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Prudent males, group adaptation, and the tragedy of the commons

Hanna Kokko and Katja U. Heubel

H. Kokko (hanna.kokko@anu.edu.au), Div. of Evolution, Ecology and Genetics, Research School of Biology, Australian National Univ., ACT 0200, Australia. – HK and K. U. Heubel, Lab. of Ecological and Evolutionary Dynamics, Dept of Biosciences, Univ. of Helsinki, Finland.

For almost five decades three threads have coexisted in the evolutionary and ecological literature, with their links only recently becoming visible and some of them still not properly addressed. These are the levels of selection debate, the metaphor of the tragedy of the commons, and the evolutionary study of sexual conflict. We analyze the eco-evolutionary dynamics of a curious system where an asexual all-female fish species (the Amazon molly *Poecilia formosa*) requires sperm from other species as a developmental trigger, without utilizing the genes from sperm. The dynamics of such a system bear strong resemblance to host–parasite dynamics, and populations of the sexual 'host' species persist much better if males avoid mating with Amazons. However, such avoidance may compromise their current mating success, and if this is the case, prudent mating becomes an altruistic trait that helps to keep an accumulating problem of a competing species at bay, and Amazon-free space can be seen to form a common good that a population should maintain for future generations. A model shows that the evolution of altruistic mating restraint is possible but selection for short-term gains means that it will remain less than perfect. This helps to explain why the anomalous gynogenetic system can persist, but it also raises questions about what kinds of traits can be classified as adaptations when optimization is not perfect and traits evolve to achieve short-term goals better than long-term performance. Contributing to the levels of selection debate, we encourage researchers to study the implications of the different timescales involved in the eco-evolutionary process.

Ever since the group selection debate in the 1960s (Wynne-Edwards 1962, Williams 1966, for discussion see Leigh 2010) it has been known that natural selection can promote traits or behaviours that are detrimental to the survival of larger units such as individuals (as opposed to their genes), or species (as opposed to individuals they consist of). Another extremely important thread of literature likewise begun with a paper published in the 1960s: Garrett Hardin published his idea of the tragedy of the commons (Hardin 1968) which likewise predicts that individuals acting in their own best interest can have detrimental consequences for the common good for a population. While he did not put his essay in a directly evolutionary context, he discussed the idea that tragedies can be avoided with 'mutual coercion, mutually agreed upon' – by which he means policing to protect the common good. This raises the evolutionary question why and how tragedies might be avoided in organisms that generally lack the cognitive capabilities required for such collective decision-making. The links between these two threads – levels of selection in evolutionary biology, and the tragedy of the commons – have only slowly become more visible in the literature (Kerr et al. 2006, Rankin et al. 2007a, Foster 2009, Frank 2010a). The link is the following: does selection favour individuals that act maximally selfishly even if this means behaving in group-detrimental ways? If they do, evolutionary theory predicts 'tragedies' to be

common. If individuals instead show restraint and act in group-beneficial ways, there is no tragedy but the explanation of such traits is very challenging because it becomes intimately linked with levels of selection and the evolution of altruism. The emergence of such cooperative tendencies has recently been quoted as 'the biggest unsolved problem in evolutionary biology' (May 2007).

Theoretical progress on the analysis of group-beneficial traits has been fast in recent years (Traulsen and Nowak 2006, Fletcher and Doebeli 2009, Gardner and Grafen 2009, see Foster 2009 and Leigh 2010 for a summary) but it has also given rise to debates that are heated enough (Wilson and Wilson 2007, Kohn 2008, West et al. 2008, Wild et al. 2009, Nowak et al. 2010, Wade et al. 2010, Abbot et al. 2011) that they have been viewed as unhealthy (Okasha 2010). Ignoring for a moment the details of the semantics that underlies these arguments – we will return to this issue in the Discussion – we would like to put emphasis on a very noteworthy and healthy aspect of the recent debate: the role of demography is finally receiving welcome attention (Frank 2010a, Lehmann 2010, Lehmann and Rousset 2010, Nowak et al. 2010). As we will argue in this paper, explicit ecological thinking including non-equilibrium scenarios is essential for understanding the evolution of group-beneficial tendencies.

In addition to the levels of selection debate and the discussion of evolutionary tragedies, a different, third thread

has become strong in the evolutionary biology literature in recent years: that of male–female interactions and sexual conflict. Intriguingly, this area has not yet developed good links with ideas of levels of selection, cooperation and demography. This is an odd omission, given that groups in general are not expected to perform maximally when they consist of individuals whose interests differ from each other, and a population of males and females forms a good potential example of such a group. This is because males' and females' interests are often significantly divergent (Parker 1979; for numerous new examples see Arnqvist and Rowe 2005, Chapman 2006, van Doorn 2009). It thus follows that considering sexual behaviour in a group or population context is important – yet much understudied (for exceptions see Rankin and Kokko 2007, Fernandez and Morris 2008, Bonduriansky 2009, Eldakar et al. 2009a, b, Long et al. 2009, Rankin et al. 2011).

The lack of attention to the 'tragic' aspects of sexual reproduction is curious given that the very existence of males has for a long time been argued to be a result of evolution that resembles parasitism: males are commonly argued to have evolved from ancestral isogamous organisms because producing numerous sperm is a profitable way to exploit the provisioning of offspring provided by eggs (reviewed by Lessells et al. 2009, Parker and Pizzari 2010). In an interesting parallel to the general debate on conflict versus cooperation in natural systems, some authors have recently promoted the idea of conflict-free evolution of maleness and femaleness (anisogamy) (Iyer and Roughgarden 2008, Roughgarden and Akcay 2010), sometimes expressing explicit dislike of the idea that males could be 'parasites' (Yang 2010). Although theory can predict cases where selection for efficient mate-searching under low densities makes gamete size evolution surprisingly cooperative in character (Lehtonen and Kokko 2011), it remains undeniably the case that the primordial sexual conflict of male gametes parasitizing female reproductive effort is the very reason why sexual populations experience the twofold cost of sex (Maynard Smith 1982, Jennions and Kokko 2010).

Our aim in this paper is to analyze a thought-provoking example of an evolutionary 'tragedy' related to sexual reproduction and the twofold cost of sex. We investigate a case where females (not males) behave in ways that resemble parasitism, and where it is possible that males evolve self-restraint to promote group survival. While it is already known that prosocial behaviours can evolve (the debate is more about how many distinct mechanisms there are and what level they are best understood at, Nowak 2006, Gardner 2009, Leimar and Hammerstein 2010), we believe that our example has general appeal for several distinct reasons. Concrete examples of restraint in any context are still scarce (microbial work perhaps forming the best exception, MacLean 2007, Eshelman et al. 2010), the analysis of population consequences of male behaviours is in its infancy (Rankin and Kokko 2007, Long et al. 2009, Rankin et al. 2011), and finally, as pointed out by e.g. Frank (2010a), current theory does not yet handle phenomena well in which short-term interests of individuals allow detrimental behaviours to spread but this leads to frequent group-level collapse. We will provide an example in which

it is crucial to think about the timescales of evolutionary change in this context.

The Amazon molly and its sexual hosts

Mollies of the genus *Poecilia* feature a curious reproductive system giving rise to a species complex with fascinating population dynamics. The Amazon molly, *P. formosa*, originally arose as a likely hybrid between *P. latipinna* and *P. mexicana*. It does not live in the Amazon region (rather in Mexico and southeastern states of US); instead its common name is derived from the mythical Amazon women of ancient Greek legends who did not tolerate any males in their communities. These women could not reproduce without visiting neighbouring tribes who still kept their men alive. Amazon mollies differ from mythical women in that mollies form an all-female species (male offspring need not be killed as they are never produced) yet with the striking similarity that they cannot reproduce without males (Schlupp 2010). As a vestigial trait reflecting a long evolutionary history of sexual reproduction prior to the emergence of Amazon hybrids, these females still need sperm to trigger embryogenesis (termed 'pseudogamy' or 'gynogenesis', Beukeboom and Vrijenhoek 1998, Schlupp 2010). The males who 'donate' sperm obviously belong to a different species than the Amazons, with *P. latipinna* or *P. mexicana* most often used a hosts. Sperm functions as a purely developmental trigger: male genes are not incorporated in the genome of the offspring except for some 'leakage' (Lamatsch et al. 2009) that can occur if there is a breakdown of the cellular mechanisms of the Amazon egg that normally destroy male chromosomes (Schlupp 2010).

The fact that Amazons still require this developmental trigger before eggs develop obviously constrains them to occur in sympatry with their sexual 'host' species who they use as 'sexual parasites'. (Note that the word 'parasitism' is somewhat loosely applied in this context because there may be no immediate costs to the males of the host species, however there is a population-level cost that we will explore in great detail below). It is conceivable that a mutant Amazon who can trigger embryonic development in a fully emancipated asexual way will arise and spread one day. Such a female would be able to reproduce regardless of male availability, and the fact that no such females have been found forms a good example that achieving a full transition to asexuality is not always fast over evolutionary time scales (Engelstädter 2008).

