

**HABITAT SELECTION AND THE EVOLUTION OF SPECIALISTS IN
HETEROGENEOUS ENVIRONMENTS**

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ABSTRACT

Recent advances in studies of habitat selection and resource use provide a framework not only for estimating resource specialization, but also for predicting future success of specialist and generalist strategies. The protocol merges resource selection functions with fitness and population dynamics to assess the evolution of competing strategies that change with density-dependent habitat selection. These strategies are revealed by resource selection coefficients derived from marked individuals that can then be used to predict each individual's fitness at different population sizes. Simulated consumer resource dynamics confirm the theory's ability to identify strategies of habitat and resource use with simple statistical models that summarize rather complex systems. The theory produces excellent fits with simulated data when strategies depend on density, and when the success of a single strategy interacts with others. Specialist strategies yield highest fitness at low population density, whereas generalists have highest fitness in dense populations. When applied to female red deer living on the Isle of Rum, Scotland, the theory correctly predicts an equilibrium distribution of competing strategies dominated by specialization on *Agrostis/Festuca* grassland. Specialization declined as population density increased through time. Simultaneously, changes in the genetic structure of the population reflected the increased opportunity for outbreeding as individuals became less specialized. Thus, it appears that theory effectively assessed competing strategies of resource use, and predicted their density- and frequency-dependent evolution.

Keywords: evolutionary strategies, generalists, habitat selection, population dynamics, red deer, resource selection functions, specialists

INTRODUCTION

Theories on the evolution, coexistence, and persistence of specialist and generalist species are frequently used to help explain the origin and maintenance of local biodiversity. Many of these models assume that specialist trade-off increased performance on some fitness-enhancing traits at the expense of reduced performance on others (e.g., Levins, 1962; MacArthur and Levins, 1964; Rosenzweig, 1974; Lawlor and Maynard Smith, 1976; McPeck, 1996). The shape of the trade-off alters the contours in adaptive landscapes that favor the evolution of relatively specialized versus generalized species. Coexistence and persistence of generalists and specialists is most likely in heterogeneous environments where no single species can maintain a selective advantage over others (e.g., Brown and Pavlovic, 1992; Wilson and Yoshimura, 1994; Holt, 1996; Egas et al., 2004; Abrams, 2006a,b, and references therein).

The number of viable strategies competing for evolutionary opportunity and ecological dominance is enhanced by strategies of habitat selection (Fretwell and Lucas, 1969), and their emergent density- and frequency-dependent evolution, that create fluid (Morris, 2003a; Vincent and Brown, 2005), and, perhaps, even holey (Gavrilets, 1997) "landscapes". Although theory reveals many of the conditions leading to specialists and generalists, there are few tools to help assess which theories are closest to reality, and which strategies are most likely to displace others. If such tools exist, we can likely find them in the same processes of habitat selection that help to determine winning and losing strategies in heterogeneous environments. A useful tool will first quantify the strategy, and second, help us predict its ecological and evolutionary dynamics.

Fortunately, we can measure the strategy of habitat and resource specialization directly from habitat preference and probabilities of resource use (resource selection functions: Boyce and McDonald, 1999; Manly et al., 2002). When habitat use is coarse-grained (MacArthur and Levins, 1964), a graph of the density of individuals occupying adjacent habitats (the habitat isodar, Morris, 1987, 1988) reveals the underlying evolutionary strategy of density-dependent habitat selection (Morris, 2003a). And, when resource use is fine-grained, the pattern of resource selection reveals the relative specialization of different populations or species, and signals which key resources are selected along underlying resource gradients. If we can link these patterns of habitat and resource use to fitness, then it should be possible to predict which strategy is most adaptive, and whether or not the population could evolve toward increased specialization. If we can also link habitat and resource use to population dynamics, then it should be possible to predict the transient ecological and evolutionary success of competing strategies. We aim to do both.

We begin by developing a simple theory demonstrating how to use resource selection functions (RSFs) to model density- and frequency-dependent strategies of specialization. We do this by linking RSFs and density to lifetime reproductive success. The value of a resource selection function depends on the availability of alternative resources. Thus, there is a risk that resource selectivity estimated by RSFs could simply reflect the local availability of resources rather than revealing the degree of specialization. This

statistical problem depends on the dynamics of resources and consumers. Changes in consumer density will alter resource abundance and vice versa. So, we test the ability of multiple regression models to estimate specialization by simulating consumer–resource dynamics.

Our simulations evaluate multiple scenarios of specialized versus generalized consumers that lead to the coexistence of consumer and resource populations. We use these simulated data to construct RSFs, and then use the simulated RSFs to verify that resource selectivity produces a tight fit with specialization. The intent is to verify that our statistical approach can indeed detect density-dependent changes in preferred strategies in relatively complex systems for which we control the dynamics.

After confirming that the theory works with simulated data, we illustrate the method with data on resource use, density, and reproductive success of individual red deer (*Cervus elaphus*) living on the Isle of Rum, the National Nature Reserve, off the west coast of Scotland (McLoughlin et al., 2006). We use the theory to predict which strategy should “win” at different population sizes, then evaluate whether data on the dynamics and genetics of Rum’s red deer population fit our expectations. They do. At low density, a strategy specializing on grassland has highest fitness, while at high density, a more generalized strategy is favored. Long-term trends in red deer population dynamics, and a gradual reduction in genetic structure, are consistent with the habitat-use data and the theory’s ability to predict specialization strategies.

