

**IJEE SOAPBOX:  
HABITATS AND SEASONS**



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All naturalists know that the world is heterogeneous in space and time, for almost any physical property and at almost any scale one cares to examine. The diversity of life—the number of species that exist, and how they are organized into complex communities—must reflect in some way the magnitude and structure of that heterogeneity. Ecologists use random quadrats to sample the world. The insightful set of essays in this compendium bring out the many consequences of the fact that organisms, by contrast, judiciously choose habitats to live in from the palette provided by environmental heterogeneity, and that habitat selection can have profound consequences for many aspects of ecological systems. To understand the life of an organism, we have to look at the world through its own eyes, and to recognize that in effect organisms are their own quadrats, which they place in a decidedly non-random way upon the landscape.

After reading through the articles in this special issue on habitat selection, I decided to read again the original writings of Steve Fretwell, who coined the terms “ideal free distribution” and “ideal despotic distribution” that are such a familiar part of today’s ecological and behavioral lexicon. The original paper (Fretwell and Lucas, 1969) does not seem to be readily available online. [Ironically, although one cannot get to the paper on the Web of Science, one *can* get a citation to Fretwell (1991)—an essay he wrote for Current Contents (the paper predecessor to the Web of Science) because Fretwell and Lucas (1969) was deemed a “Citation Classic”.] So instead, I looked again at Fretwell’s 1972 monograph, **Populations in a Seasonal Environment**, in which he summarized and extended the insights of the Fretwell–Lucas paper.

What immediately struck me is that Fretwell himself viewed habitat selection theory as part of a broader theoretical program addressing the influence of seasonality on population dynamics and regulation. In his own conclusion as to what he had accomplished in his book, he states:

*“Most populations live in a seasonal environment. My thesis is that this makes a difference. The primary part of my analysis is the development of seasonal models...”*

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*The IJEE Soapbox* provides an informal forum for leading ecologists and evolutionary biologists to expound on issues that they find particularly exciting, thought provoking, and novel.

Robert D. Holt is our first invited *IJEE Soapbox* essayist. Bob is Professor of Zoology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

So, though his book is mainly cited today in papers dealing with habitat selection, the author's own perspective is that its primary contribution was in clarifying the consequences of seasonality in population biology.

The development of those seasonal models is found in chapters 1–4 of the monograph, which even today provide interesting reading, and indeed have provocative conclusions yet to be fully explored in the literature. For instance, Fretwell argues that organisms with generation lengths equal to or longer than the seasonal cycle can exhibit multiple alternative states, and that if density-dependence in deaths is strong in one season, then increases in birth rates in the alternate season can actually depress equilibrium abundance. For organisms with short life cycles, relative to the seasonal cycle length, their abundance may be determined largely by conditions in just part of the seasonal cycle, depending on the exact temporal pattern of variation in demographic parameters through time. Fretwell further suggests that there are qualitative differences between the dynamics of species utilizing resources that cannot be overexploited (e.g., abiotic resources with fast renewal rates), and resources that can be overexploited (e.g., effective predators overexploiting their prey).

These were all prescient thoughts. Work in subsequent years has led to a considerable body of interesting work on the diverse consequences of temporal variation in ecological systems (e.g., Nisbet and Gurney, 1982; Henson, 2000; Chesson, 2003; Holt and Barfield, 2003; Ives et al., 2004; Greenman and Benton, 2005). Yet we are still far from a full synthesis of the dynamical and evolutionary implications of seasonality (Holt, 2008). One manifestation of seasonality is that species experience periods when there is a flush of resources. For instance, in northern temperate woodlands, a rich flora of spring wildflower species blooms during a transient period in each annual cycle of heightened light and nutrient levels, before the canopy closes (Anderson and Eickmeier, 1998). Insectivorous birds enjoy a peak of caterpillar abundance in early summer, which they garner to feed their young. And each fall in those same woods, streams receive a pulse of falling leaves—a fresh bolus of resources sustaining an entire aquatic food web based on detritivores.