The most interesting question in the current evolutionary scenario concerns the behaviour of males of the sexual host species. Data show that they are to some extent able to prefer conspecific females over Amazons (Aspbury and Gabor 2004, Gumm et al. 2006, Gabor and Aspbury 2008, Heubel and Schlupp 2008, Gabor et al. 2010) – yet obviously many heterospecific matings with Amazons do occur, otherwise Amazons could not exist at all given their present evolutionary constraints. We do not consider genetic leakage a possible explanation for why males of sexual host species agree to mate with Amazons, because offspring with leaked genes are gynogenetic fish that are not only less fit than other Amazons (Lamatsch et al. 2009) but also, more importantly,

any leaked genes that influence male mating success will never again find themselves in males which would allow them to be expressed (and thus visible to selection). We therefore need to consider male mate choice theory: positive Bateman gradients for males, i.e. a positive relationship between number of mates and reproductive success, predict that they are a priori expected to accept most mating opportunities (Bateman 1948, Parker 2006, Servedio and Lande 2006, Jennions and Kokko 2010, Barry and Kokko 2010). It turns out that in the context of the Amazon molly, this a priori expectation of indiscriminate mating comes with a cost to the entire group (population) that is paid by later generations than the current one. This makes male mate choice evolution a question that extends beyond sexual selection, into an area where demography and the maintenance of a common good intertwine in ways relevant to the evolution of tragedies and the levels of selection debate.

Male mating restraint as a group-beneficial trait

The reason that the Amazon molly system is a thought-provoking example for the evolution of group adaptations arising as a direct consequence of the twofold cost of sex. Amazon females do not waste any reproductive effort on producing males, which implies that if local conditions are equally favourable for Amazons and their sexual hosts, the Amazon lineage will grow at the (proportional) expense of its sexual host species. As a simple numerical example, consider a population with 20 sexual fish (half of them male) and 10 Amazon females. If populations are currently experiencing a growth phase, such that one female can give rise to four recruits, and all females receive sufficient sperm supplies, then the sexual population will double to 20 males and 20 females, and the ten Amazons will quadruple to 40 Amazon females. The sex ratio (counting all fish) will have changed from $10/(20 + 10) = 0.33$ (10 male sexuals, $10 + 10$ sexuals in total, 10 Amazons) to $20/(40 + 40) = 0.25$ (20 male sexuals, $20 + 20$ sexuals in total, 40 Amazons), i.e. males become rarer. If these 20 males are still able to fertilize the eggs of all 60 females, the next generation sex ratio is $40/(80 + 160) = 0.167$ (40 male sexuals, $40 + 40$ sexuals in total, 160 Amazons). The proportion of males, pitted against females of both types (conspecific sexuals and cloned Amazons), declines continually from one generation to the next. Note that no sex ratio selection will kick in at any point to favour producing more males. Fisherian sex ratio theory (West 2009) only balances the sex ratio within the sexual species. Since males do not gain any reproductive success by fertilizing Amazons, males' reproductive value does not elevate beyond that of (sexual) females despite the high total number of females (sexual + Amazon) present. Consequently nothing selects for deviations from 1:1 primary sex ratios within the sexual species, even when male fertilization potential has become scarce.

In the above example, absolute numbers of both species are still growing (no density dependence). If populations grow until they become limited by resources, but in a way that neither favours or disfavours sexuals, then density dependence implies that the ever-decreasing proportion of

males makes their absolute numbers fall to zero, and the same applies for the number of sexual females which equals that of males. After the sexual host is extinct, sperm-dependent Amazons must go extinct as well (Kiester et al. 1981, Kokko et al. 2008). Field data show this not to be a mere theoretical prediction (Heubel 2004).

Male mate choice has the potential to revert the march towards deterministic extinction (Schlupp 2010). The above argument assumes that sperm is equally available to all females; sperm may begin to limit reproduction as the proportion of males becomes ever smaller, but if this does not harm Amazons to any greater degree than the sexuals, extinction is unavoidable (Kiester et al. 1981, Heubel et al. 2009). However, if male choice exists, it can (if strong enough) guarantee coexistence or, in a much wider parameter space, delay extinction to such a degree that other coexistence-promoting mechanisms, such as a wider metapopulation structure, can kick in to maintain stability over large spatial scales (Heubel et al. 2009). This means that whatever the selective reasons behind male preferences, these may maintain the common good of providing (relatively) Amazon-free space for future generations of the sexual species. We take issue, however, with a recent statement that variability in male mate choice can on its own strongly promote coexistence (Mee and Otto 2010), for the reason that their model unrealistically assumes female fecundity to benefit from an increased proportion of males across all conceivable sex ratios. In reality, lack of males most likely limits female reproduction at low male densities only. If we remove the assumption that sexuals always enjoy heightened fecundity when males prefer them, this will favour the spread of asexuals and make extinction more likely.

If male behaviour is crucial to explaining the ecology of the system, it is conversely also important to understand the selective environment that determines the evolution of male behaviours. In general, one might expect males to be choosy when there is very large variation in the fitness prospects offered by some females (conspecifics) versus others (Amazons: zero). However, male mate choice theory predicts that males should not evolve discrimination very easily if each mating, including ones of low profitability, takes only little time or energy (Barry and Kokko 2010), as the best strategy is then to never reject any opportunity. This principle can extend to scenarios where some matings are accepted even if they yield zero fitness (Schmeller et al. 2005). The reason is analogous to why one should not in principle reject either small or large sums of money found lying on the street, if the time cost of picking up money is negligible, and if one's fitness is entirely dependent on this source of income. Given the assumption that the act of grabbing the coin is essentially cost-free, even 'zero money' (e.g. a laundry token that looks like money) should be taken, as long as there is a chance that it could have been a real coin. Amazon females closely resemble the females of the 'parental' species that originally created Amazons as hybrids, and these species have since been used as the sexual hosts of Amazons. Selection does not act strongly against male mistakes if they are cheap but harmless 'laundry coin pick-ups'. Note that here 'harmless' only applies within a generation (no time cost paid) since the long-term effect may be extinction.

The reasoning, even within a generation, becomes different if matings are not cost-free, which is possible once

Amazons greatly outnumber sexual females. Males then have to take part in an ever increasing number of 'futile' matings with Amazons, and sperm may become limiting. A male who saves sperm for productive conspecific matings should then have an advantage over his less discriminating competitors. Yet there are reasons why this selective pressure may still remain weak. Firstly, significant sperm limitation only takes place in those generations where Amazon frequency is already high. Such populations may already be on their way to extinction, still following behavioural rules that were valid during generations when sperm limitation was not yet a problem, and during which prudent, discriminating males were not selected for. It is unclear how selection taking place in the last few generations before extinction could leave its mark on any gene pool of the future. Secondly, discriminating males might be penalized in each generation simply because discrimination is rarely cost-free either in terms of time or for its potential for mistakes. If a prudent male hesitates too long before inseminating a female, a less discriminating male may fertilize her eggs first. This cost applies in those generations when males are still common, while another subtype of cost applies whether males are common or not: erroneously rejecting a conspecific female is always worse for male fitness than erroneously accepting a heterospecific 'laundry token'. Thus if there is a nonzero probability that a prudently mating male rejects a conspecific female, his compromised mating success with conspecifics selects strongly against discriminating males.

There are additional hypothesized reasons why discriminating male behaviour might be selected against: there is evidence that being seen to mate may elevate male attractiveness as viewed by other females (Heubel et al. 2008). Thus, a male who inseminates an Amazon might benefit by increasing his mating success with other females. Favouring discrimination, on the other hand, is the simple fact that male attention directed at one female compromises his simultaneous ability to target another one. It is then perhaps a fair summary to state that the within-generation selection for prudent mating behaviour (we define 'prudent' here as a tendency to discriminate against Amazons) can in principle be either positive or negative. However, the direction of selection at the local population level is much clearer. Local populations that consist of males who all discriminate against Amazons are predicted to be much longer lived (Kokko et al. 2008); such populations slow down the growth of the Amazon population, who then cannot reap full advantage from their avoidance of the twofold cost of sex.

If all males in a local population refused to mate with Amazon females, future generations of the sexual fish would be freed from a competing fish species that grows 'cancerously' and dooms the sexual population to extinction. The prevention, or slowing down, of the growth of the Amazon population is perfectly analogous to an environmental problem that appears small at first (initially males can fertilize all females without trouble) but accumulates over generations until it is the most pressing problem a population can face: being acutely threatened by extinction. The problem is hard for an evolutionary process to solve, however, because in any one generation a male who cares little about maintaining the common good (of keeping the sexual population relatively Amazon-free) may have the highest reproductive success.

This occurs for all the reasons mentioned above that may favour indiscriminate mating within a generation. If males evolve to maximize their current mating success, they may inadvertently promote a 'tragedy of the commons' that spells doom on all their offspring in relatively distant future generations.

It is worth specifying the magnitude of 'relatively distant' here. The path to extinction in this system is often predicted to take between 10 and 20 generations (Heubel et al. 2009). Although recent theory helps to analyze the evolutionary maintenance of a common good across generations (Frank 2010a, Lehmann 2010, Leimar and Hammerstein 2010), such theory has only been developed for demographically stable populations so far. The selective environment of the molly system is highly labile, shifting from no sperm limitation to extreme limitation followed by local extinction. For the lack of an analytical approach capable of dealing with such complexity, we therefore resorted to an extensive simulation approach to investigate whether 'altruistic' male choice – prudent behaviour at the expense of a male's current mating success – can spread in a metapopulation consisting of extinction-prone subpopulations.

