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Review

Adaptation and habitat selection in the eco-evolutionary process

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The struggle for existence occurs through the vital rates of population growth. This basic fact demonstrates the tight connection between ecology and evolution that defines the emerging field of eco-evolutionary dynamics. An effective synthesis of the interdependencies between ecology and evolution is grounded in six principles. The *mechanics* of evolution specifies the origin and rules governing traits and evolutionary strategies. Traits and evolutionary strategies achieve their selective value through their *functional relationships* with fitness. Function depends on the underlying *structure* of variation and the temporal, spatial and organizational *scales* of evolution. An understanding of how changes in traits and strategies occur requires conjoining ecological and evolutionary *dynamics*. *Adaptation* merges these five pillars to achieve a comprehensive understanding of ecological and evolutionary change. I demonstrate the value of this world-view with reference to the theory and practice of habitat selection. The theory allows us to assess evolutionarily stable strategies and states of habitat selection, and to draw the adaptive landscapes for habitat-selecting species. The landscapes can then be used to forecast future evolution under a variety of climate change and other scenarios.

Keywords: adaptation; ecology; evolution; habitat selection; mammals; natural selection

1. INTRODUCTION

Biodiversity is in crisis. The combined effects of habitat loss, exploitation, invasive species and climate change imperil species in all regions on Earth (e.g. [1–3]). Although we now possess the grim statistics, we have much to learn about forecasting possible futures for biodiversity.

Current forecasts use a variety of metrics [4], including physiological tolerances [5], phenology [6] and species-distribution models [7]. But we generally lack evolutionary projections even though it is increasingly acknowledged that ecology and evolution are intertwined in a single eco-evolutionary process [8–10]. Studies on a variety of model systems document clearly the to-and-fro of eco-evolutionary dynamics [11] and the resulting feedback between ecology and evolution [12]. Despite significant advances (e.g. [9,13–15]), we do not yet have a general framework to guide theory uniting the two disciplines [11]. Developing such a theory is difficult because it must include not only the feedback between traits and genetics at a variety of scales, it must also incorporate stochastic variation [16–18]. The theory is nevertheless crucial because forecasting the ecological and evolutionary consequences of climate change and other impacts on populations, communities and ecosystems is essential if we are to conserve biodiversity and avert further extinctions [19,20].

An effective eco-evolutionary synthesis must find common themes within which we can cast existing and

future theory. Morris & Lundberg [21] suggest that such a framework emerges from six pillars of evolution. ‘*Mechanics*’ includes the genetic and non-genetic origins of traits, phenotypes and strategies, as well as the nuts and bolts of population growth. Traits and strategies receive evolutionary value only through the ‘*functions*’ they perform in modifying reproduction and survival. The potentially complex interactions among traits, strategies and functions with the environment describe evolution’s ‘*structure*’, which varies with ‘*scales*’ of time, space and biological organization. Changes in the distributions of alleles, traits and strategies occur only through the ‘*dynamics*’ of populations and communities. ‘*Adaptation*’ tells us why there is a splendid but imperfect fit between form and function, why there is diversity and progression in life and why species are not everywhere abundant.

I evaluate the suitability of this ‘world-view’ by applying it to our understanding of habitat selection. All organisms occupy habitat and most, if not all, are capable of density-dependent habitat selection at some life stage and scale (including plants [22]). I use theory and a selective review of case studies to document the six pillars in the context of habitat selection. I then merge theory with research on Arctic lemmings, where we have obtained the requisite density-dependent data, to evaluate whether it is possible to forecast likely consequences of global warming, and other forms of environmental change, on future habitat choice.

I begin with a short review of theories outlining the mechanics of habitat selection. Rather than simply assessing habitat use relative to its availability, which is sometimes called ‘habitat selection’ (e.g. [23,24]), I concentrate on active habitat choice whereby individuals with

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the option of using different habitats choose to occupy, move from or remain in some habitats rather than others [25]. I demonstrate that habitat choice has a variety of functional relationships with reproduction and survival, and that its structure corresponds to the way that fitness covaries with habitat use and density. I assess the scale and dynamics of habitat selection, then use the interaction between ecological and evolutionary dynamics to predict patterns of future habitat occupation. I conclude with a short reflection on the utility of this approach to our understanding of habitat selection and adaptive evolution.

2. MECHANICS: HOW HABITAT SELECTION WORKS

In order to select a habitat, organisms must ‘move’ in space or time. Appropriate lower level processes include imaginative mechanisms of motility (demonstrated by bacteria that rise up and walk [26]), timing and vectors of movement and the physiology of hibernation and diapause. The panoply of influences modifying departure and settlement options available to, and decisions by, individuals represent another level associated with the mechanics of dispersal (electronic supplementary material, table S1). Descriptions of, and debates about, these mechanisms can be found in a large and sometimes complex literature (e.g. [27–29]). I focus, instead, on additional mechanics associated with strategies of density-dependent habitat occupancy that determine the rules of habitat choice.

