.
- Fiegna, F. & Velicer, G.J. 2003. Competitive fates of bacterial social parasites: persistence and self-induced extinction of *Myxococcus xanthus* cheaters. *Proc. R. Soc. Lond. B.* **270**: 1527–1534.
- Forslund, P. 2000. Male competition and large size mating advantage in the European earwigs *Forficula auricularia*. *Anim. Behav.* **59**: 753–762.
- Foster, K.R. 2004. Diminishing returns in social evolution: the not-so-tragic commons. *J. Evol. Biol.* **17**: 1058–1072.
- Foster, K.R., Shaulsky, G., Strassmann, J.E., Queller, D.C. & Thompson, C.R.L. 2004. Pleiotropy as a mechanism to stabilise cooperation. *Nature* **431**: 693–696.
- Frank, S.A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* **377**: 520–522.
- Frank, S.A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton.
- Gardner, A., West, S.A. & Buckling, A. 2004. Bacteriocins, spite and virulence. *Proc. R. Soc. Lond. B.* **271**: 1529–1535.
- Geritz, S.A.H., Kisdi, E., Meszina, G. & Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**: 35–57.
- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* **8**: 1114–1127.
- Hardin, G. 1968. The tragedy of the commons. *Science* **162**: 1243–1248.
- Jakobsson, S., Brick, O. & Kullberg, C. 1995. Escalated fighting behaviour incurs increased predation risk. *Anim. Behav.* **49**: 235–239.
- Juhas, M., Eberl, L. & Tümmler, B. 2005. Quorum sensing: the power of cooperation in the world of *Pseudomonas*. *Environ. Microbiol.* **7**: 459–471.
- Keller, L., ed. 1999. *Levels of Selection in Evolution*. Princeton University Press, Princeton.
- Keller, L.F. & Waller, D.M. 2002. Inbreeding effects in wild populations. *Trend. Ecol. Evol.* **17**: 230–241.
- Killingback, T., Doebeli, M. & Knowlton, N. 1999. Variable investment, the Continuous Prisoner's Dilemma, and the origin of cooperation. *Proc. R. Soc. Lond. B.* **266**: 1723–1728.
- Kokko, H. & Brooks, R. 2003. Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zoo. Fenn.* **40**: 207–219.
- Kokko, H. & Rankin, D.J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philos. Trans. R. Soc. B.* **361**: 319–334.
- Leigh, E.G. 1977. How does selection reconcile individual advantage with the good of the group? *Proc. Natl. Acad. Sci. USA* **74**: 4542–4546.
- López-Sepulcre, A. & Kokko, H. 2005. Territorial defense, territory size and population regulation. *Am. Nat.* **166**: 317–329.
- Lynch, M. & Gabriel, W. 1990. Mutation load and the survival of small populations. *Evolution* **44**: 1725–1737.
- Matsuda, H. & Abrams, P.A. 1994. Runaway evolution to self-extinction under asymmetrical competition. *Evolution* **48**: 1764–1772.
- Mougeot, F., Redpath, S.M., Leckie, F. & Hudson, P.J. 2003. The effect of aggressiveness on the population dynamics of a territorial bird. *Nature* **421**: 737–739.
- Nowak, M.A. & May, R.M. 1992. Evolutionary games and spatial chaos. *Nature* **359**: 826.
- Nowak, M.A., Sasaki, A., Taylor, C. & Fudenberg, D. 2004. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**: 646–650.
- van der Ploeg, J.R. 2005. Regulation of Bacteriocin Production in *Streptococcus mutans* by the quorum-sensing system required for development of genetic competence. *J. Bacteriol.* **187**: 3980–3989.
- Radesäter, T. & Halldórsdóttir, H. 1993. Two male types of the common earwig: male–male competition and mating success. *Ethology* **95**: 89–96.
- Rankin, D.J. & López-Sepulcre, A. 2005. Can adaptation lead to extinction? *Oikos* **111**: 616–619.
- Ratnieks, F.L.W. & Wenseleers, T. 2005. Policing insect societies. *Science* **307**: 54–56.
- Riley, M.A. & Wertz, J.E. 2002. Bacteriocins: evolution, ecology and application. *Ann. Rev. Microbiol.* **56**: 117–137.
- Riley, M.A., Goldstone, C.M., Wertz, J.E. & Gordon, D. 2003. A phylogenetic approach to assessing the targets of microbial warfare. *J. Evol. Biol.* **16**: 690–697.
- Saccheri, I., Kuussaari, M., Vikman, P., Fortelius, W. & Hanski, I. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**: 491–494.
- Saether, B.E. & Engen, S. 2004. Stochastic population theory faces reality in the laboratory. *Trend. Ecol. Evol.* **19**: 351–353.
- Stephens, P.A. & Sutherland, W.J. 1999. Consequences of the allee effect for behaviour, ecology and conservation. *Trend. Ecol. Evol.* **14**: 401–405.
- Suzuki, S. & Akiyama, E. 2005. Reputation and the evolution of cooperation in sizable groups. *Proc. R. Soc. Lond. B.* **272**: 1373..
- Tomkins, J.L. & Brown, G.S. 2004. Population density drives the local evolution of a threshold dimorphism. *Nature* **431**: 1099–1103.
- Travisano, M. & Velicer, G.J. 2004. Strategies of microbial cheater control. *Trends Microbiol.* **12**: 72–78.
- Waxman, D. & Gavrillets, S. 2005. 20 Questions on adaptive dynamics. *J. Evol. Biol.* **18**: 1139–1154.
- Wenseleers, T. & Ratnieks, F.L.W. 2004. Tragedy of the commons in *Melipona* bees. *Proc. R. Soc. Lond. B.* **271**: 0S310–S312.
- Wolf, J.O. 1997. Population regulation in mammals: an evolutionary perspective. *J. Anim. Ecol.* **66**: 1–13.
- Wright, J., Berg, E., De Kort, S.R., Khazin, V. & Maklakov, A.A. 2001. Safe selfish sentinels in a cooperative bird. *J. Anim. Ecol.* **70**: 1070–1079.