The model

Our model is an individual-based model in continuous time. This approach takes advantage of the Gillespie algorithm (Gillespie 1977, 1992) which avoids assuming discrete time steps for processes that can occur in real time, but simultaneously allows each individual to be a discrete entity, in keeping with reality. Below we will explain how this combination is achieved by modelling all state transitions as realizations of continuous-time rates that specify how often stochastic events occur.

We model $n \times m$ local populations of fish, such that each individual fish has coordinates i and j at any given moment ($1 \leq i \leq n$, $1 \leq j \leq m$). The model in principle allows for any spatial arrangement of the populations, characterized by the dispersal rates $d(i_1, j_1, i_2, j_2)$ from patch $\{i_1, j_1\}$ to $\{i_2, j_2\}$ (e.g. complete isolation results from setting these to zero). In our examples we investigate a 'river-based' spatial arrangement where dispersal is much easier between neighbouring patches along the j-axis than along the i-axis. Dispersal is not assumed to shift both i and j simultaneously. This does not set an upper limit to the distances covered in any particular time unit, however, because multiple dispersal events can follow each other in quick sequence.

While our model could be easily modified to let dispersal rates or life history characteristics (birth or death rates) evolve, we treat these as fixed and keep our focus on one evolving trait: male mating behaviour of the sexual species, denoted D (for 'discrimination'). This trait will be under direct selection based on within-species competition for mates, but additionally we will evaluate its evolution when the trait has local population dynamic consequences because male mating traits influence the success of the parasitic Amazon females (Heubel et al. 2009). The comparison between 'parasite-free' and 'parasitic' simulation runs will then be used to shed light on levels of selection for male mating behaviour.

The simulation proceeds as follows.

Initialization phase

At the start of the simulation, at time $t = 0$, N_P parasites and N_H hosts are distributed randomly and independently among the $n \times m$ patches. In some runs (see Results for details) we set $N_P = 0$ to track evolution of the host in the absence of Amazons, and in yet others we distribute the N_P parasites only at a later stage (e.g. $t = 10$, i.e. when a total 10 units of time have passed). In the last case, the hosts have evolved on their own for some generations.

To be able to follow the fate of each individual, they are given a unique integer identifier number I. The sex of each individual of the host species is randomly determined (yielding a 1:1 sex ratio on average within the sexual species). Each individual of the host species, whether male or female, is additionally characterized with an allelic value D that can take any real number value between 0 and 1, with an uniform distribution (mean 0.5) between these boundaries in the beginning of each simulation run, independently drawn for each individual. This haploid trait is only expressed in males. It influences mating behaviour such that high values of discrimination D make males less likely to mate with Amazons (for details including effects on conspecific mating success see below). $D = 0$ corresponds to random mating, and $D = 1$ means that a male never mates with an Amazon female. We assume that in the absence of selection values of D evolve through drift where upwards and downwards mutations are equally likely. The neutral expectation in the bounded range [0, 1] thus becomes $D = 0.5$.

Evolution

At any (continuous) point in time, each individual is in a state specified by its location i and j, and sex s that also serves as a species identifier (0 = asexual parasite, 1 = female host, 2 = male host). Sexual individuals also have their individual allelic value of the haploid trait D. Time t proceeds from one 'event' to the next, without a fixed time interval between any two events (for a similar modelling exercise see Rankin et al. 2011). An event may be a birth, a death, a mating, or dispersal. Some of these events occur at randomly drawn time points that are exponentially distributed with a parameter describing the rate at which the events occur. For others, there is a fixed time interval between events (e.g. a pre-defined time span from mating until a female gives birth – this may however be interrupted if the female dies first). We will first describe those events that are drawn from distributions, i.e. do not occur after a pre-defined time spans. We will first calculate potential event times, and then describe how to choose among them.

Death

To avoid unlimited population growth, we assume density dependence such that mature individuals die at a rate $\mu(I)$ that is positively related to the density of individuals in the local population. All individuals who reside in the same location (with identical i and j) thus share the same death rate. In our examples we model this rate as $\mu_0 + cn_{i,j}$, where μ_0 is a constant 'background' death rate, c is a constant that denotes the strength of density dependence, and $n_{i,j}$ is the sum of all mature individuals in the local patch (our examples use

$\mu_0 = 1$ and $c = 0.1$). Because of demographic stochasticity, individuals with the same death rate do not necessarily share the same death time. Instead, each individual is independently given a potential death time $t_{death}(I) = t + T_{death}$, where T_{death} is drawn from an exponential distribution with the mean $\mu(I)^{-1}$. This time is called a 'potential' time because other events – the death of some other individual, or e.g. a birth – may intervene first.

Note also that mortality $\mu > 0$ but there is no upper limit on μ. A high value of μ, say $\mu = 12.5$, means that an individual's expected future lifespan is only $\mu^{-1} = 1/12.5 = 0.08$ time units. Because μ increases with $n_{i,j}$, an individual may be very short-lived in a very dense population, but simultaneously this does not mean that density dependence makes the entire local population doomed. Each individual's death counts as an event after which all remaining individuals in the local population will have their death rates, and their new potential death times, recalculated. Thus, after the local density gets reduced, the remaining individuals have their expected lifespans adjusted upwards; they essentially become the survivors of a bottleneck.

Dispersal

Potential dispersal times $t_{disp}(I)$ are calculated analogously to potential death times: $t_{disp}(I) = t + T_{disp}$, where T_{disp} is drawn from an exponential distribution with the mean d denoting dispersal rate (our examples are derived assuming $d = 1$).

Mating

Mating rates, and hence potential mating times, are calculated for males only, as the necessary interaction with the female will be dealt with once a mating happens. We compute two potential mating times for each male: time of the next mating with a conspecific $t_{con}(I)$, and with a heterospecific (sexual parasite), $t_{het}(I)$. Sensible assumptions about mating rates must fulfil the following criteria:(1)Mating rates should increase with the number of potential mating partners in the patch, and equal zero if there are none (the potential mating time then becomes infinite).(2)Male discrimination, D, should by definition decrease the mating rate with parasitic Amazon females. This behavioural trait may, however, either increase or decrease the mating rate with conspecifics, depending on biological assumptions such as the presence of mate copying by females, or the time it takes to examine females which yields a risk that they swim out of reach or are inseminated by a competitor. The model also takes into account the possibility that a high value of D introduces type II errors such that males erroneously reject conspecifics, which is another reason why a high D may reduce the mating rates with conspecifics. If, on the other hand, discriminating is easy and fast so that discriminating males free some time to pursue profitable (i.e. conspecific) females, a high D may increase the mating rate with conspecifics.

We thus model the time of the next conspecific mating for a specific male with his individual discrimination level D_I as $t_{con}(I) = t + T_{con}$, where T_{con} is drawn from an exponential distribution with a mean $[n_F (1 + \alpha D_I)]^{-1}$. The conspecific mating rate of the male is the inverse of the time it takes to mate, i.e. $n_F (1 + \alpha D_I)$. This increases with n_F, the current number of sexual females in the local patch, and if $\alpha > 0$ it also increases with his own discrimination level

D_I. Conversely, if $\alpha < 0$, then a males' mating rate with conspecific females is harmed by being discriminating. The neutral case is given as $\alpha = 0$. We investigate values of α ranging between –1 and 1.

The time at which the same male mates with a heterospecific (Amazon) female is derived analogously, but following the definition of D, discriminating always reduces the mating rate with Amazons. Thus $t_{het}(I) = t + T_{het}$ where T_{het} is drawn from an exponential distribution with the mean $[n_A (1 - D_I)]^{-1}$. Here n_A is the current number of Amazon females in the local patch. If $D_I = 1$, the mating rate with Amazons, $n_A (1 - D_I)$, becomes zero. Note that the strongest possible within-generation selection against discrimination occurs when $\alpha = -1$, as this implies that fully discriminating males ($D_I = 1$) do not mate with conspecific females either (their mating rate with both Amazons and conspecifics is zero).

Note that the model includes male-male competition even though we do not assume that mating rates decrease with the number of competitors (other males) in the population. Mating rates remain unchanged because matings are brief and females can mate multiply in quick succession. The presence of competitors nevertheless matters to a male because we assume an effect on paternity such that the Fisher condition, i.e. the requirement that reproduction of males in a local population is limited by the offspring production actually achieved by females (Houston and McNamara 2005, Kokko and Jennions 2008), is automatically satisfied. In our case, we achieve this by assuming that the last male to have mated with a female fertilizes the eggs. Thus, while females may mate multiply (potentially in quick succession if there are many males), only one of the potential sires actually gains paternity in the current brood. Also note that the sire of the brood can differ from the sire of the same female's previous brood, and that the model also implicitly includes a potential Allee effect: female reproduction can become delayed if males are in short supply.

Consequences of mating: offspring are born

This is an event type that can occur up to three times after a fixed time interval after a mating has happened. A fertilized female is assigned three different birth times $t_{b1}(I)$, $t_{b2}(I)$ and $t_{b3}(I)$ which are, in our examples, 0.1, 0.2 and 0.3 units from the moment of fertilization. The assumption of three events follows from the ability of females to store sperm. Note that all births do not necessarily happen; the female may die before that.

We also collected data on the average age of mothers at the moment of birth, to give an estimate of the generation time. Generation time is not predefined in our model as there are no discrete generations; the age of mothers instead depends on mortality which is density dependent and thus varies across populations. However, as the average age for a mother at a birth event typically fluctuated between 0.2 and 0.3, we can state that one time unit corresponds to approximately four generations in our simulations.

