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**Edited by Simon A. Levin Stephen R. Carpenter, H. Charles J. Godfray,  
Ann P. Kinzig, Michel Loreau, Jonathan B. Losos, Brian Walker & David S. Wilcove:  
The Princeton Guide to Ecology**

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# I

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## Autecology

Jonathan B. Losos

Autecology refers to how a single species interacts with the environment; its counterpart is synecology, which refers to how multiple species interact with each other. This latter term is mostly congruent with the field of community ecology, the subject of part III of this volume.

Integral to any discussion of autecology is the concept of the niche. This concept has a long and checkered history in the field of ecology, and the term itself has taken on different meanings through time (chapter I.1). In the most general sense, however, we may think of the niche of a population as the way members of that population interact with their environment, both biotic and abiotic. In other words, the term “niche” refers to where organisms live and what they do there.

The first step in considering how organisms interact with their environment is investigating how the specific phenotypic characteristics of members of a population allow them to exist in a particular environment. The environment poses a wide variety of challenges to organisms: for example, they must be able to obtain and retain enough water, withstand high or low temperatures, and obtain enough nutrients to survive. More than a century of research has revealed that species, and even populations of species, are often finely tuned to the specific conditions in the environment in which they live. In recent years, increasingly sophisticated approaches and instrumentation have allowed an exquisitely detailed understanding of the physiological basis of organismal function (chapters I.2–I.4).

Animals—and, in some sense, fast-growing plants—also can influence the way they interact with their environment through behavioral means. For example, animals can choose the habitat in which they occur and thus can determine, to some extent, the environment they experience throughout their lives (chapter I.5). Many organisms move from their birth site at a particular stage in life; although for plants and some animals, dispersal is passive, other species actively choose where to settle (chapter I.6).

Behavior, of course, is a key component of how most animals interact with their environment. Almost

all aspects of the natural history of animals have a behavior component. In part I, we consider foraging (chapter I.7) and social behavior (chapter I.8). Other topics are included in parts II and VI of this volume.

Most plants have relatively little ability to determine the environmental conditions they experience. But plants often have another option available—they frequently exhibit substantial phenotypic plasticity, which allows a plant to alter its phenotype in an advantageous way to be better suited to its environment. Scientists have long appreciated this ability in plants, and zoologists have come to realize relatively recently that many animal species exhibit adaptive phenotypic plasticity as well (chapter I.9).

Organisms adapt in yet another way, by molding their life cycle—what is termed “life history”—to the particular environment in which they live (chapter I.10). Thus, species in environments in which resources are abundant and threats are common may have short generation times and early reproduction. Conversely, in environments in which resources are more scarce but threats are not as severe, a more successful strategy may be to defer reproduction and to invest in becoming better competitors for resources, delaying reproduction and ultimately producing fewer, but better provisioned, offspring.

No species occurs everywhere in the world. The behavior and physiological capabilities of a species determine where a species can and cannot occur. In the last few years, advances in remote sensing technology have provided the capability to visualize the distribution of environmental conditions with great precision over large spatial scales (chapter I.11). Combined with records of species occurrences and, ideally, an understanding of species’ physiological capabilities, these geographic information systems approaches have opened new vistas for understanding how and why species occur where they do; these approaches are also of great importance in predicting how species will respond to rapidly changing environmental conditions

(see parts IV and V). Of course, the distribution of a species is not only a function of its physiological capabilities and other aspects of its ecology. Rather, Earth geography and history also are important—a species cannot occupy an area that it has never had the opportunity to colonize. Consequently, biological and historical factors combine to determine the geographic range of any species (chapter I.12).

Integral to an understanding of how organisms interact with their environment is the concept of adaptation, the idea that natural selection has molded the characteristics of populations so that they are well suited to the particular circumstances in their environment (chapter I.13). Of course, this is not to say that organisms are optimally adapted to their current conditions, nor that every feature exhibited by a population represents an adaptation for some aspect of the environment. Quite the contrary, natural selection is only one of many processes that affect how populations evolve (chapters I.14 and I.15); in some circumstances, processes other than natural selection will predominate, leading populations to be less well adapted to their current circumstances.