The proportional use of different habitats by members of a population represents the strategy of habitat occupation. The strategy can be either genetic or behavioural [30], and either pure (each individual occupies only one habitat) or mixed (individuals adjust the proportion of time that they spend in different habitats). There are but three broad mechanisms underlying such strategies. (i) Patterns of habitat distribution and abundance are determined entirely by within-patch population dynamics: there is no habitat selection. (ii) Habitat differences in density caused by population dynamics are modified by dispersal independent of density. (iii) The patterns reflect intrinsic dynamics coupled with density-dependent habitat choice.

Theories of density-dependent habitat selection share the assumption that fitness, as measured by the instantaneous change in production of future descendents, depends on population density [31–33]. The accounting necessary to calculate fitness is seldom easy and is complicated by local circumstances and the degree of relatedness. These complexities are not, however, crucial to understanding theories of habitat selection. Individuals choosing among habitats with different fitness functions should occupy those habitats that maximize their expectation of fitness. This simple mechanistic rule yields a distribution of these ‘ideal’ individuals among habitats that equilibrates when an individual’s expected (but not necessarily the population mean) fitness is similar in each one [31–34].

The ability to achieve an ideal distribution is constrained by limits on acquisition, value, and reliability of information (all of which will vary with population density [35,36] and with the spatial and temporal autocorrelation in habitat [37–39]), mobility, cognitive and non-cognitive [40] capabilities to process and respond

to the information acquired, causes of dispersal unrelated to habitat selection and whether individuals are free to settle where they choose. Each constraint can cause populations to either undermatch or overmatch population density relative to habitat quality. Such ‘departures’ have frequently been inferred from behavioural studies of patch use (e.g. [41]), as well as from the field where surrogates of fitness differ between habitats [42], fail to match differences in resources [43] or where animals occupy apparently low-quality habitat [44]. None of these departures limits the utility of ideal habitat selection as a conceptual model to guide our understanding of spatial distribution and abundance and may even be somewhat irrelevant because simple patch-leaving rules also yield ideal distributions [45].

3. FUNCTION: HABITAT SELECTION’S RELATIONSHIP WITH DENSITY

The function of any trait (or strategy) involves not just the task performed, but also its relationships with other traits and tasks, and most importantly, how it maps onto density and fitness [21]. In a finite world, fitness in a single habitat must, beyond a critical threshold, decline with increasing density. The simplest mapping function that we can use to illustrate this effect is given by logistic population growth

$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left(1 - \frac{N_i}{K_i} \right), \quad (3.1)$$

where N_i is the density of individuals living within habitat i , r_i is the instantaneous rate of population growth and K_i is the habitat’s carrying capacity. Habitats will vary in r , K or both (figure 1). If, for simplicity, we imagine only two habitats, then all possible strategies are uniquely identified by the proportion (p) of individuals living in habitat 1 ($0 \leq p \leq 1$), or alternatively (q) in habitat 2 ($p + q = 1$). The mean fitness of any p strategy is, thereby,

$$p \cdot r_1 \left(1 - \frac{N_1}{K_1} \right) + q \cdot r_2 \left(1 - \frac{N_2}{K_2} \right), \quad (3.2)$$

which can then be plotted as the adaptive landscape of habitat selection in both the ecological (variation in population size) and evolutionary (different strategies) dimensions (figure 1). The slopes of this adaptive landscape represent the density-dependent selection gradients acting directly on the proportional occupation of habitat (different values of p).

Logistic population growth is a useful caricature for drawing adaptive landscapes of density-dependent habitat selection, but the general approach will work for any functional form of density dependence. Quite different functions can emerge, for example, with Allee effects [31], when individuals interfere with one another [46], or when early colonists pre-empt occupation of high-quality sites by later arriving individuals [47–51]. Fitness functions will be strongly concave if interference has a multiplying effect, such as when each arriving individual consumes or secures an equal proportion of remaining resources [52–55]. The functions shift towards inverted sigmoidal curves when individuals occupy sites in the order of their individual, rather than average, quality (e.g. [47,48,56]).