Consequence of offspring being born: juveniles mature

Newborn offspring do not directly enter the pool of mature adults. Instead they are assigned a maturation time that is 0.1 units in the future from their birth time.

Choosing among events

The choice of the next event is based on the time assigned to each event. The earliest event (smallest t) is chosen to actually occur, and the population is updated accordingly. If the event is a 'death', the corresponding individual is simply removed. If the event is 'dispersal', then we must additionally specify the new coordinates of the individual. With probability p this occurs within a river, and with probability $1–p$ to a neighbouring river (examples derived using $p = 0.99$). In either case, if movement is possible in two directions, this choice is randomly determined.

If the event is a mating, then the male is assigned a female, with the female's identity randomly chosen among the available females of the correct type (heterospecific or conspecific). This female becomes fertilized and has a birth time assigned to it. If the event is a birth, the number of offspring is not yet defined, but potential offspring are recorded as having a maturation time that is 0.1 units in the future. If the event is one of juveniles maturing, the number of offspring is determined as a Poisson-distributed random number with mean 2 (note that the low number reflects that many juvenile fish die without leaving an impact on the population). In case of a sexual mating, the offspring follow a 1:1 primary sex ratio (randomly for each offspring) and haploid inheritance of D from either the mother or the father, with 50% probability of each. D may mutate, with a low probability m, to a newly drawn random number between 0 and 1; we used $m = 0.01$ to derive our examples. Note that females may mate multiply, and we assume last male sperm precedence (the last male of a female is assumed to be the sire). All Amazon offspring are, of course, female. The juveniles mature in the location $\{i,j\}$ combination where their mother resided when she gave birth. Thus, we assume that juveniles do not automatically follow their mother after birth if she disperses in between. Their movements are independent and only occur after maturation.

After the consequences of an event have been tracked, global time gets updated to its new value (e.g. to $t_{con}(I)$ if the event was a conspecific mating). All events that rely on stochastic distributions then have their values redrawn, as the population state (e.g. density) is likely to have changed as a result of the event, and this will impact the distribution of new events.

Results

The dynamics of Amazon infestation

Figure 1 depicts an example of a simulation that has progressed for 2.5 time units (approximately 10 generations). The four different rivers harbour very different populations, whereas differentiation between subpopulations is less marked along each river. This pattern is expected from higher dispersal rates along than between rivers, which has synchronizing effects on behaviour and dynamics alike. The numbers in Fig. 1 refer to the mean value of the discrimination allele D averaged across all local males. In river 1, males discriminate strongly against Amazons, and populations have reached high densities but also experience some Amazon infestation. River 2 is similar, but with lower values
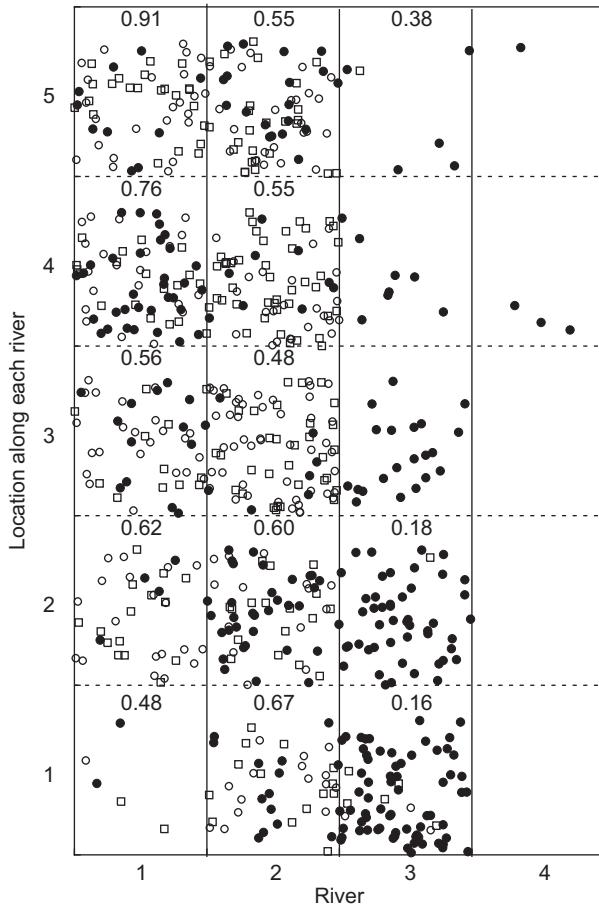
Figure 1. An example of a population initiated with that has been running for 2.5 time units (approximately 10 generations). Each individual's location is indicated with a symbol: filled circles are Amazon females, open circles sexual females, and open squares sexual males. The location within each subpopulation is scattered for illustrative purposes only; all individuals within the same $\{i,j\}$ square belong to the same subpopulation. Location-specific numbers give the average current discrimination level D, averaged across all males currently present in a subpopulation.

of D. Amazon infestation in river 3 has progressed to the point where almost all sexual individuals have vanished. The few remaining males discriminate poorly, reflecting a recent past where Amazons have been able to reproduce freely. This reproductive advantage for the Amazons has come to an abrupt halt, however, in river 3's subpopulations 3 and 4, where there are no sexual individuals left (and hence no D value can be recorded). These Amazon females will not be able to reproduce unless dispersal mixes populations soon enough to make them find a male. This extinction process has progressed much further in river 4, where the last remaining Amazon females still persist before likewise perishing unless they encounter a dispersing male or disperse themselves to find one (yet either option is unlikely because all nearby populations largely lack males too).

Although this particular example is provided for illustration only and its evolutionary trajectory was thus not tracked further, it is likely that the future next generations in this run would experience an increase in the global value of D

because of imminent extinctions in subpopulations that currently still have males with low D (although it should also be noted that these subpopulations already contribute insignificantly to the global distribution of D as they harbour very few males by now). The resultant empty patches will eventually be colonized again, possibly leading to sexually-only subpopulations that can grow rapidly for a while before being invaded by Amazons.

The presence of Amazons creates a selection pressure for better discrimination

Figure 1 is based on an evolutionary scenario with $\alpha = 0$, i.e. discriminating males suffer no intraspecific competitive cost nor do they enjoy an advantage when competing for conspecific matings. The within-generation dynamics is thus selectively neutral, and this is confirmed by repeated running of the model for 20 time units (approximately 80 generations), replicating the entire simulation 20 times in the absence of Amazons ($N_P = 0$). The populations then do not evolve to deviate from the initially set average $D = 0.5$ (Fig. 2A, case (1)). However, in addition to the case with no Amazons, we ran three additional sets of 20 runs where a population is duplicated and then each of the two copies is subjected to a specific treatment. This follows the gist of microbial experimental evolution procedures where the same population can be split in (near) identical subsets. In our case, we explored evolution when (1) Amazons are absent throughout, (2) the population in (1) is duplicated at time $t = 10$ and one of the replicates is subjected to an invasion by Amazons (N_P Amazons are at that point distributed randomly among all localities), (3) Amazons are present from the start (N_P distributed at $t = 0$) but then instantaneously removed at $t = 10$, and (4) the population of (3) is run from $t = 10$ onwards without removing the Amazons (the 'Amazons present throughout' case). All cases were run for a total of 20 time units, i.e. approximately 80 generations. Confirming the intuition of Fig. 1, population-wide D evolves upwards whenever there are Amazons present (Fig. 2A). Case (3) shows a tendency to revert back to the neutral value $D = 0.5$ after $t = 10$. Note that this is the expected null level in a bounded set of allele values: mutations on average cause upwards drift for $D < 0.5$ and downwards drift for $D > 0.5$.

In the examples of Fig. 2A, discrimination D is selectively neutral in male-male competition but populations with higher D are better protected against the invasion of Amazons. This example thus confirms that global D can evolve based on its effects on maintaining Amazon-free space, an important common good for the sexual population. However, it is far more interesting to ask if D can evolve upwards even if high D causes competitive inferiority when males compete for conspecific matings. Assuming a relatively mild effect of $\alpha = -0.2$, this proves to be the case (Fig. 2B).

