

Habitat-dependent life history

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Abstract

Life-history research, commonly treated as the study of age and stage-dependent vital rates, often invokes a role for habitat but seldom in the context of theories of density- and frequency-dependent habitat selection. Merging life-history research with habitat selection theory is crucial because habitat and habitat selection modify the partial interactive effects of genetics, traits, demography, and environment on adaptive evolution. The density and frequency dependence of habitat selection feeds back onto life histories whenever the relationship between fitness and density varies among habitats and individuals occupy the habitat yielding highest fitness. Comparisons of life history and habitat selection in rodents, fishes, and fisheries support the habitat-dependent perspective but also reveal manifold processes in need of further theoretical and empirical study.

Key words: adaptive evolution, habitat selection, ideal free distribution, litter size, salmonids

“Isn’t it curious how our understanding of life history depends on the organisms we study?” —Jeffrey Hutchings in conversation.

Introduction

Life histories evolve through age- and stage-dependent bidirectional feedback with fitness. Fecundity and survival at different ages and stages interact to determine the number of descendants—the number of descendants mediate survival and fecundity through fitness-enhancing traits emerging from processes such as density-dependence, spatio-temporal variation, mating strategies, intra- and inter-specific interactions, and many more. The ability of the feedback to achieve an adaptively optimum life history depends on tradeoffs among underlying traits (e.g., [Stearns 1976](#); [Roff 2002](#)) and whether those traits are constrained or enhanced by phylogeny, genetics, development, stochasticity, behaviour, environmental conditions (e.g., [Murren et al. 2015](#)), genotype × environment interactions ([Via and Lande 1985](#)), gene flow, the “hardness” of selection ([Kawecki and Ebert 2004](#)), genetic architecture ([Leimar et al. 2019](#)), and spatial distribution ([Kawecki and Stearns 1993](#)). Many of those tradeoffs, constraints, and enhancements depend in some way on **habitat** (see Glossary) and its relative use.

The habitats that organisms occupy, the options available for evolution, and thus the ability to study life history vary among taxa. The number of offspring produced by birds and mammals, for example, is constrained by environments favouring more-or-less constant adult body sizes and requirements of substantial investment in individual offspring. These taxa have played a disproportionate role in our understanding of optimal clutch and litter sizes ([Lack](#)

[1947, 1948](#)) and associated parental investment ([Smith and Fretwell 1974](#); [Brockelman 1975](#); [Morris 1985, 1992a](#); [Pettifor et al. 1988](#)). Indeterminant growth and developmental flexibility in organisms as divergent as fishes and plants provide opportunities for empirical research on how tradeoffs and frequency-dependent selection influence the age and number of reproduction events (e.g., [Christie et al. 2018](#)) and phenotypic plasticity ([Schlichting 1986](#); [Hutchings 2011](#)) including alternative mating strategies (e.g., [Gross 1985](#); [Hutchings and Myers 1994](#)) and their consequences ([Rowe and Hutchings 2003](#)). The somewhat capricious dependence of plants and insects on environmental characters such as temperature and rainfall affords opportunities for studies on bet hedging (e.g., [Cohen 1966](#); [Hopper 1999](#); [Simons 2011](#)). Empirical studies of semelparity are limited to organisms that reproduce only once in their lifetime (e.g., [Hutchings and Morris 1985](#)). Numerous other examples of taxon-related research directions exist in the vast literature on life history evolution. Even so, the majority of emergent strategies are, at some scale, associated with habitat and habitat selection.

I explore the apparent universality of habitat-dependent life histories by outlining the historical and conceptual contexts of habitat-dependence in general terms of adaptive evolutionary change. I expand the concepts to explicitly incorporate habitat and habitat selection through their effects on fitness. I illustrate how different forms of density-dependent habitat selection illuminate our understanding of habitat-dependent evolutionary change and demonstrate the interconnection between habitat selection and **dispersal**. I place the details of the interesting special case of reciprocal dispersal, and the caveats of my approach, in

appropriate **appendices** (A and B, respectively). I highlight the trans-taxon applicability of predicted outcomes with cogent examples and explore their likely consequences for the evolution of life histories. I conclude by discussing the crucially important roles that habitat and habitat selection play in our understanding of adaptive evolution.

Historical context

The influences of habitat and habitat selection on vital rates and life history are documented in numerous taxa. Examples include 1, protective cryptic colouration from predation among small mammals (Dice 1940; Vignieri et al. 2010; Barrett et al. 2019), lepidoptera (industrial melanism reviewed by Cook and Saccheri 2013), guppies (*Poecilia reticulata*), and other fishes (Endler 1980); 2, habitat differences in avian clutch size (e.g., between hedgerow and woodland nesting great tits, Krebs (1971), between high and poor-quality breeding territories occupied by tits, Dhondt et al. (1992), between open versus wooded islands inhabited by common eiders (Kilpi and Lindström 1997; Öst et al. 2008), and among regions occupied by ground nesting European wood warblers (Maag et al. 2022); 3, weaker selection on clutch size by blue tits living in urban versus forest ecosystems (Branston et al. 2021); and 4, a source of spatial synchrony in vital rates of hole-nesting birds (Vriend et al. 2023). Comparisons between high-versus low-predation habitats reveal differences in body size, sexual maturity, egg size, egg number, and reproduction intervals in guppies, and age at maturity and reproduction in killifish (*Rivulus hartii*) (Reznick and Endler 1982; Reznick and Travis 2019). Growth form, seed shedding, and yield of bent grass (*Agrostis tenuis*) varies among pastureland habitats in central Wales (Bradshaw 1959). Investment in future growth and module size differentiates fast-growing Bryozoans (*Watersipora subtorquata*) in deep habitat from thrifty phenotypes in shallow habitats (Lange et al. 2016). White-footed mice (*Peromyscus leucopus*) produce smaller litters in forest than they do in fencerows (Morris 1998). Roff (2002) cites many other examples of habitat and site-dependent life-history traits.

Habitat's potential role in life history evolution is further exemplified by Grime's (1974, 1977) pioneering classification of plant life strategies along and within triangular axes of competition, stress, and disturbance. Extreme strategies congregate at the vertices of the triangle. Competitive plant species occur in habitats of high productivity and low disturbance. Stress-tolerant species are typically found in habitats of low disturbance and low productivity, and ruderal species in highly productive habitats with high disturbance. Southwood (1977) proposed a similar three-dimensional model but with different axes. The first axis represented paired components of durational stability and the constancy in "favourableness". The second axis referenced spatio/temporal variance in favourableness, and the third isolation and unpredictability.