A MODEL TO PREDICT STRATEGIES IN COMPLEX SYSTEMS

Our approach represents an empirical method to “unpack” (sensu Rosenzweig, 1991) fitness-generating functions (G-functions; Vincent and Brown, 1984, 2005) so that they can be used to assess evolutionary strategies in real populations (our method applies equally well to the parallel approaches of adaptive dynamics, e.g., Metz et al., 1996; Geritz et al., 1997). A suitable G-function for assessing different strategies employed by individuals of a single consumer species exploiting multiple resources can be written as

$$G(\mathbf{v}, \mathbf{u}, \mathbf{p}, \mathbf{y}, \mathbf{n})|_{\mathbf{v}=\mathbf{u}_i} = H_i(\mathbf{u}, \mathbf{p}, \mathbf{y}, \mathbf{n}), i = 1, \dots, l_s \quad (1)$$

where \mathbf{v} is the set of “virtual strategies” used to assess the fitness of any actual strategy \mathbf{u}_i (represented by RSFs), \mathbf{p} is the set of frequencies of the different strategies in the consumer population, \mathbf{y} is the set of resource densities, \mathbf{n} is the set of consumer population sizes, and H is the actual fitness function for strategy i of s possible strategies. This formulation specifies that each strategy is explicitly density- and frequency-dependent. If we then substitute realistic models for the respective population dynamics of the consumer and its resources, it is possible to evaluate the future success of competing consumer strategies by jointly solving their evolutionary and population stability (so-called Darwinian dynamics; Vincent and Brown, 2005).

We propose an analogous six-step empirical solution to evaluate the adaptive value of resource-selection strategies:

- (1) Begin by collecting baseline data on resource use and fitness proxies of marked individuals through time.
- (2) Record population densities and resource availability at the same time.
- (3) Define the strategy set by describing the resource selection patterns of each marked individual.
- (4) Link the individual RSFs with the fitness proxies while controlling for the effects of density and potential interactions with, and among, other strategies.
- (5) Predict the range of population densities where each strategy achieves greatest fitness.
- (6) Evaluate the prediction by examining changes in phenotypes and genetics through time.

Imagine that we have estimates of resource use for a population, proxies of fitness, population density, and resource availability. Imagine further that we use resource selection functions (Manly et al., 2002) to describe the response of animals to individual resources or modifying covariates (such as elevation, slope, aspect, and distance to water or a refuge). RSFs are popular descriptors of habitat use (Lele and Kleim, 2002) and are typically built by comparing habitat features at locations used by animals with those observed from a large number of random locations (Boyce, 2006). The relative value of each habitat variable to the RSF score is revealed by its RSF coefficient, α (often estimated with logistic regression; these are sometimes called selection coefficients, a term we avoid because it has a very different meaning in population genetics). A thoughtfully constructed RSF will enhance our understanding of a population's natural history and thereby simplify assessment of habitat selection.

Resource selection functions can also be estimated for individuals if one collects data on multiple sightings of each animal. These individually-based RSFs can then be used to identify variation in individual resource selectivity. If we can connect the individual RSFs to fitness (e.g., with estimates of lifetime reproductive success), the relationships with fitness will represent alternative resource-selection strategies available to adaptive evolution, providing that RSFs are heritable. In self-limiting populations (e.g., Turchin, 2001), fitness should eventually decline with density.

The suite of individually-based RSFs thus represents the set of available strategies to be tested by natural selection. Their relationships with fitness, and the dependence of fitness on population dynamics, provide the opportunity to determine which strategies should become rare, merely persist, or perhaps flourish with changes in population size.

We can evaluate the RSFs' evolutionary potential by describing the functional relationships between fitness proxies and RSF coefficients. Statistical problems (colinearity) arise when RSF coefficients (or fitness estimates) are correlated with one another. If this occurs, we can use principal components analysis to summarize their joint effects on fitness (McLoughlin et al., 2007). To control for density- and frequency-dependent evolution, we must also determine the relationships among the fitness proxies, the average population density experienced by the focal individuals, and the frequency of different strategies with changes in population size (interaction between density and strategy).

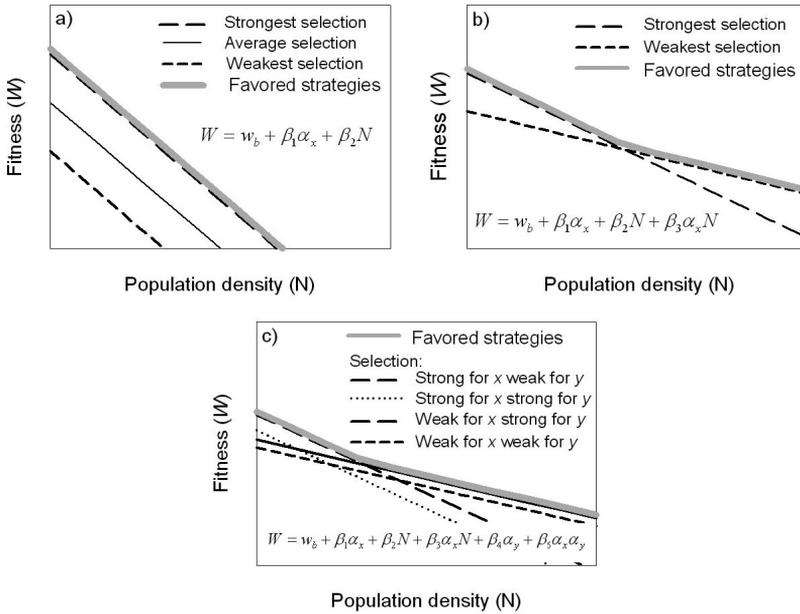


Fig. 1. Strategies of resource selection leading to distinct density-dependent fitness (W) functions, as depicted by three regression models. The constant w_b included in the multiple regression models represents the fitness achieved at low population density, independent of resource selection. Individual variation in fitness associated with resource use is depicted by different bold lines. Resource-use strategies yielding the greatest fitness are displayed in gray. Three scenarios are outlined. In (a), fitness associated with selecting x (α_x) is independent of density. In (b), fitness associated with selecting x also depends on density (a significant $\alpha_x \cdot N$ interaction). Scenario (c) illustrates an example where fitness depends not only on selection for x (α_x), but also for y (α_y), and where fitness associated with α_x also depends on both density and α_y . Despite the complexity, it is still possible to map the favored strategies against density.

