Evolutionary disarmament in interspecific competition

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Competitive asymmetry, which is the advantage of having a larger body or stronger weaponry than a contestant, drives spectacular evolutionary arms races in intraspecific competition. Similar asymmetries are well documented in interspecific competition, yet they seldom lead to exaggerated traits. Here we demonstrate that two species with substantially different size may undergo parallel coevolution towards a smaller size under the same ecological conditions where a single species would exhibit an evolutionary arms race. We show that disarmament occurs for a wide range of parameters in an ecologically explicit model of competition for a single shared resource; disarmament also occurs in a simple Lotka–Volterra competition model. A key property of both models is the interplay between evolutionary dynamics and population density. The mechanism does not rely on very specific features of the model. Thus, evolutionary disarmament may be widespread and may help to explain the lack of interspecific arms races.

Keywords: adaptive dynamics; arms race; asymmetrical competition; coevolution

1. INTRODUCTION

Competitive asymmetry, which is the advantage of having a larger body or stronger weaponry than a contestant, is thought to drive spectacular evolutionary arms races in intraspecific competition (Dawkins & Krebs 1979; Clutton-Brock *et al.* 1980; Roberts 1996; Simmons & Scheepers 1996; Loison *et al.* 1999; Székely *et al.* 2000; Dunn *et al.* 2001). Similar asymmetries are well documented in interspecific competition (Persson 1985; Alatalo & Moreno 1987; Dickman 1988; Morin & Johnson 1988), yet they apparently seldom lead to exaggerated traits.

The lack of interspecific arms races is traditionally attributed to the relatively smaller importance of the shared resources for which members of different species may compete (Krebs & Davies 1987, pp. 143–144). Most within-species arms races occur in males that compete for females (Clutton-Brock *et al.* 1980; Simmons & Scheepers 1996; Loison *et al.* 1999; Székely *et al.* 2000; Dunn *et al.* 2001), i.e. for their chance to reproduce, which amounts to genetic life or death. By contrast, interspecific competition may occur for food, shelter or, in some cases, territory. The ‘life–dinner’ principle (Dawkins & Krebs 1979) suggests that competition for interspecifically shared resources is not intense enough to drive arms races.

However, many dinners eventually amount to life. If a species is competitively superior such that it monopolizes some non-substitutable resource, then it excludes its competitors. Competition for an essential limiting resource should drive interspecific arms races similar to the intraspecific ones (for an account of the failure of the life–dinner principle, see, for example, Abrams (1986)).

Interspecific competition may differ from intraspecific competition, not only in the importance of the resources contested, but also in the size distribution of competing individuals. Here we demonstrate that if two species substantially differ in size, then both species may evolve

towards a smaller size rather than towards a larger size. Parallel coevolution towards a smaller size, henceforth called evolutionary disarmament, occurs under the same ecological conditions where a single species would exhibit an evolutionary arms race. First, we show that disarmament occurs for a wide range of parameters in an ecologically explicit model of competition for a single shared resource. Next, we briefly describe a simple Lotka–Volterra competition model that also exhibits disarmament. In both models disarmament results from the interplay between evolutionary dynamics and population density. This mechanism does not rely on very specific features of the model. Thus, evolutionary disarmament may be widespread and may help to explain the lack of interspecific arms races.

2. AN EXPLICIT RESOURCE COMPETITION MODEL

We consider a trait, such as body size, that influences success in competitive contests. The evolution of such a trait is determined by two opposing forces. Being larger than opponents is advantageous for winning resources and, therefore, for achieving high fecundity. On the other hand, large size entails some opponent-independent cost either in terms of the resources used for maintenance or in reducing the chances of survival. We assume that the population is limited by a single resource, that size does not affect the efficiency of searching for or handling the resource and that density dependence operates exclusively via resource limitation.