A more recent example is Pecuchet et al.'s (2018) search for similarities in life history among disparate groups of North Sea marine taxa. Correspondence of combined traits between copepods and fish reflected a predominant south-

north depth and seasonality gradient. Such correspondence, where it exists, is compromised by differences in lifestyle and habitat (Pecuchet et al. 2018). So, although it is tempting to classify organisms based on their relative positions along major environmental axes, habitat characteristics are often more complex. Different vital rates often exhibit opposing environmental trends capable of compensating for their separate effects on populations (Villellas et al. 2015). Further complexity emerges from plastic life-history traits tuned by habitat to reflect local conditions and ecological opportunities.

Conceptual context

Fitness, and thus the vital rates of life history, emerge through the nested mappings of genetics onto traits, the translation of traits into demography, and the conversion of demography into fitness,

$$(1) \quad w = f(D(T)(G))$$

where w = fitness, D corresponds to demographic rates of survival and reproduction, T = the trait or traits of interest, and G = genotype(s) (Coulson et al. 2006). The general form of eq. 1 becomes more useful when expanded to include the separate and interacting effects of genetics, demography, and traits on the marginal change in fitness,

$$(2) \quad \frac{\partial w}{\partial G} = \frac{\partial w}{\partial D} \frac{\partial D}{\partial T} \left[\left(\frac{\partial T}{\partial G} \frac{\partial T}{\partial E} \right) \right] + \frac{\partial D}{\partial E}$$

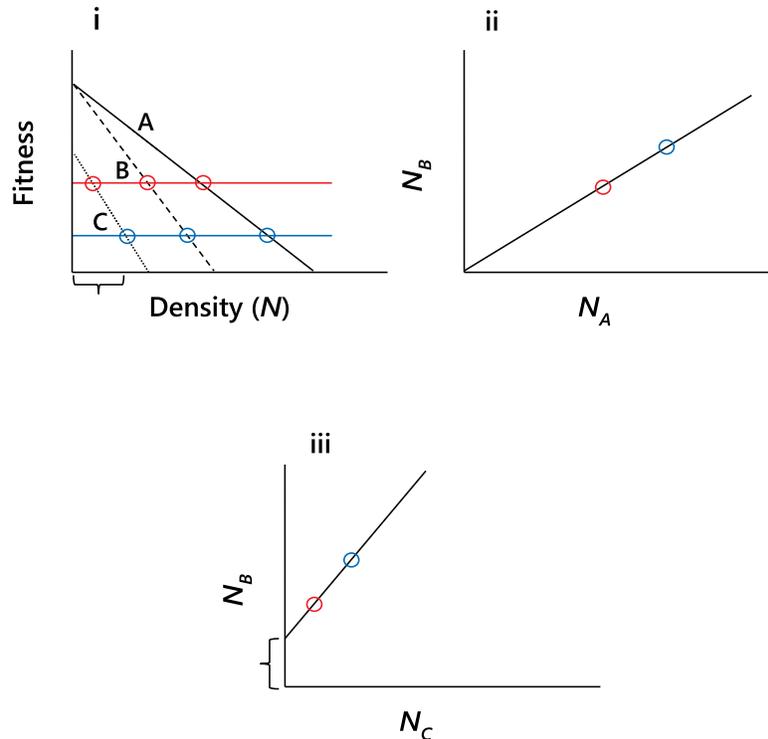
where $\partial w/\partial G$ represents adaptive evolution (natural selection) on genes, $\partial w/\partial D$ is the opportunity for selection, $\partial D/\partial T$ is the marginal effect of trait value on demography (selection), $\partial T/\partial G$ is the response to selection associated with heritable trait values, $\partial T/\partial E$ is the effect of environment on trait value (phenotypic plasticity/reaction norm), and $\partial D/\partial E$ is the effect of environment on demography (as through density and frequency dependence; Coulson et al. 2006; Morris and Lundberg 2011; Morris 2018). Each of these terms can be translated into life history, and each varies with habitat.

If a population occupies only one habitat, then trait evolution will occur via eq. 2. But when a population occupies more than a single habitat, trait evolution will depend not only on the habitats' separate values of eq. 2, but also on the proportions of the population living in each habitat. Potential evolutionary outcomes fall along the population's adaptive function (Levins 1962, 1968) that weights the fitness in each habitat with respect to its use.

We can make the evolutionary outcome explicit by considering the influence of two habitats, 1 and 2. In our first example, imagine that the habitats are exploited by **fine-grained** foragers (each organism uses the habitats in the proportions (p and q ; $0 \leq p \leq 1$, $q = 1 - p$) in which they occur in the environment). Under these conditions, the adaptive function (A) is simply the product of fitness achieved in each habitat multiplied by its proportion,

$$(3) \quad A = pw_1 + qw_2$$

Fig. 1. Illustrating how relationships between fitness and density are converted into habitat isodars. (i) Linear density-dependence in fitness for three habitats (A = solid line, B = dashed line, C = dotted line). With ideal free habitat selection, fitness is equal in all habitats even though population size varies. (ii) The isodar graph of the densities in habitats A and B at two different population sizes ($N_B = bN_A$). Both habitats are always occupied, the linear isodar passes through the origin, and the proportional use of the two habitats is equal at all population sizes. (iii) The isodar graph of the densities in habitats B and C ($N_B = a + b'N_C$). Only habitats B and A are occupied at low population size so the isodar for B and C has a nonzero intercept. The proportion of the population in each habitat varies with population size. The third isodar between habitat A and C is easily inferred by substituting the solution from the isodar for habitats A and B ($N_A = \frac{a+b'N_C}{b}$). Horizontal lines and circles denote ideal free equilibria at low (red) and high (blue) population sizes. Circles on the isodars equal the paired values of density for the same densities in (i). N_i equals the density in habitat i . The bracket equals the isodar intercept (a) for habitats B and C.



(Levins 1962, 1968). The optimum value of a trait corresponds to the position on the adaptive function where fitness is maximized. We want to know whether habitat selection might alter this outcome.