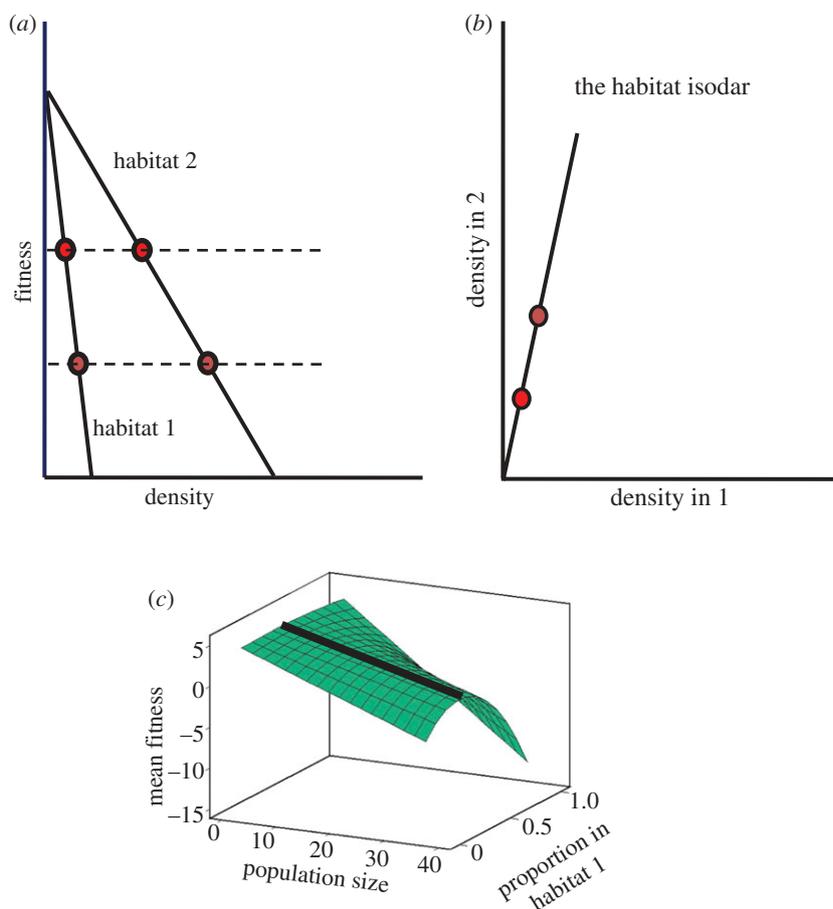


Figure 1. An illustration of the functional relationships between density and fitness for two habitats that produce a fixed optimum strategy of habitat selection. (a) The underlying fitness–density functions. Circles indicate densities with equal fitness in each habitat. (b) The resulting habitat isodar obtained by plotting all possible densities where fitness is equal in both habitats. (c) The map (adaptive landscape) of mean fitness for all possible strategies (proportions) of habitat occupancy at different population sizes. The maximum height of the landscape (bold black line) represents the optimum strategy of habitat selection at all population sizes.

4. STRUCTURE: HOW HABITAT SELECTION MAPS ONTO FITNESS

The adaptive landscape of habitat selection illustrated in figure 1 sinks and changes shape with increasing population size. At low density, all strategies yield similar fitness: the adaptive landscape is relatively flat (shallow selection gradients). This pattern quickly gives way to rather intense stabilizing selection on p with steep gradients at high density. Evolution towards the optimum strategy (the value of ' p ' that maximizes fitness) is thus much more rapid when the population exists at high density than when it exists at low density. Fitness varies with density, but the selection gradients converge on a single optimum value of p (a single strategy of habitat selection) at all population sizes.

This conclusion depends critically on the relative slopes and intercepts of each habitat's fitness function. If one habitat yields a higher potential growth rate at low density than does the other, then p varies with changes in population size (figure 2). Individuals occupy only habitat 2 at low density, then occupy habitat 1 at an increasing ratio with each increase in population size.

The adaptive landscapes in figures 1 and 2 may appear similar (both decline and change shape with population size: selection gradients in each example are shallower at low population size than they are in large populations),

but the emergent strategies of habitat selection depart dramatically from one another. Selection in figure 1 is always stabilizing around a single optimum p , whereas selection in figure 2 is directional towards 100 per cent occupation of habitat 2 at low population size, and stabilizing around varying habitat preferences at higher population sizes.

We can reveal the optimum strategy by plotting the system's habitat isodar: the set of densities in each habitat such that an individual's expected fitness is identical in each [33]. In the case where linear fitness curves diverge from a single point of high fitness, the isodar passes through the origin (constant p , figure 1b). But when fitness at low density is higher in one habitat than in the other, the optimum strategy (p) changes with population size (the isodar intercept is greater than zero, figure 2b).

Isodars represent the solution to the habitat-selection game played by currently available phenotypes. The game will change if new phenotypes (or mutants) invade the population. Phenotypes are likely to vary in their relative ability to perform vital functions in the different habitats that they exploit. Improved aptitude to one habitat will frequently be traded off against lost ability in another (e.g. [57]). These trade-offs represent the range of possible habitat-selection strategies that might evolve. But can all of them lead to potentially viable alternatives?