Theoretical studies of the impact of seasonality upon population dynamics have revealed a rich palette of possible behaviors. The basic protocol is to take a model developed for a constant environment, and then to express one or more of the model parameters as a function of time. For example, if the birth rate of a prey species is determined by resource availability, seasonal resource variation might be portrayed as sinusoidal variation in prey births. Some species tend to oscillate following disturbance, even in constant environments, and others can cycle or show irregular unstable oscillations in perpetuity, because of strong density dependence and interactions with other species. Superimposing seasonal variation on such systems can lead to resonance, where the amplitude of oscillations is magnified by the interplay of intrinsic instability and environmental forcing (Nisbet and Gurney, 1976; Rinaldi and Muratori, 1993; Turchin and Hanski, 1997). In predator–prey interactions with driven seasonal variation in prey intrinsic growth rates, population cycles arise with a much longer period than the annual cycle, and seasonal forcing can even generate chaotic dynamics (King and Schaffer, 1999).

Seasonality can either depress or increase average population size; which occurs depends on many system-specific details. Seasonal variation in the carrying capacity  $K$  of a logistic equation reduces time-averaged mean abundance (Nisbet and Gurney, 1976), but by contrast seasonal variation in the intrinsic growth rate  $r$  can increase average abundance (Cushing, 1987). Experimental studies in controlled microcosms provide empirical demonstrations of some of these predicted effects. For instance, Jilison (1980) experimentally showed that periodic variation in the flour resource supporting lab populations of *Tribolium* increased their average numbers, consistent with the outcome of theoretical models tailored to this system (Henson and Cushing, 1997). Likewise, Orland and Lawler (2004) forced seasonal variation in resource supply rates onto microcosms harboring the protist *Colpidium striatum*, and found that resonance between this forced variation and intrinsic dynamical processes increased average abundance. They argued that metabolic nonlinearities coupled with internal resource storage during periods of high resource abundance boosted the average population size of the beetles.

This example illustrates the general point that resource storage in a season of plenty can buffer population decline through a season of scarcity (see also Genesis 41–42). In the absence of such storage, following each resource pulse during which population size grows, there is an inevitable trough of resource shortage, during which density dependence may be intensified, precisely because a season with a surfeit of resources boosts population size. For a long-lived species to persist, it must be able to cope with or evade such crunch periods. The persistence of small-bodied and short-lived species by contrast may depend simply upon rapid growth during good times leading to numbers at the end of the favorable season sufficient to survive as a population through even a lengthy decline phase.

One consequence of seasonality is thus that all species that persist must have mechanisms for surviving the worst times of the year. Many species have evolved storage mechanisms such as internal fat bodies (Grover, 1991), external hoards (e.g., seed caches in desert rodents and ants), or durable age/stage classes (Chesson, 2003) in response to seasonality. But another nearly ubiquitous adaptation to temporal variation in the environment, including seasonality, is movement across space, ranging in scale from adaptive habitat selection in local landscapes to migration across the globe. In effect, organisms which disperse do a “space for time” substitution, moving from sites where conditions are likely to deteriorate to locales where conditions are more favorable, rather than hunkering down and toughing it out without moving among habitats.

I believe this basic line of reasoning is one reason why Steve Fretwell felt that a theory of habitat selection and spatial distribution would fit organically into a broader theory of population dynamics in seasonal environments. The other, more concrete, reason is that he loved birds, and in the life of temperate bird species both seasonality and spatial variability in habitats loom large, so a full accounting of their dynamics must consider how populations respond both to temporal variation and habitat heterogeneity. He left academia long ago, and I have not been able to trace him, so cannot directly confirm this interpretation of his rationale for the structure of his 1972 monograph.

To understand the world, it is sometimes useful to imagine alternative possible worlds

which differ in some major, salient way from the one we actually inhabit. For instance, if we are to understand why there are two sexes, it is instructive to consider the consequences of living in an imaginary world where there are instead three (or more) sexes. [The earliest reference I could find for this observation is Maynard Smith (1986), but I think the insight goes back to some earlier doyen of evolutionary biology.] Reasoning about counterfactual conditions is challenging and rife with subtleties (Lewis, 2001), but a dose of science fiction can at times help illuminate science itself.

So what would our world be like, were there no seasonality? It is after all an accident of astronomical history that the axis of the Earth tilts as it does, so that we experience a regular seasonal cycle. If we could go back in time and do a little astro-engineering, the Earth could have been placed the same distance from the sun, but on a circular orbit and with no tilt, hence no seasons. The major latitudinal and altitudinal gradients would still be present, other drivers of spatial heterogeneity such as geomorphological and tectonic processes would still march along, and spatial and temporal heterogeneity might as well arise from self-organizing and at times dynamically unstable ecological systems, but there would be a monotonous temporal regularity to life, with each day on average being the same as the day before. Would this world broadly resemble the one we inhabit, or would it likely differ in some fundamental respects?