Imagine that individuals occupy habitat in a way that maximizes fitness (ideal), and that no other individuals interfere with their choice (free). The population of such individuals will achieve an **ideal free distribution** (IFD; Fretwell and Lucas 1969) in which mean fitness is equal in both habitats ($\bar{w}_1 = \bar{w}_2 = \bar{w}$). The adaptive function thus collapses to

$$(4) \quad A = \bar{w} (p + q) = \bar{w}$$

One should not interpret eq. 4 to mean that the proportional use of the two habitats has no effect on the adaptive function, but rather that its singular mean value depends on those proportions. The proportions, in turn, may or may not vary with population density. To evaluate this second effect, we first incorporate the density-dependent frequency of use of each habitat into the adaptive

function,

$$(5) \quad A = f_1(N) p \bar{w}_1 + f_2(N) q \bar{w}_2$$

(Morris and Lundberg 2011) where $f_i(N)$ is the frequency of use of habitat i with changes in population size N . We can then calculate the frequencies from the habitat's **isodar** (Fig. 1; Morris 1988), the set of densities in a pair of habitats such that an individual's expectation of fitness is the same in each. Assuming that fitness declines linearly with density, the isodar for a pair of habitats is given by the straight line,

$$(6) \quad N_2 = a + bN_1$$

where the intercept a is proportional to the difference in fitness (e.g., intrinsic rate of increase) at low density and the slope, b , is the ratio of the slopes of the underlying fitness functions (Morris 1988). When habitats differ in both maximum fitness and the slope of fitness with density, the proportion of the population in each habitat, and thus the

weighting of the adaptive function, varies with population size. But if habitats differ only in their fitness slopes, $a = 0$, the linear isodar passes through the origin, and the frequencies of habitat use are constant with changes in population size (Fig. 1).

To calculate the fraction of the population using habitat 2, we assume for simplicity that the habitats are equal in size. Doing so allows us to substitute abundance for density in our calculations (habitats of different sizes can be accommodated with weighting terms). We can then calculate the fraction using habitat 2 (f_2) by dividing the isodar solution (left side of eq. 6) by total population size,

$$f_2 = \frac{N_2}{\sum_{i=1}^2 N_i}$$

The fraction using habitat 1 = $1 - f_2$. Merging isodars with Levins' equation thus yields the density- and frequency-dependent weighting of adaptive evolution in heterogeneous environments.

Habitat isodars allow us to expand the one-habitat scenario to pairs of habitats (the analyses are somewhat more complex when more than two habitats are occupied) because they enable a simple calculation of the frequencies of habitat use. For the special case of a linear isodar passing through the origin, the frequencies are constant at all population sizes, and thus so are the effects of environmental variability. Mean fitness in this special case varies with population size, but not the relative contributions to adaptive evolution caused by habitat differences in density-dependence.

If the population occupies both habitats but individuals use only one at a time (**coarse grain**, Levins 1962, 1968), then fitness obtained from the two habitats accrues multiplicatively and the adaptive function is given by the product,

$$(7) \quad A = w_1^p w_2^q$$

(Levins 1962, 1968). Mean fitness is equal at the IFD, the adaptive function collapses to $A = \bar{w}$, and the frequency dependence of adaptive evolutionary change can again be inferred from the isodar.

Habitat-dependent evolution

Processes of natural selection depend on whether an individual's absolute fitness responds only to density (density-dependence), only to the frequencies of other phenotypes in the population (frequency-dependent), to both density and the frequencies of other phenotypes (**soft selection**) or is independent of both density and frequency (**hard selection**; Wallace 1975; Fig. 2). Processes of habitat selection parallel those of natural selection. Habitat selection can be independent of, or dependent on density and similarly independent of, or dependent on the frequency of habitats available (Fig. 2). Although habitat selection and natural selection can both be classified according to patterns of density and frequency dependence, a key difference is that those influences on habitat selection are easily evaluated with isodars (Fig. 3).

Fig. 2. The four discrete influences of density and frequency on adaptive evolution and habitat selection (derived after Wallace 1975).

| | | Density | |
|-----------|-------------|----------------------|------------------------|
| | | Dependent | Independent |
| Frequency | Independent | Density Dependent | Hard |
| | Dependent | Soft | Frequency Dependent |

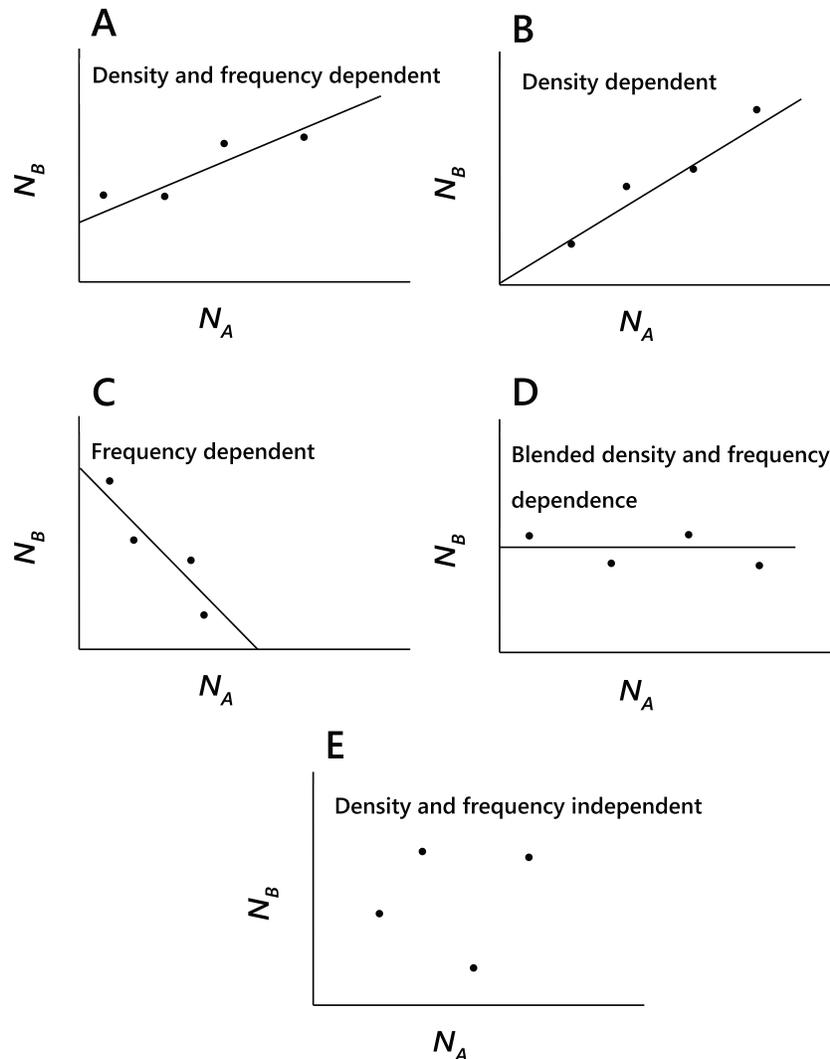
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When the frequency of use depends on density (linear isodars with nonzero intercepts), habitat selection is both density and frequency dependent, and so too are its effects on natural selection (soft, Fig. 3A). The soft selection induced by habitat feeds back onto habitat preference. Significant curved or nonlinear isodars (not shown) also document situations in which the frequencies of individuals occupying a habitat change with density.