Each time an individual finds a resource item, a Poisson-distributed random number of opponents challenge that individual and the resource is then consumed by the individual with the largest resource holding potential. An individual’s resource holding potential is the sum of its size as a heritable component plus a normally distributed random deviation that changes between contests and reflects temporary effects such as satiation or errors in perceiving opponents’ size (Parker 1983; Maynard Smith & Brown 1986; Abrams & Matsuda

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1994). Fecundity is proportional to the amount of resource gained minus the amount necessary for maintenance. First, we assume a maintenance cost proportional to size; later we shall also consider nonlinear costs. The number of resource items consumed by the entire population is a saturating function of population size (see Appendix A for the model equations).

The dynamics of evolution are derived from the species' fitness gradient, i.e. by investigating whether a slightly larger or a slightly smaller size ensures higher fitness in a given resident population. This approach assumes small intraspecific variation in size (Taper & Case 1992; Abrams *et al.* 1993a).

Evolution in a single species can lead to a considerably large size despite the cost of being large (figure 1a). When the arms race eventually comes to a halt, the trait value attained lacks evolutionary stability such that size is under disruptive selection (Abrams *et al.* 1993b; Taylor & Day 1997). Strategic models of evolution predict that, at this point, the population undergoes evolutionary branching, i.e. it splits into two subpopulations with increasingly different trait values (Geritz *et al.* 1998). Evolutionary branching occurs with diploid multilocus genetics if mating is (or evolves to be) assortative and branching then amounts to speciation (Dieckmann & Doebeli 1999; Drossel & McKane 2000). Even if genetic constraints prevent speciation (Abrams *et al.* 1993b), the single-species ecosystem remains susceptible to invasion by a second species. Note that two species limited by a single resource can coexist in the case of asymmetrical competition (Maynard Smith & Brown 1986; Abrams & Matsuda 1994; Geritz 1995; Geritz *et al.* 1999; Kisdi 1999): the small species, which can maintain its population at a low resource level, is able to invade the large species by using only resources left unattended by chance, whereas the large species can invade the small species by winning resources in contests.

The coevolution of two species is markedly different from single-species evolution (figure 1a). The two species engage in evolutionary disarmament, i.e. they engage in parallel evolution towards a smaller size for a range of trait values. Disarmament also occurs at trait values where each species alone would exhibit an arms race evolution towards a larger size. The smaller species in figure 1a evolves to the cost-free minimal size, whereas the final size of the larger species is well below the size produced by a single-species arms race. The precise shape of the evolutionary trajectory depends on the relative amount of additive genetic variance in the two species, which sets the relative speed of evolution (see Appendix A). However, the fitness gradients of the two species (which are denoted by shading in figure 1) ensure that the evolutionary dynamics remain qualitatively the same irrespective of the precise amount of genetic variances available. Mutation-limited evolution (Dieckmann & Law 1996; Matessi & Di Pasquale 1996) has qualitatively the same dynamics.

A single species attains a locally evolutionarily stable size rather than an evolutionary branching point if the fitness in a competition-free environment is a sufficiently concave function of size (this may be the case, for example, if, without competition, size is under stabilizing selection). Disarmament nevertheless occurs if a sufficiently smaller

Figure 1. Evolutionary disarmament with (a) linear and (b) concave costs. (a) A single-species ($x_1 = x_2$) arms race leads to an evolutionary branching point (dot), whereas two-species coevolution leads to a smaller size in both species. (b) A single-species arms race reaches a locally evolutionarily stable size (dot). If a sufficiently smaller species invades, the two species undergo disarmament until they reach an evolutionarily stable community (open circle). The shading in both panels indicates the sign of the fitness gradient: light shading, negative in both species (disarmament); medium shading, positive in the small species and negative in the large species (convergent evolution); dark shading, negative in the small species and positive in the large species (divergent evolution); very dark shading (only in b), positive in both species; no shading, the two species cannot coexist. The symmetry is due to the arbitrary labelling of species 1 and 2. See Appendix A for the methods and parameter values.

immigrant species invades (figure 1b). Note that an invading species that is much smaller than the resident species will displace the former resident and may subsequently undergo a single-species arms race; repeated invasions then lead to single-species evolutionary cycles (see also Maynard Smith & Brown 1986; Abrams & Matsuda 1994).