This result is remarkable because it suggests that males may evolve to sacrifice their own current mating success to help maintain a common good for the use of future populations. Their prudency (high D) diminishes the growth of a competing species that has the potential to eventually reap too many local resources from the sexuals in any density-dependent setting. Prudent mating evolves despite the possibility of uncooperative cheats spreading in the
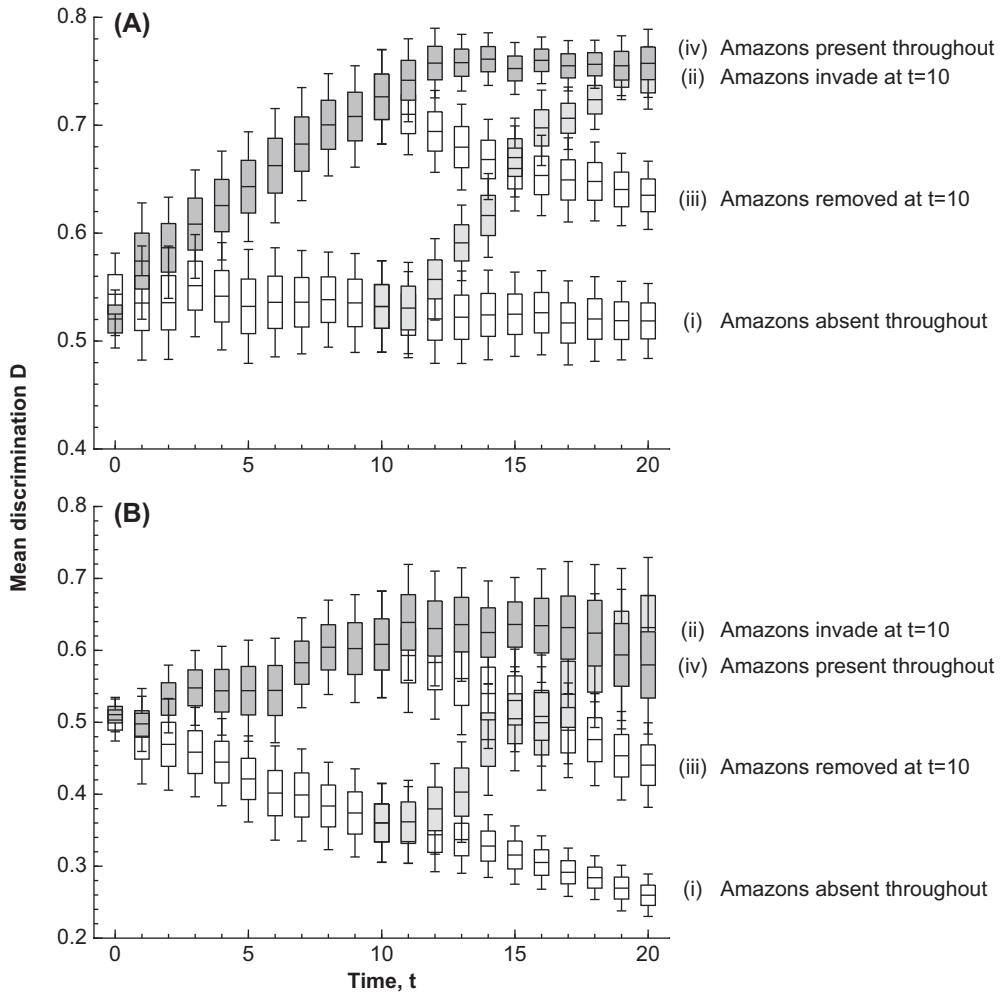
Figure 2. Snapshots of the evolutionary process as measured at each integer value of time t. Note that while t is not confined to integer values, the population can still be measured at arbitrary intervals including integer values of t. The measured trait is the mean D averaged across all males in the global population, and the box plots gives this mean $\pm$ SE and 90% confidence intervals, as the mean from 20 simulation runs. White box plots show evolution when no Amazons exist in the system, light grey indicate their arrival at $t = 10$, and dark grey are the cases with Amazons present throughout. Data from simulation runs in which Amazons went extinct despite their intended presence were discarded for this plot; this was achieved by the sexual populations that discriminated most strongly, which explains the slight drop in mean D and the broader confidence intervals in (B) towards the end of the simulations. In (A), there is no within-generation selection for or against male discrimination ($\alpha = 0$), and accordingly case (1) with no Amazons ever present does not deviate from its initial distribution that includes the neutral expectation 0.5 within its confidence interval. In (B), within-generation selection favours smaller values of D ($\alpha = -0.2$). Populations consequently evolve smaller D but this trend becomes strongly reversed in the presence of Amazons, regardless of whether they exist from the beginning or if they invade later.

population. A cheating (i.e. freeriding) male who uses a lower D will experience a higher mating success among conspeficic females. Consider, for example, a male with $D = 0.2$ who is an immigrant or a mutant in a population where other males use $D = 0.8$. With $\alpha = -0.2$, the low-discriminating male achieves a mating rate of $n_F \times 0.96$, which is a 14% increase over $n_F \times 0.84$ reached by other males who use $D = 0.8$. This makes the lower D spread within a population – jeopardizing the common good and hastening extinction. The interesting question is whether the hastening of extinction is a sufficient penalty for the freeriding alleles. Any gene copies are unlikely to survive in a population on a fast-track to extinction. Quoting a phrase by Leimar and Hammerstein (2010), however, individuals comprising a group do not completely 'stand or fall together'. They share a common interest in the

survival of their group, but dispersal means that lineages can also reap the local benefits and escape before extinction strikes. This makes the question of prudent local resource management highly non-trivial, in gynogenetic systems as well as elsewhere (van Baalen and Sabelis 1995, MacLean 2007, Wakano et al. 2009, Eshelman et al. 2010).

Selection at the subpopulation level

There are many possible ways to quantify levels of selection phenomena (Foster 2009). Our system is dynamically complicated, which makes it difficult to plug in any of the standard approaches. We will first simply provide the outcome (evolved global D) as this most clearly shows what actually evolves as a net effect of all selective processes (Fig. 3).
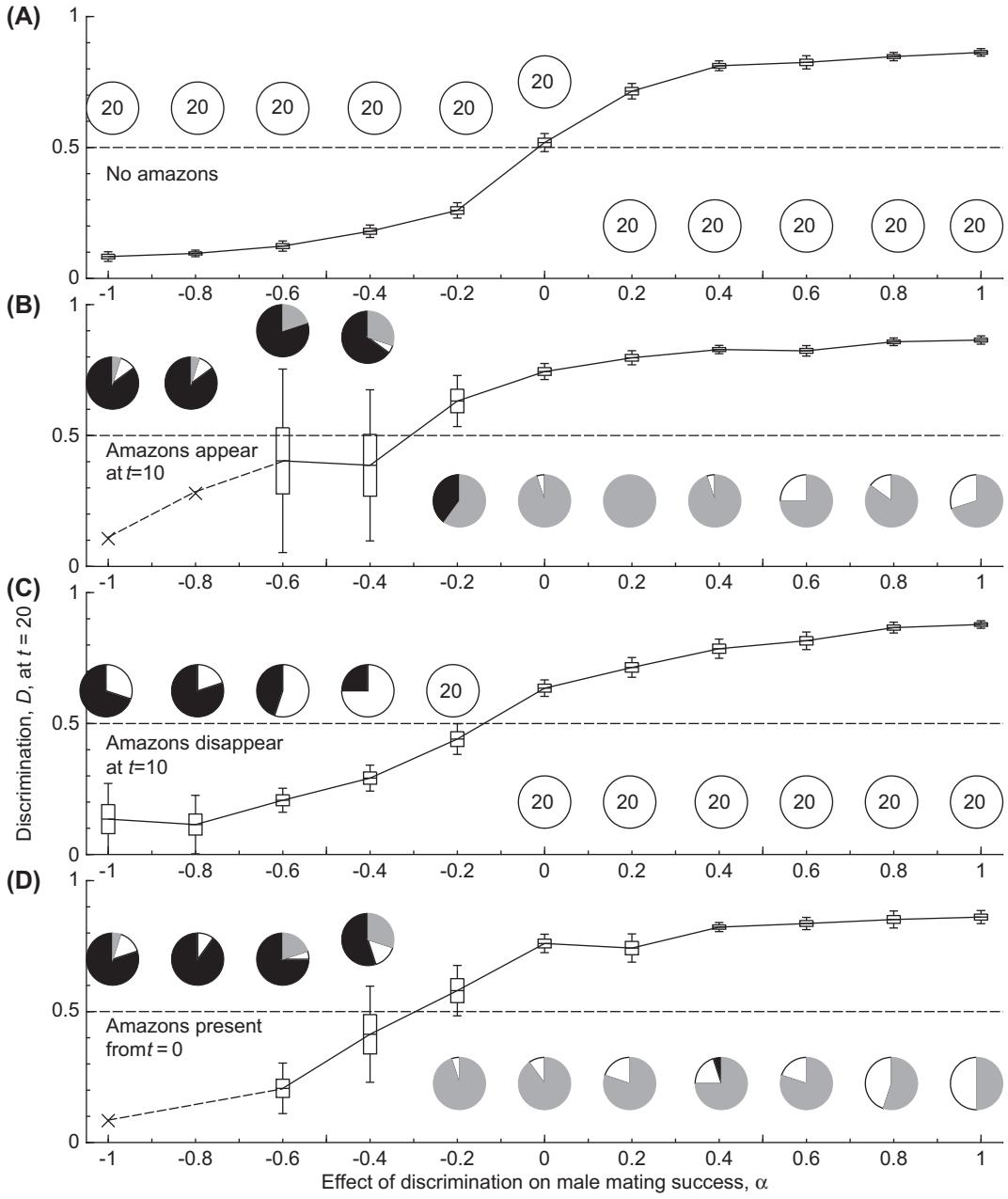
Figure 3. Evolved discrimination D by males (box plots) at $t = 20$, in cases where (A) no amazons are ever present, (B) amazons are present initially and are removed at $t = 10$ (i.e. approx. 40 generations), (C) amazons are absent initially and appear in the system at $t = 10$ (i.e. after approx. 40 generations), (D) amazons are present throughout. Box plots give the mean $\pm$ SE (box) and the 95% confidence interval (vertical lines) for data that consists of 20 independent runs of mean D at $t = 20$, each data point giving the average over all males present at $t = 20$ within each simulation. The box plots only use data from runs where the sexual species did not go extinct: pie charts give the number of runs, with maximum 20, ending in total extinction (black), coexistence with amazons (grey), or only the sexual species present (white). As an additional requirement, in (B) or (C), only data from coexisting populations are used to form the box plots, leaving in some cases only isolated data points (1 out of 20 populations persisting: marked as a cross and dashed line). This is to ensure that (B) and (C) reflect evolution in the presence of amazons throughout; the omitted data experiences evolution towards similar values as in (A) and (C) once Amazons no longer exist in the system.

