Evolutionary Ecology, 1994, **8**, 667–686

The evolution of traits that determine ability in competitive contests

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Summary

We analyse mathematical models of the evolution of a trait that determines ability in contest competition. We assume that the value of the competitive trait affects two different components of fitness, one measuring the benefit of winning contests and the other measuring the cost of developing the competitive trait. Unlike previous analyses, we include the population dynamical consequences of larger competitive trait values. Exaggeration of the competitive trait reduces the mean probability of survival during the non-competitive stage of the life cycle. The resulting lower population density reduces competition and, therefore, reduces the advantages of greater competitive ability. Models without population dynamics often predict dimorphism in the competitive trait when resource possession is decided by interactions with many other individuals. If the competition involves a contest with a single other individual, models without population dynamics often predict cycles of increase and collapse in the trait or a continual increase, possibly resulting in extinction. When population dynamics are included, both of these results become less likely and a single stable trait value becomes more likely. Population dynamics also make it possible to have dimorphism when individuals have a single pairwise contest and alternative stable trait values when an individual has many contests. Increases in the value of the resource being contested may increase or decrease the evolutionarily stable size of the trait. Competition between very differently sized species will often decrease size in the larger species (character convergence).

Keywords: arms race; competition; contest; evolution of size; evolutionarily stable strategy; extinction; frequency dependence; mathematical model

Introduction

Biologists interested in the evolutionary effects of competition have more often studied exploitative competition between species than interference or contest competition within a species. Thus, there is a large amount of literature on character displacement (reviewed in Arthur, 1982; Abrams, 1986a; Grant, 1986; Taper and Case, 1985, 1993), while the evolution of ability in competitive contests has only received sporadic attention. However, those analyses that have been done (Parker, 1979, 1983; Maynard Smith and Brown, 1986) suggest that the evolution of traits determining competitive ability in contest situations within a species can sometimes result in an 'arms race'. This refers to a situation in which the selectively favoured value of a trait increases as the mean value of the trait increases. The theoretical work by Parker (1979, 1983) and Maynard Smith and Brown (1986) suggests that such competitively driven evolution can produce perpetual increase or perpetual cycles in the mean value of the trait. More recent

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0269–7653
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reviews (Dawkins, 1986; Vermeij, 1987; Seger, 1992) argue that arms races may have been a major reason for the occurrence of rapid evolution and co-evolution.

Unfortunately, there is no convincing experimental evidence of such evolutionary escalation and evidence from the fossil record is generally subject to many interpretations (see, e.g. Gould's (1974) discussion of the supposed escalation of antler size in the Irish elk, *Megaloceros giganteus*). The previous theoretical studies (Parker, 1979, 1983; Maynard Smith and Brown, 1986) assume that the nature of the competition does not change with changes in population size. It is therefore unclear to what extent they might apply to a more typical situation in which more exaggerated trait values reduce population size and, therefore, reduce the prevalence of competition.

This article analyses a number of simple models of contest competition in which the population dynamical consequences of evolutionary change are taken into account. We are interested in determining how parameters of the interaction affect the exaggeration of the trait and in determining whether perpetual increase or cycles in the trait are likely outcomes. Because larger body size frequently confers a greater competitive ability (Brooks and Dodson, 1965; Rummel and Roughgarden, 1985; Maynard Smith and Brown, 1986), these models are particularly relevant to the evolution of body size.

The evolution of traits determining competitive ability is one of many ecologically important evolutionary processes that are usually frequency dependent (Maynard Smith and Brown, 1986; Taper, 1988; Abrams, 1989; Seger, 1992; Abrams *et al.*; 1993b). The frequency dependence arises because the fitness associated with a trait involved in competition depends on the traits of other individuals. Evolutionarily stable strategy (ESS) models have been used extensively to analyse the outcome of frequency-dependent evolution and this is the approach that will be used here. A number of recent studies have shown that ESS models predict outcomes very similar to quantitative genetic models under a broad range of conditions (Charnov, 1989; Charlesworth, 1990; Iwasa *et al.*, 1991; Taper and Case, 1992; Abrams *et al.*, 1993a,b).

Models of contest competition

Under contest competition, the individuals with the greatest competitive ability have the greatest chance of winning one of a limited number of high-quality resources. For convenience, we will use the terms 'large' and 'small' to refer to individuals with high or low values of the trait determining competitive ability. Small and large individuals prefer and are capable of using the same resources, but small individuals cannot get the best resources if larger individuals are sufficiently abundant relative to the abundance of resources. It is important to remember that developing a larger value of the competitive trait generally entails a cost. We incorporate such a cost and make a number of more specific assumptions to simplify the analysis and to maintain consistency with the previous work by Parker (1983) and Maynard Smith and Brown (1986).

The organism we model is assumed to have a semelparous life history with two stages, a pre-adult or juvenile stage and an adult or reproductive stage. The juvenile component of fitness is the probability of survival to the adult stage and the adult component is the expected reproductive output (measured by the expected total number of offspring if the population is asexual or otherwise by the number of female offspring). Contest competition only occurs in the adult stage and the outcome of the competition determines an individual's expected reproductive output. These assumptions are likely to be satisfied for at least some insect species with adult-stage competition for mates or territories (Thornhill and Alcock, 1983; Wickman, 1985). We follow Parker (1983) in making a number of more specific assumptions. First, we assume that the probability of survival through the juvenile stage is determined by an individual's genotype. This

Table 1. Definitions of mathemetical symbols

$B(S,s^*,N)$	Expected reproductive output of an adult phenotype S in a population with mean genotype s* and population size N
D	Slope of linear mortality rate versus size relationship
k	Additive genetic variance (assumed constant and small)
$m(s)$	Instantaneous mortality rate of individual with genotype s (dm/ds is denoted m'; d^2m/ds^2 is denoted m″)
N	Population size measured at newborn stage
q	Frequency of small type in a dimorphic population
$p(S,s)$	Probability density of phenotypes S produced by genotype s
Q	Reproductive output of non-resource holder
R	Range of triangular distribution function
S	Individual's phenotype (competitive trait value)
s	Individual's genotype (expected competitive trait value)
s^*	Mean genotype within a population or morph
T	Threshold phenotype required to obtain a resource (free for all)
V	Additional reproductive output of resource holder (above Q)
$W(s,s^*,N)$	Expected relative fitness of rare genotype s in a population with mean genotype s* and population size N
Z	Number of resource items
σ	Standard deviation of phenotypic distribution

is appropriate when the genotype specifies the length of the juvenile period or the growth rate during that period. However, there is assumed to be considerable environmental variation in the size attained by a given genotype, due to variation in factors such as temperature and food supply. The outcome of the adult-stage competition is determined by an individual's phenotype (i.e. its size). Population density may affect juvenile survival, the adult probability of winning or the adult pay-off from winning contests.

Table 1 summarizes the symbols used in the model. An individual's size (competitive trait value) is denoted by S, while the mean size specified by its genotype is given by s. The distribution of individual sizes, S, produced by genotype s has a mean value of s and the shape of the distribution is assumed to be independent of the mean. The distribution function of sizes produced by genotype s is denoted $p(S,s)$; we assume a normal or other simple unimodal distribution function when it is necessary to derive exact results. We assume (again following Parker (1983)) that there is relatively little genetic variability in the population. As with most ESS models, haploid genetics are implicit. The mean genotypic value of newborns in the population is denoted s^*; most individuals in the population have this genotype, but there are also mutants with slightly different values of s. (Our methods also apply to a case where S is a quantitative trait with a unimodal distribution with a small additive genetic variance; Abrams *et al.*, 1993b). Because the genotypic distribution is narrow, adults will have approximately the same mean genotypic value as newborns.