When the coevolving species are considerably different in size, then it is mainly competition with conspecifics and not with the other species that selects for large size

Figure 2. Evolutionary patterns with linear cost of size. Light grey shading, disarmament; dark grey shading, disarmament if parental survival is sufficiently large; black shading, no disarmament; no shading, no single-species arms race (evolution to the smallest possible size); dotted shading, non-equilibrium population dynamics (these points were excluded from the present analysis). See Appendix A for the methods and parameter values.

(Matsuda & Abrams 1994). The reason for this is that a small increase in size is beneficial when contestants have similar sizes, but a small increase in size is unnecessary for a giant when competing with a dwarf and is ineffective for a dwarf when competing with a giant. Evolutionary disarmament is facilitated if the evolution of one species relaxes intraspecific competition in the other species and, hence, relaxes selection for large size in the other species and vice versa.

How does intraspecific competition change during coevolution? A decreasing size of the giants implies less cost and, thus, a higher equilibrium density for the giant species. The dwarf species then finds fewer resources and suffers from more attacks by the giants. Consequently, the density of the dwarf species decreases, i.e. intraspecific competition relaxes, which favours disarmament in the dwarf species. On the other hand, a decreasing size and increasing density of the dwarf species has two opposing effects on the density of giants. First, the dwarf species will capture more resources and thereby deprive the giants of the resources, but at the same time provide more opportunities for the giants to attack and take resources away from them. The first effect dominates for most parameter values and the density of the giants decreases, which facilitates disarmament in the giants. Disarmament in any one species thus invokes further disarmament in the other species, thereby maintaining parallel evolution towards a smaller size. If however resources are very hard to find (i.e. parameter b , which describes how fast the number of resource items captured by the entire population saturates with population density, is small compared to z , the probability that a given individual will participate in a given contest), then the density of the giants can increase, which selects for even larger size. The giants may grow so large that they become dependent on the dwarf population for finding resources, i.e. they need the dwarfs as 'scouts' to locate resources, which they take away from the dwarfs in contest. This heuristic argument assumes that the two species are considerably different in size and that the population density is low such that only

Figure 3. The competition coefficient of the Lotka–Volterra model as a function of the difference in size. Disarmament is possible if the competition coefficient remains positive, even for a large size advantage (solid curve) and there is no disarmament if much smaller competitors have a vanishing effect (dashed curve).

pairwise interactions have to be considered. However, numerical analysis of the model shows that disarmament occurs for a wide range of parameters (figure 2).

3. A SIMPLE LOTKA–VOLTERRA COMPETITION MODEL

Next we show that disarmament can also occur in a simple Lotka–Volterra competition model. Although this model is not mechanistic (i.e. it is not derived from the ecological details of competition), its simplicity is attractive for highlighting the necessary conditions for disarmament.

Consider a Lotka–Volterra model of the form

$$\frac{1}{N_i} \frac{dN_i}{dt} = r(x_i) - \sum_j \alpha(x_i - x_j) N_j, \quad (3.1)$$

where N_i is the density of species i with size x_i , $r(x_i)$ is the intrinsic growth rate that incorporates the cost of size and $\alpha(x_i - x_j)$ is the competition coefficient that depends on the difference in size (cf. Law *et al.* 1997; Kisdi 1999). Whether disarmament can or cannot occur in this model depends crucially on the shape of the competition coefficient function $\alpha(x_i - x_j)$ (figure 3). If the competition coefficient becomes zero when the opponent is much smaller, then the large species is unaffected by the small species' evolution and will not disarm (figure 4a). In order for disarmament to occur, the large species must experience at least some competition, even from a considerably smaller species (figure 4b). This occurs if the small species can 'sneak' resources away without being challenged by large individuals as in our ecologically explicit model. Note that the model frequently exhibits repeated branching.

4. DISCUSSION

The models highlight the conditions that are necessary in order for evolutionary disarmament to occur. The distribution of size needs to be strongly bimodal. In the face of recombination, this is only possible with two reproductively isolated species; male competition for conspecific females will thus not lead to disarmament.