We will then proceed to providing a conceptual tool where we calculate selection differentials for entire subpopulations as if they were organisms, as this allows us to state to what extent subpopulations differ in their productivity ('fecundity' and 'lifespan') depending on the type of individuals they consist of (Fig. 4). This latter approach provides necessarily a much less complete picture than simply reporting all outcomes, yet we believe its worth lies in it guiding thinking in useful directions, as net outcomes on their own state little about the selective processes that underlie the observations.

The outcomes indicate, nevertheless, that maintaining the 'common good' is important, and populations can evolve to achieve this. This generalizes to values beyond $\alpha = 0$
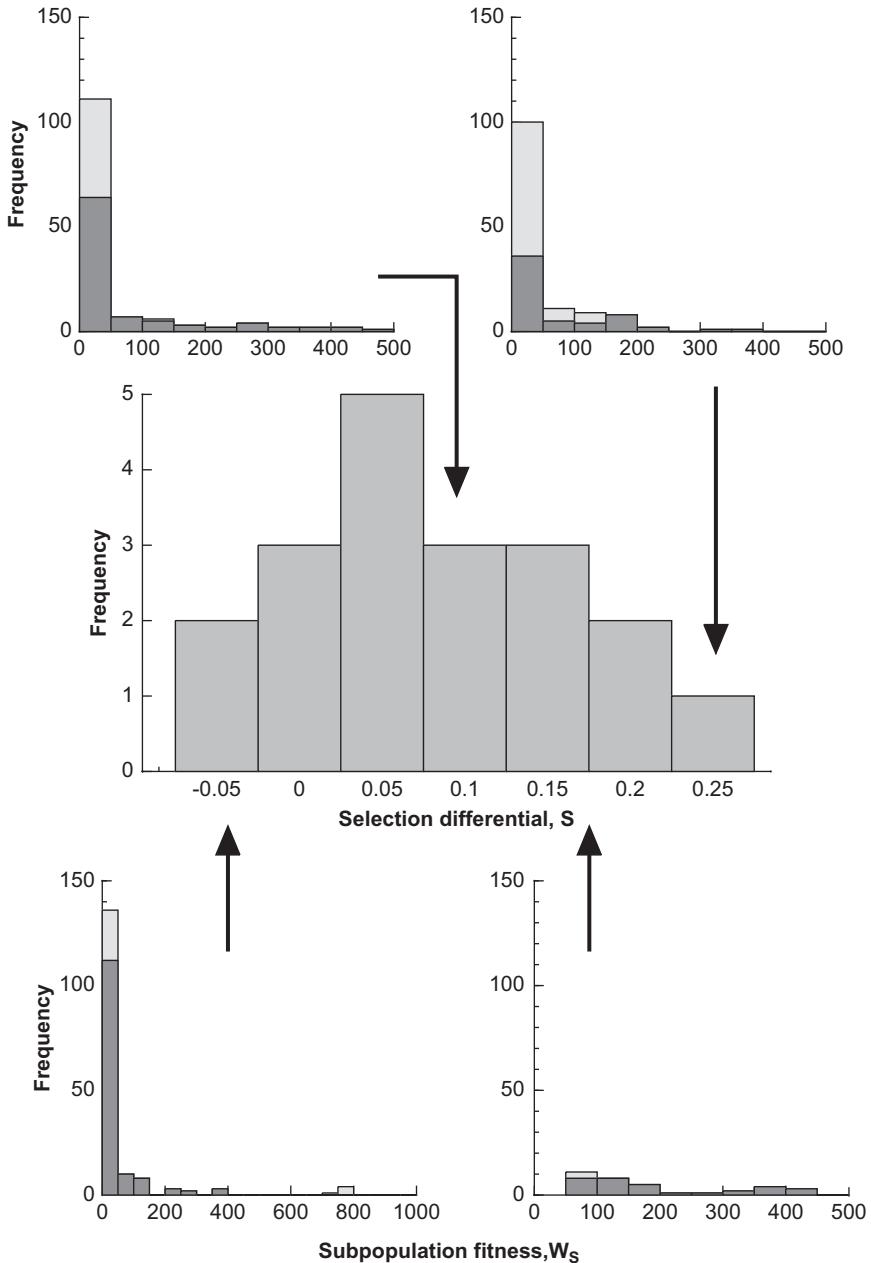
Figure 4. Selection to maintain the common good in the example case of α = –0.2. The main figure in the centre shows the selection differential *S* calculated across all 19 valid simulation runs, where entire subpopulations are treated as entities that have fitness W_S. This allows defining *S* as the mean value of D_S of a subpopulation from where a new individual originates minus the average D_S of all subpopulations ever present. Four example cases are depicted in greater detail, showing the distribution of subpopulation fitness (W_S = lifespan of subpopulation × mean number of sexual females). Arrows indicate the value of the selection differential that each fitness distribution gives rise to. In the example histograms light shading indicates an uncooperative population, dark indicates a cooperative population, where a cooperative population is defined as $D_S > 0.5$. This definition is for illustration only, as S is computed without any arbitrary thresholds for D_S.

or α = –0.2 (Fig. 3), but not uniformly across the entire range from α = –1 to α = 1. The higher α, the higher and more uniform the evolved values of *D*. Very high values of α describe cases where discriminating males enjoy strongly elevated mating success. Unsurprisingly, this predicts that males will easily evolve high levels of discrimination. The common good of defence against Amazons exists regardless of whether Amazons are actually present, and this is not surprising because both selection within a generation and the longer term ecological process both favour these 'cooperative'

tendencies. Cooperation involves no altruism when α > 0, and the outcome is better classified as byproduct mutualism. The more interesting finding is that even when α is very high, only about half of these populations rid themselves of the entire Amazon infestation (Fig. 3D). This finding is in line with results from ecological dynamics (Heubel et al. 2009) where high *D* permits coexistence if males are generally efficient sperm produces.

The parameter space of mild within-generation selection, from α = –0.2 to α = +0.2, is arguably the most

interesting one. Here the presence of Amazons clearly elevates D to higher levels than it would evolve to in their absence (Fig. 3). The common interest among individuals to produce an Amazon-free space for future generations is a strong enough selective force to elevate D above its neutrality line ($D = 0.5$) in all the cases, including the case with negative within-generation selection ($\alpha = -0.2$).

When negative within-generation selection becomes stronger still ($\alpha < -0.2$), the pattern changes again. The fate of populations becomes more variable, with some displaying much higher D than others, and an increasing proportion of populations experience global extinction. These extinctions are at their most numerous when α is lowest. Here, within-generation selection against discrimination is so strong that males simply fail to evolve the cooperative tendencies required to maintain the necessary common good for future generations. If the resulting empty areas were to be colonized again, the immigrants would have to come from areas where the common good is better maintained – possibly elevating D again over a larger spatial scale – or from areas not recently invaded by Amazons such that the sexual population was safe.

To be able to quantify the importance of maintaining the common good (future Amazon-free space) in this setting, we split up the time flow within each simulated locality into sections where there is a viable sexual population present (defined as at least one sexual female and one sexual male residing in the locality), or no such viable population exists locally. The time slices that had a viable population were then scored for their lifespan and average number of sexual females, sexual males and Amazons, together with the mean D found during the lifespan of this subpopulation. These numbers fluctuate over time due to immigration and emigration as well as births or deaths, which makes their quantification somewhat challenging. We used the same time-weighted procedure for all these quantities, exemplified for D in the following way: we aim at the unbiased estimate of the D that a researcher would find if randomly sampling sires of all the offspring produced in this subpopulation over the subpopulation's lifetime. Thus we computed a weighted average of D over time with weights that are male numbers between time points t_i to t_{i+1}, multiplied by the duration of the time interval $t_{i+1} - t_i$. (Note that since the population only changes in composition when i changes, the number of males remains unchanged between t_i to t_{i+1}.) For example, consider a population that at $t = 0$ started with one male with $D = 0.5$ and another with $D = 0.53$, then at $t = 0.03$ the first male dies, then 0.013 time units later (at $t = 0.046$) the 2nd male dies. The average D is a weighted average of the trait of two males for a duration of 0.03 time units and of the one remaining male for a subsequent duration of 0.013 time units, and its value is (0.03 × (0.5 + 0.53) + 0.013 × 0.53) / (0.03 × 2 + 0.013) = 0.5177. We call this time-weighed quantity the subpopulation-specific D, denoted D_S. Note that the same locality {i,j} can harbour several subpopulations over time, these simply must be temporally non-overlapping.