When there is no effect of population density, the pre-adult survival of individuals of genotype s is given by $\exp(-m(s))$, where $m(s)$ is the instantaneous mortality rate, which is an increasing function of s. When there is density dependence, m may be an increasing function of N as well as s, where N is the number of newly recruited individuals at the beginning of the generation.

The adult component of fitness for an individual is always influenced by two factors: (1) its phenotype, S and (2) the distribution of phenotypes in the adult population (determined by s^*). In addition, in some cases the adult fitness may also depend on adult population size; if N is the

number of newborns, the adult population is $\exp(-m(s^*))N$. The adult fitness of an individual with phenotype S in a population with genotype s^* and (newborn) population size N is denoted $B(S, s^*, N)$. Combining the two components of fitness allows the fitness of a rare genotype s in a population with genotype s* to be given by

$$W(s, s^*, N) = \exp(-m(s, N))\int p(S, s)B(S, s^*, N)\mathrm{d}S \tag{1}$$

where the integral is taken over the range of the mutant individual's phenotypic distribution. The population is assumed to be at a population dynamical equilibrium, so $W(s^*,s^*) = 1$.

A necessary condition for s^* to be evolutionarily stable is that individual fitness does not change with a slight deviation of an individual's genotype, s, from the population mean. This means that s^* must satisfy the following condition:

$$(\partial/\partial s)[W(s, s^*, N)]|_{s=s^*} = (\partial/\partial s)[\exp(-m(s, N))\int p(S, s)B(S, s^*, N)\mathrm{d}S]|_{s=s^*} = 0 \tag{2a}$$

where the integral is again taken over the range of the mutant's distribution function and the mutant type s is assumed to be very rare. In addition, evolutionary stability requires that, if the mean genotype changes slightly from the value specified by Equation 2a, natural selection acts to restore that value. This requirement was termed 'continuous stability' by Eshel (1983) and is represented mathematically by

$$(\mathrm{d}/\mathrm{d}s^*)\{(\partial/\partial s)[W(s, s^*, N(s^*))]|_{s=s^*}\} = (\partial/\partial s^*)\{(\partial/\partial s[\exp(-m(s, N))\int p(S, s)B(S, s^*, N)\mathrm{d}S]|_{s=s^*}\} < 0 \tag{2b}$$

This expression assumes that population dynamics are sufficiently fast relative to evolutionary dynamics that N can be represented as a function of s^*. Given that the distribution of genotypes, s, is very narrow, the dynamics of change in s^* can be described by $\mathrm{d}s^*/\mathrm{d}t = k\partial W/\partial s_{s=s^*}$ where k is the additive genetic variance of s (Taper and Case, 1992; Abrams *et al.*, 1993b). Inequality 2b requires that the equilibrium of this dynamic equation be stable. It should be noted that this condition is often not equivalent to the requirement that s^* represents a (local) maximum of individual fitness (Eshel, 1983; Taylor, 1989; Taper and Case 1992; Abrams *et al.*, 1993b). Individual fitness is maximized at the value specified by Equation 2a provided that

$$(\partial^2/\partial s^2)[W(s, s^*, N)]|_{s=s^*} = (\partial^2/\partial s^2)[\exp(-m(s, N))\int p(S, s)B(S, s^*, N)\mathrm{d}S]|_{s=s^*} < 0 \tag{2c}$$

In the analysis below, an evolutionarily stable trait value is one that satisifies Equation 2a and Inequality 2b. Because N is either assumed to be constant or a function of s^*, fitness will be expressed as a function of the two variables, s and s^*.

Inequality 2b is a local condition for evolutionary stability. If mutant types with sizes very different from s^* can arise and breed true, then it is also necessary to confirm that $W(s, s^*)$ is smaller than $W(s^*, s^*)$ for all other values of s, when s^* satisfies Equation 2a and Inequality 2b. This is most likely to occur if a similar species that competes for the same resources can invade the system, but it may also occur intraspecifically when there are alleles with large effects on the trait value. If invasion by a significantly different phenotype of the same or a different species is possible and the original local ESS is denoted $s_1{}^*$, then there will be another value of s, denoted s_2, which is a local maximum of $W(s, s_1{}^*)$, with $W(s_2, s_1{}^*) > W(s_1{}^*, s_1{}^*)$.

If invasion by a second type is possible, it is then necessary to check whether there can be a stable dimorphic ESS (Brown and Vincent, 1987). If population dynamical and evolutionary time scales are sufficiently different, there will be two sets of conditions for such a dimorphic system to be stable. The first is that the population dynamical system consisting of the two types reaches a stable equilibrium. The second is that, given the equilibrium population density, the two

equations describing the trait dynamics of the two types also have a stable equilibrium. The rate of change of the two population densities can be expressed by dynamical equations for the change in total population size, N and for the change in the frequency, q, of type 1. Necessary conditions for this system to have a stable equilibrium are that the fitnesses of the two types are both equal to one at equilibrium and the fitnesses are negatively frequency dependent (i.e. increases in the frequency of either type reduce its relative fitness). Additional conditions may be required if the dynamics of N can produce instability, but this will not be considered here. If q denotes the frequency of the type with genotype s_1, these necessary conditions for a stable equilibrium are

$$W(s_1^*, qs_1^* + (1-q)s_2^*) = \exp(-m(s_1^*, N))\int p(S, s_1^*)B(S, q, s_1^*, s_2^*, N)\mathrm{d}S = 1 \quad (3a)$$

$$W(s_2^*, qs_1^* + (1-q)s_2^*) = \exp(-m(s_2^*, N))\int p(S, s_2^*)B(S, (1-q), s_2^*, s_1^*, N)\mathrm{d}S = 1 \quad (3b)$$

$$(\partial/\partial q)[\int p(S, s_1^*)B(S, q, s_1^*, s_2^*, N)\mathrm{d}S] < (\partial/\partial q)[\int p(S, s_2^*)B(S, (1-q), s_2^*, s_1^*, \mathrm{N})\mathrm{d}S] \quad (3c)$$

where the competitive-stage fitness function B now depends on the frequencies of both types and their genotypic values, s_1^* and s_2^*, as well as the total population size, N. Equations 3a and 3b imply that both types must just replace themselves at equilibrium. Inequality 3c indicates that an increase in the frequency of either type reduces its relative fitness.

The existence of a stable dimorphic state does not rule out the existence of a stable state with greater than two strategies, however, this was not observed in simulations of any of the models we investigated. There were models in which Equations 3a and 3b were satisfied, but Inequality 3c was not. Simulations of these cases, assuming that a broad array of genotypes was maintained by mutation or migration, always resulted in perpetual cycling of the strategies as illustrated in Maynard Smith and Brown (1986, Fig. 2) and Packer and Abrams (1990, Fig. 4). A large genotype or a group of large genotypes is excluded by a very small one, which then increases in size and is again excluded by a small genotype. If mutation only produces genotypes that are close to those that are present, indefinite increase in size occurs.

