

HABITAT AND HABITAT SELECTION: THEORY, TESTS, AND IMPLICATIONS

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Ancient Nabateans prospered in a green patchwork Negev by harvesting its sparse rainfall with an ingenious system of hillside dykes and catchments. They anchored their commerce with way-stations taxing the long lines of spice-laden camel caravans that, like tall ships, sailed the dunes and barren, rocky landscapes of the Middle East. Even now, flocks of the Negev's nomadic Bedouin slake their thirst in the Nabatean's long-abandoned, hand-hewn, bedrock cisterns.

Modern Negev immigrants see the Nabateans as an inspirational parable for gritty determination, hard work, and invention. The Nabatean desert "experiment" is also a parable for habitat and habitat selection. At their peak, Nabatean cities were inhabited by only a few thousand people. Most of the Negev was too harsh to support even their creative agriculture.

In the parlance of ecology, the Nabateans strived to eke out their precarious existence in a landscape containing a few fragile source habitats embedded in an inhospitable sink. As the Nabatean cities grew, so too did their demands on the sources. Wonderfully engineered agriculture was necessity as much as invention. Irrigated land subsidized formerly lush oases. The Nabateans lived on the razor's edge. Wars, the age of sail, and altered trade-routes sealed their fate. The Nabatean economy collapsed and the Negev returned to the nomads.

Similar stories are written large in all human history. The Polynesian migration through the South Pacific is not so much a legacy of heroic adventure and superb navigation as it is an escape from poverty and starvation. The great human migrations to North and South America also can be understood as density-dependent dispersal by destitute people leaving lands of hardship in favor of the promise of future prosperity in an under-populated new land. Today's refugees from famine, war, and persecution swarm the globe in search of a better life.

Humans, like all species, require space in which to live. And, like all other species, our abundance varies across space. We disperse our descendants to live in new places.

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So we might suspect that theories of habitat selection would be deeply imbedded in our BIDE (Births, Immigration, Deaths, Emigration) models of population dynamics. Alas, those phenomenological models seldom include mechanisms of habitat occupancy that generate spatial and temporal variation in fitness and migration.

The role of migration is explicit, however, in metapopulation models that integrate space and time into a more comprehensive understanding of populations. Early models concentrated on the pulse of local extinctions and colonization without reference to density dependence or other mechanisms influencing those probabilities. Density-dependent dispersal is explicit in more sophisticated models that assess movement through landscapes of varying habitat quality. Also, dispersal kernels and movement rules often are used by landscape ecologists to predict abundance and distribution in heterogeneous environments. But few models of spatial dynamics successfully merge density-dependent habitat selection with landscape pattern and dynamics.

Habitat stands front and center in wildlife management and conservation, where ecologists use sophisticated tools to describe spatially explicit resource use. These empirical models often are then used to map habitat quality at various spatial scales and to inform managers on the future availability and use of habitats. Resource-selection functions can be used to identify “critical habitat” of endangered or threatened species, to help assess the viability of populations, and to aid in understanding the consequences of changing land-use and climate. Yet again, the density-dependent mechanisms of habitat selection, their ramification as frequency-dependent patterns in habitat use, and evolutionary change in habitat preference, are seldom included.

Meanwhile, theories of habitat selection have increasingly influenced our understanding of dispersal, source–sink dynamics, occupation and avoidance of ecological traps, the assembly and structure of ecological communities, and the evolution of niches. Yet we lack consensus on definitions of habitat, the scale of habitat selection, the connection between habitat selection and patch use, the role of stochasticity in population dynamics and habitat selection, and the degree to which we can use patterns in density to infer habitat quality and selection.

So we scoured the world in search of scholars who could bring sense and synthesis to our understanding of habitat, habitat selection, and its implications to management and conservation. We realize that any collection such as this will be eclectic and unable to cover the broad array of mechanisms influencing habitat selection and its manifest roles in such areas as ecology, evolution, wildlife management, and conservation biology. We hope, nevertheless, that this collection of papers will serve as a benchmark against which future scientists can gauge progress. Several authors highlight new approaches and insights that can, and should, guide future research. And, if we are lucky, perhaps others will pick up the gauntlet and use habitat selection to gain knowledge of the spatial and temporal dynamics of humans that, along with other factors, must be understood to improve the basis for resource management and conservation decisions.