We then computed the selection differential for D_S at the subpopulation level, beginning by defining a subpopulation's fitness W_S as the time-weighted average of numbers of sexual females in the subpopulation, multiplied by the lifespan of the entire subpopulation. For example, consider a population that consists of one female from $t = 0$ to $t = 0.031$, then of two females from $t = 0.031$ to 0.034, then again of only one female from $t = 0.034$ to 0.421, and then this female dies or disperses so that the entire subpopulation is now extinct. W_S will then equal (0.031 × 1 + 0.003 × 2 + 0.0081 × 1)/(0.421) × 0.421 = 0.0451. Females are the relevant measure here when we take the male's genes point of view, as male reproductive rates increase with the number of sexual females present. We then computed S, the selection differential, as the expected difference between the D_S of a 'parent' subpopulation (one that is observed to have produced a new offspring, e.g. a disperser) and the average D_S of all subpopulations that existed throughout the simulation run. In other words, we computed the difference $\dfrac{W_S D_S}{\Sigma_{all} S W S} - \bar{D}_S$

where $\bar{D}_S$ is the mean of D_S taken over all subpopulations that existed in one simulation run. This computation is exactly analogous to selection differentials calculated for traits in normal organisms. Statistically, a subpopulation elevates its chances of being the 'parent' of an offspring by (a) being viable during the time that the offspring is observed to be born, which creates the correlation between long lifespan of a subpopulation and its fitness, and also by (b) exhibiting, on average, high fecundity; this favours subpopulations that host a large number of females, as these are the potential mothers of young produced. If 'parental' subpopulations tend to be those in which males protect the common good well (high male discrimination D_S), this will be reflected in a positive value of the selection differential S.

Our hypothesis that subpopulations that maintain a high D_S are large and long lived, and that this should be reflected in high subpopulation fitness W_S whenever Amazons are present, was confirmed (Fig. 4). We computed S for all simulation runs of category (4) that resulted in a global population of Amazons persisting throughout the simulation. For $\alpha = -0.2$, this meant including 19 out of 20 simulation runs, as in one case high discrimination against Amazons drove them extinct which thereafter changes the evolutionary trajectory to resemble that of case (1). The 19 values of S are depicted in Fig. 4, with four individual simulation runs illustrated in detail. These detailed histograms underlying each particular value of S show the fitness W_S distribution among subpopulations that were highly cooperative ($D_S > 0.5$, dark bars) or cooperated poorly ($D_S < 0.5$, light bars); poorly cooperating subpopulations tend to form a clear low-fitness cluster. Note that the arbitrary threshold $D = 0.5$ is illustrative only and not used in the computation of S itself.

In most runs, the selection differential S for maintaining the common good is positive (Fig. 4). As an example, the top right histogram shows that a few cooperative subpopulations reached very high $W_S > 150$, and all of these were classified as cooperative; the majority of poorly cooperative subpopulations had W_S close to zero. This pattern leads to a very high S. However, we also observed some runs with a negative S. The lower left histogram shows how this can arise when in addition to many uncooperative low-fitness subpopulations there are also a few that reach very high

fitness despite, loosely speaking, their slack attitude towards maintaining the common good. The reason is simple: this simulation produced one river that never happened to experience much Amazon infestation, and subpopulations in this river enjoyed exceptionally high fitness despite remaining totally unprotected against any invasion that might happen in the future. We never excluded the possibility of such safe spatial pockets in the simulations, yet the overall distribution of S remained positive. This means that as a whole, a newly born sexual individual is more likely to have been produced by a cooperative (high D_S) than an uncooperative (low D_S) population.

We also quantified the lifespan of subpopulations separately, as one might argue this to be the more important population-level trait from a male perspective than any measure that is weighted by female numbers (since large numbers of females may covary with large numbers of males who then form competitors for any focal male, negating the benefit of large female numbers). Again exemplified with $\alpha = -0.2$, and excluding the one simulation where sexuals rid themselves of all Amazons, there is usually a clear positive relationship between subpopulation lifespan and subpopulation-specific D_S within each simulation (Fig. 5). This pattern is broken three times (out of 19), when populations that happen to avoid Amazon infestation experience a long and healthy life despite their continued vulnerability (negative slopes in Fig. 5).

The patterns depicted in Fig. 4 and 5 use a particular value ($\alpha = -0.2$) as an example as altruism is at its clearest at this point, but these patterns prove generally robust. The entire dataset of 220 simulation runs (20 replicates for each of 11 values of α) produced a total of 123 cases where Amazons were present throughout from $t = 0$ to $t = 20$. A total of 110 out of these 123 cases yielded a positive S, and 109 out of 123 yielded a positive logistic regression coefficient between the lifespan of the sub-
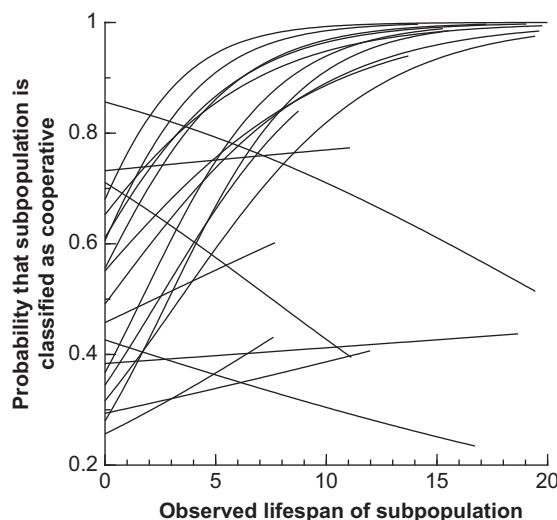

Figure 5. Long subpopulation lifespans are, with a few exceptions, strongly associated with these populations being of a cooperative type ('cooperative' defined as $D_S > 0.5$). The 19 logistic regressions are shown for the lifespan data range observed within each run of the case $\alpha = -0.2$.

population and whether it was classified as cooperative (with $D_S > 0.5$).

Discussion

Depending on who is asked, the levels of selection debate has experienced a revival in recent years (Wilson and Wilson 2007) or has reached unhealthy levels of animosity between researchers (Okasha 2010). Here we wish to interpret our findings making several points of interest in this debate.

We shall first, however, comment on the biological lessons regarding the particular gynogenetic species complex of Amazon mollies and their host species. An evolutionary pattern that favours discrimination in the presence of Amazon mollies is clearly operating, based on evidence that males discriminate more strongly if they originate from populations with a history of coexisting with mollies, than from allopatric populations (Ryan et al. 1996). The level at which selection favours such discrimination is, however, far from clear. Our results show that if discrimination is favoured at the within-generation level (i.e. if discriminating males achieve better fertilization success with conspecific females, $\alpha > 0$), then there is nothing very puzzling about the system. Maintaining the common good can then arise as a byproduct of males doing what is best for them individually. The fact that extinctions still occur in this case is an example of a tragedy of the commons: a consequence of the fact that the common good is not maintained well enough to prevent all Amazon trouble (this would require very high discrimination D; see Heubel et al. 2009). The interesting lesson that we learn in the $\alpha > 0$ case is that evolution cannot be expected to operate with sufficient foresight to prevent negative population consequences. Far from it: conflicts between individuals or within their genomes often predict deterministic reductions in population size (Rankin et al. 2007a; for sexual examples see Rankin and Kokko 2007 and Connallon et al. 2010).

However, it is also possible that within-generation selection works against discrimination ($\alpha < 0$). Above we have discussed a number of reasons for this, from mate choice copying to the fact that immediate male fitness is more harmed by erroneously rejecting a conspecific female than by erroneously mating with a heterospecific. Within-generation selection may therefore act 'against' strong discrimination. If $\alpha < 0$ for mollies, then the evolved discrimination against Amazon females could be an interesting case of 'altruistic' restraint where an individual suffers a within-generation fitness cost (reduced mating success) but discrimination improves long-term population performance sufficiently to compensate for this.

As such, it is no news that such processes can occur. Proper fitness measures must take more than one generation into account (Metz et al. 1992), and altruism always has to find its explanation by 'explaining it away'. Ultimately the number of gene copies must increase for the altruist as opposed to the non-altruist, so the former never was a true altruist in the long-term genetic sense. (As an aside, similar arguments apply for spite; at some point the removal of competitors must benefit the spiteful actor or its descendants, usually via density dependence. One simply labels it 'spite' when the effect is somewhat delayed.) Our results show that negative

population consequences, when they act fast enough over relevant spatial scales, can limit the spread of freeriding cheats, and that this can occur in an example that is rooted in documented biology (reviewed by Schlupp 2010). Such an example is perhaps a welcome deviation from the abstract behaviours typically modelled when addressing the evolution of common interest and mutual dependency among individuals (for examples see Eshel and Shaked 2001, Kokko et al. 2001, Roberts 2005, Frank 2010b, but see also Garay 2009 and Driscoll and Pepper 2010 for concrete examples).

While examples involving much biological detail are welcome, addressing the relevant complexities has a clear downside in the form of reduced analytical tractability. Even so, we believe there are a number of important conceptual insights to be derived from our exercise. Much of the recent debate has revolved around whether social behaviour can all be usefully understood using inclusive fitness models or not (Wild et al. 2009, Nowak et al. 2010, Wade et al. 2010), and whether this means that we should distinguish between 'selection' – which can operate across multiple levels – and 'adaptation' which has been argued to only apply at the organism level, based on kin-selected principles (Gardner 2009).