Figure 4. Simulated evolutionary trees with the competition coefficient as (a) the dashed line and (b) the solid line in figure 3. (a) No disarmament; the branch of large size is unaffected. (b) Evolutionary branching is followed by disarmament.

The shared resource may not be monopolized by the large species if the two species are to coexist. A more subtle but crucial condition is that the small species must affect the population dynamics of the large species by pre-empting the shared resource, such that the density of the large species declines if the density of the small species increases. This rules out disarmament, for example, in light competition in plants: however abundant, a short species cannot shade light away from tall plants. These predictions are in broad agreement with the observation that arms races most often occur in intra-specific competition for mates (Dawkins & Krebs 1979; Clutton-Brock *et al.* 1980; Simmons & Scheepers 1996; Loison *et al.* 1999; Székely *et al.* 2000; Dunn *et al.* 2001) and only in specific cases of interspecific competition, such as in light competition in plants (Givnish 1982; Weiner 1986).

Asymmetrical competition within a species may drive an evolutionary arms race to the extinction of the species (Matsuda & Abrams 1994; Gyllenberg & Parvinen 2001). If a second species immigrates, the direction of evolution can be reversed by mutual disarmament and extinction can thereby be avoided. Note that disarmament will be detectable as a significant parallel shift towards a smaller size only if a single species lives first in isolation long enough for a spectacular arms race to occur, which is then reversed after the immigration of the second species. If the two species coexist from the onset, then the arms race is blocked by the mechanism that underlies disarmament.

Evolutionary disarmament may be hard to tell apart from a lack of an arms race. If, for example, the resource handling time is very short, such that competitors have no time to challenge the individual who captured a food item, then contests rarely take place and armaments will not evolve in single species either. Intraspecific arms races in competition for mates are facilitated by lengthy mating as well as by active mate choice of the females.

Assuming a single limiting resource, our model is ecologically much simpler than the classic model of asymmetrical competition set up by Rummel & Roughgarden (1985) and subsequently analysed by, for example, Brown & Vincent (1987), Taper & Case (1992), Vincent *et al.* (1993) and Matsuda & Abrams (1994). The latter model

assumes not only competitive superiority of larger individuals, but also partial niche segregation between individuals of different sizes through differential consumption of a resource continuum. Like ours, this model also predicts evolution to a fitness minimum (i.e. to an evolutionary branching point). If the population at the fitness minimum is invaded by a substantially different species, then parallel evolution in either direction may follow depending on the invader's size and cycles of invasion and extinction can occur (Taper & Case 1992, 1993). An example given by Cohen *et al.* (1999) shows parallel evolution to a smaller size following evolutionary branching in this model. Abrams & Matsuda (1994, pp. 678–679) found that, in a model for asymmetrical competition for space, a minimum-sized species can invade a species that has undergone an evolutionary arms race and this invasion triggers the evolution of lesser armament in the large species.

The Lotka–Volterra model we have described is the same as the one that was used by Law *et al.* (1997) and Kisdi (1999), but these authors assumed that the competition felt by the large species vanishes as the size difference increases (see the dashed line in figure 3). As our explicit resource competition model highlights, this need not be the case and, if this assumption is relaxed, disarmament can commence.

Parallel evolution is even possible with symmetrical competition for a single resource (Abrams 1987), but its existence and direction depends on the details of the model and it presumes that coexistence is possible by additional density dependence of growth rates for some reason other than resource competition.