Robert Holt and Michael Barfield (Holt and Barfield, 2008, this issue) tackle the problem head-on with a theory that evaluates the conditions under which species' niches can evolve to convert sink into source habitat. Niche expansion in previous models was

prevented by the assumption that all individuals participated equally in migration to and from sink habitat. The new models relax this assumption and allow phenotypic variation in dispersal. The models teach us that habitat selection can facilitate adaptation to sink habitats. But adaptive evolution toward sinks can be very slow, even under the most promising conditions. And it can be further constrained by stabilizing selection in the source.

Ultimately, habitat selection emerges only because organisms are better adapted to live and reproduce in some places than they are in others. Each species is dealt a death card that eliminates it from the game of life. But the dealer plays favorites. Some taxa are at the table for a single hand while others hang on with the same general body plan and habitat preference for millions of generations. One explanation for these patterns is that niches are conservative. Habitat selection constrains the niche to source habitats. As long as source habitats persist, so do their occupants. But previous models assumed that novel mutants obeyed the same dispersal rule as did the average individual in the population. When Bob Holt and Michael Barfield relax that assumption, and allow each mutant to play to its strength, they find that the adaptive ability to exploit new habitats, including fitness sinks, is enhanced. Although niches may not be as conservative as we once thought, they are hardly liberal. As mutants leave the source population, they reinforce adaptation to the source habitat by those they leave behind, and reduce the phenotypic variance in that population. If early dispersers successfully adapt to their new habitat, then disruptive selection can create new species. But if they are unsuccessful, then the lost genetic variance may constrain future evolution.

A long-standing yet exciting problem in habitat selection theory has been to link individuals' fitness measures with their habitat choices made over multiple rather than single life-cycle events. Undaunted by the magnitude of this challenge, Daniel Fortin, Doug Morris, and Phil McLoughlin (Fortin et al., 2008, this issue) model the temporal dynamics of simulated populations to predict the fitness of individuals adopting divergent resource specialization strategies under varying population density. The ability of relatively simple statistical models to predict favored strategies is impressive. This is illustrated most effectively by showing that lifetime reproductive success of female red deer living on the Isle of Rum was related to their specialization on specific plant communities located near the coast and inland as population density changed. Like other papers in this compendium, we believe that this work is exciting for two principal reasons. First, the modeling approaches described by Fortin et al. provide a strong conceptual framework for evaluating the consequences of habitat selection and potential for evolutionary change. Despite some evidence of genetic changes in response to increased population density and more generalized habitat use in red deer, a key unanswered question is whether habitat choice has a genetic basis or simply results from maternal (phenotypic) effects or imprinting associated with early exposure in offspring. This question arises frequently but has not been resolved adequately in most vertebrates. Second, underlying causes of habitat choices, the consequences of those decisions, and tests of the theory, have a profound impact on wildlife management and conservation programs.

Nearly 40 years ago Steve Fretwell and H.L. Lucas proposed a simple model of den-

sity-dependent habitat selection that led to the idea of an ideal free distribution (IFD) in which animals move among habitats in ways that maximize mean fitness (Fretwell and Lucas, 1969). Daryl Moorhead and colleagues (Moorhead et al., 2008, this issue) have studied two experimental systems, classic published data on flour beetle coexistence, and more recent studies of red-backed voles in Lakehead University's Habitron. Numerous, often complicated, mechanisms have been proposed to explain the outcomes of Park's famous flour-beetle experiments (Park, 1948). Moorhead et al. (2008, this issue) show how all of these mechanisms can be simplified when we recognize the role of density-dependent habitat selection. The existence and importance of an IFD is supported in both the beetle and vole examples. The connection of experimental designs with computer models is relatively exceptional in habitat studies; therefore, these results are particularly important.

However, such IFD results do not always obtain because social interactions among individuals, e.g., territoriality, can maintain variability in fitness leading to what Fretwell and Lucas termed an ideal despotic distribution (IDD). One possible outcome of interference competition can be nonlinear isodars, as illustrated by Tom Knight et al. (2008, this issue), using experimental data from brook trout.