What can we say about discrimination D (or more precisely, any particular numerical value of it) as an adaptation? Our selection differential approach to understand its evolution is helpful but mathematically incomplete. In particular, we have not attempted to cast the evolution of D in terms of kin selection, simply because this task appears extremely daunting when the selective environment changes rapidly from one generation to the next, and when temporal changes in relatedness obey different rules in populations of varying size. For example, an immigrant cheater male arriving in a population with only one male left will change D_S much more, and have much faster extinction-causing potential, than one arriving in a large population.

This is not equivalent to saying that kin selection is not useful (the viewpoint stated by Nowak et al. 2010). Discriminating males who reside in spatially subdivided populations experience kin structure. Indeed, the very reason why they should care about maintaining the common good for future generations is that these are likely to contain related descendants (Lehmann 2010). In this sense, we fully agree with the usefulness of striving towards understanding evolutionary processes from an inclusive fitness point of view, although it must be said that dynamically complicated cases provide computational challenges that may cast doubt on whether truly new insights would be gained for this particular biological system by attempting to derive the relevant equations. This, however, reflects not a failure of inclusive fitness theory but the far more general principle that there is a tradeoff between model generality and precision (Levins 1966). In other, more general contexts, suitable simplifications have proven impressively useful for understanding empirical patterns and generating new testable predictions (West et al. unpubl.), which makes their complete dismissal by Nowak et al. (2010) very odd.

Simultaneously, however, statements that adaptation can only occur at the (kin-selected) individual level even if selection can operate across multiple levels (Gardner 2009) appear too strong to us. This debate involves the definition of adaptation as an answer to the question 'what does an entity (e.g. an organism) appear to be optimizing?' In the case of our discriminating males, one definition of adaptation is that males sacrifice some of their mating success to maintain the common good of Amazon-free space for future generations. Alternatively, a researcher could state that (sub)populations evolve to maintain the common good. The latter view smacks more of naïve group selection than the former, a fact that we will comment on below. However, both views fail to capture some aspects of reality in important ways. At the individual level, our models show that males maintain the common good in a very unsatisfactory manner: we always find some populations that are on their way out because of insufficient attention paid to the common good. Similarly, the adaptive process at the subpopulation level is painfully imperfect as it is plagued by clear conflict between individuals that live in this population (freeriders can spread).

A strict interpretation of Gardner (2009) would predict that only one of these levels make any sense. As pointed out by Foster (2009), however, there are numerous cases where adaptation does not work brilliantly, and it may then be a too strong claim to assign one level the label of 'adaptation' and claim that any other level makes no sense. Our case appears to fall in this category of imperfections. Males do not produce an adaptation to prevent all Amazon reproduction, nor do they maximize their within-generation success except in very short-lived populations. If one accepts that their behaviour is an awkward temporally shifting compromise between short and long term selective processes, it is not fully clear to us if there is any level of optimization that will satisfy the criteria of 'adaptation' as promoted by Gardner and Grafen (2009) and Gardner (2009).

Of course, one could envisage a valid attempt to rescue the argument of adaptation as inclusive fitness operating at the individual level, by developing models similar to Lehmann (2010) and using them to reiterate that males evolve adaptations that maximize the quantity that a suitably complicated inclusive fitness model predicts them to optimize. Such a result, if successful (see van Veelen 2009 and Marshall 2011 for why this might be difficult), would have to track all spatiotemporal scales until it automatically stretches the definition of adaptation to become identical with selection – which explicitly was not the intention of Gardner (2009). Also, such an exercise could be criticized for following an a priori goal to 'define' adaptation as the outcome viewed from a particular angle, when other angles (e.g. subpopulations riddled with internal conflict) could be similarly and validly used as a basis for any relevant relatedness calculations as well.

Instead, we would like to offer the following viewpoint. Adaptation is clearly about something that an entity has evolved to do well. Recent and frequently occurring events have a greater influence on the current distribution of genotypes than rare events, and it follows that adaptations are mostly found in response to the former type of challenges. An example helps to make this point: Tasmanian devil populations are currently in trouble because they suffer from a facial tumour that spreads from one devil to another (McCallum et al. 2009). Should one consider the dispersal ability of a tumour an adaptation? If yes, was it still an adaptation in the sadly possible scenario of the near future where the last devil is dead? Instead of defining adaptation to occur at any

particular level, it is better to define it broadly as 'evolved optimization' and then simply remember that one cannot expect an evolved entity to solve rare problems as proficiently as commonly occurring ones. Short-term growth or transmission can be near optimal because selection for these is ever-present, simultaneously nothing prevents the solution from drifting far away from being able to solve a rare or hitherto never encountered challenge (e.g. finding a new host when devils are no longer available).

In non-social contexts, it is very clear that biological entities evolve apparent foresight when the challenges are frequent. Examples are responses to the photoperiod that allow organisms to behave as if they knew that winter is approaching, and the maintenance of general immune systems even though not every generation encounters every possible disease. In social systems, one speaks of common interest among individuals when group or population level processes are sufficiently fast that adaptations take them into account to some appreciable extent. The global distribution of molly genotypes in our model shows a significant effect of local extinctions because these have occurred frequently enough in the recent past.

Thus, when the temporal scales of within-generation selection and the longer term population consequences overlap sufficiently, one can validly speak of an adaptation to avoid extinction. In the more usual cases where population turnover is less dramatic, such language is hardly useful. The very infrequency of extinction allows lineages to persist for a long time and evolve traits that make them more vulnerable to extinction, summarized as no adaptation to avoid extinction in a foresighted manner. This helps to restore the distinction between multi-level selection and adaptation. Organisms with high dispersal capacity aren't considered to have evolved their long wings 'to avoid extinction' even though range sizes do covary with wing length (Böhning-Gaese et al. 2006) and large range sizes ultimately help lineages avoid extinction (Powell 2007). Recent selection may have favoured either type within a population, in other words, selection in the short term will not avoid producing short wings on the basis that this might increase eventual extinction risk. This should not make us classify short wings as any less adapted than long wings (to the relevant current environmental conditions encountered by each population).

Perfectly optimal behaviour will be rare even for frequently occurring challenges, but adaptations to solve a complex problem evolve much more easily if there is strong common interest among biological entities (Leigh 2010, Leimar and Hammerstein 2010). The great success of individuals, as opposed to any other type of groups, in achieving adaptive responses may thus reflect the specific power of the evolutionary innovation of active suppression of within-genome conflict (fair meiosis, Leigh 2010), rather than there being anything magical about inclusive fitness arguments applying at the individual level only.

We would therefore like to end this paper with two conclusions. One is to provide a reminder that evolution operates across multiple time scales. This gives rise to a view of adaptation in the context of a dynamic equilibrium where the more short-sighted solutions are continually on their way out, and imperfection is the rule at least when outcomes are judged for long-term performance. Examples abound far beyond weird gynogenetic systems (Rankin et al. 2007a, López-Sepulcre et al. 2009, Korb and Foster 2010). To mention a few examples, evolutionary biologists understand that cancer is an evolutionary short-term strategy (Pepper et al. 2009, Perkins and Swain 2009), where some cells proliferate by avoiding the policing that normally keeps selfish tendencies of cells at bay, but this causes a fully blown tragedy of the commons: the death of the entire organism. Cancer may be hard to think of as an adaptation, yet when viewed over sufficiently short time scales (cell lineage growth within a body), 'successful' cancers no doubt are those that are good at extracting resources from the body. Cancer's short-term success is essential for understanding why at any point in time very many cancerous cells exist on this planet, and ditto for the Cape honey bee where the 'social cancer' of uncooperative egg-laying workers spreads from colony to colony, spelling doom for colony function (Härtel et al. 2006). Since extinction at the species level is known to be highly non-random too, even species level selection must ultimately be included in a proper understanding of what exists in a world and why (McPeek 2007, Rankin et al. 2007b, Jablonski 2008, Goldberg et al. 2010), even if adaptation to avoid extinction of entire species must be rare or non-existent.

Our second message is to remind researchers that much of the battle about levels of selection is ultimately about how we teach students about evolution. For some reason, most laymen who accept evolution think of natural selection as something that ensures the survival of a species. Student generation after student generation, bright young minds must be made aware of the flaws lurking in naïve group selection thinking before they can hope to argue clearly about evolution. These problems extend to scientific fields close enough to benefit from evolutionary thinking (e.g. microbiology) but far enough that most researchers have not thought deeply about how rife conflict can be within a species and how easily this can hamper group-level adaptation. The mainstream approach of evolutionary biologists in dealing with this problem is to learn to label all 'group' arguments as inherently dodgy.

Given the number of dodgy arguments ever produced, this rule of thumb is often valid. Still, recent theoretical work creates the very valid question by any deeply thinking student: if kin and group selection really are two sides of the same coin (Lehmann et al. 2007), why is one 'good' and the other 'bad' in our textbooks? The crux of the issue seems to be no particular scientific result, but the fact that for some unknown reason it is much more natural for people to come up with naïve (wrong) group selection arguments than naïve (wrong) kin selection arguments, and evolutionary biologists consequently have to be trained to be very wary of the former. Probably this practice has to continue as long as we find no other remedy for the layman's and freshman student's inherent tendency. However, among experts, it might be time to move on from petty semantics to a true appreciation of demographic consequences of cooperation and conflict (for examples see Kerr et al. 2006, Weinig et al. 2007, Lion and Boots 2010, Brockhurst et al. 2010), and the rich tapestry of evolutionary outcomes that can arise over different time scales, whichever the favoured mathematical method each person chooses to employ.

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