Ecologists are increasingly interested in the evolutionary time scale. On one hand, it has become clear that, in many cases, we can understand the current state of species and of entire communities only by considering their history. Species are not blank slates, to be molded by selection to the optimum configuration for their environment; rather, they have a historical starting point, and selection can work to modify species

only from this point (chapter I.13). Similarly, communities, too, have histories—the current state of a community is a result of which species have managed to get to a given locality and how those species interact once there. Methods to incorporate evolutionary information, in the form of phylogenies (or evolutionary trees), are now widely utilized and becoming increasingly sophisticated (chapter I.16). Conversely, evolutionary biologists have clearly demonstrated over the last several decades that evolutionary change can occur very rapidly (chapter I.17). Consequently, ecologists ignore evolution at their own peril—populations can adapt quickly enough that evolution can have effects even on ecological time scales.

Evolution is important in another respect. The components of ecological interactions are species. The study of speciation—how new species arise—has long been the province of evolutionary biologists, but in recent years it has become clear that ecology may play an important role in affecting rates of speciation. In particular, the concept of ecological speciation—the idea that speciation is intimately tied to ecological divergence—has gathered great support (chapter I.18). Hence, in this respect as well, ecological and evolutionary perspectives are strongly intertwined. Finally, over larger time scales, certain groups of organisms diversify greatly, producing not only a large number of species but also occupying a great variety of ecological niches. Some scientists consider this phenomenon, known as adaptive radiation, to be responsible for the majority of life's diversity (chapter I.19).

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# I.1

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## Ecological Niche

Thomas W. Schoener

### OUTLINE

1. Three concepts of the ecological niche
2. The recess/role niche and seeking ecological equivalents
3. The population-persistence niche and mechanistically representing competition
4. The resource-utilization niche and understanding the evolution of species differences
5. Environmental niche modeling and analyzing niches on a macroscale
6. Conclusion

It may come as something of a surprise that *ecological niche*, a term so common in the popular media, has three distinct meanings among scientists, each with an associated conceptual basis: these are the recess/role niche, the population-persistence niche, and the resource-utilization niche.

### GLOSSARY

**character displacement.** The situation in which two species are more different in geographic locations where they overlap than between locations where they occur alone

**community.** Those species populations occurring at some location

**competition.** Ecological interaction in which two or more species negatively affect one another by consuming common resources or by other harmful means

**convergence.** Development of increasing similarity over time, usually applied to species somewhat unrelated evolutionarily

**niche dimension.** Environmental variable along which a species' niche is characterized, e.g., food size, and typically represented as the axis of a graph

**polymorphism.** The existence of two or more forms, differing in morphology or some other way, in the same population

**population.** Those individuals of a species occurring at some location

**population growth rate  $r$ .** The per capita rate at which a population changes size, typically computed as the birthrate minus the death rate

### 1. THREE CONCEPTS OF THE ECOLOGICAL NICHE

#### The Recess/Role Niche

The first use of “ecological niche” appeared in a report on ladybugs written by R. H. Johnson nearly a century ago, although the term was used shortly thereafter by the zoologist Joseph Grinnell, who is generally given credit for its original development. The meaning was very close to figurative usage: the ecological niche of a species is its “role,” “place,” or more literally “recess” (in the sense of a “nook” or “cubbyhole”) in an ecological community. Thus, the California thrasher, one of Grinnell’s major examples, is a bird of the chaparral community that feeds mostly on the ground by working over the surface litter and eating both animal and plant items of a suitable size. Escape from predators is similarly terrestrial, with the well-camouflaged bird shuffling off through the underbrush on the rare occasions when it is threatened.