The form of the competition function B depends on the number and nature of contests that occur during the competitive stage of the life cycle. We assume that the contests are disputes over a resource with a 'value', V, measuring the expected additional reproductive output from holding a resource item. For simplicity, we assume that an adult can only hold a single resource item during its lifetime. Individuals that do not obtain a resource have an expected reproductive output given by Q. Individuals that obtain the resource have an expected reproductive output of $Q + V$. We again follow Parker (1983) in examining two ends of a continuum of possible ways that contests may determine which individuals obtain the resource. The first ('pairwise') is one in which each individual that survives the pre-competitive stage engages in a single contest with another individual from the population; the phenotype of the opponent is assumed to be independent of that of the given individual. The form of B is then, $B(S,\ldots) = Q + V(\text{probability}(S > S^\dagger)$, where $S^\dagger$ is the phenotype of a randomly chosen individual from the population. This type of competition is most likely if the individuals are sessile after a brief dispersal phase and therefore only compete with a neighbouring individual. If individuals are not sessile, it is difficult to imagine how there could be a single contest with a randomly chosen other phenotype; mobile individuals that lose their first contest are expected to engage in additional contests. The second ('free-for-all') is a case in which individuals engage in sufficiently many contests that all adults with a size greater than a threshold value, T, obtain the valuable resource and those with sizes smaller than T do not obtain the resource. In this case T will generally depend on the number of resources present, the population size and the mean genotype s^*. Here, the form of B is $B(S,\ldots) = Q$ if $S < T$ and $B(S,\ldots) = Q + V$ if $S > T$. Maynard Smith and Brown (1986) only considered pairwise competition, while Parker (1983) considered both types,

Table 2. Outcomes of the evolution of contest-related traits

Outcome	Conditions when observed
One evolutionary stable $s^* \geq 0$	Whenever the marginal cost of increased size is sufficiently large
Dimorphism ($s_1^* = 0$ and $s_2^* > 0$)	Free-for-all competition and a small enough cost of increased size; most likely with no population dynamics
	Pairwise competition and juvenile mortality after settlement (model 1 from the section on pairwise competition with population dynamics)
Cycles in s^*	Pairwise competition when invasion of small types is possible and the marginal cost of increased size is small; most likely when population size is constant
Indefinite increase in s^* ending in extinction	Pairwise competition when invasion of small types is impossible and the marginal cost of increased size is small; most likely when population size is constant
Alternative stable s^* (depending on initial conditions)	Free-for-all competition with population dynamics under a narrow range of conditions

but did not discover all of the possible types of evolutionary outcomes. Parker (1983) refers to pairwise competition as 'random structuring of resources' and refers to free for all competition as 'perfect structuring of resources'.

The following four sections analyse four types of competition; pairwise and free for all, with and without population dynamics. The two models without population dynamics are analysed first; here, the treatment is brief because many of the results have been derived previously in Parker (1983) or Maynard Smith and Brown (1986). For each type of competition, we begin with a verbal explanation of the possible evolutionary outcomes, followed by the mathematical details. Table 2 summarizes the qualitatively different outcomes and the conditions required to produce each one.

Pairwise competition with a constant population density in the competitive stage

A constant population density can be maintained by several different mechanisms; density-dependent (but size-independent) juvenile mortality or a density-dependent factor that affects the reproductive rates of all adults multiplicatively. A small increase in genotypic size always results in a significant increase in an individual's probability of winning its single contest; this increase is independent of the current mean size. The selection pressure for increased size is balanced by the cost of developing the large trait. If the marginal cost increases as trait value increases, a large size is often evolutionarily stable. However, if the marginal cost does not increase, size may increase indefinitely. Continual increase may be halted if a second population of small individuals invades the system. Even if there is a large trait value at which marginal costs of larger size equal the benefits, this size may be so large that small individuals which lose all of their contests nevertheless have greater lifetime fitness. When invasion by small individuals is possible, the small individuals replace the large ones, because the relative fitness of small individuals increases as their frequency increases. Increased frequency of the small type increases the probability that they will win a contest because of being matched against a second small individual. However, once the large individuals have been excluded by small ones, there is again selection for increased size, restarting the cycle. Thus, there are three possibilities: a stable large size, indefinite increase in size or cycling of sizes. Maynard Smith and Brown (1986) provide more details on this scenario.

Because population size is constant, it can be ignored in the analysis and Equation 2a may be rewritten as

$$m'(s^*)(\int p(S,s)B(S,s^*)\mathrm{d}S|_{s=s^*}) = (\partial/\partial s)(\int p(S,s)B(S,s^*)\mathrm{d}S)|_{s=s^*} \quad (4)$$

where the right-hand side of the equation and the integral on the left-hand side depend on the form of the distribution function, p, but are independent of its mean, s^*. If p has a normal distribution (with variance σ^2) and B has the form described above, Maynard Smith and Brown (1986) show that Equation 4 simplifies to

$$m'(s^*)(Q + (V/2)) = V/[2\sigma\sqrt{\pi}] \quad (5)$$

Applying the equilibrium Equation 2a, the stability Inequality 2b can be reduced to $m'' > 0$. Thus, for an evolutionarily stable size to be maintained, the instantaneous death rate must rise at an accelerating rate with size. If $m'' < 0$, size may either increase or decrease indefinitely, depending on its initial value; if $m'' = 0$, size will always increase or always decrease depending on the relative values of the two sides of Equation 4 (equality of the two sides will not occur when $m'' = 0$, unless there is extremely unlikely balancing of parameter values).

If s^* increases indefinitely or if the evolutionarily stable value specified by Equation 4 is large enough, then individuals with $s = 0$ (i.e. s equal to some minimum value) will increase in the population, provided they can arise and breed true. Thus, it is necessary to see whether there can be a dimorphic population. Here we show that Inequality 3 for a stable dimorphism cannot be satisfied. Assume that the fitnesses of two genotypes are equal when the frequency of the smaller type ($s_1{}^*$) is q, i.e.

$$\exp(-m(s_1{}^*))(Q + qV/2) = \exp(-m(s_2{}^*))(Q + qV + (1 - q)V/2) \quad (6)$$

The derivative of the left-hand side of Equation 6 with respect to q is larger than the derivative of the right-hand side. Thus, if there is a state with equal fitnesses (Equation 6 satisfied), any increase in the frequency of the smaller type increases its fitness relative to the larger type. This results in replacement of the larger type by the smaller, but the smaller type is then subject to selection for increased size. Our simulations of this case assumed that $s = 0$ types and an array of other s values are constantly introduced into the population at a low rate by mutation or migration. These simulations confirmed Maynard Smith and Brown's (1986; see their Fig. 2) results; repeated cycles occur in s^*, with gradual increase in the mean size followed by rapid decrease to $s^* \simeq 0$.

Free for all competition with constant population density in the competitive stage

This case differs from the preceding in that a small increase in genotypic value may not result in a significant increase in the probability of winning a resource. This is true, for example, if most individuals obtain resources. If there is enough of an advantage to becoming larger that size does become very large, then there is also a difference in the consequences of invasion by a very small type. In this case, increases in the frequency of the small type decrease its fitness relative to that of the large type, resulting in a stable dimorphism. An increased frequency of the small type does not affect its fitness (because the small type is still below the threshold value T required to obtain a resource). However, an increased frequency of small individuals does increase the fitness of the large type (because smaller individuals of the large type are now more likely to be above the threshold value T).

Equation 4 still gives the necessary condition for an ESS (Parker, 1983) although the function B is different. If we assume a normal distribution for p, the defining and stability conditions for an ESS become

$$m'(s^*)[Q + V\int_T^\infty(1/(\sigma\sqrt{[2\pi]}))\exp(-(S - s^*)^2/(2\sigma^2))\mathrm{d}S] = (V/(\sigma\sqrt{[2\pi]}))\exp(-(T - s^*)^2/(2\sigma^2)) \quad (7a)$$

$$\partial/\partial s^*\{-\mathrm{m}'(s^*)[Q + V\int_T^\infty(1/(\sigma\sqrt{[2\pi]}))\exp(-(S - s^*)^2/(2\sigma^2))\mathrm{d}S] + (V/(\sigma\sqrt{[2\pi]}))\exp(-(T - s^*)^2/(2\sigma^2))\} < 0 \quad (7b)$$

where T is the threshold character value required to obtain a resource. If it is assumed that a fixed fraction of all adults obtain a resource and the number of adults is constant, then T is equal to the mean character s^* plus some constant number of standard deviations, σ. This assumption makes $\exp(-(T - s^*)^2/(2\sigma^2))$ independent of s^*. This dependence of T on s^* also means that the integral on the left-hand side Equation 7a is independent of s^*. Consequently, Equation 7a will have a solution for some unique s^* only if m'' is non-zero and the point will be stable only if $m'' > 0$ (Parker, 1983). This means that there can be a continual increase, decrease or stable equilibrium of size, depending on the second derivative of the death rate function, m''.