Speaking metaphorically, evolution seems to seek out every nook and cranny in the diversity of the physical world, crafting some organism that can cope with all kinds of unusual conditions. Microbes with strange chemistry abide in deep rocks, near-boiling hot springs, and in lakes buried under the Antarctic ice, and strange and wonderful denizens wander across the eternally black deserts of the deep sea. Seasonality provides an extra and quite major dimension of variability in the physical world, and many lifestyles have evolved precisely to take advantage of seasonal forcing in the environment. Many species of migratory birds, mammals, insects, and fish exploit seasonal pulses of resources in one place, and then hunker down somewhere else during resource troughs. Were there no seasonality, entire lifestyles would be missing from the spectrum of organic diversity.

Moreover, in the absence of seasonality, even non-migratory organisms might have fewer reasons to move from one place to another. Dispersal can evolve even in constant environments (due to competition among kin, Rousset, 2004), but the natural history of migration and dispersal shows that temporal variation, including seasonal forcing, is a powerful driver of movement. If dispersal were considerably reduced in an aseasonal world (versus the one we know), my suspicion is that we would see a much more depauperate biota emerging over evolutionary time scales. Within species, a moderate amount of dispersal can boost the pool of genetic variation that is brought to bear on local adaptation to any one site; conversely, if dispersal is very low, local adaptation might be constrained by a paucity of genetic variation. After a species originates, if overall rates of dispersal are very low, even slight barriers could constrain its ultimate range to the region near its site of origin. Rich local communities can only arise if many species' geographical ranges overlap, and if ranges are strongly constrained by dispersal limitation, there is less opportunity for overlap. Mechanisms of coexistence that depend upon dispersal in metacommunities (Holyoak et al., 2005) would contribute much less

to species diversity, so local species richness would be reduced because of species interactions as well. All these single-species and community-level effects of reduced dispersal would have macroevolutionary consequences, in that a given species would be less likely to be the progenitor of daughter species across space. Local communities on continents might then resemble the biota of small, distant oceanic islands today, which because colonization is so rare are strikingly depauperate in the communities of plants and animals they contain.

And now, back to habitat selection. We could carry out a similar thought experiment, and ask how much diversity we would see on our planet, if organisms dispersed only at random and could not choose to reside in habitats so as to improve their fitness. My hunch is that again diversity would be greatly constrained. Habitat selection permits resource specialization to be maintained in a heterogeneous landscape, which is an important dimension of species coexistence. The richest slice of the Earth's biota is comprised of plants, specialist herbivorous insects, and their specialized parasitoids, most of which are rare, in an absolute sense. It is difficult to imagine a species of *Heliconius* butterfly persisting in a rain forest, were it unable to seek out with some degree of effectiveness the sparsely dispersed patches of *Passiflora* it requires for oviposition.

These counterfactual conjectures might be assessed to some degree using laboratory microcosms and *in silico* experiments. Whether or not my hunches about imaginary worlds are correct, I have no doubt that habitat selection has been a vital ingredient in generating and maintaining the rich panoply of life we see around us today, in the spatially heterogeneous and seasonally driven world that actually exists (Rosenzweig, 1995). As humans destroy and reconfigure the landscape of this world, we preclude or distort avenues for habitat selection by many taxa and thereby further degrade their environment. In a temporally varying environment, habitat selection may be particularly important for species persistence (Schmidt, 2005). A deep understanding of habitat selection is essential for conservation, restoration, and the wise management of natural resources.

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I would like to thank Steve Fretwell for his kindness to me many years ago. In 1978, when I was still a student, my parents were living in Manhattan, Kansas, and Steve was a professor there at Kansas State University. Over the Christmas break, I went home, and being a keen birder, contacted Steve (much of whose work was motivated by empirical studies of dickcissels and other bird species). He took a break from his own family festivities and drove me to walk across the Konza tallgrass prairie reserve, where as a wind lightly salted with snowflakes gusted across the hills, we flushed my first Greater Prairie Chicken. After I moved to the University of Kansas in 1979, over the next several years he and I had a number of stimulating conversations about a wide range of topics in evolutionary biology, from habitat selection to food web interactions to the awkward interface between evolution and religious faith. I am honored to have known this stimulating and creative scientist.

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