Population cycles can maintain foraging polymorphism

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The maintenance of genetic variability in morphological traits that affect fitness is poorly understood. We present a simple Mendelian model of genetic traits affecting foraging efficiency in grazing ungulates, based on a trade-off between rates of energy extraction at low versus high levels of plant abundance. The model suggests that variation in foraging efficiency could be maintained via lottery competition arising as a direct consequence of dynamically unstable interactions between consumers and their food resources. Lottery competition is a plausible mechanism for explaining wide variability in foraging efficiency, such as that documented in unstable Soay sheep populations on the St Kilda archipelago.

Keywords: foraging; genetic mechanisms; morphology; polymorphism; population cycle; Soay sheep

1. INTRODUCTION

Understanding the processes that maintain genetic variation in adaptive traits within a single population is one of the most challenging questions in population genetics (Hedrick 1986; Barton & Turelli 1989). The issue is particularly perplexing for traits that have an unambiguous fitness value, such as those affecting foraging. Despite compelling evidence that variation in feeding morphology and behaviour can be highly heritable (Smith 1993; Hori 1993) and that selection gradients on foraging traits can be strong under typical ecological conditions (Robinson & Wilson 1994; Illius *et al.* 1995; Schluter 1994, 1995), many wild populations maintain substantial amounts of phenotypic variation in trophic characters (Skulason & Smith 1995). It is widely agreed that spatial variation in the environment could explain some cases of foraging polymorphism. It is currently less clear, however, whether temporal variability in closed, panmictic populations could also maintain polymorphic traits (Hedrick 1986; Barton & Turelli 1989).

Consider a well-studied example. Soay sheep of the St Kilda archipelago are subject to severe fluctuations in population density at frequent intervals. Time-series data for the Hirta island population in the St Kilda archipelago (Clutton-Brock *et al.* 1991, 1997; Grenfell *et al.* 1992) suggest that such fluctuations are cyclic, typically with a periodicity of three to four years. These cycles are thought to reflect overcompensatory responses in both mortality and juvenile recruitment to the population (Clutton-Brock *et al.* 1997), stemming from persistent effects of the early environment experienced by young sheep (Clutton-Brock *et al.* 1992) coupled with depletion of energetic reserves during periods of food scarcity (Clutton-Brock *et al.* 1997; Illius & Gordon 1998).

During these recurrent population crashes, there is strong selection for foraging traits maximizing energy gain in depleted swards (Illius *et al.* 1995). Of particular interest is the observation that body mass and jaw width are strongly correlated with survival (Illius *et al.* 1995), probably because animals with broad muzzles are more efficient at cropping sparse grass than are animals with narrow muzzles (Gordon *et al.* 1996). What is puzzling is that Soay sheep retain an appreciable amount of variation in both body mass and jaw width, in spite of pronounced directional selection gradients (Illius *et al.* 1995). This immediately begs the question: what sustains variability in adaptive foraging traits?

Here we show that temporal variability in selection, such as that experienced by an animal like the Soay sheep with recurrent population crashes, could readily enhance genetic variability, provided that all genotypes occasionally have the chance to win the annual fitness lottery (Fagerstrom 1988; Ellner & Hairston 1994). We first consider an explicit Mendelian model of genotypic variation in foraging efficiency resulting from muzzle shape and imbed that population genetic model in a plant–herbivore food chain to evaluate the impact of dynamic instability.

2. POPULATION AND EVOLUTIONARY DYNAMICS

To model the population genetics of foraging, we assumed that foraging efficiency is determined by two alternate alleles (0 and 1) occurring at a single locus. We assume dominance of allele 1 over allele 0. We refer to the proportion of each genotype in the population using a subscript notation, where g_{11} is the proportion of homozygous dominant individuals, g_{00} is the proportion of homozygous recessive individuals, and $g_{01} + g_{10}$ gives the proportion of heterozygous individuals (which have the same phenotype as homozygous dominants). Incorporating

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Figure 1. Consumer fitness in relation to resource density for different genotypes, according to the Mendelian model described in the text. Individuals with narrow jaws are homozygous recessive, with foraging parameter values of $a=0.4$ and $b=1.0$, whereas individuals with wide jaws are either homozygous dominant or heterozygous, with foraging parameters $a=0.8$ and $b=1.4$. Note that each phenotype has a range of resource densities over which it is most fit.

dominance in this way eliminates any possibility of heterozygote advantage.