The density- and frequency-dependent effects can be graphed to yield a heuristic understanding of the evolution of competing strategies (Fig. 1). We consider three scenarios. In the first and simplest, fitness is a function of selection for resources (or their modifying covariates) of type x (α_x) as well as the density of consumers (N). Resource selection in this instance has an additive effect on fitness that is independent of population density (Fig. 1a). Nevertheless, fitness will decline with increasing density. The relationship between fitness (W) and population density (N) then takes the form:

$$W = w_b + \beta_1 \alpha_x + \beta_2 N \tag{2}$$

where β_1 and β_2 are regression coefficients for α_x and N , respectively (β_2 is negative). A significant intercept ($w_b + \beta_1 \alpha_x$) reveals the minimum fitness (w_b) that is achieved at low

population density, plus the fitness increment associated with the density-independent selection for x . The variation in α_x observed within the population reflects the range of individual strategies. Since the effect of habitat selection on fitness in this scenario is independent of density, a single strategy yields maximum fitness at all population sizes. That single strategy would correspond to strong preference for a habitat attribute that enhances fitness (i.e., β_j and α_x both positive) as displayed in Fig. 1a, or to the strong avoidance of an attribute that reduces fitness (i.e., β_j and α_x both negative). In the context of evolutionarily stable strategies, individuals holding any other available strategy will have lower fitness and should become increasingly underrepresented in the population through time.

The second scenario (Fig. 1b) illustrates a situation where fitness gains accrued through resource specialization depend on population density. Specialists (strong selectors), for example, could be favored at low population density, whereas generalists (weak selectors) could achieve greater fitness when population density is high (Fig. 1b). This density-dependent switch in relative fitness payoffs would be revealed in a regression model by a significant interaction between strategies and population density:

$$W = w_b + \beta_1\alpha_x + \beta_2N + \beta_3\alpha_xN \quad (3)$$

where β_3 represents the regression coefficient associated with the interaction term α_xN . Solving the equation will identify which strategies have greatest fitness at different values of N . Somewhat more complicated models can be used to illustrate density- and frequency-dependence when fitness responds to preference for multiple resources (Fig. 1c). Just such a model of density- and frequency-dependence appears necessary to explain resource use by red deer (details below).

COMPETING STRATEGIES IN SIMULATED CONSUMER-RESOURCE SYSTEMS

Readers may wonder whether our simple phenomenological models can reveal the adaptive potential of different strategies in communities undergoing rather complex consumer-resource dynamics. We shared that concern, so we simulated the dynamics of a one-consumer-two-resource system, calculated the resource selection functions and fitness, and tested whether we could predict fitness from eq 2.

We based our simulations on Lotka-Volterra models that accounted for the diet preference of consumers exposed to exploitation and interference competition (Fryxell and Lundberg, 1997, eqs 2.10–2.12 and 6.6). The consumer population was comprised of specialists (S) consuming only resource 1, and generalists (G) consuming both resources without discrimination. Consumers were allowed equal access to two types of randomly distributed resources (R_1 and R_2) with R_1 more profitable than R_2 (i.e., $e_i/h > e_j/h$, where e_i is the energy content of resource i and h is handling time). The model assumes that consumers do not search while handling resources and resources simply have additive effects (i.e., no nutritional synergism) on energy intake. Consumer-resource dynamics of this system is given by:

$$\frac{dR_1}{dt} = r_1 R_1 \left[1 - \frac{R_1}{K_1} \right] - \sum X_{1j} N_j \quad (4)$$

$$\frac{dR_2}{dt} = r_2 R_2 \left[1 - \frac{R_2}{K_2} \right] - \sum X_{2j} N_j \quad (5)$$

$$\frac{dN_j}{dt} = c N_j (e_1 X_{1j} + e_2 X_{2j}) - N_j d \quad (6)$$

where N_j is the density of specialists (N_S) or generalists (N_G), R_i is the density of resource i , r_i is the maximum per capita rate of increase, K_i is carrying capacity, c represents a coefficient converting energy consumption into consumer offspring, and d is the per capita rate of consumer mortality. The rate of consumption of resource i by consumers adopting strategy j is given by X_{ij} , such that

$$X_{ij} = \frac{a \phi_{ij} R_i}{1 + a(\phi_{1j} h_1 R_1 + \phi_{2j} h_2 R_2) + a q_i (\phi_{iS} N_S + \phi_{iG} N_G)} \quad (7)$$

where a is the area searched per unit time and q_i is the time spent interacting with competitors when feeding on resource i . The probability of attack against each resource item encountered (ϕ_i) is $\phi_{iS} = 1$ and $\phi_{iG} = 0$ for specialists, and $\phi_{iG} = 1$ and $\phi_{iS} = 0$ for generalists.