Density-dependent habitat selection occurs when the ratio of habitat use is constant even though fitness varies (linear isodars through the origin, Fig. 3B). Frequency-dependent habitat selection emerges when population density is held constant while the frequency of habitat use changes (e.g., a linear isodar with slope = -1 , Fig. 3C). A peculiar blend of density- and frequency-dependent habitat selection is revealed when a consistent mean difference in density is independent of the density in alternative habitats (Fig. 3D). The density in the most preferred habitat is constant, while the density in the alternative changes as does the frequency of habitat use. Such a situation can arise when the population in one habitat is well regulated, while that in another is not, as might occur with some forms of source-sink dynamics (Shmida and Ellner 1984; Holt 1985; Pulliam 1988; Dias 1996). Neither density- nor frequency-dependent habitat choice occurs between pairs of habitats in which there is no difference in mean density and no relationship between their densities (no isodar, hard selection; Fig. 3E).

The most interesting outcome of habitat's influence on life history occurs when the density-dependence of traits differs between habitats. Consider, for example, a situation in which adults choosing between two habitats are more susceptible to predation in one than in another. The ratio of juvenile to

Fig. 3. Five categories of density and frequency dependence revealed by linear habitat isodars. Filled circles correspond to a subset of relevant data points, lines represent expected best fits with the data.



adult survival will be higher in the more lethal habitat. Selection there will favour earlier maturity and increased reproductive effort (Gadgil and Bossert 1970; nicely summarized in Hutchings 2021). Selection on age and effort at maturity will be different in the safer habitat that has a lower ratio of juvenile to adult survival. Assuming a well-mixed ideal free population, selection will depend on the proportional use of the two habitats (soft selection; the resultant “mean” life history emerges directly from habitat-dependent choice).

If the proportion of the population using each habitat is constant with population size (a linear isodar through the origin), then density-dependent habitat selection has no additional effect on evolution. That is not the case where the proportional use of the two habitats varies with population size as occurs with a significant isodar intercept. The proportion of the population influenced by habitat differences in predation varies with population size. Selection is still soft, but its “softness” varies with population size because the frequencies of exposure to the habitats’ different predation regimes change with population size.

Habitat-dependent dispersal

The relative frequencies of habitat use arise through the density-dependence of fitness (Fig. 1) and through the life history of dispersal (e.g., Ronce 2007; Beckman and Sullivan 2023; Lustenhouwer et al. 2023). The consequences of dispersal, or its absence, are realized through the choices for, and occupation of, habitat. To make this point explicit, consider the discrete population growth equations for two habitats, A and B,

$$(8) \quad N_{A(t+1)} = N_{A(t)} + r_A N_{A(t)} - \gamma_A N_{A(t)}^2$$

and

$$(9) \quad N_{B(t+1)} = N_{B(t)} + r_B N_{B(t)} - \gamma_B N_{B(t)}^2$$

where r is the maximum discrete rate of population increase and γ is the decline in growth rate with each habitat’s population density (size). Letting fitness equal the per capita increase

in population size, $(N_{i(t+1)} - N_{i(t)}) / N_{i(t)}$, the resulting isodar for which fitness is equal in both habitats is given by

$$(10) \quad N_B = \frac{r_B - r_A}{\gamma_B} + \frac{\gamma_A}{\gamma_B} N_A$$

An interesting dynamic occurs when the number of individuals predicted by the isodar is not the same as the number of individuals produced by population growth (Appendix A). For example, if population growth without dispersal yields more individuals in habitat B than predicted by the isodar, that habitat will be oversaturated, and ideal habitat selection will be attained only if some of those individuals disperse to habitat A. The habitat that is oversaturated depends on the habitats' relationships between fitness and density, population size, and whether the population is growing or in decline (Morris et al. 2004; Appendix A). If populations fluctuate through time, as often occurs for seasonally reproducing species, then the identity of the oversaturated habitat will change with periods of population growth and decline, as will the direction of dispersal (reciprocating dispersal; Morris et al. 2004; Appendix A). So too will habitat's influence on other life-history traits.

Evidence for habitat-dependent life history

Although theory predicts widespread adaptive effects of habitat and habitat selection on life history, affected traits will vary among taxa. An assessment of the generality of habitat-dependent life history must thus include evidence for habitat's influence on life history across taxa, as well as evidence for underlying processes of habitat selection and dispersal.

Density-dependent growth and survival

The simplest case of habitat's influence on life history emerges when a population occupies a single habitat. Adaptive evolution responds only to the fitness accrued in that habitat. A similar effect can emerge when independent populations occupy different qualities or mixtures of habitat. A possible example is given by brook trout (*Salvelinus fontinalis*) occupying small, isolated rivers in Newfoundland where they evolved distinctly different life histories (Hutchings 1993). Female fish living in Freshwater River, where the ratios of adult-to-juvenile growth rate and adult-to-juvenile survival were low, matured earlier and with greater reproductive effort than did females from Cripple Cove River with higher ratios of growth and survival. Cripple Cove females matured later with less reproductive effort than those in Freshwater River (Hutchings 1993). The divergence between populations belies significant heterogeneity within rivers in growth rate-dependent life history (Hutchings 1996). Those differences appear to reflect each river's habitat and habitat-dependent densities, but it is also possible that they originated independently through alternative evolutionary mechanisms.