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APPENDIX A

Here we outline the mathematical details of the two models described in the main text. In the explicit resource competition model, the fitness (annual growth rate) of size y in a population with size x is calculated as

$$W_x(y) = vR(y-x) - \gamma y + p(y), \quad (\text{A } 1)$$

where $R(y-x)$ is the amount of resource gained by an individual of size y in a population with size x , γy is the maintenance cost of size y , $vR(y-x) - \gamma y$ is the number of offspring produced and $p(y)$ is parental survival, which may also depend on size. In order to calculate $R(y-x)$, we assume that the total amount of resource captured by the entire population of N individuals is

$$C(N) = K(1 - e^{-bN}). \quad (\text{A } 2)$$

A saturating function for $C(N)$ is plausible *a priori*. The above functional form holds if N individuals search randomly and independently for K resource items that

are present at the beginning of each year. The amount gained by an individual of size y is given by

$$R(y-x) = C(N) \sum_{k=0}^{\infty} P_k \frac{k+1}{N} a^{(k)}(y-x), \quad (\text{A } 3)$$

where P_k is the probability that, when a given resource item is found by one individual, k more opponents appear to contest the resource. P_k is given by a Poisson distribution with parameter zN . $(k+1)/N$ is the probability that the focal individual of size y is part of the $k+1$ contestants and $a^{(k)}(y-x)$ is the probability that it wins the resource against k opponents of size x . In order to calculate $a^{(k)}(y-x)$, we assume that an individual of size x has a normally distributed resource holding potential ξ centred around x and that the resource is won by the individual with the highest ξ (cf. Parker 1983). Then

$$a^{(k)}(y-x) = \int_{-\infty}^{\infty} f(\xi, y) F^k(\xi, x) d\xi, \quad (\text{A } 4)$$

where $f(\xi, x)$ and $F(\xi, x)$ are the probability density and cumulative distribution functions, respectively, of the normal distribution with mean x and variance σ^2 . For a resident size of ($y=x$) $a^{(k)}(0) = 1/(k+1)$ and, therefore, $R(0) = C(N)/N$. In population dynamic equilibrium the resident's annual growth rate must be unity; the equation $W_x(x) = vC(N)/N - \gamma x + p(x) = 1$ can be used for determining the equilibrium resident density N . We assume throughout that population densities are at a stable equilibrium and parameters where the population densities exhibit non-equilibrium dynamics are excluded from the analysis (see figure 2).

The fitness $W_{x_1 x_2}(y) = vR(y-x_1, y-x_2) - \gamma y + p(y)$ in a two-species community with residents of sizes x_1 and x_2 is calculated analogously. Here, the resource gained by an individual of size y is

$$R(y-x_1, y-x_2) = C(N_1 + N_2) \sum_{k_1=0}^{\infty} \sum_{k_2=0}^{\infty} P_{k_1} P_{k_2} \frac{k_1 + k_2 + 1}{N} \times a^{(k_1, k_2)}(y-x_1, y-x_2), \quad (\text{A } 5)$$

where N_1 and N_2 are the equilibrium densities of the two resident species, P_{k_1} and P_{k_2} are the probabilities that k_1 individuals of the first species plus k_2 individuals of the second species contest the resource with the focal individual (which are given by a Poisson distribution with parameters zN_1 and zN_2 , respectively) and

$$a^{(k_1, k_2)}(y-x_1, y-x_2) = \int_{-\infty}^{\infty} f(\xi, y) F^{k_1}(\xi, x_1) F^{k_2}(\xi, x_2) d\xi \quad (\text{A } 6)$$

is the probability that the focal individual wins the resource item. Note that the double summation in equation (A 5) can be rewritten as

$$\frac{\exp(-zN)}{N} \int_{-\infty}^{\infty} f(\xi, y) \exp(zN\Pi) (zN\Pi + 1) d\xi, \quad (\text{A } 7)$$

where $N = N_1 + N_2$ and $\Pi = F(\xi, x_1)N_1/(N_1 + N_2) + F(\xi, x_2)N_2/(N_1 + N_2)$ and, thereby, the numerically cumbersome double summation can be avoided. We determined the equilibrium densities (N_1, N_2) by simulating

the joint population dynamics of the two species and calculated equation (A 5) by numerical integration.