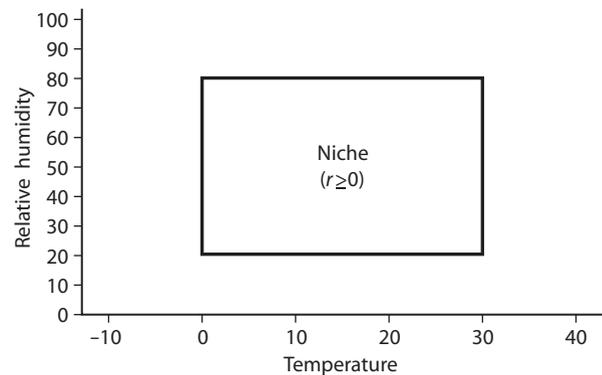
The idea that there exists a set of characteristic habitat and food types with accompanying behavioral, morphological, and physiological adaptations leads to the notion of ecological equivalents. These are defined as two or more species with very similar niche characteristics that occur in completely different localities. An example from Grinnell’s writings is the kangaroo rat of North America, which “corresponds exactly” to the jerboa (another desert rodent species) of the Sahara. The existence of ecological equivalents would imply that rather invariant rules determine the niches available for occupancy in a particular kind of environment, e.g., a desert. Moreover, niches can be empty in the sense that a suitable species does not occur within a

locality, perhaps because it never got there or was unable to evolve in situ.

But to what extent do ecological equivalents really exist? Decades after Grinnell's work, we now know (section 2, below) that although some examples can certainly be found, perhaps more commonly, species of similar environments (e.g., deserts) among distant localities are neither identical nor often even similar. Perhaps such considerations helped to engender the two other meanings of ecological niche, each with its accompanying set of ideas about how the ecological world works.

### The Population-Persistence Niche

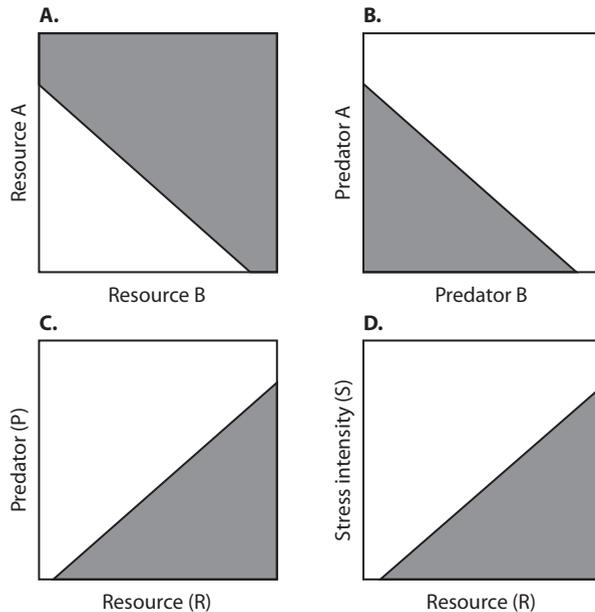
The *population-persistence niche* has its roots in papers written in the mid-twentieth century by the ecologist and limnologist G. E. Hutchinson. This concept focuses on the species, in this case its population, rather than on the environment. Hutchinson formulates the ecological niche as a quantitative description of the range of environmental conditions that allow a population to persist in some location; the term *persist* means having a positive or at least zero (break-even) population growth rate,  $r$  (if  $r$  is negative, the population dwindles away to extinction). An example of an environmental condition is temperature; a second example would be humidity (for organisms on land) or salinity (for organisms in water). If we represent an environmental condition by the axis of a graph, a *range* is an interval along that axis, e.g., temperature from 0°C to 30°C (figure 1). A second interval, say for relative humidity, might range from 20% to 80% along the humidity axis. We can have as many different environmental axes as necessary to characterize the population growth rate. If  $r$  for a given axis is uncorrelated with the values of variables of the other axis (e.g., if the range of temperatures allowing  $r \geq 0$  is the same for any value of humidity), then the niche is rectangular (as in figure 1); otherwise it will have other shapes. Hutchinson labeled his concept the cumbersome " $n$ -dimensional hypervolume" (imagine three or more environmental axes). The more succinctly labeled *fundamental niche* is that portion of niche space where the species population can persist. The fundamental niche is visualized as being in the absence of other species that compete with the given species for resources and thereby affect its persistence. To account for this latter circumstance, Hutchinson defined the "realized niche" as that portion of the fundamental niche not overlapping the fundamental niches of competing species, plus that portion overlapping the competing species' niches where the given species can still persist (have  $r \geq 0$ ).



**Figure 1.** Example of Hutchinson's population-persistence niche. Rectangle encloses the ranges of temperature and humidity in which the species' population can persist (where  $r \geq 0$ ).