Appendix 1

Finding the evolutionary singular strategy (ESS)

The resident population is assumed to be at ecological equilibrium. From eqn (1), assuming logistic growth, such that $l(N) = \mu N$, the equilibrium population density of the resident is calculated as being:

$$\hat{N} = \frac{b - g(\bar{z})}{\mu} \quad (\text{A1})$$

If a strategy is to be an ESS, the following condition must be satisfied:

$$0 = \left. \frac{\partial w'}{\partial z'} \right|_{z'=\bar{z}} \quad (\text{A2})$$

Where z' is the amount a mutant invests in competition (the 'mutant' strategy), \bar{z} is the average population investment in competition (the 'resident' strategy) and w' is the fitness of the mutant strategy. Solving this for eqn (2) will give us z^* , the ESS. In the simple case where we define $f(z', \bar{z}, \hat{N}) = (z'/\bar{z})^\alpha$, the benefit individuals gain from fighting does not depend on density. In this case, using $g(z) = cz^\beta$, and solving eqn (A2), we obtain the following ESS:

$$z^* = \left(\frac{b\alpha}{\beta c} \right)^{\frac{1}{\beta}} \quad (\text{A3})$$

In the situation where the benefit changes with the number of individuals in the population, such that $f(z', \bar{z}, \hat{N}) = (z'/\bar{z})^{\alpha\hat{N}/(\hat{N}+\gamma)}$, there two possible ESS':

$$z^* = \left(\frac{\beta\gamma\mu + b(\alpha + \beta) - \sqrt{-4b^2\alpha\beta + (\beta\gamma\mu + b(\alpha + \beta))^2}}{2\beta c} \right)^{\frac{1}{\beta}} \quad (\text{A4a})$$

$$z^* = \left(\frac{\beta\gamma\mu + b(\alpha + \beta) + \sqrt{-4b^2\alpha\beta + (\beta\gamma\mu + b(\alpha + \beta))^2}}{2\beta c} \right)^{\frac{1}{\beta}} \quad (\text{A4b})$$

Properties of the ESS

Following Geritz *et al.* (1998), we can investigate the properties of the ESS given in (eqns A2 and A4). The ESS will be stable if:

$$\left. \frac{\partial^2 w'}{\partial z'^2} \right|_{z'=\bar{z}=z^*} < 0,$$

and will be convergence stable if:

$$\left. \frac{\partial^2 w'}{\partial z'^2} \right|_{z'=\bar{z}=z^*} - \left. \frac{\partial^2 w'}{\partial z'^2} \right|_{z'=\bar{z}=z^*} < 0.$$

For evolutionary suicide to occur, the ESS must be convergence stable. Using these two equations one can show that as long as the parameters are all positive, the

ESS given by eqn (A3) will be ESS-stable if $\beta > \alpha$ and will always be convergence-stable. i.e. if $\beta > \alpha$, the population will always evolve towards this ESS, and once it gets there, no other strategy will be able to invade. The ESS given by eqn (A4a) is both ESS-stable and locally convergence stable, so the population will always evolve towards an ESS, and will be stable once it reaches it.

Calculating the extinction threshold

Rearranging eqn (A1) for when $\hat{N} \leq 0$ reveals that evolution will evolve towards the extinction boundary if the ESS is:

$$z^* \geq \left(\frac{b}{c} \right)^{\frac{1}{\beta}}$$

Using the ESS given by eqn (A3), where the benefit from competing does not depend on density, we see that the population will go extinct if $\alpha\beta$. In other words, if the increase in the relative benefit increases faster than the cost of expressing the trait, for each mutational step, then the population will evolve towards a point which drives the population extinct.

If the benefit of investing in competition does depend on density, the criterion for a population to go extinct if it reaches the ESS given by eqn (A4) is $4b\beta^2\gamma\mu < 0$. As all variables are positive in the model, the effect of density dependence prevents the population from going extinct.

Appendix 2

Intensity of density-dependence affects equilibrium population density

As the degree of density dependence γ affects the ESS, it will also have an impact on the equilibrium population density. Density-dependence will increase equilibrium population density if:

$$\frac{\partial \hat{N}^*}{\partial \gamma} > 0$$

where the population density is evaluated when z is at the ESS: $\hat{N}^* = \hat{N}|_{z=z^*}$. This inequality is always positive, so increasing the strength of the density-dependent incentive will always increase population density. We may therefore say that populations with a higher effect of density-dependence on the incentive to compete will have larger population densities than those that do not.

Received 9 May 2006; revised 6 July 2006; accepted 7 July 2006