The evolutionary ambiguity is eliminated in comparisons between limnetic and benthic ecotypes of three-spined stick-

lebacks coexisting in small freshwater lakes (Schluter and McPhail 1992). In Alaska, large benthic females breeding in shallow bays produce fewer and larger eggs than do coexisting slender limnetic females breeding along steep rocky shorelines (Baker et al. 2005). Differences in egg size correlate with habitat differences in water temperature that influence embryo development. The pattern calls for genetic studies and common garden experiments to determine whether the habitat-dependent differences in egg size and number are plastic or fixed traits.

Genetic differentiation is clearly documented for the life histories of two coexisting Atlantic cod ecotypes living along the southeastern coast of Norway (Knutsen et al. 2018). The fjord ecotype is genetically distinct from the sympatric North Sea ecotype. Despite a shared dependence of juvenile body size on vegetation cover, differences between ecotypes emerge through their respective interactions with wave exposure and sampling year (Knutsen et al. 2018). It will be interesting to learn whether other life history characters respond similarly.

Density- and frequency-dependence revealed by fish isodars

The heterogeneous growth rates observed in brook trout emanate from a combination of stochastic opportunities to acquire resources early in life and emergent dominance that enables large individuals to secure and retain the best sites available (Hutchings 1996; Knight 2000). Theory for **despotic** or **pre-emptive distributions**, such as would appear appropriate for trout occupying pool and riffle habitats, predicts curved isodars (Morris 1994). In each case some individuals secure better breeding sites than do others with concomitant impacts on life history, such as size-dependent site selection and fecundity. Knight et al. (2008) designed experiments to generate habitat isodars of brook trout occupying lower and upper reaches of two isolated Newfoundland rivers, including one (Drook) studied by Hutchings. The experiments confirmed that the isodars were curved, that they varied within and between rivers, and that each isodar correctly predicted variation in body size (Knight et al. 2008) crucial to brook trout life history.

The results of Knight et al. (2008) are mirrored by analyses of 26 years of data from 14 populations of spawning Chinook salmon (*Oncorhynchus tshawytscha*) along the Oregon coast (Falcy 2015). Densities between high versus low gradients in spawning channels yielded curved isodars similar to those of brook trout. The effects of density and frequency dependence are enhanced if spatially separated populations, such as those of anadromous salmonids, remain distinct through natal site fidelity (Keefer and Caudill 2014).

The generality of density-dependent habitat selection is reinforced in another long-term study across an extensive spatial scale. Fifty years of data collected on the distribution of pike (*Esox lucius*) in England's Lake Windermere's two basins revealed that fish disperse along a gradient that equalizes fitness between habitats (Haugen et al. 2006). Habitat selection by the pike modified population abundance, and thus its correlated traits of survival and fecundity. However, in this case,

the linear isodar's intercept was not different from zero. The frequency of use of the two habitats, and thus their influence on pike evolution in the lake, is constant with changes in population size.

Habitat-dependent litter size in white-footed mice

White-footed mice regularly inhabit nest boxes in the northeastern limit of their geographical range (Nicholson 1941; Morris 1986) affording unique insights into small-mammal life history. Recruitment is a lottery in which most litters are unsuccessful at recruiting offspring to the adult nest-box population, and the probability of success is independent of litter size (Morris 1986). Even so, litters of size six and greater produce fewer recruits than expected because survival “falls off the cliff” in large litter sizes (Mountford's hypothesis; Mountford 1968; Morris 1996). The result is a bet-hedging strategy of frequent iterated reproduction.

Female white-footed mice produce smaller litter sizes in forest habitat, but with higher rates of juvenile survival, than they do in adjacent edge and nearby fencerow habitats (Morris 1986, 1996). The pattern of habitat-dependent litter sizes is inconsistent with most evolutionary expectations from classical life-history theory in which high rates of juvenile-to-adult survival favour increased female effort (Gadgil and Bossert 1970; Schaefer 1974; Stearns 1976). Might this apparent contradiction be explained by density-induced state dependence? Large females produced larger litter sizes, on average, than did smaller females, but there was no difference in female body size among habitats. Female body size varied between seasons and among years; litter size did not (Morris 1992b). Thus, the explanation for habitat-dependent litter sizes must lie elsewhere.

White-footed mouse litter size declines with population density ($\partial D/\partial E$ in eq. 2; Morris 1989), but it appears to do so differently in the three habitats. The linear isodar between forest and edge passes through the origin (constant frequency of use). The isodars between forest and fencerow, as well as between the edge and fencerow, are curved upwards (frequency varies with population size). Those patterns warn us that the importance of density and frequency dependence can vary among landscapes and that ignoring habitat and habitat selection can misinform our understanding of life history (Morris 1992b).

Do habitat differences in litter size create the evolutionary adjustments predicted by eq. 2? Standardized selection gradients for increased litter size at the “8th research site” where mice occupy forest, edge, and fencerow habitats are overwhelmingly positive (Morris 2018). Yet 29 years of data yielding approximately 60 mouse generations failed to reveal any increase in mean litter size. This was not the case at a different site (“Mary”) composed only of fencerows. Litter size increased marginally despite no consistent pattern in standardized selection gradients (Morris 2018). The anomaly is associated with site-dependent differences in predation and predation risk. Weasel predation is high at the 8th site where litter sizes did not increase through time and is non-existent

at the Mary fencerow site where litter sizes were larger than in the same habitat at the 8th.

Density- and frequency-dependent dispersal

The differences among sites and habitats occupied by white-footed mice are nevertheless consistent with differences in dispersal and associated environmentally induced effects. Mice at the 8th site disperse from the high-density forest habitat to lower density edge habitats when population size increases. They emigrate from edge into forest when populations decline (reciprocating dispersal; Morris and Diffendorfer 2004). In apparent contradiction with theory (e.g., Fig. 1), dispersal occurs even though the linear isodar for those two habitats passes through the origin. Mean fitness, however, tends to be higher in the forest (Morris 1991). The result is that the expectation of fitness used by mice, and that thus generates the “isodar”, is based on perceived habitat quality rather than actual quality (e.g., Fretwell and Lucas 1969). Differences in fitness affect the differential habitat-dependent population growth necessary for reciprocating dispersal.

Bidirectional dispersal homogenizes selection among habitats, hinders the evolution of genetic differences in trait values within habitats, and expands the potential for phenotypic plasticity ($\partial T/\partial E$). In environments where dispersal among habitats is frustrated or otherwise impossible, as in white-footed mice occupying fencerows at the Mary site with no accessible alternative habitat, environmental effects on demography can more readily translate into population differences in mean life history. Reduced predation risk at the Mary site transformed the litter size \times habitat interaction and caused a small increase in mean litter size despite normalizing selection (Morris 2018).