Hutchinson's concept is important for several reasons. First, it provides a precise, quantitative way to characterize the ecological niche. Second, it focuses on what the species itself does rather than on the opportunity for a species to exist or not in a community (the latter being the "recess" concept of Grinnell). Thus, ecological equivalents are not necessarily expected and, if they do not occur, are not troubling to the concept: for Hutchinson, there are no "empty niches."

Such a precise formulation of the niche is not without its drawbacks, however. Chief among them perhaps is the difficulty of finding out what the population-persistence niche of a species actually is in nature. Presumably, for each point of the  $n$ -dimensional hypervolume—say for each value of temperature and humidity—one needs to culture populations or otherwise determine their population growth rate  $r$ ; and one repeats this for different points until one has all combinations of temperature and humidity for which the population can persist. The difficulty of so doing for all but microorganisms (at best) is easy to imagine. A second problem is that certain niche characteristics as conceptualized by Grinnell are not easily ordered along an environmental axis. An example is food size: at any given real location, food comes in a variety of sizes (rather than there being one food size for each location). Of course, one can use average food size, but such a concept is not as plausible as using average temperature because animals come across a variety of food sizes on a daily basis. Animals of a particular body size (and therefore a particular size of feeding apparatus, e.g., mouth) have limitations on the extreme values of food size that can be consumed: items too large cannot be swallowed, and those too small cannot be handled deftly (or eaten in an energetically profitable way). Hence, a more detailed



**Figure 2.** Chase-Leibold concept of the population-persistence niche. Each panel has two regions, a shaded region where  $r \geq 0$  and an unshaded region where  $r < 0$ . The niche is the shaded region. (A) A species with two substitutable resources (the axes measure resource density); (B) a species with two predators; (C) a species with a predator and a resource; (D) a species with a stress and a resource. (Figure courtesy of J. M. Chase.)

description than the average food size available at a location is desirable. Third, Hutchinson's niche is one-sided in the sense that it assumes a rather passive species that does not affect other species in the community in a way that eventually feeds back onto the given species. Fourth, Hutchinson focuses almost exclusively on one type of ecological interaction, competition between species; for example, his distinction between the fundamental and the realized niche. In this way, his concept was not as inclusive as that of Grinnell.

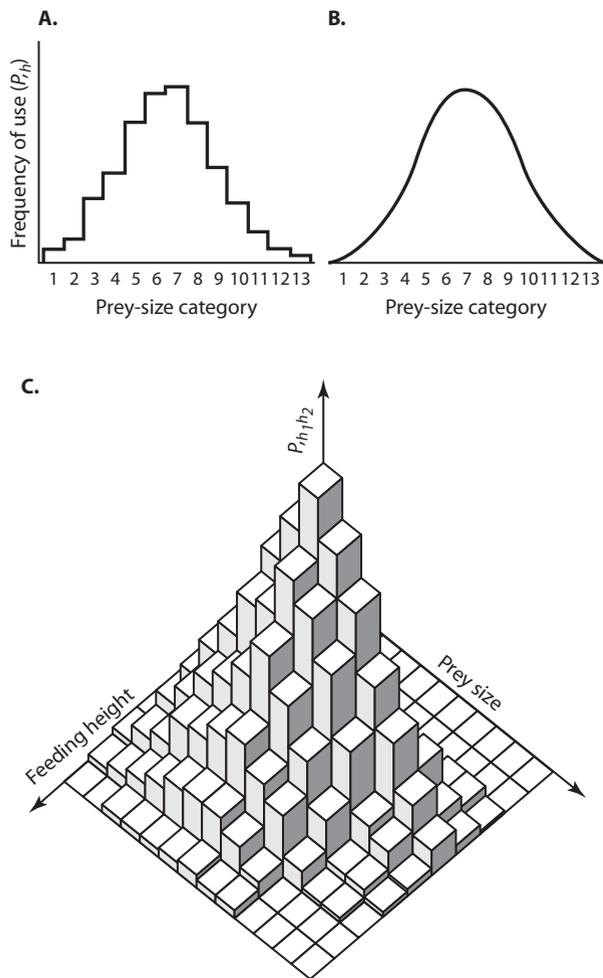
In part as a reaction to the latter two drawbacks, Jonathan Chase and Mathew Leibold have substantially extended the population-persistence niche. In a recent but already very influential book, they define the niche as a joint specification of environmental conditions or variables that allow a species to have  $r \geq 0$  along with the effects of that species on those environmental variables. Niche axes are quite broadly construed and can include a variety of factors that impact populations (and vice versa); examples include amount of a given resource, abundance of a given predator, and degree of a physical stress such as wind speed (figure 2). Thus, one can incorporate effects of species on environmental conditions, and one can specify a given region of niche space where a species has  $r \geq 0$  (figure 2).