The rate of foraging by terrestrial mammals grazing on dense swards of evenly distributed plants often saturates with increasing plant biomass (Black & Kenney 1984; Short 1985; Laca *et al.* 1992; Gross *et al.* 1993; Wilmschurst *et al.* 1995) and is well-predicted by Holling's (1959) type-II functional response

$$\text{intake} = \frac{aN}{1 + abN}, \quad (1)$$

where N is vegetation biomass, a the rate of search by the forager and b the time to handle each unit of biomass consumed. We assume that each of these parameters is dependent on genotype, with both a and b smaller for homozygous recessive individuals than for homozygous dominant or heterozygous individuals. As we will shortly explain, large values of the parameter a enhance foraging efficiency at low resource levels, whereas small values of b enhance foraging efficiency at high resource levels; hence we assume that no genotype can perform best under all environmental conditions.

Depending on the genotype of the forager, energy gain either increases rapidly with initial increase in plant biomass and levels off at a modest asymptote, or else increases modestly with initial increase in plant biomass and levels off at a high asymptote (figure 1). These differences are intended to represent outcomes of different jaw morphologies, ranging from individuals with a wide dental arcade (those with the dominant allele 1) to individuals with narrow arcade breadth (those homozygous for the recessive allele 0). Arcade breadth commensurately affects muzzle shape, such that narrow jaws tend to protrude more than wide jaws (Gordon & Illius 1988; Janis & Ehrhardt 1988), and this could influence ability to feed selectively from the sward.

On an interspecific level, variation in jaw shape is often associated with different feeding styles: grazers have wide jaws whereas browsers have narrow jaws (Gordon & Illius 1988; Janis & Ehrhardt 1988). Browsers are commonly more selective in their foraging behaviour than are grazers; we presume that this difference in selectivity is at least partly associated with differences in jaw shape. Hence, our model postulates that individuals vary genotypically in jaw shape and that this trait is associated with trade-offs in foraging efficiency. Animals with shallow, wide jaws would be favoured at low resource availability, because their morphological structure makes them adept at clipping short plants (figure 1). At high plant biomass, animals with a deep, narrow jaw would be most adept at selecting the most nutritious plant parts, which are often the most rapidly digested, thereby reducing the handling time within the digestive tract (figure 1). Protruding jaws sweep a narrower path across the grass sward, reducing the effective rate of search. There is some experimental evidence of such a trade-off in efficiency among large grazing ungulates inhabiting the Serengeti savannah grasslands (Murray & Illius 1994).

This simple algorithm for genetic determination of foraging efficiency can be readily imbedded in a set of consumer–resource equations, incorporating density-dependent recruitment by resources linked with a saturating functional response on the part of consumers (Caughley 1976):

$$\text{resources: } \frac{dN}{dt} = rN(1 - N/K) - P \sum_{i=0}^1 \sum_{j=0}^1 \frac{g_{ij}a_{ij}N}{1 + a_{ij}b_{ij}N}, \quad (2)$$

$$\text{consumers: } \frac{dP}{dt} = P \left(\sum_{i=0}^1 \sum_{j=0}^1 \frac{g_{ij}a_{ij}N}{1 + a_{ij}b_{ij}N} - c + \varepsilon_i \right), \quad (3)$$

where N is resource population density, P is consumer population density, r is maximum per capita rate of resource growth, K is resource carrying capacity, g_{ij} is the proportion of genotype ij in the consumer population, c is the expected per capita rate of mortality of consumers, which we assume to be independent of genotype, and ε_i is stochastic variation in consumer mortality rate from year to year. We assumed that ε was normally distributed, but truncated to prevent illogical cases of 'positive' mortality, which could otherwise occur if $\varepsilon > c$ for deviates drawn from the right-hand tail of the normal distribution. The purpose of adding environmental noise was to generate a small amount of temporal variation in abundance even for locally stable populations so we could better visualize selection gradients. Changes in genotype distribution clearly affect foraging rates and therefore community dynamics. Changes in genotype distribution depend in turn on individual fitness and independent assortment of gametes, as described below.