Habitat selection thus appears to modify white-footed mouse life history. At the 8th, adaptive evolution occurs at the scale of a population in which density- and seasonally dependent dispersal creates sufficient gene flow to override local spatial and temporal adaptation. A similar process was postulated for tits breeding in good versus poor habitats in Belgium (Dhondt et al. 1990). Environmentally dependent plasticity could nevertheless enable some degree of “habitat specialization” (Roff 2002). Dispersal disappears when there is no suitable alternative habitat as at the Mary fencerow site. In that case, zero gene flow among (nonexistent) “habitats” enables local adaptation to a single habitat.

Density- and frequency-dependent phenotype matching

The importance of habitat selection is reinforced when individuals match their phenotypes with habitat. Stream and river-dwelling fishes that escape predation are associated with dramatic and adaptive differences in life history (Reznick 2016; Reznick and Travis 2019). In other systems, such as the occupation of isolated watersheds by brook trout (Hutchings 1993), differences in flow rates and productivity interact with density-dependent movements between pools and riffles (Knight et al. 2008) that can enhance adaptive divergence of populations to stream-wide characteristics.

Adaptive divergence in such cases is likely associated with genetic predispositions, such as differences in aggression or other personality traits, that allow some individuals greater opportunity to occupy the “best” sites or habitats (Cote et al. 2010).

Individuals that match their personality with habitat induce covariance between genotypes and environments (eg. through the product $\frac{\partial T}{\partial G} \cdot \frac{\partial T}{\partial E}$ in eq. 2; Edelaar et al. 2008; Holtman et al. 2017). For example, fish occupying favourable sites are likely to achieve more rapid growth rates and larger sizes than competitors, providing the selective gristmill for further life history evolution.

Evidence for personality-linked habitat choice is equivocal in stream-living salmonids. Principal components analysis (PCA) on behaviours of young-of-the-year Atlantic salmon (*Salmo salar*) revealed repeatable personalities. The PC scores were not linked to the complexity of habitat where fish were captured even though two of the three PCs were significantly different between complex versus open enclosures (Church and Grant 2018). Brown trout (*Salmo trutta*) parr also displayed consistent personalities but with effects opposite to a priori expectations. More cautious (shy) individuals, rather than bold individuals, grew faster in the wild (Adrianenssens and Johnsson 2011).

Other studies suggest behaviourally mediated habitat use. Wild adult brook trout in north-central Pennsylvania appear to exhibit mobile versus sedentary life histories that enable high-survival mobile phenotypes opportunities to find and occupy the most profitable patches (White and Wagner 2021). But while captive 1-year-old brook trout possessing more exploratory behaviour also tended to be more aggressive, personality had no effect on average resource use (White et al. 2019). No doubt some of the variation arises because different personality-dependent mechanisms can underly general patterns such as dispersal. Both risk-averse shy individuals and risk-prone bold individuals might disperse to avoid predation (Cote et al. 2010).

Salmon species appear to select habitat similarly. Wild juvenile Atlantic salmon occupy habitat in accordance with an ideal free distribution (Hedger et al. 2005), but older individuals appear to occupy habitat in a way more representative of pre-emptive habitat use (Gibson et al. 2008). Manipulative experiments yield somewhat different results suggesting important roles for competitive abilities (as in juvenile coho salmon, *Oncorhynchus kisutch*; Grand 1997), mixtures of ideal free and ideal despotic distributions in Atlantic salmon (Bult et al. 1999), and pre-emptive size-dependent distributions in brook trout (Knight 2000; Knight et al. 2008).

Size-dependent site selection by brook trout is echoed with matching habitat choice by spawning sockeye salmon (*Oncorhynchus nerka*, Camacho and Hendry 2020). Large three-ocean female salmon, that are most susceptible to predation by bears in shallow water, preferentially used deeper water than did salmon in other sex and age classes. Selection, estimated by a measure of nest defense (the length of time that females remained alive after spawning), was mostly associated with the cost large females would pay if they mismatched their body size to water depth. Three-ocean females compensate for higher mortality by producing larger

clutches with larger eggs deposited in deeper nests than smaller females. In this way, the size and age distribution of spawning salmon matches that expected from age- and size-specific tradeoffs between mortality and spawning success (Cunningham et al. 2013). It is thus obvious that habitat selection in its various guises feeds back directly onto life history. It is just as obvious that life history influences habitat selection, and that both interact in adaptive evolution.

Density- and frequency-dependent habitat selecting fishers

Perhaps the best evidence in favour of habitat-dependent selection comes not from fish but from the behaviour of fish harvesters. Several analyses of fishing effort from different commercial fleets, fish stocks, and simulated fisheries yield agreement with theories emanating from ideal free habitat selection (Gillis et al. 1993; Gillis and Peterman 1998; see assumptions and caveats in Gillis 2003). Best-fit isodars emerged from models that included nonlinear effort in which various forms of interference can undermatch effort with habitat quality (Gillis and Van der Lee 2012). Interference and fleet dynamics, such as fleets with numerous centrally managed vessels, provide opportunities for direct feedback that can enhance the ability to interfere with choices by smaller independent companies. The applicability of the modified model was confirmed by Van der Lee et al.’s (2014) analysis of 4 years of groundfish trawl data from NAFO Division 4 X. The isodar model outperformed a more complicated individual choice model maximizing fishers’ utility.

Although studies of salmonids and fish harvesters provide novel insights into habitat selection, we know much less about the correspondence between habitat and life history in these systems, and especially that related to density-dependent habitat choice. An exception is the comparison of brook trout habitat use in streams with and without anadromous trout. Juvenile brook trout possessed generally higher densities in low current velocities (e.g., pool habitats) than in higher current velocities (e.g., riffles) in streams lacking anadromous fish (Morinville and Rasmussen 2006). There was no difference in density in streams with migrant fish. The brook trout habitat preferences in these streams mimic differences in morphology and metabolic rates between resident and anadromous forms. Phenotype-habitat matching, such as that exhibited by sockeye salmon (Camacho and Hendry 2020), also provides tantalizing evidence of feedback of density- and frequency-dependent habitat choice on life history.