We used the contribution to total population growth by individuals adopting strategy j (i.e., $[1/N]dN_j/dt$, where $N = N_S + N_G$) as a fitness surrogate. The per capita rate of population increase is commonly considered as a proxy for fitness in models of habitat selection (Morris, 1987, 2003b; Fryxell and Lundberg, 1997). We explored a subset of possible dynamics consistent with our phenomenological models' assumptions so that we could assess their ability to distinguish among different strategies of density-dependent resource harvest. We varied the input parameters in eqs 4–6 to match the assumptions of each statistical scenario. We simulated the dynamics, defined RSF coefficients for resource 1 as $\alpha_1 = 1$ for specialists and $\alpha_1 = 0$ for generalists, and substituted the predicted values of $[1/N]dN_j/dt$ and their associated variables (100 different values of N) into the corresponding statistical model (e.g., eq 2). We then assessed the fit of each model with a single linear multiple regression analysis. The fit with each model was nearly perfect ($F > 1,000$; $r^2 = 0.99$).

Let's first consider our simulations with strong interference when foragers compete for resource 2. Per capita growth rate declined with increasing consumer density. At low consumer density, specialists had higher per capita growth rate (fitness index) than generalists, whereas at higher consumer density, generalists were favored. The switch from specialist to generalist in this model occurred at a consumer density of approximately 8.4 individuals per unit area. The consumer population stabilized over time at a total ($N_S + N_G$) density of 12.8 individuals (Fig. 2b), a density where generalists had the greatest fitness (Fig. 2a). This conjoining of evolutionary and population dynamics reveals, as the

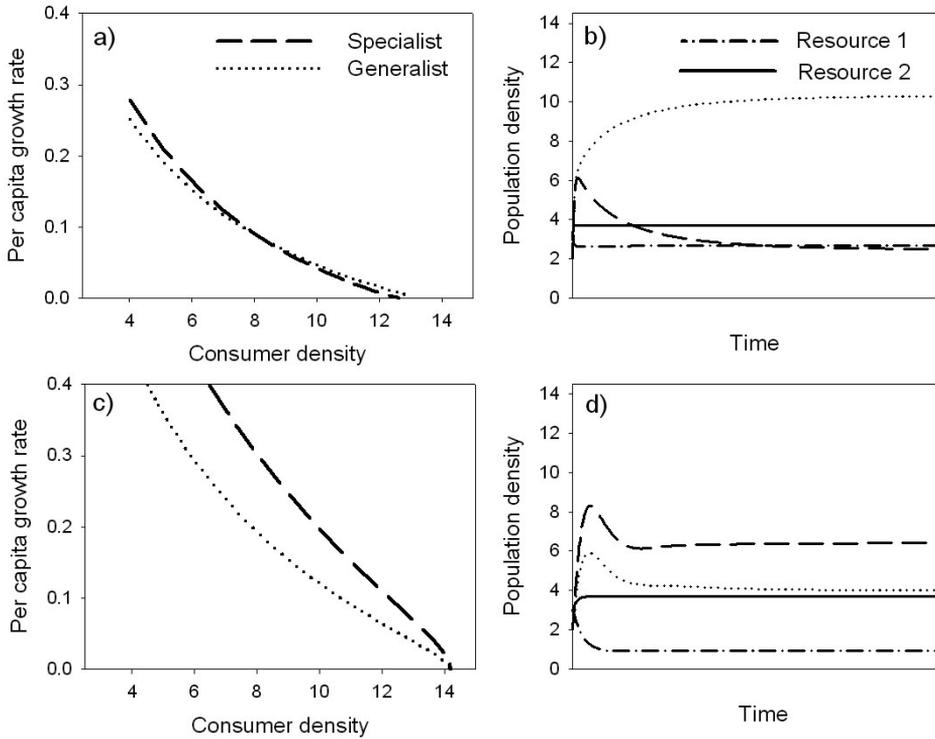


Fig. 2. Per capita contribution to total population growth as a function of total population density for generalists or specialists on resource 1, as well as temporal trends in population dynamics. The simulations for (a) and (b) were based on resource handling time ($h = 1$), the area searched per unit time ($a = 1$), the time spent interacting with competitors when feeding on resource 1 or 2 ($q_1 = 2.5$, $q_2 = 12$), the maximum per capita rate of increase ($r_1 = r_2 = 1$), the carrying capacity of resource of type 1 or 2 ($K_1 = K_2 = 4$), the energy content of each resource item of type 1 or 2 ($e_1 = 4$, $e_2 = 1$), a coefficient converting energy consumption into consumer offspring ($c = 1$), the per capita rate of consumer mortality ($d = 0.3$), and the probability of attack against resource type 1 or 2 for specialists ($\phi_{1S} = 1$, $\phi_{2S} = 0$) and for generalists ($\phi_{1G} = \phi_{2G} = 1$). Initial population density for resource type 1 and 2 was $R_1 = R_2 = 3$, whereas the density of specialists and generalists was $N_S = N_G = 2$. Parameter values for (c) and (d) were as in (a, b), except that $q_1 = 1$.

system approaches stability, that generalists are more than four times as abundant as specialists. Moreover, our interpretations of the simulated data are exactly what we expect when they are fitted to the statistical model $\{[1/N]dN_j/dt = 0.516 + 0.067\alpha_1 + (-0.202 \ln(N)) + (-0.030\alpha_1 \ln(N)), (r^2 = 0.99)\}$ and predict a switch from specialists to generalists around a population density of 9.3 (notice that, given the form of eq 3, $[1/N]dN_j/dt = [1/N]dN_G/dt$ when $N = \exp[-\beta_1/\beta_3]$, which here corresponds to $\exp[-0.067/-0.03] = 9.3$). The predicted switch point is close to the actual switch point (8.4) revealed in Fig. 2a.