If each genotype has a fitness of $w_{ij} = a_{ij}N/[1 + a_{ij}b_{ij}N]$ and mating is non-assortative with respect to foraging genotype, then the proportion of haploid genotypes (h) among consumer gametes can be calculated by the following set of equations:

$$h_1 = \left(w_{11}g_{11} + \frac{w_{10}g_{10} + w_{01}g_{01}}{2} \right) \left(\frac{1}{\bar{w}} \right), \quad (4)$$

Figure 2. Changes in consumer density and frequency of the dominant allele (allele 1) over time, with two different sets of parameter values. (a,b) Stable, $K=3$; (c,d) unstable, $K=6$. In each case, the coefficient in variation of mortality was 10% of the mean. Foraging parameters were as follows: $r=1$, $c=0.40$, $a=0.4$ and $b=1.0$ for homozygous recessive individuals, whereas $a=0.8$ and $b=1.4$ for heterozygotes and homozygous dominant individuals.

$$h_0 = \left(w_{00}g_{00} + \frac{w_{10}g_{10} + w_{01}g_{01}}{2} \right) \left(\frac{1}{\bar{w}} \right), \quad (5)$$

where the mean fitness of individuals in the consumer population equals $\sum_i \sum_j w_{ij}g_{ij}$. The frequency of offspring genotypes that can be produced through randomly mixing these gametes (γ_{ij}) is calculated according to the binomial distribution: $\gamma_{00} = h_0^2$, $\gamma_{10} + \gamma_{01} = 2h_0h_1$, and $\gamma_{11} = h_1^2$. It is subsequently straightforward to calculate changes in the proportion of each genotype by adding recruits and subtracting deaths ($dP_{ij}/dt = \bar{w}\gamma_{ij}P - cP_{ij} + \varepsilon_i P_{ij}$, $g_{ij} = P_{ij}/P$). Simulations were run for 5000 time-steps, using a discrete-time Euler approximation with 100 sub-steps to model the continuous Lotka–Volterra differential equations. We used a stochastic uniform distribution to set initial frequencies of each genotype in the population. Simulations were started with the plant population at its carrying capacity and herbivores one-tenth as common as plants. To ensure the possibility of reinvasion of rare genotypes with higher than average fitness (to be consistent with Maynard Smith's (1982) definition of an evolutionarily stable strategy), we set a lower limit of 10^{-4} for the density of each genotype.

3. RESULTS AND DISCUSSION

We first consider the fitness of different genotypes relative to resource availability. The consumer population would be unchanging when the per capita fitness gain obtained via foraging ($aN/[1+abN]$) exactly matches the risk of mortality ($c + \text{mean } \varepsilon$). Hence, one can evaluate evolutionary outcomes by simply determining which genotype would perform best at a given level of mortality averaged over time. Individuals with narrow muzzles are

less efficient than other grazers when resources are scarce, but feed better than other genotypes when resources are abundant (figure 1). Hence, if average mortality risk is high, then equilibrium plant biomass would be high, and genotypes with narrow muzzles would tend to be favoured (right-hand portion of dotted line in figure 1). Low risk of mortality correspondingly favours individuals with broad muzzle dimensions (left-hand portion of solid line in figure 1).

Given the nature of trade-offs in foraging efficiency, each genotype has a level of resource abundance at which it performs best. Temporal variation in resource abundance could therefore contribute to variation in foraging efficiency, provided that all genotypes are most fit at some time or another, albeit temporarily. Such variation in resource abundance could arise naturally through dynamic instability induced by the consumers themselves.

One way to destabilize simple trophic models such as ours is to increase the resource carrying capacity, the so-called 'paradox of enrichment' (Rosenzweig 1971; Gilpin 1972; May 1972). Parameter combinations conferring unstable population dynamics lead to an increased degree of polymorphism relative to their stable counterparts (figure 2). This is because of shifts in fitness advantage as resource density fluctuates slightly out of phase with that of the consumers, as previously described for systems with pure exploitative competition among distinct consumer species (Armstrong & McGehee 1980; Waltman 1983). Hence, this dynamic can be interpreted as a form of lottery competition (Fagerstrom 1988), with lottery conditions imposed by dynamic interactions between consumers and their resources. Maintenance of variability in foraging efficiency in the dynamically unstable case does not arise as some kind of curious form of heterosis.