Parker (1983) did not explore the consequences of invasion by $s = 0$ individuals. Such an invasion is possible whenever there is a continuous increase in s (due to $m'' \leqslant 0$) or when the stable value of s that satisfies Equation 7a (or its analogue for a different distribution function) is sufficiently large. If there is a frequency q of the $s = 0$ individuals at which fitnesses of the two types (0 and s_2) are equal, then

$$Q\exp(-m(0)) = \exp(-m(s_2^*))(Q + f(q, s_2^*)V) \quad (8)$$

where, $f(q, s_2^*)$ is a function giving the probability of an individual with genotype s_2^* having a phenotype greater than the threshold value T for obtaining a resource. The value of s_2^* is determined by an equation analogous to Equation 7a, in which the threshold phenotypic value, T, depends on q; if there are more $s^* = 0$ individuals, a larger fraction of the large individuals will be able to obtain a resource. Equation 8 assumes that, in a dimorphic population, $s_1^* = 0$. This is justified because, by becoming any larger than the minimum size, small individuals still cannot win any resources and they suffer the disadvantage of poorer survival in the pre-competitive stage. The fact that the threshold value T decreases with q means that, if Equation 8 is satisfied for some q, that equilibrium will be stable.

There are thus two possible results of free for all contest competition with no effect of mean size on the competitive process: (1) a single ESS size, at which the fitness of the population is greater than $Q\exp(-m(0))$ (the fitness of individuals with the minimum size) or (2) a dimorphic state in which one of the two types has the minimum possible size and the fitness of each type is equal to $Q\exp(-m(0))$. Equation 7a shows that, all else being equal, a narrow phenotypic distribution is likely to result in a large ESS size or dimorphism; narrowing the distribution increases the right-hand side of Equation 7a and this increases the s value needed to satisfy the equation, because $m'' > 0$ is necessary for an ESS to exist. A larger s^* decreases the mean fitness of the population, increasing the likelihood of successful invasion by $s = 0$ types. Equation 7a also implies that, for a given variance, an intermediate value of T will result in the largest ESS size and be most likely to result in dimorphism. If T is much smaller than s^*, most individuals obtain resources and large size has little advantage; the right-hand side of Equation 7a is then close to zero and size will be close to the minimum possible. Similarly if T is much larger than s^*, few individuals obtain resources, regardless of their size and there is little benefit to large size; the right-hand side of Equation 7a is again close to zero and the ESS size will be small. Qualitatively similar results would follow from any unimodal phenotypic distribution function.

Free for all competition with population dynamics

The assumptions of the preceding section require a very strong sort of density dependence to maintain constant population size. More commonly, if mean size increases, survivorship in the

pre-competitive (juvenile) stage decreases and the adult population density will then decrease. A sufficient decrease in the adult stage population density will result in all individuals obtaining resources, which eliminates any selection for larger size. The outcome is then usually a single, stable large size.

If a fixed number of resource items are being contested and individuals can only hold a single resource, the threshold phenotype required to obtain a resource, T, must depend on the population size during the adult (competitive) stage. If there are Z resources and the adult population is smaller than Z, all individuals will obtain a resource and there will be no competition. The way that T changes as s^* increases is determined by the details of the model. We will illustrate this by considering a model in which the density regulation arises from the limited number of high quality resources and the assumption that individuals without a high quality resource have $W < 1$. There are a fixed number of resources, Z, that cannot be subdivided; individuals holding a resource have reproductive output $Q + V$, while other individuals have output Q.

The assumption that non-resource holders cannot replace themselves means $Q < 1$. An increased population size means that a larger fraction of the population fails to obtain a (high-quality) resource, eventually reducing mean fitness to one. The population dynamics are described by.

$$N_{t+1} = \exp[-m(s^*)]N_t(Q + V) \quad \text{if } Z > \exp[-m(s^*)]N_t \tag{9a}$$

$$N_{t+1} = (\exp[-m(s^*)]N_t - Z)Q + Z(Q + V) \quad \text{if } Z < \exp[-m(s^*)]N_t \tag{9b}$$

Equation 9a describes situations in which the number of adults is less than the number of resources, while Equation 9b applies when the number of adults is larger than the number of resources. These equations again assume that mutant types are rare enough to have little effect on population dynamics. Equation 9b means that the equilibrium population density of new-borns is $N_e = ZV/(1 - Q\exp(-m(s^*)))$, provided the mean size is small enough that some adults fail to obtain resources. The fraction of adults obtaining a resource is $Z/(\exp(-m(s^*))N_e) = (\exp(m(s^*)) - Q)/V$, provided this quantity is less than one. As the genotypic trait value of the population, s^*, increases, the relative trait value $(T - s^*)$ required to obtain a resource decreases.

We begin by showing that selection cannot produce either an indefinite increase in size or dimorphism. If s^* becomes large enough so that $m(s^*) = \ln(Q + V)$, all individuals obtain resources (Equation 9a applies) and any selection for an increase in s^* disappears, while an increased s^* still implies reduced juvenile survival. We denote the value of s^* that satisfies this equation by s_{max}; size cannot increase beyond this value. Thus, selection cannot produce an indefinite increase in s^*, regardless of the shape of the function $m(s)$ or the distribution function, $p(S, s)$. In addition, this means that s^* will not increase to the point where there are unused resources. Individuals with $s^* = 0$ cannot invade because they never obtain resources and the 'losers fitness', Q, is <1. For the same reason, there can be no dimorphism in which the smaller type always loses contests.

These general results do not determine $s_e{}^*$, the ESS genotype or how it is affected by the other parameters of the system. If we assume that the phenotypic distribution function is unimodal, it is impossible for selection to increase s^* to the point (s_{max}) where all individuals obtain the resource. This is because the threshold size T needed to acquire the trait approaches the minimum trait value in the population as s approaches s_{max}. The right-hand side of Equation 7a then approaches zero, while the left-hand side does not. Although Equation 7a assumes a normal distribution, the result $s_e{}^* < s_{max}$ holds for any unimodal phenotypic distribution where $p(S, s)$ approaches 0 when S is sufficiently different from s. The exact form of the relationship

between T and s^* depends on the mortality function, m and the distribution function, p and must generally be determined numerically. To provide a concrete example, we investigate a model with the specific assumptions that $m(s) = Ds$, where D is a constant and the phenotypic distribution $p(S, s)$ is triangular with a range from $s - R$ to $s + R$ and a maximum value of $1/R$ at s, i.e. $p(S, s) = (R - s)/R^2 + S/R^2$ if $S < s$ and $p = (R + s)/R^2 - S/R^2$ if $S > s$. Under these assumptions, the evolutionary dynamics can be described by

$$\mathrm{d}s^*/\mathrm{d}t = k(\partial W/\partial s|_{s=s^*}) = k\partial/\partial s\{\exp(-Ds)[Q + V\textstyle\int_T^{s+R} p(S, s)\mathrm{d}S]\}|_{s=s^*} \tag{10a}$$

$$\begin{aligned} &= -kD + kV\exp(-Ds^*)(R + s^* - T(s^*))/R^2, \text{ if } T(s^*) > s^*, \text{ and} \\ &= -kD + kV\exp(-Ds^*)(R - s^* + T(s^*))/R^2, \text{ if } T(s^*) < s^* \end{aligned} \tag{10b}$$

These equations have been simplified by using the fact that the integral (i.e. the fraction of individuals of the mean genotype that obtain a resource) is, as shown above, $(\exp(Ds^*) - Q)/V$. This result also allows T to be expressed as a function of s^*, as is shown in the Appendix. The full analysis of this system is rather complicated and is relegated to the Appendix. There are three possible equilibria, denoted s_e^*; $s_e^* = 0$ and two positive values of S_e^*, where S_e^* again denotes an evolutionarily stable equilibrium of s^*. The parameter values producing different equilibria are illustrated in Fig. 1. Large enough values of the product of the size-related death rate D and the phenotypic range, R, imply $s_e^* = 0$, while smaller values of DR produce a positive equilibrium s_e^*. There is a small range of parameter values for which $s_e^* = 0$ and a larger s_e^* are alternative equilibria (see Fig. 1B). If $s_e^* = 0$, juvenile survival will be high and only a small fraction of the surviving juveniles will obtain the resource. This means that there is little advantage to increasing size. On the other hand, if the initial mean size is sufficiently large, few juveniles survive and the threshold size required to obtain a resource is smaller relative to the mean; this can favour, an increase in size, although it will stop at some point less than s_{max}.