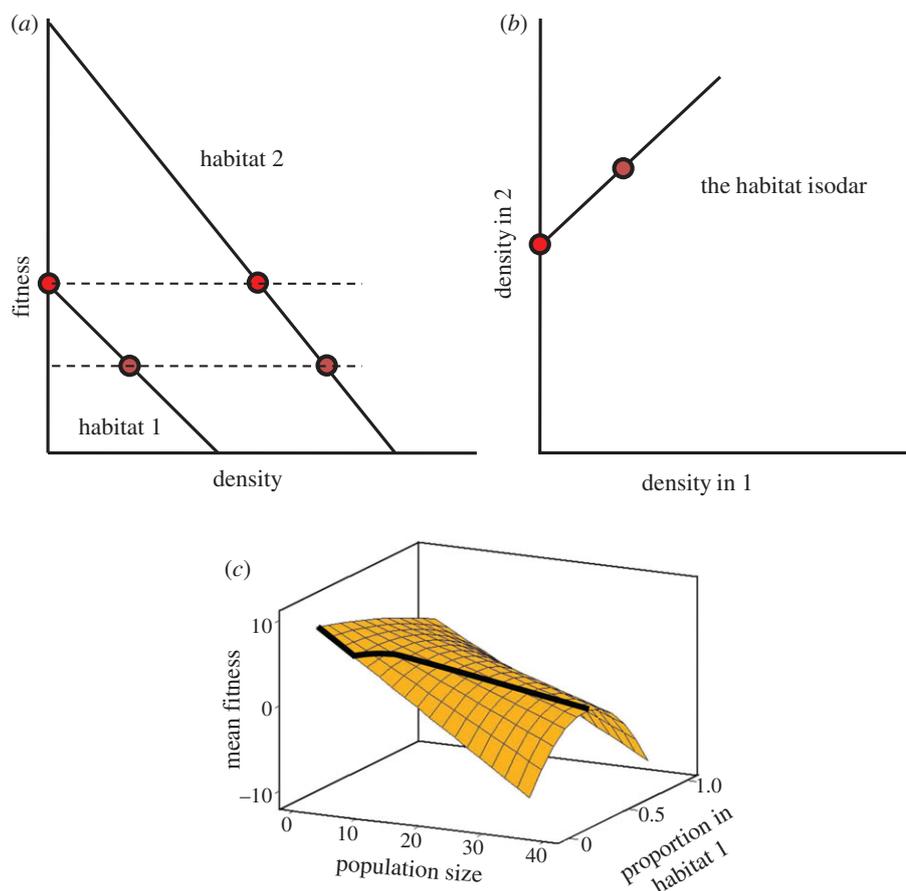


Figure 2. An illustration of fitness functions that yield changing optimal strategies of density-dependent habitat selection. (a) The fitness–density functions. Circles indicate densities with equal fitness in each habitat. (b) The habitat isodar. (c) The adaptive landscape and the varying optimum habitat-selection strategy (bold black line).

Figure 3 provides the answer by illustrating fitness functions of an initial resident phenotype (black lines) and two of an infinite number of possible mutants. Mutant 1 (red lines) trades improved aptitude over the resident in habitat 2 against reduced aptitude in habitat 1. Whether it can replace the resident depends on the net density-dependent fitness gain or loss associated with the trade-off. Mutant 2 (blue lines) has a similar trade-off, but accrues less fitness than the resident in both habitats. Mutant 2 thus represents a possible alternative, but it cannot replace mutant 1 because its fitness in both habitats is less than that of the resident at all population sizes. Definitive experiments testing these predictions will herald a significant advance in our understanding of eco-evolutionary feedback on habitat selection.

Our general theory imagines fixed habitats occupied by identical individuals. The models thus ignore much of the underlying structure of habitat selection. Habitat choices will vary, for example, with an individual's age and state if different habitats yield different age- and state-dependent relationships between reproductive value and density. The characteristics of a habitat, such as temporal and spatial variation in productivity and predation risk, will also vary among replicates (and through time), as will the resulting relationships between fitness and density.

The effect of such heterogeneity on habitat isodars will depend on the magnitude of the (often stochastic) variation within and among states and habitats (e.g. [58]),

as well as measurement error [58,59]. If habitats are dramatically different from one another, then between-habitat differences can be expected to predominate and yield relatively homogeneous isodars. But if habitat comparisons are too fine, then within-habitat heterogeneity might easily swamp the isodar signal. It will often be advisable, therefore, to evaluate heterogeneity statistically by searching underlying gradients for habitat clusters [60], by accounting for random temporal or spatial variation in mixed-effects models or by assessing for differences in habitat use among age and state classes [46,61].

5. SCALE: THE DIMENSIONS OF HABITAT SELECTION

Few topics in habitat selection have attracted more interest than the problem of scale. Many treatments view habitat selection as a hierarchical (statistical) process whereby the 'order of selection' is conditional on scale [24,62]. Occupation of a home range or territory, for example, is considered a second-order process because it must be included within the species' geographical range. Selection among habitats by an individual is third order because it depends on habitat availability within the home range. Although this approach is useful for comparisons of use relative to availability, it begs the question of how geographical ranges expand and contract, as well as what sequences and scales of choices are made by individuals when choosing a home range or territory.

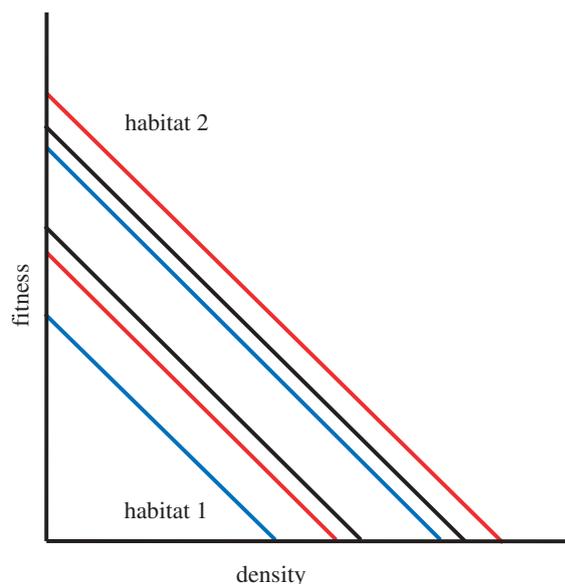


Figure 3. Fitness functions in two habitats for a resident strategy (black lines) and two possible mutant strategies. Mutant 1 (red lines) is a viable alternative to the resident because it trades off increased fitness in habitat 1 for reduced fitness in habitat 2. Mutant 2 (blue lines), which has the same relative trade-off, is suboptimal because its fitness at all densities is less than either of the other two strategies. The curves need not be linear or parallel.