The shading in figure 1 indicates the sign of the fitness gradient in the two species as evaluated numerically, i.e.

$$\left. \frac{\partial W_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i} \quad (i=1,2). \quad (\text{A } 8)$$

The evolutionary trajectories are obtained from the dynamics

$$\frac{dx_i}{dt} = c_i \left. \frac{\partial W_{x_1, x_2}(y)}{\partial y} \right|_{y=x_i}, \quad (\text{A } 9)$$

with equal speed constants ($c_1 = c_2$) in the two species (see Taper & Case 1992; Abrams *et al.* 1993a).

Size is measured in units of σ with zero being the smallest possible value. The model has three independent parameters, namely vKz , b/z and $\gamma\sigma$ and the function $p(x)$ is to be specified. We assumed no parental survival ($p=0$) in figure 1a and parameter values of $vKz=1.6$, $b/z=2.5$ and $\gamma\sigma=0.5$. There was no maintenance cost ($\gamma=0$) in figure 1b, but there was a cost affecting parental survival is given by $p(x) = 0.9 - 0.05x - 0.05x^2$. The other parameters were $vKz=0.8$, $b/z=5$ and $\sigma=1$.

We produced figure 2 by calculating evolutionary trajectories starting from the evolutionary branching point for various values of b/z and $\gamma\sigma$, holding parental survival (p) constant at various values and setting $vKz=1.6$. We concluded that disarmament had occurred when the size of both species became smaller than the size reached in the single-species arms race. Note that adding a constant p to equation (A 1) is equivalent to a coordinate shift of $(x-x_0)$ in the trait value. The evolutionary branching point with a larger value of p is at a larger trait value relative to the smallest biologically feasible trait value ($x=0$) and disarmament can occur more easily before the smaller species hits $x=0$. The plot remains similar for $vKz=0.8$, except that a single-species arms race only occurs at lower values of $\gamma\sigma$.

The competitive coefficient in the Lotka–Volterra model depended on size difference according to

$$\alpha(x_i - x_j) = c \left[1 - \frac{1}{1 + v \exp(-k(x_i - x_j))} \right] + a \quad (\text{A } 10)$$

(modified from Law *et al.* (1997) and Kisdi (1999)), where $v=1.2$ and $k=4$ and either $c=2$ and $a=0$ (dashed line in figure 3) (see also figure 4a) or $c=1$ and $a=1$ (solid line in figure 3) (see also figure 4b). In the simulations $r(x) = 4 - x$. The simulation procedures are as in Geritz *et al.* (1998), except that the demographic stochasticity of rare mutants was taken into account according to Dieckmann & Law (1996).

REFERENCES

- Abrams, P. A. 1986 Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy. *Evolution* **40**, 1229–1247.
- Abrams, P. A. 1987 Alternative models of character displacement and niche shift. 2. Displacement when there is competition for a single resource. *Am. Nat.* **130**, 271–282.
- Abrams, P. A. & Matsuda, H. 1994 The evolution of traits that determine ability in competitive contests. *Evol. Ecol.* **8**, 667–686.