The presence of a significant interaction term $\beta_3\alpha_x N$ (eq 3) does not necessarily imply a density-dependent shift in the favored strategy. We illustrate this by a simulation that decreased interference competition on resource 1 ($q_1 = 1$ instead of 2.5). The fitness curves converged, but never crossed within the range of positive fitness values (Fig. 2c). Adaptation thus favored the specialist in all extant populations. Total consumer population density ($N_G + N_S$) stabilized at 10.4 individuals in this model, and produced an equilibrium ratio of 1.6 specialists for each generalist in the population (Fig. 2d). The regression model describing the fitness function also includes the appropriate interaction term accounting for the fitness convergence of the alternative strategies: $\{[1/N]dN_j/dt = 0.903 + 0.385\alpha_1 + (-0.339\ln(N)) + (-0.134\alpha_1\ln(N)), (r^2 = 0.99)\}$. If we solve for the convergence predicted by the regression, then generalists and specialists would achieve equal fitness at a consumer density of 17.7 individuals per unit area, well beyond the maximum density in the simulations. Thus, even in this rather complex mechanistic consumer–resource system, the statistical model would have correctly predicted evolution toward specialists.

Difficulties can arise if consumer–resource dynamics cycle through time. Weak interference competition among consumers ($q_1 = q_2 = 0.1$), for example, can produce stable limit cycles (Fig. 3a). Even if the per capita rate of energy intake consistently favors specialists at low resource density, and generalists at high density (Fig. 3c), the overall gains associated with each strategy depend on the unstable dynamics of resources. Both high and low resource gain (and fitness) can be observed across a range of consumer population densities (Fig. 3b,d). With long-term data, the resulting cyclical selection would increase the variance in fitness and make it impossible to statistically predict evolutionary strategies unless one incorporates the underlying time series describing system dynamics. Alternatively, an investigation conducted over a limited number of generations would fail to identify cyclical ecological dynamics and would mislead our evaluation of adaptation. Neither criticism refutes the model. An appropriately specified model (with long-term temporal dynamics included) could correctly predict changes in strategies through time.

Our final simulation assessed an equally complicated example where fitness depends on density for some resources and not for others, and where selection of some resources influences the fitness achieved from others (density and frequency dependence, Fig. 1c). This scenario can be described by extending eq 3:

$$W = w_b + \beta_1\alpha_x + \beta_2N + \beta_3\alpha_x N + \beta_4\alpha_y + \beta_5\alpha_x\alpha_y \quad (8)$$

where β_4 and β_5 are regression coefficients associated with the RSF coefficient (α_y) of resource y (or a modifying covariate) and with the interaction $\alpha_x\alpha_y$, respectively.

To evaluate the reliability of eq 8, we imagined that densities of the two resources were fixed at their respective carrying capacities. We then introduced a third resource that increased fitness ($[1/N]dN_{jm}/dt$) directly, as well as indirectly by modifying the assimilation of resource 1:

$$\frac{dN_{jm}}{dt} = cN_{jm}(e_1X_{1jm} + e_2X_{2jm}) + c\phi_{mj}v(1 + X_{1jm}) - N_{jm}d \quad (9)$$

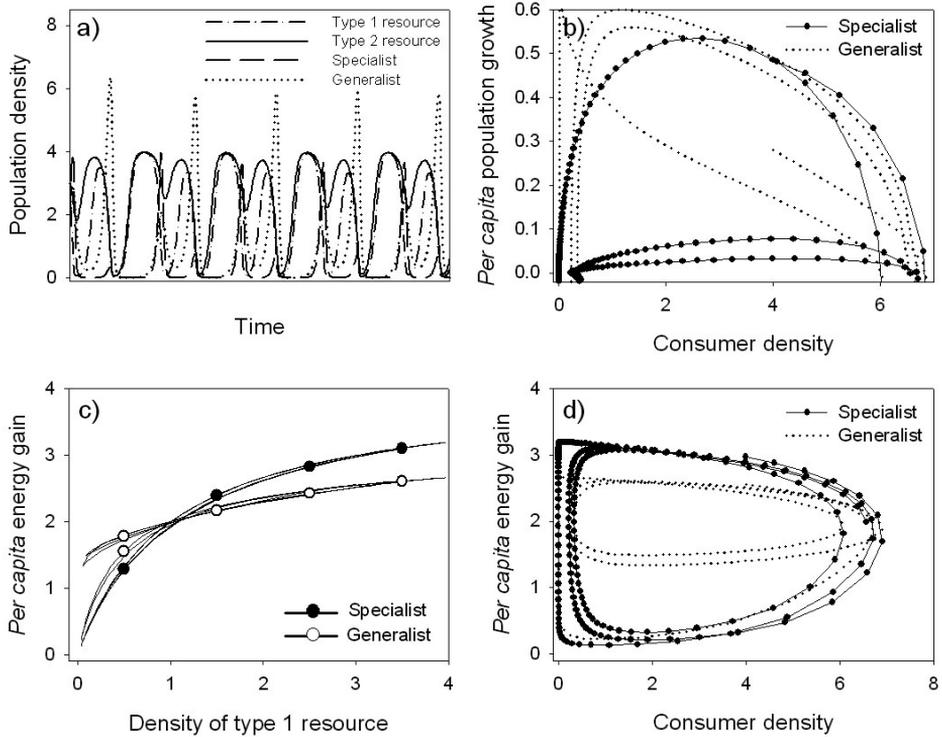


Fig. 3. An illustration of the dynamics of two resource populations consumed by generalists competing with specialists on resource 1. (a) Temporal dynamics of consumer and resource population densities. (b) Trajectories of per capita contribution to total population growth during the increasing phases of the population dynamics. (c) Per capita energy intake rate of consumers as a function of the density of resource 1 or (d) of the total consumer density. Parameter values as in Fig. 2a, except that $d = 0.2$, $e_2 = 2$, $q_1 = q_2 = 0.1$. In such systems where interference competition among consumers is weak, overall gains associated with a given strategy depend on the unstable dynamics of resources (see text for additional details).