Numerous studies, for example, have associated density or distribution with meticulous point measurements of structure to document species' so-called microhabitat preferences without first accounting for larger scale (macrohabitat) differences. Operationally, macrohabitat frequently coincides with the scale at which one might estimate density for isodars [63]. Inspection of figure 2 reveals an additional problem. The relative use of the two habitats varies with population density. Only one of the habitats is acceptable (=statistically available) at low population size. So, any study that ignores population dynamics and adaptive (fitness-maximizing) behavioural choices in assessing use relative to availability has a high probability of misinforming habitat preference [64]. Unfortunately, this is likely to be a rather large set because many of these studies consider neither dynamics nor fitness [65].

Habitat scale also has profound influences on evolutionary dynamics. We can explore these effects within a generation using a caricature of models designed to assess constraints on local adaptation [66–68] that were developed further by Dan Cohen [69]. The weighted mean fitness of a heritable strategy (or trait) U within a well-mixed population exploiting several habitats can be written as

$$\hat{W}_U(U) = \sum_i H_i R_i W_i(U), \quad (5.1)$$

where H_i is the proportion of the population exposed to habitat i , R_i is the expected net lifetime reproduction of an individual experiencing that habitat and $W(U)$ is the relative fitness of the strategy. The main point is that the weighted mean fitness is determined by exposure to habitat. The global optimum will depend much more on common habitats than it will on sparse ones. Thus,

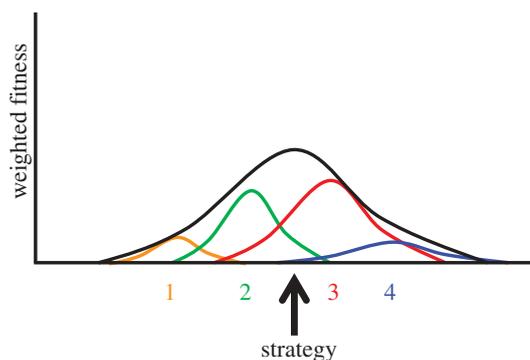


Figure 4. An example demonstrating that the optimum strategy emerging as the weighted mean fitness in several habitats may depart substantially from the optimum strategy in any single habitat. The bold black curve and arrow signify the weighted mean fitness and weighted optimum, respectively. Coloured curves correspond to the weighted fitness functions in four different habitats. The optimum strategy in any single habitat (indicated by numbers) will often differ from the overall weighted optimum. After Cohen [69].

individuals living in relatively rare habitats, or habitats with low density, may be poorly adapted to local conditions (figure 4).

The applicability of Cohen's model is closely linked to the spatial scale of habitat selection that can determine how thoroughly populations are mixed. The assumptions of the model are easiest to attain in a fine-grained environment [70] where individuals use each habitat in direct proportion to its availability. Movement among patches is at a maximum in such an environment [71], and so too is the potential for gene flow. In coarse-grained environments, however, individuals exploit only a single habitat, and dispersal is often either minimal or directed by habitat selection. Directed dispersal depends on the relative fitness differences among habitats and the cost of habitat selection [72], both of which will often vary with population size (figure 2).

A thoughtful reviewer noted that equation (5.1) also applies to apparently coarse-grained life histories where individuals 'born and raised' in a single habitat emerge to join a common (mixed) breeding pool before re-entering the matrix of habitats to reproduce. Local adaptation will thus be constrained by gene flow that is proportional to the production of descendants from each habitat. The function of different trait values will nevertheless vary among habitats, as will the survival and future reproduction of the individuals possessing them. Whether these potential differences in recruitment are realized will depend on the degree of developmental and behavioural plasticity available to neutralize fitness differences among environments.

Pelagic differences among rodent species represent a suitable system to evaluate Cohen's model. Relatively simple mutations cause cryptic colour variation in rodents [73–75] that reduces predation from both aerial and terrestrial predators [76]. Colour variants of beach mice (*Peromyscus polionotus*) occupying different dune environments in Florida and Alabama occur in populations with little gene flow and are thus capable of local adaptation. Gene flow is high, however, among populations of pocket mice (*Chaetodipus intermedius*) occupying areas with light-coloured rocks versus dark lava flows in New Mexico and

Arizona [77]. Frequency-dependent selection on pocket mice, presumably through differential mortality, overrides gene flow that must nevertheless produce large numbers of sub-optimal phenotypes. Contemporary gene flow in the pocket-mouse populations is likely to inhibit local adaptation, and particularly so in rare habitats, an interpretation bolstered by asymmetries in both migration and selection experienced by animals on the two substrate types [78].