If there is a positive s_e^*, larger DR reduces that value, while a larger V increases it, as might be expected. A larger Q increases s^* when more than half the adults obtain a resource, but decreases s^* when fewer than half the adults obtain a resource. The dependence on the fraction of individuals obtaining a resource occurs because the selection is strongest when exactly half of the individuals obtain a resource; at this point, a unit increase in genotypic size has the largest effect on the chance of obtaining a resource.

There are a variety of ways to introduce density dependence into the free for all model besides the requirement $Q < 1$, analysed above. One possibility is that the death rate in the juvenile (pre-competitive) stage is an increasing function of N. Another is that either or both reproductive rate parameters, Q and V, are decreasing functions of adult population density, $\exp(-m(s^*))N$. We will not present detailed analyses of these cases here. A variety of different dynamical behaviours are possible in theory. However, it is clear that an indefinite increase in s^* is prevented in these cases by the same mechanism described above. Larger size implies decreased juvenile survivorship or decreased reproductive output. At some size, survivorship or reproduction will be sufficiently low that all individuals obtain a resource and further increases in size will have no advantage. Dimorphism is also a possible outcome in many models with direct effects of population density on m, Q or V. A large enough trait value can reduce population density to the point where the $s = 0$ genotype has a fitness greater than one, allowing it to invade. The case of constant adult population, analysed in the previous section, can be produced by a model with $Q > 1$ and very strong density-dependent mortality in the juvenile stage.

Pairwise competition with population dynamics

The assumption of strictly pairwise competition for resources of fixed value seems to require a sessile competitive stage, as described above. It also requires that the number of individuals that

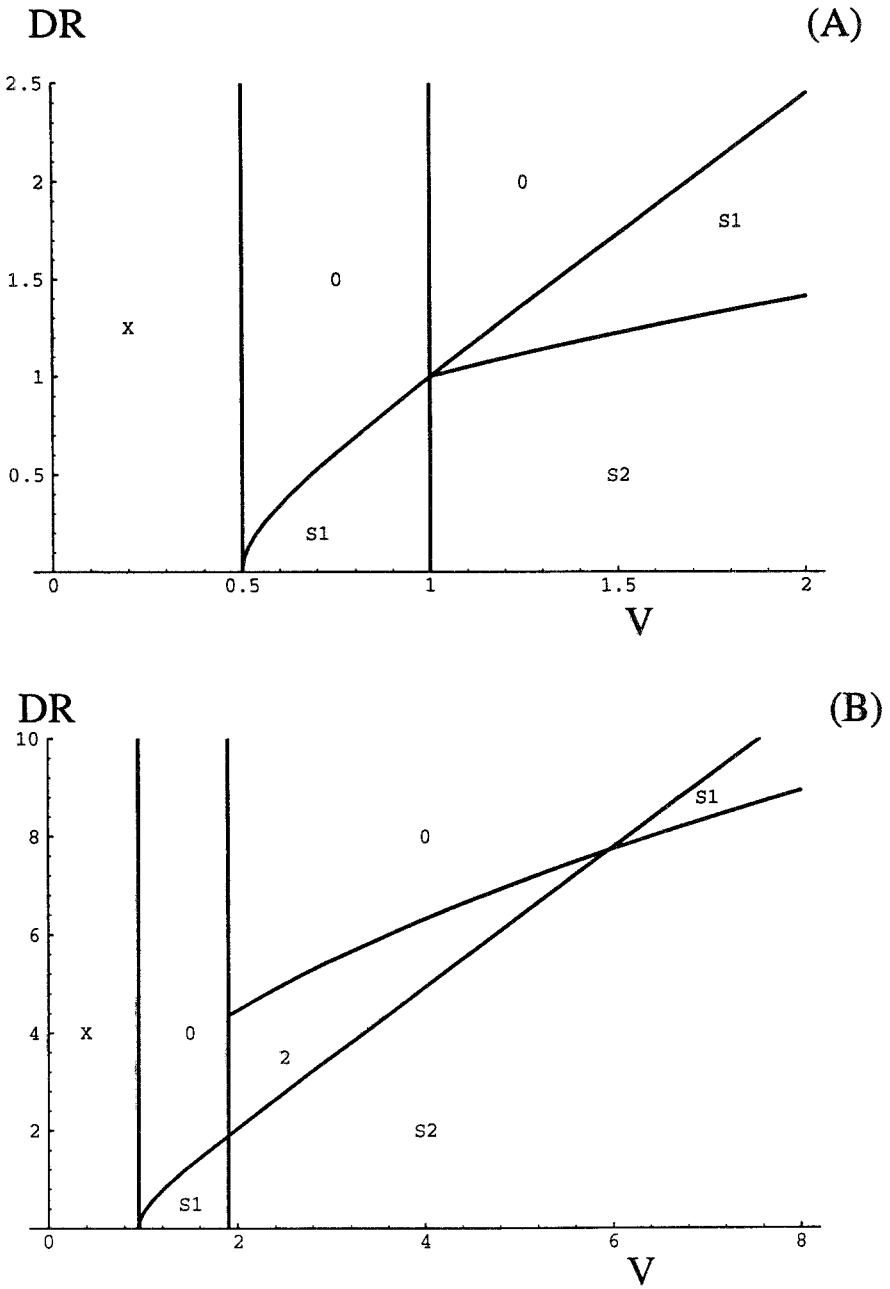

Figure 1. The evolutionary equilibrium size for different parameter values for the model described by Equations 10a and 10b and analysed in the Appendix. The formulae for s_1^* and s_2^* are given in the Appendix. The figure shows the effects of V (additional reproduction from holding a resource) and DR (R, range of phenotypes; D, slope of juvenile mortality versus size relationship) for two values of Q (reproduction by individuals without a resource). (A) $Q = 0.5$ and (B) $Q = 0.05$. The region labelled X denotes parameter values that lead to extinction of the population. The region of parameter space that results in either $s_e^* = 0$ or $s_e^* = s_2^*$ being stable is denoted by 2 in (B). Values of DR larger than those illustrated result in $s_e^* = 0$ being the only stable equilibrium when V is large enough for the population to persist.

arrive at the competitive stage be limited by another, size-independent type of competition earlier in the life cycle. Two alternative models fit these criteria. In the first, the dispersing young settle by a 'lottery mechanism' (i.e. the competitive phenotype does not influence whether an individual obtains a settling site). The number of settling sites is equal to twice the number of sites that can be occupied by an adult and sites are arranged in pairs. Survival of settled individuals to the competitive stage depends on the value (size) of the competitive trait. If both members of a pair survive, they engage in a competition that determines which individual obtains or dominates the site as an adult. The loser will have a reduced (or zero) reproductive output. The second model assumes that the size-dependent mortality occurs before individuals settle and survival from settling to the competitive phase is 100%. There are again twice as many sites for settling as there are sites that can be dominated by an adult. There is no need to assume any additional type of density dependence in either model, since population size cannot exceed the number of adult sites. We consider each of these two models in turn. In the first model, the cycles that occurred with fixed population density are replaced by dimorphism. When small individuals increase in frequency, their relative fitness decreases. This is because they are better off settling next to a large individual (which is likely to die before the competition) than next to another small individual (which always survives, although it only wins the contest 50% of the time). In the second model, the mortality occurs before settling, so the frequency dependence is similar to that with fixed population size and can result in cycles.