where j distinguishes the strategies linked to the consumption of resources 1 and 2 (generalist or specialist), and where m represents the strategies related to the use of resource v . Consumers interfere with one another only while foraging on resources 1 and 2. Consumers are thus associated with one of four possible strategies (NSH , NSL , NGH , NGL). Each strategy identifies whether individuals are specialists (S) or generalists (G), whether their probability of attack when encountering resources 1 or 2 is high (H) or low (L) ($\phi_{1Sm} = 1$, $\phi_{2Sm} = 0$; $\phi_{1Gm} = 1$, $\phi_{2Gm} = 1$), and whether probability of attack by either S or G against resource items of type v may be either high or low ($\phi_{jH} = 0.7$, $\phi_{jL} = 0.5$).

The consumer population in this simulation stabilized at a density of 34.1 individuals per unit area. Consistent with the fitness functions (Fig. 4), strategy N_{GH} dominated the

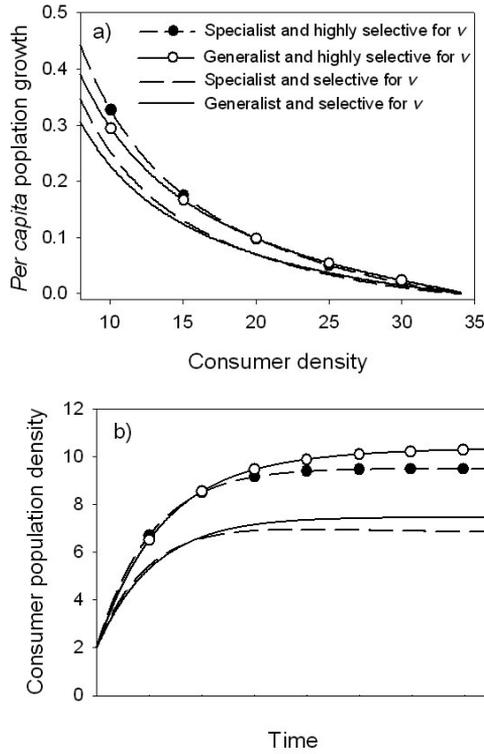


Fig. 4. An illustration of the effects of multiple resources on resource specialization. Specialists and generalists on resources 1 and 2 can also display different levels of selection for a third resource (v). (a) Per capita contribution to total population growth as a function of population density for resource 1 and 2 generalists, or specialists on resource 1. (b) Population dynamics of the four consumer strategies. Parameter values as in Fig. 2a, except that $d = 0.5$, $e_1 = 3$, $q_1 = 1$, $q_2 = 4$, $v = 2$, $\phi_{1Gm} = \phi_{2Gm} = \phi_{1Sm} = 1$, $\phi_{2Sm} = 0$, $\phi'_{jH} = 0.7$, $\phi'_{jL} = 0.5$.

system, while N_{SL} became the least common one. More importantly, the fitness functions associated with each strategy were expressed by the corresponding regression (i.e., eq 8): $\{[1/N]dN/dt = 0.837 + 0.160\alpha_1 + (-0.333\ln(N)) + (-0.065\alpha_1\ln(N)) + 0.324\alpha_v + 0.034\alpha_1\alpha_v, (r^2 = 0.99)\}$, which correctly predicted the superiority of N_{GH} , and inferiority of N_{SL} , at high consumer density.

Collectively, the simulations suggest that rather simple regression models can be used to infer favored strategies of resource specialization in real populations. So we searched for a system where we could exploit requisite data on resource use and availability, correlates of fitness, and population dynamics. All of these data have been collected through years of intensive study of free-ranging red deer on the Isle of Rum.

CAN WE PREDICT FAVORED STRATEGIES OF RESOURCE SPECIALIZATION IN REAL POPULATIONS?

McLoughlin et al. (2006) reported that the individual-pooled lifetime RSF for red deer hinds living along the Kilmory River on the Isle of Rum could be expressed as:

$$\text{RSF}_{\text{score}} = \exp [(-2.480 \alpha_{\text{Calluna}}) + (-1.932 \alpha_{\text{Eriophorum}}) + (-2.480 \alpha_{\text{Molinia}}) + (2.526 \alpha_{\text{Juncus}}) + (0.622 \alpha_{\text{Agrostis/Festuca}}) + (-7.86 \times 10^{-8} \alpha_{\text{Distcoast}^2})]$$

where $\text{RSF}_{\text{score}}$ is proportional to the probability of occurrence. The regression coefficients (α_i) are equivalent to resource selection ratios (Manly et al., 2002), and their exponentiated values can be interpreted directly as odds ratios (Boyce et al., 2003). In other words, negative coefficients signify low probability of red deer occurrence, whereas positive values increase this probability. The probability of occurrence of individual hinds thus generally covaried positively with habitats represented by *Agrostis/Festuca* grassland and *Juncus* marsh, and negatively with habitats corresponding with communities of *Molinia* flush, *Calluna* heath and heather moorland, *Eriophorum*-dominated bog, as well as with distance from the coast (*Distcoast*²). There was also substantial variation amongst individuals in their responses to habitat and to the distance from the coast, much of which McLoughlin et al. (2006) accounted for by estimating lifetime reproductive success (LRS) with respect to these gradients. The fitness surrogate of individual LRS was related to the lifetime RSF coefficients and conspecific density following the relationship:

$$\text{LRS} = \exp [0.516 + (-0.019 \alpha_{\text{Calluna}}) + (0.00006 \alpha_{\text{Eriophorum}}) + (-0.289 \alpha_{\text{Molinia}}) + (0.0036 \alpha_{\text{Juncus}}) + (1.143 \alpha_{\text{Agrostis/Festuca}}) + (-195,167 \alpha_{\text{Distcoast}^2}) + (-0.0048 \alpha_{\text{Density}}) + (-99,577 \alpha_{\text{Agrostis/Festuca}} \times \alpha_{\text{Distcoast}^2}) + (-0.0148 \alpha_{\text{Agrostis/Festuca}} \times \alpha_{\text{Density}})]$$

where α_i is the RSF coefficient for variable i (McLoughlin et al., 2006).

This model of LRS follows the general form given by eq 8, corresponding to our scenario 3 (Fig. 1c). The fitness associated with selecting the *Agrostis/Festuca* community declined with density and when individuals were farther from the coast (the coefficients associated with *Calluna*, *Eriophorum*, and *Juncus* were not significantly different from zero).

We display the LRS–density relationship for strong and weak selectors of *Agrostis/Festuca* and distance from the coast to illustrate the resulting set of strategies that can be expected from this complex association (Fig. 5). We illustrate only the density-dependent variation in LRS for specialists (represented by the 9th decile of observed RSF coefficients: +1) and generalists (i.e., RSF coefficient: 0) that either strongly avoided areas away from the coast (represented by the 1st decile of RSF coefficients: -3.33×10^{-06}) or selected such areas (9th decile of RSF coefficients: $+9.15 \times 10^{-08}$). We exclude negative coefficients because they correspond to individuals that do not benefit from consuming the resource and thus provide no additional information about the potential for evolution of specialization for *Agrostis/Festuca*. Other RSF coefficients were held constant at their median value because their influence is additive and does not change with density or selection for the *Agrostis/Festuca* community.

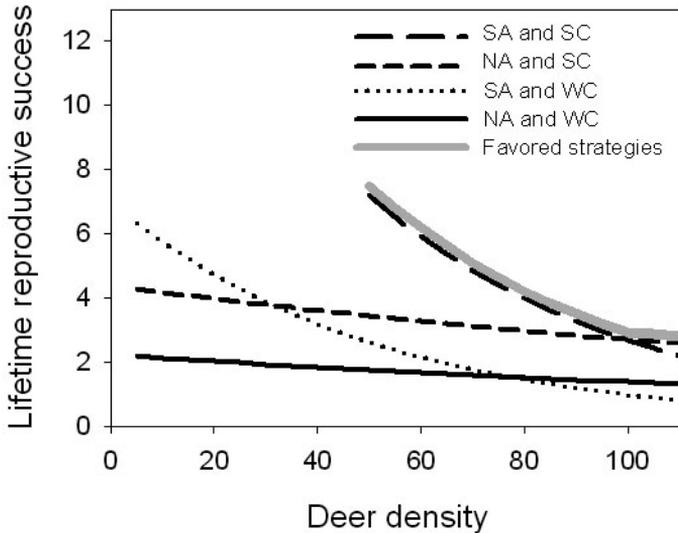


Fig. 5. An illustration of density-dependent declines in lifetime reproductive success (LRS) of red hinds adopting four selection strategies. Strategies correspond to individuals with high RSF coefficients for the *Agrostis/Festuca* community (strong selectors, SA), individuals not selecting (NA) the *Agrostis/Festuca* community, and individuals with strong (SC) versus weak selection (WC) for areas near the coast.

Over most of the observed range of deer density (including the average density of 72.3, McLoughlin et al., 2006), the strategy of strong selection for the *Agrostis/Festuca* community near the coast (SA + SC) yields the highest LRS (Fig. 5). At very high deer density, however, generalist hinds that do not select the *Agrostis/Festuca* community (NA), while still selecting areas near the coast (SC), achieve the highest fitness. The strategy of habitat selection by female red deer depends on density and on the frequency of alternative strategies.

DISCUSSION

Theories such as those related to adaptive (Metz et al., 1996; Geritz et al., 1997) and Darwinian (Vincent and Brown, 2005) dynamics allow us to explore the joint consequences of ecological processes underlying density- and frequency-dependent evolution. Evolutionary ecologists also possess the appropriate tools to apply the theory to resource adaptation and adaptive strategies of resource selection. The proof of concept comes from our ability to reveal habitat-selection strategies in simulated consumer–resource systems, and in a free-ranging red deer population, by conjoining resource selection functions with estimates of fitness and population density. This method appears to work

even when a strategy's fitness varies with population density and depends on alternative strategies.

Our assessment of resource selection strategies by red deer hinds illustrated an intriguing convergence of fitness for strong selectors of the *Agrostis/Festuca* community near the coast with coastal generalists. Red deer in this system use these areas in a manner consistent with ideal habitat selection (Conradt et al., 1999; McLoughlin et al., 2006). Thus, as population size increases, and the fitness of the *Agrostis/Festuca* specialists declines, we expect a greater proportion of individuals to adopt alternative competing strategies with less specialization on the *Agrostis/Festuca* community. This pattern is exactly what McLoughlin et al. (2006) demonstrated with the red deer RSF. Selection for the *Agrostis/Festuca* community diminished with density because individual hinds increased their use of alternative plant communities.