6. DYNAMICS: HOW DENSITY AND FREQUENCY ALTER HABITAT SELECTION

The grain of habitat selection provides a convenient platform on which to evaluate how the struggle for existence reduces a strategy's fitness (figures 1 and 2). Imagine a population living in a fine-grained two-habitat environment where U different strategies (such as the proportion of time spent in each one) trade-off fitness procured from the two habitats, and that we plot the respective fitnesses against one another. The resulting fitness set [70] details the expected fitness in both habitats. The best strategy maximizes mean fitness determined by overlaying the fitness set with Levins' [70] adaptive function

$$W_2 = \frac{A}{q'} - \frac{p'}{q'} W_1, \quad (6.1)$$

where W is fitness, A represents the (arbitrary) weighted fitness of both habitats combined and p' and q' ($p' + q' = 1$) are the respective proportions of habitats 1 and 2 in the landscape (this model, unlike Cohen's, does not include the proportion of individuals exposed to each habitat). Mean fitness at any fixed population size is given by the point of tangency between the adaptive function and the outer edge of the fitness set. Levins' [70] model includes the frequency of habitats, but neither the density nor frequency dependence of the habitat-selection game. The strategy that maximizes mean fitness is appropriately discounted by the relative weights of habitat distribution, but only for a single value (slice through the adaptive landscape) of population size.

Yet it is clear that fitness varies with density and strategy (figures 1 and 2). The mean fitness of an individual that uses habitats in a particular ratio thus depends on density and on the frequency of habitat use by other individuals (the alternative strategies of habitat selection). These complexities limit the utility of using Levins' analysis to determine the evolutionarily stable strategy of habitat selection.

The limitations of fitness sets are mostly overcome by Brown [79] and Vincent & Brown's [80] fitness-generating function for habitat selection

$$G(v, u, N) = vF_1(x_1) + (1 - v)F_2(x_2), \quad (6.2)$$

where v is the virtual strategy of the proportional use of habitat assessed against all feasible strategies u ($u \in [0, 1]$) at population size N , $vF_1(x_1)$ is the fitness achieved by v in habitat 1 at total population size N for all u and $(1 - v)F_2(x_2)$ is the fitness achieved in habitat 2. The adaptive function is subsumed in each habitat's relationship between fitness and density. Fitness in Brown's model depends on strategy, density and the frequency of other strategies in the population. Frequency-dependent habitat selection demonstrates the superiority of the G -function approach because frequency represents an additional

factor that can warp fitness sets away from their underlying tradeoffs in aptitude. It is nevertheless important to bear in mind that the challenges to empiricists cannot be so easily simplified. Mathematical convenience does not eliminate the fact that tests of the theory must deal, in some way, with real fitness sets, adaptive functions and adaptive landscapes.

We should not assume, however, that an ideal-free distribution yields a single strategy played equally by all. When individuals occupy habitat such that their expected fitness is the same in each, all receive the same payoff. This outcome is not equivalent to each being identical in either phenotype or strategy to all others. Rather, the ideal-free distribution's Nash equilibrium collapses the fitness set for all extant strategies to a line of slope 1 (all strategies achieve equal fitness in both habitats [21]). Any adaptive function will intersect the linear fitness set along the same vector of equal fitness. Linear fitness sets represent a form of emergent neutrality [81], enabling persistence of many different habitat-selection options. It will thus often be most informative to think of the ideal-free distribution as an evolutionarily stable state [82] where many different strategies following the same general behavioural rule coexist (similar 'multiple solutions' to ideal-free habitat selection occur in predator-prey habitat-selection games [83–85]).

7. ADAPTATION: PUTTING HABITAT SELECTION TO WORK

The process of adaptation to habitat unites ecological with evolutionary dynamics to yield the evolutionarily stable strategy or state that solves the habitat-selection game. Each has three key properties [86]: the strategy or state must be convergence stable (reaches a fitness peak), it must resist invasion from other competing strategies or states and it must be able to invade other strategies or states when rare.

Two of the three properties (convergence stability and resistance to invasion) can be inferred directly from adaptive landscapes as illustrated in figures 1 and 2. Fitness converges along a single ridge of habitat choice that maximizes fitness. The third property requires that we evaluate whether this fitness-maximizing strategy, when rare, can invade neighbouring strategies when they are common (the so-called neighbourhood invader strategy [86]). We can expand the analysis to a global invader strategy when considering only two habitats because our adaptive landscapes include all possible values of p .

First, we calculate the fitness of all strategies as in figures 1 and 2. Then we calculate, for each of these strategies, the difference in fitness that would accrue to one individual if it had instead followed the rule of ideal-cost-free habitat selection: 'occupy habitat in the proportion that maximizes individual fitness'.

Figure 5*a* illustrates the global invader strategy landscape for the diverging fitness functions in figure 1(*a*). The optimum ideal-free strategy runs down the valley-bottom of the invader landscape. An individual playing the ideal-free strategy obtains higher fitness, at all population sizes, than it would by playing any other strategy.

Figure 5*b* illustrates the corresponding invader strategy landscape for the converging fitness functions in figure 2*a*.