The first model is defined by the fact that mortality occurs after settlement. The number of potential adult sites is Z and the number of settling individuals is always $2Z$. As before, we assume that adult winners of competition have reproductive output $V + Q$ and losers have output Q. If the size-dependent mortality phase occurs between settling and competition, then the relative fitness of a rare s mutant type in an s* population is given by

$$\exp(-m(s))\{Q + V(1 - \exp(-m(s^*))) + \exp(-m(s^*))V[\text{probability}[S > S^*]\}$$

where the second term within { } represents cases in which an individual's neighbour dies before the competitive stage, so it obtains the resource 'by default'. The probability that $S > S^*$ in the third term within { } depends on the phenotypic distribution function and the difference between s and s^*. This fitness expression assumes that enough young are produced so that there are more than $2Z$ recruits available. If we assume a normal distribution function, the necessary condition for s^* to be an ESS, $(\partial W/\partial s\,|_{s=s^*} = 0)$, becomes

$$-m'(s^*)[Q + V - (V/2)\exp(-\mathrm{m}(s^*))] + V\exp(-m(s^*))/(2\sqrt{[\pi\sigma^2]}) = 0 \tag{11}$$

The stability criterion (Equation 2b) is

$$\begin{aligned} &-m(s^*)''[Q + V - (V/2)\exp(-m(s^*))] - (V/2)(m'(s^*)^2)\exp(-m(s^*)) \\ &\quad - Vm'(s^*)\exp(-m(s^*))/(2/\sqrt{[\pi\sigma^2]}) < 0 \end{aligned} \tag{12}$$

This is always satisfied if $m'' = 0$ and will only be violated if m'' has a sufficiently large negative magnitude. It is possible to determine the effects of the parameters Q, V and σ on the equilibrium s_e^* by implicit differentiation of Equation 11; s_e^* always decreases with increases in Q or σ, but s_e^* increases with V.

It is also necessary to determine whether a mutant $s = 0$ individual can increase when the rest of the population has a larger value, s_e^* (that satisfies Equation 11 or its analogue for a different distribution function). Such an invasion is possible when

$$\exp(-m(s_e^*)) < \{Q + 2V - \sqrt{(Q^2 + 2V^2 + 2QV)}\}/V \tag{13}$$

A sufficiently large s_e^* will satisfy this inequality. Whether this leads to a stable dimorphism or cycles of increase and collapse of the trait value, depends on how the relative fitnesses of the two types change with an increase in the abundance of the $s = 0$ type. If the proportion of $s = 0$ individuals is q, the fitnesses of the two types are given by

$$W(s^*,qs^*) = \exp(-m(s^*))\{Q + V(1 - \exp(-m(s^*)))(1 - q) + (V/2)(1 - q)\exp(-m(s^*)) + V_q\} \tag{14a}$$

for the larger type and

$$W(0,qs^*) = \{Q + V(1 - \exp(-m(s^*)))(1 - q) + (V/2)q\} \tag{14b}$$

for the $s = 0$ type. These expressions make the simplifying approximation that individuals with $s = 0$ never have a large enough phenotype to win a competition with the larger type. The derivative of Equation 14b with respect to q is always less than the derivative of Equation 14a with respect to q. This indicates that if there is an equilibrium with equal fitnesses, it will be stable. The same result can be obtained for any pair of sizes $s_1^* > s_2^*$; the relative fitness of the larger type increases with increases in the frequency of the smaller type. The cycles that were observed in the model without population dynamics therefore cannot occur here. The equilibrium proportions of $s = 0$ and the larger type (s^*) may be determined from the requirement that the two fitnesses (Equations 14a and 14b) must be equal; this implies that

$$q = \{2(Q + V)(1 - \exp(-m(s^*)) + V\exp(-m(s^*))\,((\exp(-\,m(s^*)) - 2)\}/\{V(1 - \exp(-m(s^*)))^2\} \tag{15}$$

The necessary conditions for q to represent a proportion ($0 < q < 1$) are that

$$\{Q + 2V - \sqrt{(Q^2 + 2V^2 + 2QV)}\}/V < \exp(-m(s^*)) < (2Q + V)/(2Q + 2V) \tag{16}$$

If Inequalities 16 are not satisfied, one of the two types will exclude the other.

Assume that a second species having $s^* = 0$ invades a system with a single species whose phenotype satisfies Equation 11 and Inequalities 12 and 13 and the two species attain a stable equilibrium. The new equilibrium phenotype for the first (larger) species will then be smaller than its original phenotype. This can be shown from the expression for the evolutionarily stable phenotype of the larger species in such a dimorphic system:

$$-m'(s^*)[Q + V - (V/2)(1 - q)\exp(-m(s^*))] + V(1 - q)\exp(-m(s^*))/(2\sqrt{[\pi\sigma^2]}) = 0 \tag{17}$$

Implicit differentiation of this expression with respect to q shows that increases in the frequency of the $s = 0$ type, q, result in a smaller s_e^*. This means that the size of the larger type converges toward the smaller.

The effects of parameter values on the evolutionarily stable size can be better investigated using a specific example; we again take the simple case of $m = Ds$, where D is a positive constant. Equilibria of this system are always locally stable and are given by

$$s_e^* = (1/D)\ln[V(D\sqrt{(\pi\sigma^2)} + 1)/(2D(Q + V)\sqrt{(\pi\sigma^2)})] \tag{18}$$

It is easy to verify that s_e^* increases as V increases and decreases with increases in Q, σ or D. The value of s_e^* increases indefinitely as D or σ approaches zero. This means that, given a small enough D or σ, $s = 0$ types can invade the system, based on Inequality 13. The trait value of the larger type (species) can be calculated using Equations 15 and 17. This results in a lengthy expression and the effects of parameter values were explored using a computer algebra program (*Mathematica 2.0*; Wolfram, 1991). Size decreases with increases in V or σ and increases with

increases in Q or D. Except for the response of size to the phenotypic variance, these are all the opposite of the responses that would occur in a genetically monomorphic population. The difference occurs because the parameters affect the proportion of $s = 0$ individuals as well as changing the direct competitive advantage of an increase in size.

The second life history under pairwise competition assumes that the size-dependent mortality occurs before settling. The number of settling sites ($2Z$) is presumed to be twice the number of resources (Z) and the actual contests occur shortly before settling. Provided the number of individuals settling is greater than $2Z$, there is competition for each resource item. However, if the number of recruits is $< 2Z$, some individuals will obtain a resource without competition and if the number of recruits is $<Z$, there will be no competition. (Juveniles are assumed to avoid competitors when settling if it is possible to do so.) This leads to the following model of fitness near the population dynamical equilibrium:

$$W(s, s^*) = \exp(-m(s))[Q + V(\text{Probability}[S > S^*])] \text{ if } \exp(-m(s^*)) > 2/(V + 2Q) \quad (19a)$$

$$W(s, s^*) = \exp(-m(s))\{Q + V[2 - (2Q + V)\exp(-m(s^*))]/[1 - Q\exp(-m(s^*))] + V(\text{probability}[S > S^*])[(V + Q)\exp(-m(s^*)) - 1]/[1 - Q\exp(-m(s^*))]\} \quad (19b)$$
$$\text{if } 1/(V + Q) < \exp(-m(s^*)) < 2/(V + 2Q)$$

If $\exp(-m(s^*)) < 1/(V+Q)$, the population will go extinct, thus $\exp(-m(s^*)) = 1/(V+Q)$ implicitly defines an upper limit to the size that evolution can produce. There will be no competition when the population size is less than Z under these conditions. When Equation 19b applies, the probability that an individual occupies a site without a neighbour is

$$[2 - (2Q + V)\exp(-m(s^*))]/[1 - Q\exp(-m(s^*))] \quad (20)$$

The ESS value of s^* will be determined by the requirement that $\partial W/\partial s|_{s=s^*} = 0$; there are two alternatives to be considered, depending on whether the number of surviving settlers is greater or less than $2Z$.