Although we can frame our approach in the context of G-functions and adaptive dynamics in the search for evolutionarily stable strategies, it differs in at least two important respects. First, our simulations of population dynamics do not explicitly include an evolutionary time scale. So, even though the regression models can predict which strategies yield the highest fitness at different population sizes, they cannot predict, on their own, whether any single strategy will come to dominate the population. If one has data on population dynamics, however, then it does become possible to gain insight into the evolutionary dynamics of resource selection because the evolutionary time scale is implicit in our simulations. Second, we chose input parameters designed explicitly to yield two persisting strategies. Although other "realistic" parameter values that we explored yielded only one strategy, we evaluate only outcomes where regression has potential to differentiate adaptive scenarios of density-dependent resource use (Fig. 1).

Coexisting strategies are, nevertheless, a common feature of density-dependent habitat selection. When fitness declines with density and habitats differ in their fitness potential, habitat use necessarily expands with increasing density. Individuals move among habitats to maximize fitness, and disperse their genes by doing so. Gene flow should thus increase with density and reduce genetic structure within any population that is capable of living and reproducing in multiple habitats.

We can test the evolutionary prediction of habitat-dependent gene flow with red deer because the habitat use, population dynamics, and genetics of the Kilmory River population have been monitored intensively since 1974. Populations increased rapidly after culling ended in 1972. Densities peaked in the early 1980s and have remained more or less stable since (Coulson et al., 1997; Albon et al., 2000; Nussey et al., 2005). During that time, individual hinds have become more generalized in habitat use. If our interpretations of red deer specialization are correct, then this inevitable density- and habitat-dependent mixing of strategies should decrease genetic structure. And, as the theory predicts, a global measure of genetic structure (F_{ST}) of female red deer living in different habitats has declined since the population stabilized in the early 1980s (Nussey et al., 2005). Field observations on red deer thus tend to support the evolutionary implications of density-dependent habitat selection. We showed that such observations can be used to identify adaptive strategies of resource use.

Some readers will wonder whether or not our phenotypic gambit (Grafen, 1982, 1984) can truly represent potential for evolution. Our method is aimed explicitly toward evaluating the fitness consequences of alternative resource selection strategies. The approach is not designed to predict the evolution of traits such as conversion efficiencies that increase an individual's ability to use one habitat over another. Rather, it uses patterns of resource and habitat use, and their dependence on density, to predict which strategies yield higher fitness at different population sizes. Each individual's pattern of resource use represents a potential strategy, but not necessarily a different genetic legacy. Even so, the method can be expanded to explore invasion of new strategies by altering the fitness consequences associated with the use of specific resources and habitats. We encourage those who would like to modify our approach to assess the invasion and convergence of new strategies. Although we have much to gain by linking resource use with the evolution of specialists and generalists, a thorough analysis of invasion potential and evolutionary stability may appear to have limited utility in conservation where biologists must forecast shorter-term responses to fluctuating environments and declining population sizes. We caution that ignoring evolutionary consequences in conservation strategies can lead to disastrous consequences. Even in vertebrates, evolutionary dynamics often occur on ecological time scales (Coltman et al., 2003; Réale et al., 2003; Edeline et al., 2007).

Others may question whether the demands of individual resource use and lifetime fitness limit the approach to a handful of exceptional species. When combined with suitable caveats on its evolutionary interpretation, the method can be applied to any system where one can obtain repeated measures of resource use on marked individuals, estimates of resource availability, and correlates of fitness. Assessments of foraging behaviors, such as those obtained from quitting-harvest rates, are especially promising because they may often be closely related to fitness (e.g., Morris and Davidson, 2000).

We suspect that many of our readers are surprised, and we hope delighted, by the ability of simple statistical models to infer the evolution of resource specialization. How can such simple models encapsulate the multi-textured adaptive surfaces of ecology and evolution embedded in G-functions (e.g., eq 1)? We believe that the answer is also rather simple. The range of current resource-use strategies revealed by RSFs are survivors of long-term adaptation. Current strategies reflect the historical dynamics of their constituent populations, and should often be close to their joint ecological and evolutionary optima (Mitchell and Valone, 1990).

But what if current strategies are not close to their evolutionary equilibrium? Can we use the connections between resource selection and fitness to infer evolutionary dynamics when populations or their environment change rapidly? We suspect so. Populations caught in an ecological trap (Dwernychuk and Boag, 1972; Schlaepfer et al., 2002), for example, should possess high frequencies of resource selection strategies that nevertheless yield low fitness. And populations of pest species on the verge of an epidemic may often be characterized by underrepresented strategies of high fitness.

Ecology and studies of evolution are too often treated as separate pursuits. Too many ecologists restrict their interests to describing resource use, or the dynamics of popula-

tions and communities, without due consideration of their evolutionary implications. Too many evolutionary biologists maintain a narrow focus on adaptation of single traits removed from their ecological milieu. Meanwhile, theoreticians rarely document how their models might be tested. And empiricists spend too much time and effort on the logistics of data collection and analysis. It is as though each scientist is mining a single precious metal from the ore of evolution while discarding all others in a slag pile of missed opportunities. Deep understanding of adaptation requires synthesis between ecology and evolution, and between theory and observation. We invite each kind of scientist to join us in extracting the exciting insights that will emerge as we mine the rich seams of adaptive strategies in real populations.

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