Although this model represents a vast improvement in the concept of population-persistence niche, the operational difficulty of measurement still exists: determining the niche for figure 2 (Chase and Leibold) is not much easier than for figure 1 (Hutchinson).

### The Resource-Utilization Niche

An eminently operational concept of the ecological niche, formulated by two evolutionary ecologists, Robert MacArthur and Richard Levins, is the *resource-utilization niche*, our third meaning. Like the population-persistence niche, the resource-utilization niche is quantitative and multidimensional, but it focuses entirely on what members of a species population in some locality actually do—in particular, how they use resources. The relative use ( $\Rightarrow$ utilization) of resources along a given niche axis can be described as a frequency distribution or histogram. Take, for example, the axis food size. We can (figure 3, top) draw a histogram showing the fraction of food of different sizes consumed by all members combined of a given population; e.g., the fraction of the total population's foods between 5 and 6 mm. If we have a second dimension, say feeding height, we can graph the fraction of food items eaten at different heights in the vegetation. The two can be combined as a joint distribution or three-dimensional histogram (figure 3, bottom), and this can be further generalized (although not easily graphed) for as many dimensions as ecologists find important to describe the population's resource use. A broad classification of the kinds of niche axes used for utilizations consists of habitat, food type, and time. Within habitat, microhabitat and macrohabitat are distinguished, whereby microhabitat has a smaller spatial scale (e.g., height in vegetation) than does macrohabitat (e.g., vegetation zone such as tropical rainforest or desert). Within food type, food size and hardness can be distinguished. Within time, daily and seasonal activity can be distinguished.

The resource-utilization niche immediately frees us from the problem with Hutchinson's formulation that certain environmental variables cannot be meaningfully described using only the average. Indeed, the resource-utilization niche is nothing more than a precisely formulated description of the natural history of a species: its habitat, food types, and activity times, among other things. Such natural history can include nonfeeding habitats and activity times for behaviors such as predator escape and mating, all characterizable on its niche axes. Thus, we have a niche concept that precisely encapsulates what ecologists measure anyway. Indeed, Grinnell, the originator of the *recess/role niche* concept, measured such things in his study



**Figure 3.** An example of the resource-utilization niche. (A) A one-dimensional niche, where the dimension is prey size. Numbers give prey-size categories, indexed by  $h$ ; (B) the same utilization smoothed; (C) utilization of two resource dimensions, prey size and feeding height. (Redrawn from Schoener, 1986.)

organisms but with the assumption that, in so doing, he was discovering something about the availability of niches in the community—an availability or opportunity to which the species more or less had to conform. The resource-utilization niche, in contrast, assumes nothing about rigidly determined niche recesses in a community, nor about the necessity of ecological equivalents, nor about the existence of empty niches. The resource-utilization niche was formulated a decade or so after the population-persistence niche but, unlike the latter, has remained rather unchanged up to the present. This is despite the fact that, by emphasizing resources, it is seldom extended beyond resource use,

unlike both the recess/role niche of Grinnell and the population-persistence niche of Chase and Leibold.

We now review seriatim the kinds of research engendered by the three concepts of the niche as well as a very recent research trend called ecological niche modeling that includes elements of all three.

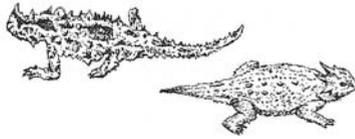
## 2. THE RECESS/ROLE NICHE AND SEEKING ECOLOGICAL EQUIVALENTS

In an early study of grassland birds inhabiting far-flung locations—Kansas, Chile, and California—Cody found that each community contained about the same number of species and the same ecological types: three or four passerines (small “perching” birds), a larger vegetarian “grouse-like” species, both a long- and a short-billed wader, and two or three raptors. Twenty pairs of ecological equivalents were identified between the two Mediterranean systems: Chile and California. However, later studies by Cody in other Mediterranean systems including Sardinia and South Africa showed a weaker pattern, especially for the latter, whose floras were very different.