- Abrams, P. A., Harada, Y. & Matsuda, H. 1993a On the relationship between quantitative genetic and ESS models. *Evolution* **47**, 982–985.
- Abrams, P. A., Matsuda, H. & Harada, Y. 1993b Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* **7**, 465–487.
- Alatalo, R. V. & Moreno, J. 1987 Body size, interspecific interactions, and the use of foraging sites in tits (Paridae). *Ecology* **68**, 1773–1777.
- Brown, J. S. & Vincent, T. L. 1987 Coevolution as an evolutionary game. *Evolution* **41**, 66–79.
- Clutton-Brock, T. H., Albon, S. D. & Harvey, P. H. 1980 Antlers, body size and breeding group size in the Cervidae. *Nature* **285**, 565–567.
- Cohen, Y., Vincent, T. L. & Brown, J. S. 1999 A G-function approach to fitness minima, fitness maxima, evolutionarily stable strategies and adaptive landscapes. *Evol. Ecol. Res.* **1**, 923–942.
- Dawkins, R. & Krebs, J. R. 1979 Arms races between and within species. *Proc. R. Soc. Lond. B* **205**, 489–511.
- Dickman, C. R. 1988 Body size, prey size, and community structure in insectivorous mammals. *Ecology* **69**, 569–580.
- Dieckmann, U. & Doebeli, M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354–357.
- Dieckmann, U. & Law, R. 1996 The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* **34**, 579–612.
- Drossel, B. & McKane, A. 2000 Competitive speciation in quantitative genetic models. *J. Theor. Biol.* **204**, 467–478.
- Dunn, P. O., Whittingham, L. A. & Pitcher, T. E. 2001 Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**, 161–175.
- Geritz, S. A. H. 1995 Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. *Am. Nat.* **146**, 685–707.
- Geritz, S. A. H., Kisdi, É., Meszéna, G. & Metz, J. A. J. 1998 Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**, 35–57.
- Geritz, S. A. H., Van der Meijden, E. & Metz, J. A. J. 1999 Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Popul. Biol.* **55**, 324–343.
- Givnish, T. J. 1982 On the adaptive significance of leaf height in forest herbs. *Am. Nat.* **120**, 353–381.
- Gyllenberg, M. & Parvinen, K. 2001 Necessary and sufficient conditions for evolutionary suicide. *Bull. Math. Biol.* **63**, 981–993.
- Kisdi, É. 1999 Evolutionary branching under asymmetric competition. *J. Theor. Biol.* **197**, 149–162.
- Krebs, J. R. & Davies, N. B. 1987 *An introduction to behavioural ecology*, 2nd edn. Oxford: Blackwell Scientific.
- Law, R., Marrow, P. & Dieckmann, U. 1997 On evolution under asymmetric competition. *Evol. Ecol.* **11**, 485–501.
- Loison, A., Gaillard, J.-M., Pelabon, C. & Yoccoz, N. G. 1999 What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.* **1**, 611–633.
- Matessi, C. & Di Pasquale, C. 1996 Long-term evolution of multilocus traits. *J. Math. Biol.* **34**, 613–653.
- Matsuda, H. & Abrams, P. A. 1994 Runaway evolution to self-extinction under asymmetrical competition. *Evolution* **48**, 1764–1772.
- Maynard Smith, J. & Brown, R. L. 1986 Competition and body size. *Theor. Popul. Biol.* **30**, 166–179.
- Morin, C. & Johnson, E. A. 1988 Experimental studies of asymmetric competition among anurans. *Oikos* **53**, 398–407.
- Parker, G. A. 1983 Arms races in evolution—an ESS to the opponent-independent costs game. *J. Theor. Biol.* **101**, 619–648.
- Persson, L. 1985 Asymmetric competition: are larger animals competitively superior? *Am. Nat.* **126**, 261–266.
- Roberts, S. C. 1996 The evolution of hornedness in female ruminants. *Behaviour* **133**, 399–442.
- Rummel, J. D. & Roughgarden, J. 1985 A theory of faunal buildup for competition communities. *Evolution* **39**, 1009–1033.
- Simmons, R. E. & Scheepers, L. 1996 Winning by a neck: sexual selection in the evolution of giraffe. *Am. Nat.* **148**, 771–786.
- Székely, T., Reynolds, J. D. & Figuerola, J. 2000 Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution* **54**, 1404–1413.
- Taper, M. L. & Case, T. J. 1992 Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* **46**, 317–333.
- Taper, M. L. & Case, T. J. 1993 Coevolution among competitors. In *Oxford surveys in evolutionary biology*, vol. 8 (ed. D. J. Futuyma & J. Antonovics), pp. 63–109. Oxford University Press.
- Taylor, P. & Day, T. 1997 Evolutionary stability under the replicator and the gradient dynamics. *Evol. Ecol.* **11**, 579–590.
- Vincent, T. L., Cohen, Y. & Brown, J. S. 1993 Evolution via strategy dynamics. *Theor. Popul. Biol.* **44**, 149–176.
- Weiner, J. 1986 How competition for light and nutrients affects size variability in *Ipomea tricolor* populations. *Ecology* **67**, 1425–1427.