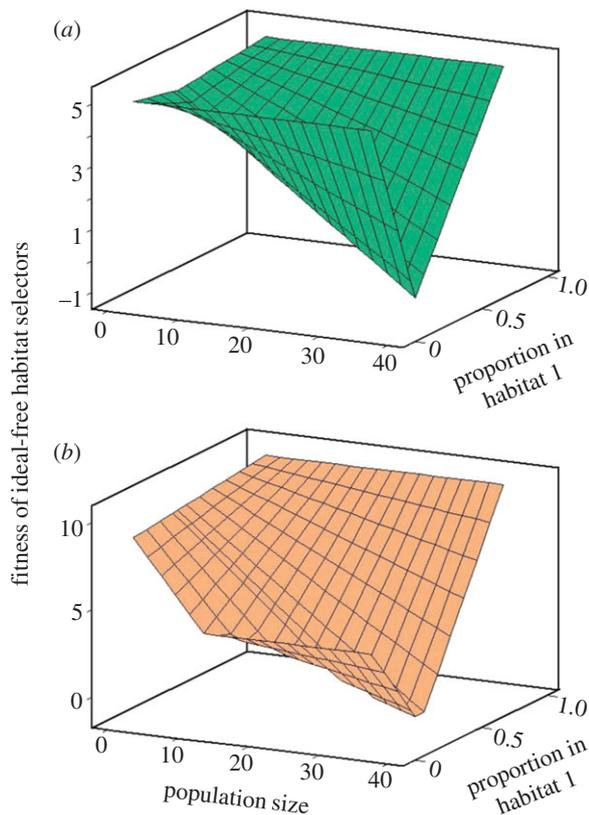


Figure 5. Global invader strategy landscapes for ideal-free habitat selection that corresponds with the fitness–density functions in (a) figures 1a and (b) 2b. The ideal-free distribution is evolutionarily stable.

Again we see that the ideal-free strategy can invade all others when both habitats are occupied (the ideal-free strategy is equal to the ‘occupy only habitat 2’ strategy at low population size).

Figures 1, 2 and 5 hint at an exciting possibility. If we can plot adaptive landscapes for real systems, then we can forecast future adaptation to habitat at different population sizes. Even more exciting is the possibility of invoking eco-evolutionary feedbacks to explore adaptive evolution under alternative scenarios that change habitat quality and abundance. Recall that the strategy of habitat selection is revealed by the system’s habitat isodar. It should thus be possible to use the isodar to infer the expected shapes of fitness functions, the underlying adaptive landscape and thus future adaptation to habitat.

Morris *et al.* [87] outlined the requisite theory. The general habitat isodar of a population exploiting habitats 1 and 2 is the simple linear equation

$$N_2 = C + bN_1, \quad (7.1)$$

where N_i is population density in habitat i . For populations growing logistically (that yield the linear fitness functions in figures 1 and 2), $C = [(r_2 - r_1)/r_2]K_2$ and $b = (r_1/r_2)(K_2/K_1)$ [51]. An empirical isodar includes estimates for both C and b , and so assuming that one can estimate the maximum growth rate and carrying capacity in a single habitat, it is possible to generate the remaining values for the second habitat [87]. Knowing the fitness functions, it is then a relatively simple task to plot the adaptive landscape (from equation (3.2)). The landscape can then be

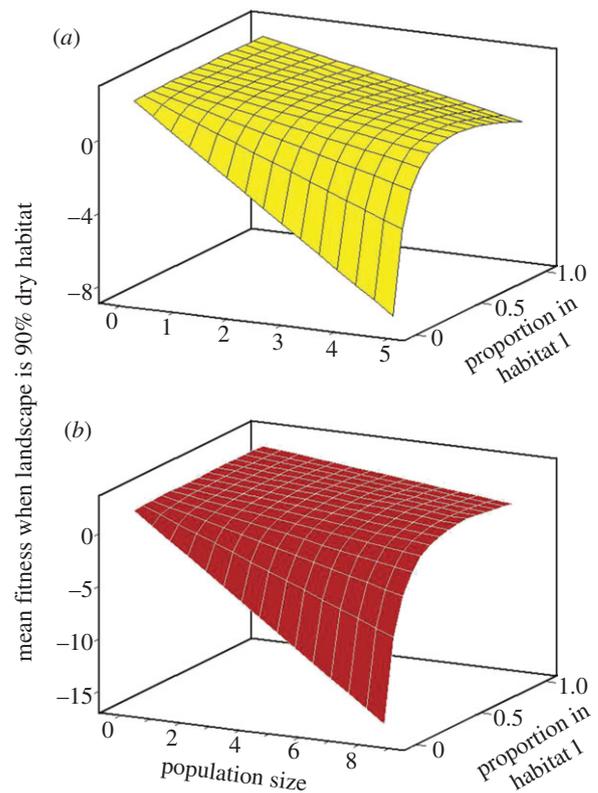


Figure 6. (a) Minimum and (b) maximum forecasts for future adaptive landscapes of habitat selection by brown lemmings on Herschel Island when 90% of the area is composed of xeric tundra. Forecasts are based on the 95% confidence intervals about the brown lemming’s calculated isodar ($Y = 0.02 + 3.42X$ and $Y = -0.11 + 6.96X$, respectively; [87]). Note differences in scale.

used to forecast future evolution under varying scenarios of habitat change and population dynamics.