In contrast to birds, plants in Chilean and Californian systems showed little convergence at the community level; for example, woody vegetation in Chile comprises less of the total cover but more total species and has a greater diversity of height layers than in California. Nonetheless, the major growth forms (e.g., broad-leaved evergreen, broad-leaved deciduous) are similar, even with regard to number of species, although several forms present in Chile (e.g., spine-stemmed shrubs) are absent from California—an apparent empty niche. Major resemblances between plant growth forms among plants with very different evolutionary lineages occur rather commonly among plants; a striking example is given by American cacti and African euphorbs.

Perhaps the least evidence for ecological equivalents after systematic search is among colubrid snakes of North, Central, and South America. Cadle and Greene find few ecological equivalents (and little evidence for community similarity); instead, a number of types (fossorial earthworm eaters, nocturnal arboreal lizard/frog eaters) in some communities are conspicuously absent in others.

Probably the most extensive work on convergence and ecological equivalents has been done on lizards. An initial study by Fuentes, again comparing Chile and California, found convergences in community characteristics as well as in individual niche traits—microhabitat, daily activity time, and food type. In a second major study, Pianka found less evidence for



**Figure 4.** An example of ecological equivalents: the horned toad (*Phrynosoma platyrhinos*) of North American deserts and the thorny devil (*Moloch horridus*) of Australian deserts. [From Pianka, E. R. 2000. *Evolutionary Ecology*. San Francisco: Harper & Row. Used by permission of Pearson Education, Inc.]

similarity in community characteristics than difference among lizards of the three warm-desert systems of North America, Australia, and Africa. Nonetheless, striking ecological equivalents sometimes exist, such as the amazing resemblance between the horned toad of North America and the thorny devil of Australia (figure 4).

Examples of ecological equivalents are most impressive when the species from widely different localities are relatively unrelated in terms of evolutionary descent: convergent evolution toward the same morphology and behavior would seem to support the idea of the niche as a functional optimum characteristic of particular types of communities (e.g., those in deserts) into which species repeatedly evolve. Nonetheless, a plausible hypothesis for lack of convergence is that major evolutionary stocks are so different that evolution is too constrained to produce much convergence. Melville, Harmon, and Losos recently examined two lizard families, the Iguanidae and Agamidae, of North America and Australia, respectively, which are closely enough related to belong to the same clade (Iguania) even though they have been geographically separate for as long as 150 million years. Using an approach that takes into account evolutionary relatedness, they found convergence in habitat use and locomotor morphology, including pairs of ecological equivalents, between the two deserts.

Another example of convergence among relatively closely related species is provided by the *Anolis* lizards of large West Indian islands: Cuba, Hispaniola, Jamaica, and Puerto Rico. Here, various ecomorphs—species occupying the same microhabitat—have independently evolved on the separate islands. Harmon, Kolbe, Cheverud, and Losos found that five functionally distinct morphological characters—body size, body shape, head shape, lamella (ridges on toes) number, and sexual size dimorphism—converge among the different islands as a function of habitat similarity. For example, lizards living on the ground and low trunks are more similar between Cuba and Hispaniola than either is to other ecomorphs (e.g., those living in tree

crowns) co-occurring on the same island and to which they are more closely related.

A final recently discovered example of convergence occurs in a completely different group: orb-weaving spiders of the genus *Tetragnatha* of the Hawaiian islands. Blackledge and Gillespie found that spiders inhabiting different islands constructed remarkably similar webs. These convergences toward ecological equivalency, which they called “ethotypes” (ethology is the study of behavior, and this emphasizes the behavioral similarity), occurred independently in evolution. Like the Australian Iguania discussed above, the group as a whole consists of relatively closely related species.