Gabriel Blouin-Demers and Patrick Weatherhead (Blouin-Demers and Weatherhead, 2008, this issue) return to the challenging but long-neglected process of linking habitat choices and fitness in ectotherms by relating habitat use to locomotion speed in black ratsnakes. These authors are well aware of assumptions implicit in making these connections that would entangle the careless writer. They recognize, for instance, that thermal conditions for optimal movement may differ strikingly from those required for other life-history traits—such as growth rate. But their approach is well-reasoned and they show convincingly that snakes use habitats non-randomly, and in ways that could yield higher fitness. Ratsnakes spend a disproportionate amount of time in habitats that provide optimal thermal conditions for avoiding lethal temperatures, as well as for capturing prey and evading predators. As argued by Blouin-Demers and Weatherhead, future work on populations of these and other ectotherms will be especially important for projecting effects of future climate and landscape changes, and for guiding conservation initiatives aimed at protecting and enhancing critical habitats.

Students of species coexistence and patch use will be familiar with a wonderful story being written in the sandy deserts of southern Israel. Michael Rosenzweig and Zvika Abramsky set the stage in 1986 (Rosenzweig and Abramsky, 1986). Allenby's gerbil and the greater Egyptian sand gerbil are embedded in a peaceful game of habitat selection. Fierce rivals for shared habitats, they nevertheless coexist in a habitat centrifuge that spins each species into its secondary preference at high density. Further studies led by former Rosenzweig students Burt Kotler and Joel Brown (Kotler et al., 1991, 1993, 2002) teach us that the competition is unequal and depends on predation risk. Large Egyptian gerbils forage early when they can skim the cream from the renewed larder of seeds redistributed by late afternoon winds. Diminutive Allenby's gerbils live off the crumbs by foraging later in the night with greater efficiency. But each species forages less in dangerous places than in safe patches.

Victor China and Noa Shefer join Abramsky with Brown and Kotler (China et al., 2008, this issue) to bring the story up to date. Habitat selection of the two protagonists depends on density, but while the more specialized Egyptian gerbil prefers semistabilized dunes at low density, the generalist Allenby's gerbil has no preference between semistabilized or stabilized habitat. The pattern of giving-up-densities in standard foraging patches revealed a greater cost of predation in stabilized habitat. The cost decayed with increasing density. Thus the gerbils appear to manage risk by exporting safety in numbers from one habitat to another via density-dependent habitat selection.

Greater sage grouse are among North America's most magnificent birds. They rival wild turkeys and Europe's capercaillie for size and charisma. The limit of their geographic range coincides with the boundary of the Great Plains stretching across the western USA and Canada. Males hoot and strut in the cool dawn mist of spring, ghostly apparitions of the prairie's native peoples whose rich culture was starved by the extinction of bison. The prairies were not empty for long. Cattle barons moved their herds north into the rich Alberta grasslands. Cattle are poor cousins of the oil and gas that feed the Alberta economy. The barons and their massive, unfenced spreads vanished into the folklore of high-prairie cowboys. Can the grouse be far behind?

Cameron Aldridge and Mark Boyce (Aldridge and Boyce, 2008, this issue) answer the question with cutting-edge models of habitat use and chick mortality. Sage grouse breed in the dry sage-brush uplands. The most successful birds raise their chicks among forbs growing along sinuous moist coulees and depressions that snake across the remaining native prairie. Cattle saved the prairie from the farmer's plow, but not from exploration and exploitation of oil and gas. The vast tracts of prairie have been carved into a patchwork quilt dotted with hundreds of well-heads and roads. The consequences for grouse are dire. Many of the wells lie in the same moist habitats that sage grouse hens need for chick rearing. Although hens can raise their chicks successfully during years with normal precipitation, recent broad-scale droughts threaten the population with extinction. These insights were possible only by merging habitat selection with its fitness consequences.

Will male sage grouse continue to herald the Canadian spring with their spectacular displays of fanned spike-pointed tail feathers, inflated gular sacs, and rigid drooped wings? Aldridge and Boyce conclude that grouse will persist only if managers expand the size of moist habitat patches and improve their quality, as well as that of adjoining grassland. Is there another option? Is there enough time for sage grouse to adapt in order to successfully exploit grassland sinks? We doubt it.