Discussion

Life histories typically refer to age- or stage-specific traits related directly to reproduction and survival (e.g., Nettle and Frankenhuys 2020); the “combination of life-history traits that determines an individual’s probability of surviving to, and reproducing at, various ages or stages” (Hutchings 2021, p. 1). Much of life-history research thus addresses patterns of growth, survival, and reproduction throughout an organism’s lifetime.

A key feature of life history evolution is that traits enhancing future survival are traded off against traits maximizing current fecundity. Dispersal through habitat selection involves similar tradeoffs between current opportunities and future survival and reproduction elsewhere. The form of those tradeoffs, and their interdependence with density, will determine the degree to which their demographic consequences influence other life-history traits, as well as the stability of habitat-dependent dispersal and its roles in adaptation (e.g., Kawecki 2008). The examples reviewed here, in numerous systems and on a variety of taxa, confirm those expectations.

Effective modelling and understanding of dispersal and habitat selection require assessments of the costs and benefits accrued by philopatry, emigration, and immigration (Anderson 1989). Each component modifies, and is modified by, demography with impacts on eco-evolutionary dynamics and covariances among traits (Lustenhauer et al. 2023), including those related to age- and stage-specific fecundity and survival. It is thus appropriate to consider dispersal as a key life-history trait (Ronce 2007; Beckman and Sullivan 2023; Lustenhauer et al. 2023). By doing so, we implicitly acknowledge that whenever habitat selection motivates, or arises from, dispersal, it too is a key life-history trait.

Habitat and habitat selection feed back onto life history through their separate and joint effects on all terms in eq. 2 and perhaps most interestingly through effects on demography ($\partial D/\partial E$) and phenotypic plasticity ($\partial T/\partial E$). When individuals occupy multiple habitats, the influences of density- and frequency-dependent habitat selection can be neutralized by reciprocating dispersal. Adaptive evolution under these conditions is likely to favour plastic life histories that depend primarily on variability in individuals' state. But when habitats are isolated from one another, dispersal is frustrated, and adaptive evolution can then respond to selection within a single habitat rather than a compromise among potentially conflicting selection gradients experienced in multiple habitats.

Understanding the correspondence between life history, habitat, and habitat selection in real systems rests on the ability to thoroughly investigate the underlying dynamics of habitat selection and dispersal. If habitat selection fits an ideal free distribution such that all individuals have equal opportunity to occupy habitat, genes flow freely among habitats, and habitat-dependent natural selection represents a compromise among habitat-dependent selection gradients. But if individuals vary in their ability to occupy and hold habitat, then selection shifts to reinforce life-history characters, such as growth rates and subsequent reproductive strategies, associated with habitat choice. Predictions become complicated if mixed strategies coexist as might occur in Atlantic salmon (Bult et al. 1999), or if individuals switch from ideal free choice at low density to despotism or pre-emption at higher densities (Morris et al. 2016). Even if a single dominance strategy exists at all densities, its success is bedeviled with peril. Highly efficient or aggressive individuals can evolve their populations to extinction (e.g., Parvinen 2005; Parvinen and Dieckmann 2013). These various idiosyncrasies foretell advances in theory, experiment, and field research

necessary to fully comprehend and appreciate the significance of habitat-dependent life history.

Glossary

| | |
|---|--|
| Coarse grain | The scale at which an individual disperses from one spatial opportunity to another (dispersal scale). |
| Dispersal | The (usually) permanent movement of an individual from one spatially defined living opportunity to another. |
| Fine grain | The spatial scale within which an individual acquires resources without dispersal. Corresponds with an organism's foraging scale. |
| Habitat | An area or volume, often distinguished by physical, chemical, and biotic properties, within which the collection of individuals expresses a different pattern of fitness accrual than do similar collections in other areas or volumes. |
| Habitat isodar | The relationship(s), often revealed by regression, between the density of individuals in one habitat and that in one or more other habitats such that the expectation of fitness is the same in each. The evolutionarily stable solution for adaptive density-dependent habitat selection. |
| Hard selection | Selection on traits whose values are independent of frequency and population density. |
| Ideal despotic distribution | The distribution of a population that emerges when dominant individuals contest and defend breeding or foraging sites from other individuals. |
| Ideal free distribution (IFD) | The freely chosen distribution of a population among habitats or foraging opportunities such that the mean fitness of individuals is the same in each. |
| Ideal pre-emptive distribution | The distribution of a population among habitats or foraging opportunities such that each succeeding individual freely occupies the highest quality breeding or foraging site available. |
| Reaction norm (norm of reaction) | The pattern of expression of one or more traits across environments. |
| Soft selection | Selection acting on traits whose values depend on frequency and population density. |

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Appendix A. Reciprocating dispersal

We can predict the number of dispersing individuals directly from the isodar. We begin by calculating total population size,

$$(A1) \quad \text{TOT} = N_B + N_A = \frac{r_B - r_A}{\gamma_B} + \frac{\gamma_A}{\gamma_B} N_A + N_A$$

letting $\frac{r_B - r_A}{\gamma_B} = \varphi$ and $\frac{\gamma_A}{\gamma_B} = \beta$

$$(A2) \quad N_A = \frac{\text{TOT} - \varphi}{1 + \beta}$$

Imagine any two points on the isodar representing population growth from $\text{TOT}_{(t)}$ to $\text{TOT}_{(t+1)}$. Fitness in habitat A is equal to that of habitat B on the isodar thus, by population growth alone, the frequencies in habitat A and B at time $t + 1$ without dispersal are the same as those on the isodar at time t , but they are mismatched with ideal habitat selection at time $t + 1$,

$$(A3) \quad N_{A(t+1)} = \frac{\text{TOT}_{(t+1)} - \varphi}{1 + \beta}$$

and

$$(A4) \quad N_{B(t+1)} = \text{TOT}_{(t+1)} - N_{A(t+1)}$$

Fig. A1A illustrates the dispersal solution. The ratio $N_{B(t)}/N_{A(t)}$ is given by the straight dashed line $N_{B(t)} = b'N_{A(t)}$. Since fitness is equal on the isodar, any increase in population size by growth alone must also fit on the same line. Whenever $\varphi > 0$ and $\text{TOT}_{(t+1)} > \text{TOT}_{(t)}$, the population growth projection will lie above the isodar solution (habitat B is oversaturated, habitat A is undersaturated). Keeping total population size constant, the number of individuals dispersing from the higher quality habitat B to habitat A is given by the dotted line orthogonal to the isodar. To calculate the number of dispersing individuals, repeat the calculation yielding **eq. 10** for the growth trajectory,

$$(A5) \quad N'_{A(t+1)} = \frac{\text{TOT}_{(t+1)}}{1 + b'}$$

then, calculate the difference between the predicted value on the isodar (**eq. 10**) and that caused by population growth.

$$(A6) \quad D_{(t+1)} = N_{A(t+1)} - N'_{A(t+1)}$$

where D is the number of dispersing individuals (in this case from habitat B to habitat A) and the prime indicates the values of the growth trajectory. Solutions in terms of habitat B are simply obtained by using **eq. A4**.