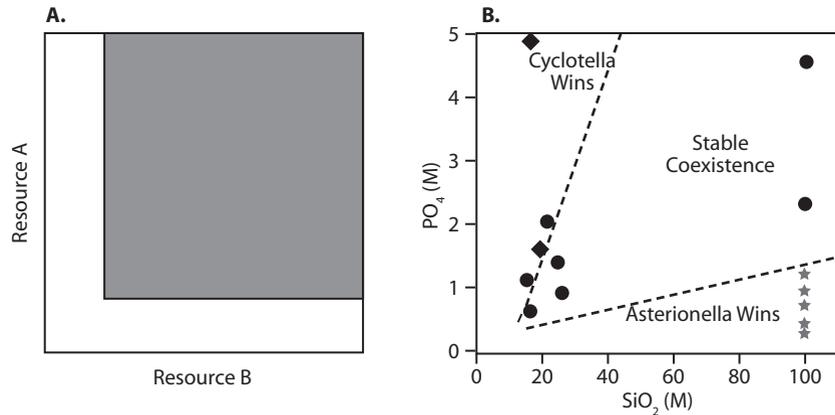
In conclusion, although the evidence for ecological equivalents is certainly mixed, more and more examples are coming to light that make Grinnell’s rather old concept seem alive if not completely well. As Schluter has suggested, to the extent that ecological equivalents exist and are independently evolved, morphology, physiology, and behavior must constrain the efficiencies with which resources and other factors characteristic of particular kinds of ecosystems (e.g., deserts) can be dealt with—ecological equivalents mark peaks in the adaptive landscape.

### 3. THE POPULATION-PERSISTENCE NICHE AND MECHANISTICALLY REPRESENTING COMPETITION

Maguire in 1973 may have been first to plot population growth rate  $r$  for real species as a function of niche dimensions and to make predictions about the competitive outcomes among them. In the 1950s, Birch had studied several species of beetle infesting stored grain in Australia; figure 5 shows Maguire’s plot of Birch’s data with respect to temperature and moisture. Isoclines of positive values of  $r$  down to zero (no population growth) show different patterns for the two species, such that *Calandra oryzae* has a higher  $r$  for lower temperatures and somewhat greater moistures than *Rhizopertha dominica*. The dashed line in figure 5 separates regions of niche space where one versus the other species has the higher  $r$ . Assuming no complications, an environment on one or the other side of the line will favor one or the other species of beetle in competition.

To illustrate their ideas about the population-persistence niche, Chase and Leibold replot data of Tilman for two species of diatoms, *Asterionella* and *Cyclotella* (figure 6). The situation is somewhat more complex than that shown in figure 2 because resources are not substitutable (which would mean that the populations can survive on either resource alone or on some combination) but rather are essential: figure 6A shows the general case, where a species must have a





**Figure 6.** (A) Chase-Leibold population-persistence niche (shaded area) for essential resources. (B) Ranges of coexistence and exclusion for two species of diatoms competing for two essential resources in chemostats. Circles give nutrient-ratio treatments where the two species coexist; stars give treatments where

*Asterionella* excludes *Cyclotella*; diamonds give treatments where *Cyclotella* excludes *Asterionella*. (Redrawn from Chase and Leibold, 2003; their figure 4.1 in turn redrawn from Tilman, D. 1977. Resource competition between planktonic algae: An experimental and theoretical approach. *Ecology* 58: 338–348)

vegetation heights and preferring different temperatures? This situation applies to predators, such as Grinnell's California thrasher, that eat a great variety of insects and other arthropods that in turn have their own populations with their own niche characteristics.