Sage grouse exemplify the increasing frequency and complexity of environmental threats that are creating an urgent need for innovative ways to quickly pinpoint where conservation actions may be most effective. Alexandre Hirzel (Hirzel, 2008, this issue) uses computer simulation to explore whether conventional time-series methods of assessing habitat suitability—typically via repeated habitat-specific counts of individuals over many years—can be replaced with methods that exploit spatial variation in abundances collected within one sampling period. In a relaxed binary world, Hirzel's "virtual species" could approximate characteristics of real organisms in being either sedentary

or vagile, or responding to density-dependence or environmental variation when living in simple or patchy landscapes. Unexpectedly, a habitat's "relative capacity" to attract individuals depended little on the species' biology but could be estimated with certainty using a variety of methods in moderately patchy landscapes. Hirzel's idea of substituting spatial for temporal variation in a species' abundances across habitats holds much promise for quickly gauging habitat suitability. The litmus test will be when we evaluate whether these methods predict habitat quality in natural populations and whether habitat suitability is linked to fitness in free-ranging animals.

Ecologists usually assume implicitly that natural selection has shaped patterns of habitat selection, and that habitat-use patterns on the landscape are adaptive. But for human-modified landscapes this might be presumptuous given the relatively short time available for natural selection to sort out which habitats confer greatest fitness. Dave Howerter and colleagues (Howerter et al., 2008, this issue) evaluate this issue directly by studying nest-site selection by mallard ducks in the Canadian prairies. Nesting success was not necessarily the best predictor of where the ducks tended to nest. In an extensive literature review on the topic, Carl Bock and Zach Jones (Bock and Jones, 2004) found a similar mismatch between components of fitness and bird abundances in human-modified landscapes. Statistical models of habitat selection, such as resource selection functions, lack any explicit connection to the fitness mechanisms that shaped patterns of habitat use. Instead, these are simply statistical models describing the sorts of places where organisms can be found. In contrast, models such as the IFD, isodars, and IDD are more mechanistic, being based on underlying principles from modern evolutionary theory.

If theories of habitat selection are to effect changes in conservation and management, we need a roadmap to guide us on what they can and cannot achieve. Niclas Jonzén's review (Jonzén, 2008, this issue) illustrates some of the best routes, which sections to avoid, and where the bumpy road toward management needs more work. Jonzén warns us that purely deterministic models might mislead the unwary theoretical tourist, and that these models must ultimately include stochastic dynamics. Other processes, such as spatially correlated stochasticity, can yield patterns similar to those created by habitat selection. Jonzén challenges field ecologists to explore how, exactly, stochasticity and habitat selection interact with population dynamics at large spatial scales and through time. Then he challenges theorists to explore how the co-evolution of dispersal and adaptation between generations is related to habitat selection and dispersal within generations. The atlas to understanding, like any other roadmap, reveals many routes to a common goal. We should hardly be surprised that competing models can yield similar patterns. Like desserts displayed in a baker's window, the test of a model's utility lies not in passersby who count the calories and move on, but in whether it can satisfy the sweet cravings of the sophisticated diner.

The wildlife science literature is replete with papers that describe habitat use in animals. Many measure habitat or resource selection. They do so by using ever more challenging and sophisticated methods. Yet relatively few tackle the central issue of quantifying the consequences of habitat choice. Despite repeated calls to tightly couple

habitat-selection theory with population ecology, those cries of encouragement have largely gone unnoticed. Studies and conservation strategies of endangered species often rely on estimates of habitat-specific abundance. They can scarcely afford to overlook the critical step of an evolutionary perspective. Using abundance estimates to design and implement recovery efforts for rare or declining species in a timely manner could be misguided. However, by explicitly incorporating estimates of fitness and an “adaptive management” cycle into these programs, habitat-specific consequences of conservation actions implemented for imperiled species could be assessed and then used to improve program effectiveness. Will our efforts on behalf of endangered species help them survive as they march, like the Negev caravans of old, from one conservation oasis to the next? Or are our images of habitat quality simply mirages that lead conservation astray in a desert of declining abundance? We believe that the theory, tests, and applications described in this compendium are crucial to conservation and management. They provide new ideas and tangible ways to help navigate the density- and frequency-dependent fitness landscapes that ultimately will determine the effectiveness of conservation and wildlife management programs.

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