The first of the two fitness expressions, Equation 19a, is identical to that used in models without population dynamics. This is because, when the defining inequality of Equation 19a is satisfied, adult population size is independent of trait value. Thus, if the evolutionarily stable value of s^* determined in the section on pairwise competition with a constant population in the competitive stage (and in Maynard Smith and Brown, 1986) satisfies the condition $(V + 2Q)\exp(-m(s^*)) > 2$, then the results from the earlier section are not changed. If the results from the earlier section predict an indefinite increase in s^* and $Q\exp(-m(0)) > ((V/2) + Q)\exp(-m(s^*))$ while the defining inequality of Equation 19a is still valid, then $s = 0$ types can invade. This again produces cycles in the mean trait value.

If the phenotypic variance is sufficiently small and $s^* = 0$ individuals cannot invade when all settling sites are occupied, then s^* will increase until fitness is determined by Equation 19b. In this case, $s = 0$ individuals can invade if $Q\exp(-m(0)) > 1$, which requires that $Q > 1$. Such an invasion always leads to replacement of the larger types and evolutionary cycles in s^*, as in the model without population dynamics. (This may be verified by simulation; a dimorphism cannot occur because, given the defining inequality of Equation 19b, s^* individuals cannot increase when they are rare in an $s = 0$ population.)

This second model shows that some population dynamical schemes can produce the same phenomena as models without population dynamics. However, it should be noted that the cyclic outcomes in this model always require that $s = 0$ individuals that lose the competition nevertheless have a positive population growth rate when there are empty settling sites.

Discussion

A large number of alternatives are considered in the above analysis. However, there are some general conclusions. First, it is unlikely that size will increase indefinitely or that size will reach such a large value that the population becomes extinct. This is a simple consequence of the fact that contest competition disappears when the population becomes small enough that all individuals obtain high quality resources. The possibility of frequency-dependent evolution leading to extinction was first suggested by Haldane (1932) and has been mentioned in the context of specific models in many subsequent works (e.g. Lande, 1976; Parker, 1983; Maynard Smith and Brown, 1986; Taper and Case, 1992; Matsuda and Abrams, 1994). While other biological situations may produce frequency-dependent extinction (Matsuda and Abrams, 1994), extinction because of the evolution of ability to win contests seems to require rather restrictive assumptions regarding population dynamics.

The possible outcomes of the evolution of traits determining ability in contest competition, other than indefinite increase, are (1) a single, evolutionarily stable size, (2) two alternative stable sizes, (3) dimorphism with some large and some small individuals and (4) cycles in which small individuals exclude large ones, but then increase in size and are eventually excluded in turn. The first possibility appears to be the most probable one in our models. Alternative states (the minimum possible size or some larger size) occurred for a limited range of parameters in the free-for-all model we studied. Dimorphism is a possibility under other models of free-for-all competition, but it requires that the reproductive output of contest losers be relatively high. Cycles in competitive ability also require that the reproductive output of losers be relatively high and that the pairwise mode of competition be an adequate description of the contests. Even under these conditions, further restrictions on the type of population dynamics and the parameter values are necessary for cycles to occur.

It seems unlikely that the conditions required for repeated cycles in competitive ability are satisfied frequently. Even in the case of sessile organisms with spatially localized competition, it is difficult to picture a situation that would result in strictly pairwise competition; organisms such as trees and barnacles typically have a number of neighbours that may usurp their space. Thus, it is likely that the competitive process will involve enough individuals and that it is better described by the free for all model than the pairwise model. The unique cyclical dynamics that Maynard Smith and Brown (1986) first described for the pairwise model requires that very small individuals have a positively frequency-dependent fitness when they first arise; this results in the exclusion of the larger type and the start of another cycle. This positive frequency dependence arises because, when the frequency of small individuals increases, pairs of small individuals sometimes compete and one member of the pair will be able to obtain the resource. Even if competition involves only three individuals, a small individual will only win when both other members of the group are small; this is very unlikely when the small type is rare. Even if there is strict pairwise competition, some population dynamic assumptions prevent cycles from occurring (e.g. when size dependent mortality occurs after settling, as in the first model in the section on pairwise competition with population dynamics).

A prerequisite for dimorphism is the ability of minimum-sized individuals to arise and breed true in the population. This is obviously possible when the small individuals are of another species. However, small types in a species with large mean size cannot breed true if the trait value is determined by the standard polygenic model with many loci having small, additive effects on the character (see e.g. Maynard Smith and Brown, 1986). Dimorphism in a single species requires a genetic system that permits a bimodal size distribution. When the dimorphic equilibrium consists of two separate species, the larger species converges in size toward the

smaller species as the result of competition between them. This adds another possibility to the rapidly growing list of possible mechanisms that produce competitive convergence (Abrams 1986a, 1987a,b, 1990a,b).

The results presented here also suggest that, in spite of the advantage that large individuals have in competition, size may often fail to increase above a value that confers minimal contest ability. The reason is that small size implies good survival, which in turn means that only a small fraction of the individuals obtain a resource. When only a small proportion of individuals can obtain the resource, the probability of obtaining a resource is low, both for the mean genotype and for genotypes which specify slightly different mean sizes. The selection pressure for larger size is therefore relatively low, because a small increase in size cannot result in a large increase in the probability of obtaining a resource. This can effectively 'trap' a population at some minimum size, even though, if the size increased above some threshold, selection might favour further increases. Whether or not there is an increase in competitive ability above a minimum value may depend on stochastic processes such as founder events and genetic drift in small populations.

The marginal cost of larger size (the magnitude of m') and the variance of the phenotypic distribution play a large role in determining the evolutionarily favoured size. Small values of both of these quantities tend to produce a large size in models with or without population dynamics.

The effect of the fitness payoffs to winners and losers (V and Q) is less straightforward. A larger payoff to winners (V) has the direct effect of favouring a larger size. However, a larger V also increases the population size, which may either increase or decrease the value of increased size. The effect of the loser's payoff, Q, is solely the result of its effect on population size and a larger Q may favour either increased or decreased size, depending on the fraction of individuals that obtain a resource. The strength of selection for larger size depends on the slope of the relationship between size and the probability of obtaining a resource. The slope is shallow either if very many or very few individuals obtain a resource. Greater reproduction decreases the proportion of individuals obtaining a resource, but this has different effects on s^* depending on whether the proportion is large or small. For the model of pairwise competition with mortality after settling, the effects of Q and V on s^* were qualitatively different depending on whether a second, small species (or type) was present.

Perhaps the main message from this analysis is the importance of including population dynamical consequences in evolutionary models. We have already noted that the qualitative outcome (e.g. minimum size versus some larger size, extinction versus persistence) depends on assumptions about population dynamics. At a more detailed level, the stability of evolutionary equilibria is also dependent on population dynamics. Thus, the special case of a death rate that increases linearly with size divides evolutionarily stable from unstable equilibria in the models without dynamics (see also Parker, 1983; Maynard Smith and Brown, 1986). On the other hand, linear mortality rate functions lead to stable equilibria in the corresponding models with the population dynamics that we considered here.