This can be readily verified by examining the mean fitness of each genotype over time. In the dynamically unstable case shown in figure 2, for example, the arithmetic mean fitness of homozygous recessive individuals (0.411) was similar to the mean fitness of heterozygous or homozygous dominant individuals (0.410). Homozygous recessive individuals had higher fitness than other genotypes during periods of resource abundance, whereas the converse was true during periods of resource scarcity. Hence, dynamic instability induced temporal alternation in fitness advantage, which in turn sustained polymorphism.

Lottery competition can only be a viable mechanism for maintaining trait variation if there is storage of temporarily weaker genotypes until ecological conditions are reversed (Ellner & Hairston 1994). Such a storage mechanism is readily visible in models with explicit age structure, such as Ellner & Hairston's (1994) model of larval recruitment dynamics. There is an implicit storage effect in models framed in continuous time, because only a fraction of the population can disappear through mortality at any point in time. Hence, substantial numbers of each allele can persist over the entire cycle period.

In order to test the generality of this process, we performed 1000 Monte Carlo simulations, in which each parameter value was independently drawn at random from a uniform distribution. (Ranges for each parameter were as follows: $r=0-1$, $K=0-10$, a for homozygous recessive individuals $=0-1$, b for homozygous recessive individuals $=0-1$, and $c=0-1$.) We assumed that the values of a and b for homozygous dominant or heterozygous individuals were 0.4 units larger than that of homozygous recessive individuals, thereby assuring trade-offs in foraging efficiency. Population geneticists often use a value of 5% as a benchmark for polymorphism. Our results showed that out of 692 simulations in which consumers did not go extinct, 163 simulations (23.6%) produced polymorphism greater than 5%. Of the remaining simulations that went to fixation, the dominant allele won about twice as frequently as the recessive allele. This Monte Carlo procedure suggests that dynamically maintained polymorphism should be commonplace in consumer-resource systems, at least in those that might conform in some sense to the simple trophic model.

It is simple to recast our genetic model to include simple additive properties. In such a case, heterozygous individuals would have search rates and handling times that are mid-way between values for individuals that are homozygous for either allele. Mortality risk of intermediate magnitude would favour individuals with moderate muzzle dimensions, neither too broad nor too narrow for conditions at equilibrium (falling between the two curves shown in figure 1). Simulations conducted with such additive genetic models suggest levels of polymorphism (12.8%) similar to those observed in the dominance model, out of 734 feasible parameter combinations derived from 1000 random draws.

Our results suggest that dynamic instability provides a plausible explanation for persistent polymorphism in foraging traits. The Soay sheep population on St Kilda has well-documented fluctuations in abundance that seem to be at least partly induced by herbivory, as would be

consistent with our model (Clutton-Brock *et al.* 1997). Nonetheless, cycles in Soay sheep have some additional biological wrinkles not incorporated in our simple trophic model. Sheep mortality is triggered by energetic reserves falling below minimum metabolic maintenance requirements; this occurs during periods of exceptionally challenging weather (Clutton-Brock *et al.* 1997; Illius & Gordon 1998). Models of overcompensatory dynamics in Soay sheep (Grenfell *et al.* 1992; Clutton-Brock *et al.* 1997; Illius & Gordon 1998) further assume age- and sex-structure, which can have a destabilizing effect on population dynamics.

Simple genetic determination of a complex physiological structure such as jaw morphology is undoubtedly unrealistic to some degree (Atchley *et al.* 1985). On the other hand, there is some evidence that jaw shape in mice may be determined by a relatively small set of major genes expressed during development that profoundly affect mandibular development (Atchley & Hall 1991; Atchley *et al.* 1992). The simple developmental 'fields' that are determined genetically may manifest more complex and profound changes in jaw shape and function.

The conditions favouring foraging polymorphism in our model are mild, demanding no special mechanism other than trade-offs in foraging efficiency at different levels of resource abundance and cyclic variation in consumer and resource abundance. It should be possible in principle, even if rather difficult in practice, to measure such foraging trade-offs; such measurements would be the simplest way to falsify the proposed hypothesis.

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