Morris *et al.* [87] applied the theory to three species of small mammals living in xeric and mesic tundra on Canada’s Herschel Island. They calculated the maximum population growth rate of brown lemmings (*Lemmus trimucronatus*) from estimates of reproductive frequency and litter size, then drew the adaptive landscape by substituting this value and an estimate of carrying capacity weighted by the frequency of each habitat on the island (73% xeric) into *Lemmus*’ linear isodar. Herschel Island is expected to become drier through climate change. It seems reasonable to assume that reduced precipitation will alter the frequencies of wet and dry tundra, so Morris *et al.* [87] projected their empirical isodar to a drier island with 90 per cent xeric habitat.

Projections on future habitat selection can only be as accurate as estimates of current habitat use, so I recalculated adaptive landscapes for a drier island using Morris *et al.*’s [87] confidence intervals about the brown-lemming isodar. Although the upper estimate of the adaptive landscape (figure 6b) is somewhat steeper than the lower estimate (figure 6a, note differences in scale), and the lower estimate exhibits somewhat more stabilizing selection, there is relatively little difference between them. In each scenario, flat selection gradients provide little traction for adaptive change at low population sizes. Selection gradients against occupation of dry habitats become progressively steeper, however, with increasing population size.

The implication for species with wildly fluctuating population sizes, such as those that typify lemmings [88], are rather profound. When lemming populations exist at low density, almost any strategy of habitat selection yields similarly high fitness. Habitat selection may thus drift away from the optimum mesic niche. But when population density is high, suboptimal strategies, and particularly those with large proportions of individuals occupying dry habitats, are replaced by individuals earning much higher fitness through their mesic preference.

Flat adaptive landscapes at low density thus alert us to a potentially very important role for drift in eco-evolutionary feedback. Low-density populations can ‘explore’ a variety of potential habitat-selection strategies to be tested later by natural selection at higher densities. Drift at low density can thereby alter trait distributions that ultimately produce different fitness functions. New fitness functions yield a new adaptive landscape to be explored by natural selection.

8. REFLECTION: HABITAT SELECTION AND THE ECO-EVOLUTIONARY PROCESS

Habitat selection has far-reaching consequences for both ecological and evolutionary dynamics. Theory and practice promise a method to predict future distribution and abundance associated with global warming and any other process that modifies the abundance and quality of habitat.

There is much work that needs our attention. Stochastic effects, for example, can mask the patterns emerging from the deterministic processes outlined here. Null models, such as those used by Haila *et al.* [89], and more recently by Campbell *et al.* [90], downplay active habitat selection as a factor determining the distribution and abundance of forest birds. Stochasticity can also influence the evolution of habitat preferences through acquisition of discriminating cues [91]. Many other forms of stochasticity have been explored by Jonzén *et al.*, including temporal differences in reproductive rates coupled with variation in sampling efficiency [59,92] and random temporal variation in fitness coupled with probabilistic habitat selection in correlated environments [58]. Temporal stochasticity raises numerous questions about the appropriate measure of fitness (e.g. [59]), which complicates decisions by habitat selectors. Choices maximizing current population growth rate may not maximize long-term fitness that depends critically on the pattern of temporal variation [93].

Stochastic models, including those that vary habitat-dependent population growth parameters and population sizes of interacting species [83,84,94], tend to produce results that can depart rather dramatically from deterministic solutions. None, however, impinges on the utility of the underlying theory, nor of isodars representing evolutionary attractors for habitat selection [58].

No population exists independently of others. Future applications of the theory must, therefore, pay increasing attention to different forms of habitat selection [95], age and stage structure, individual state and population dynamics (e.g. consumer resource models instead of Lotka–Volterra [85]), as well as trophic structures and species interactions [82,83,85]. As we embark on developing these more complex models, we should ponder the remarkable fit that simple linear models seem to

provide with highly complicated systems. Even the simplified Arctic foodweb in which we predict the eco-evolutionary future of brown lemmings has far more connections than we are likely ever to measure effectively [88]. Yet, amidst this complexity, brown-lemming habitat use on Herschel Island is revealed by a single-species linear isodar that is independent of the densities of two similar coexisting rodent species [87]. Each Arctic rodent in this three-species community is specialized on a different region along the xeric–mesic gradient [96]. The struggle for existence among conspecific individuals is the dominant interaction that determines habitat use by rodents on Herschel Island.

Interspecific competition nevertheless influences isodars in other rodent communities [46,97], and computer simulations demonstrate an ability for trophic interactions to hide otherwise apparent trends in habitat occupation between competing species [83,84]. An astute ecologist will thus test for such effects before using isodars and their underlying adaptive landscapes to forecast eco-evolutionary futures.

More importantly, perhaps, is the reality that adaptive traits and strategies are moulded by the dynamic interplay between ecology and evolution. In order to apply *adaptation* to the habitat-selection game, one first must be explicit about what strategies are being assessed and their underlying *mechanisms*, what the *functional relationships* of those strategies are with density, how the *structure* of the functional relationships and their connection to fitness varies in time and space, what *scales* in time, space and biological organization are appropriate for the mechanisms being assessed and how ecological and evolutionary *dynamics* interact with one another. Those same underlying principles are equally appropriate for evaluating other adaptive questions in the realms of evolution and ecology.

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