Repeating the same procedure for a decline in population size (**Fig. A1B**) illustrates that the better habitat B will be undersaturated and dispersal back to the isodar is from habitat A (reciprocating dispersal, **Morris et al. 2004**). When populations increase, the better habitat is the “donor”; when populations decline, dispersal flows from the poor to the better habitat (**Morris et al. 2004**).

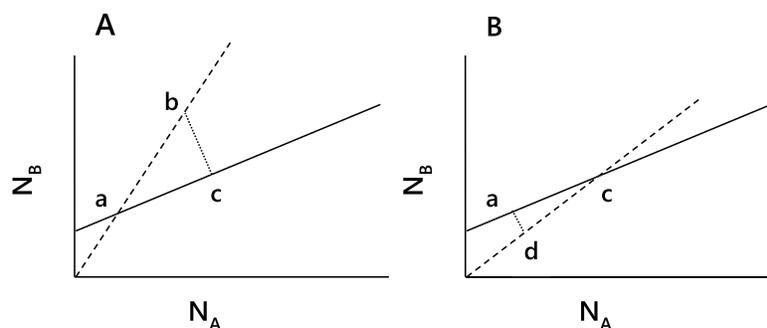
Appendix B. Caveats associated with habitat-dependent life histories

Our simplified models assumed ideal free habitat choice. Free choice is often restricted and other models are more appropriate. Options include dominance (despotic distribution; **Fretwell and Lucas 1969**), site pre-emption (pre-emptive distribution; **Pulliam 1988**; **Pulliam and Danielson 1991**; **Rodenhouse et al. 1997**; **McPeck et al. 2001**), unequal competitors (truncated phenotype distributions; **Parker and Sutherland 1986**; **Houston and McNamara 1988**), and matching habitat choice (**Edelaar et al. 2008**). Although each effect involves different processes, all are consistent with dynamics in which the probability of dispersal to higher quality patches increases with the fitness payoff (**Křivan et al. 2008**). All can be modelled with their respective habitat isodars (**Morris 1988, 2003, 2011**).

Dispersal among habitats is complicated by such features as territorial or pre-emptive behaviour, maladaptive traits expressed in a habitat different from the original, “maternal” effects associated with natal habitat feedback on development and behaviour (**Stamps 2001**; **Davis and Stamps 2004**; **Mabry and Stamps 2008**), and costs incurred during dispersal (e.g., increased risks of injury, mortality, and disease). Complications increase further with lost opportunities of within-habitat activities while dispersing, and the costs associated with search, assessment, and establishment in new habitat (**Morris and MacEachern 2013**). Dispersing individuals can also experience fitness dilution through outbreeding and selection against traits that would otherwise enable future back migration. Regardless of the above, we can safely assume that dispersal has the potential for far-reaching impacts on other aspects of life history and subsequent evolution.

Whether dispersal enhances evolutionary divergence or restricts, it depends on the possible dilution of locally adaptable genotypes (e.g., **Dhondt et al. 1990**). Genetic dilution can be reduced if individuals match inherited phenotypes with habitat (**Edelaar et al. 2008**), and particularly so if phenotype matching correlates with mate selection (**Porter and Akcali 2018**). Phenotype matching reduces habitat’s influence on phenotypically plastic traits ($\partial T/\partial E$ in **eq. 2**) and might thus

Fig. A1. Illustration of reciprocating dispersal for individuals obeying an ideal free distribution in two equal-sized habitats. The solid sloped line is the isodar. (A) The population at time t (point a) grows such that the proportion at time $t + 1$ is the same as at time t (point b ; the population in the better habitat B is overmatched relative to the IFD). To reach an ideal habitat distribution, the joint densities must converge on point c (individuals disperse from habitat B (density is reduced) to habitat A (density is increased)). (B) The same population declines from point c at time t to point d (at $t + 1$). The density in habitat A is overmatched. Individuals disperse from habitat A to habitat B. Fewer individuals disperse than in (A) because the population at time $t + 1$ is smaller. This procedure will work for any shape of isodar in populations with pulsed dynamics of reproduction and dispersal. N is population size.



help to canalize (Waddington 1942) habitat choice. The resulting habitat specialization magnifies the likelihood of habitat-specific life history.

An extreme example occurs when the cues organisms use to choose habitat make them susceptible to maladaptive habitat choice and associated ecological and evolutionary traps (Robertson et al. 2013). An additional concern is that such cues might be fixed traits or otherwise persist across generations. Experimental evolution of two-spotted spider mites (*Tetranychus urticae*; Mortier and Bonte 2020) demonstrates that maladapted cues can indeed persist across multiple generations. Ten generations of intense selection for host preference on high-fitness tomato plants failed to yield any change in the mite's preference for lower fitness cucumbers.

Adaptive phenotype-habitat matching can occur only when different habitats confer clear advantages to some phenotypes over others, such as size- or colour-dependent predation and mate choice, or when habitat-induced developmental or behavioural differences pre-adapt habitat choice. The

resulting habitat, density, and frequency-dependent soft selection (Wallace 1975) can reinforce habitat matching and the selection of traits conferring competitive advantages at high densities (Bell et al. 2021). In environments where habitat selection is devoid of density and frequency, and where all genotypes share similar habitat-dependent probabilities of risk and reward, selection is hard, population densities are more prone to vary, and adaptation is likely to favour the average number of offspring more than their individual quality (Bell et al. 2021).

Equation 2 provides a final warning. Equalizing mean fitness via an IFD is not the same as equalizing adaptive evolution because the partial effects of environmental influences [$\partial T/\partial E$ (reaction norms) and $\partial D/\partial E$ (density and frequency dependence)] are likely to vary among habitats. Thus, if one is interested in fully understanding natural selection on traits such as life history, a minimum analysis must include the density-dependence of habitat selection. That analysis is simplified in stable populations that would possess constant densities in each occupied habitat.