The models analysed here are quite simple. Some may be reasonable descriptions of adult competition in holometabolous insects, where the elements of a semelparous life history, a pre-adult cost to large size, and an adult fitness advantage in competition due to size all seem to be satisfied frequently (Thornhill and Alcock, 1983). However, it is not clear to what extent they apply to size-structured populations in which young individuals are small and must compete with adults before they attain a large size (e.g. many invertebrates and fish, as well as many other groups; see Polis (1984) and Ebenman and Persson (1988)). Another restriction of the models analysed here is the assumption that there are a fixed number of equally valuable resource items. In some types of contest competition there is a continuous spectrum of resource values, with a correlation between size of the competitive trait and the value of the resource obtained. This

seems likely to result in greater exaggeration of the competitive trait than the situation considered here. It means that, even when survival rates are so low that some resources are available, there may still be selection for increased size because the best resources are still obtained by the largest individuals.

Our assumption of a fixed number of resources with one resource per individual is often not appropriate for competitive contests for mates. In this case, a smaller population size of males will result in more females per male, but need not eliminate competition. However, even in this case, it seems likely that spatial and energetic considerations will set a maximum to the number of mates that can be monopolized. Once the lower male survival due to the large trait value has reduced the male population sufficiently, competition will also disappear in this case.

Several authors (e.g. Dawkins, 1986; Vermeij, 1987) have suggested that arms races of competitive ability may have played a large role in determining macroevolutionary patterns. Our models are not entirely inconsistent with this view, but they do suggest that there are limitations on the extent of the escalation in competitive ability. Indefinite increase or permanent escalation will not occur and very often competitive traits will not increase above minimal levels. Vermeij (1987) and Dawkins (1986) argue that evolutionary arms races are also common in predator – prey systems. However, models incorporating population as well as evolutionary dynamics frequently do not produce such an outcome (Abrams, 1986b, 1990c, 1991).

Acknowledgements

This work was supported in part by NSF grant BSR 8918646 to P.A.A. and a Guest Researcher Grant from the Swedish Natural Science Research Council (N.F.R.). We thank an anonymous reviewer, Peter Taylor and especially Mark Taper for their comments on the manuscript.

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Appendix: the behaviour of Equations 10a and 10b

The threshold character value for obtaining a resource, T, in Equations 10a and 10b is a function of the mean size of the population. Specifically, T is determined by the requirement that the fraction of individuals that obtain a resource must be $(\exp(Ds^*) - Q)/V$; this must in turn be equal to the integral of the distribution function from T to $s^* + R$. It follows that

$$T = s^* + R - R\sqrt{[(2/V)(\exp(Ds^*) - Q)]} \text{ if } (\exp(Ds^*) - Q)/V < 1/2 \tag{A1a}$$

and

$$T = s^* - R + R\sqrt{[2 - (2/V)(\exp(Ds^*) - Q)]} \text{ if } (\exp(Ds^*) - Q)/V > 1/2 \tag{A1b}$$

The value of s^* then determines which of these two threshold expressions is substituted in Equations 10a and 10b. When s^* is sufficiently small, Equations 10a and A1a may apply, while larger values of s^* always require Equations 10b and A1b. Making the substitution for T in Equations 10a and 10b in the text gives the two possible dynamic equations:

$$ds^*/dt = k\{-D + (1/R)\exp(-Ds^*)\sqrt{[(2V)(\exp(Ds^*) - Q)]}\} \text{ if } (\exp(Ds^*) - Q)/V < 1/2 \tag{A2a}$$

$$ds^*/dt = k\{-D + (1/R)\exp(-Ds^*)\sqrt{[2V^2 - (2V)(\exp(Ds^*) - Q)]}\} \text{ if } (\exp(Ds^*) - Q)/V > 1/2 \tag{A2b}$$

The behaviour of these equations can be analysed by determining the stability of the positive equilibrium points and the point $s^* = 0$. It is useful to divide the analysis into two cases depending on the relative values of V and $(1 - Q)$. If $V > 2(1 - Q)$, then Equation A2a describes the dynamics for sufficiently small values of s^*, but Equation A2b describes the dynamics for s^* larger than a threshold value. If $(1 - Q) < V < 2(1 - Q)$, then the dynamics are described by Equation A2b for all s^*. (If $V < 1 - Q$, it is impossible for the population to grow regardless of its density, so this case need not be considered.)

Case 1: $1 - Q < V < 2(1 - Q)$

There are two potential equilibrium points of the dynamic system of Equation A2b, only one of which is stable for a given set of parameters: (1) if $DR > \sqrt{[[2V(V + Q - 1)]}$ then $s_e^* = 0$ and (2) if $DR < \sqrt{[2V(V + Q - 1)]}$ then $s_e^* = s_1^*$, where

$$s_1^* = (1/D)\ln\{(1/D^2R^2)(-V + \sqrt{[V^2 + 2VD^2R^2(V + Q)]})\} \tag{A3}$$

Case 2: $V > 2(1 - Q)$

This case is more complicated, because either of the two dynamic Equations A1a and A1b may apply. Equation A2a has only one stable equilibrium (Equation A4 below). However, there are four alternative outcomes, depending on the values of V, Q and DR:

(1) if $DR > \max[\sqrt{[V/(2Q)]}, \sqrt{[2V(V + Q - 1)]}]$ then $s_e^* = 0$;
(2) if $DR < \min[\sqrt{[V/(2Q)]}, \sqrt{[2V(V + Q - 1)]}]$ then $s_e^* = s_2^*$, where

$$s_2^* = (1/D)\ln\{(1/D^2R^2)(V + \sqrt{[V^2 - 2VQD^2R^2]})\} \tag{A4}$$

(3) if $\sqrt{[V/(2Q)]} < DR < \sqrt{[2V(V + Q - 1)]}$ then $s_e^* = s_1^*$; it is important to note that both inequalities can be satisfied for some values of DR only if $V > (1 + 4Q - 4Q^2)/(4Q)$;

(4) if $\sqrt{[V/(2Q)]} > DR > \sqrt{[2V(V + Q - 1)]}$ then there are two alternative stable points depending on the initial value of s^*; $s_e^* = 0$ (which will be observed if the initial value is sufficiently small) and $s_e^* = s_2^*$ (which will be observed if the initial s^* is sufficiently large). It should be noted that the two defining inequalities for this fourth outcome can only be satisfied for $V < (1 + 4Q - 4Q^2)/(4Q)$; this inequality can only be consistent with the assumption (case 2) that $V > 2(1 - Q)$, when $Q < (2 - \sqrt{3})/2$.

The possible equilibria produced by different parameter values are illustrated in Fig. 1. This multitude of possibilities can be simplified by noting that a sufficiently small value of the product of the death rate and phenotypic range (DR) always results in a single positive value for s_e^*, although this may be s_1^* or s_2^* depending on whether V is relatively small or large. A sufficiently large DR always results in the minimal possible size, $s_e^* = 0$. For a limited range of parameter values there may be alternative equilibria at $s_e^* = 0$ and $s_e^* = s_2$. In this case, when s^* is small, population size is large enough that few individuals obtain the resource and the advantage of increasing size is outweighed by the disadvantage of higher mortality. However, if s^* is above a certain threshold, the population size is small enough that there is a sufficient advantage to contest ability that size increases to a larger equilibrium value.

This analysis also allows us to determine how the different parameters affect the equilibrium s^*. Of course, when $s_e^* = 0$, small changes in the parameter values (Q, V, D and R) have no effect. If $s_e^* = s_1^*$, the effects may be determined by taking the derivative of Equation A3 with respect to parameter values; s_1^* increases with V and Q and decreases with D or R. It might seem counter-intuitive that a larger 'loser's fitness', Q, increases the optimal size. This occurs because a larger Q increases the population size; because more than half the individuals obtain a resource at this equilibrium, a larger population increases the advantage of larger size. If $s_e^* = s_2^*$, size decreases with D, R or Q and increases with V. The different response to Q in this case is because fewer than half the individuals obtain a resource and therefore, the larger population size caused by a larger Q reduces the advantage of larger size.