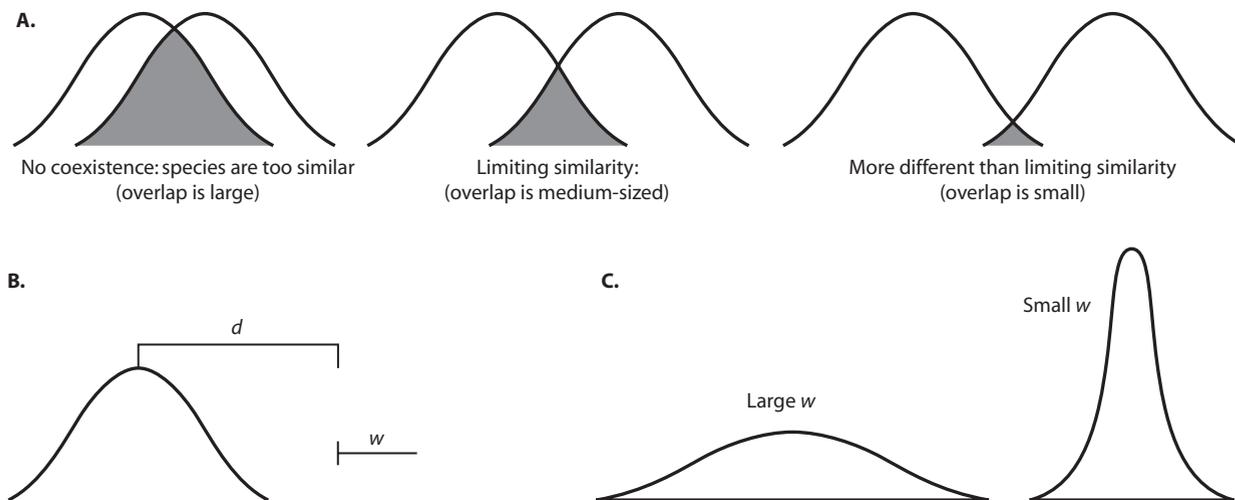
The 1967 paper in which MacArthur and Levins promoted the resource-utilization niche has as its main objective the understanding of how similar competing species can be and yet still coexist. It is sometimes said that species cannot coexist if they occupy the same niche, but the theory of MacArthur and Levins also posits that if the niches of the species are too similar (too much niche overlap), they still cannot coexist. To illustrate, imagine two species with the one-dimensional niche in figure 7; this dimension might be food size, and one species tends to eat larger food on average than the other. If the niches are too close (figure 7A, left), they are too similar (the niche overlap [shaded area] is too great), and the better competitor will eliminate the other from the community. That degree of closeness at which the species can just coexist (any closer and one is eliminated) is called the *limiting similarity* (figure 7A, middle); the niches can, of course, be farther apart and still allow coexistence (figure 7A, right).

Limiting similarity is measured in units of  $d/w$ , where  $d$  is the distance between peaks and  $w$  is the width of the niche (usually computed as the standard deviation of the utilization distribution; figure 7B). The larger the  $w$ , the more generalized the species; a specialist has a thin niche (small  $w$ ; figure 7C).

In MacArthur and Levins's theory, a  $d/w$  slightly larger than 1.0 is the limiting similarity; much subse-

quent work has shown limiting similarity to vary greatly yet be about 1 (certainly to an order of magnitude). Indeed, sometimes real species differ by almost exactly this theoretical value. A sensational example is provided by two mud snails (*Hydrobia*) studied by Fenchel in Denmark. The snails ingest particles: diatoms and inorganic pebbles covered with minute sessile organisms. About 150 years before the study, a fjord collapsed, and one species invaded the other's range. The resource-utilization niches of the species displaced away from one another, apparently independently, numerous times, to  $d/w \approx 1$  (figure 8, top left). Corresponding to this niche difference is a difference in body (shell) size such that larger species ingest larger particles (figure 8, top right), and the body sizes of the species had diverged (in a process called character displacement) to a ratio of 1.3–1.5 (figure 8, bottom). Consistent with the theory of Taper and Case (see below), this ratio is higher than the ratio of  $d$ 's for the two resource utilizations of 1.2.

So far we have represented the resource-utilization niche as a distribution summing together the food-size or other niche characteristics of all individuals in a population. However, individuals may differ in their niche characteristics, sometimes just by chance opportunity (e.g., what they happen to come across to eat), but sometimes because they have different morphologies and behaviors that make them specialized for a certain portion of a niche axis (just as species can be specialized). Figure 9 shows the two extreme possibilities for such component individuals; note that each individual can be a generalist (figure 9, left) or a



**Figure 7.** (A) One-dimensional resource-utilization niches of two species showing no coexistence because niches are too similar (left), limiting similarity—species can just coexist (middle), and

greater than limiting similarity also allowing coexistence (right). (B) Niche distance  $d$  and niche width  $w$  for two species. (C) Niches of generalist (large  $w$ ) and specialist (small  $w$ ) species.

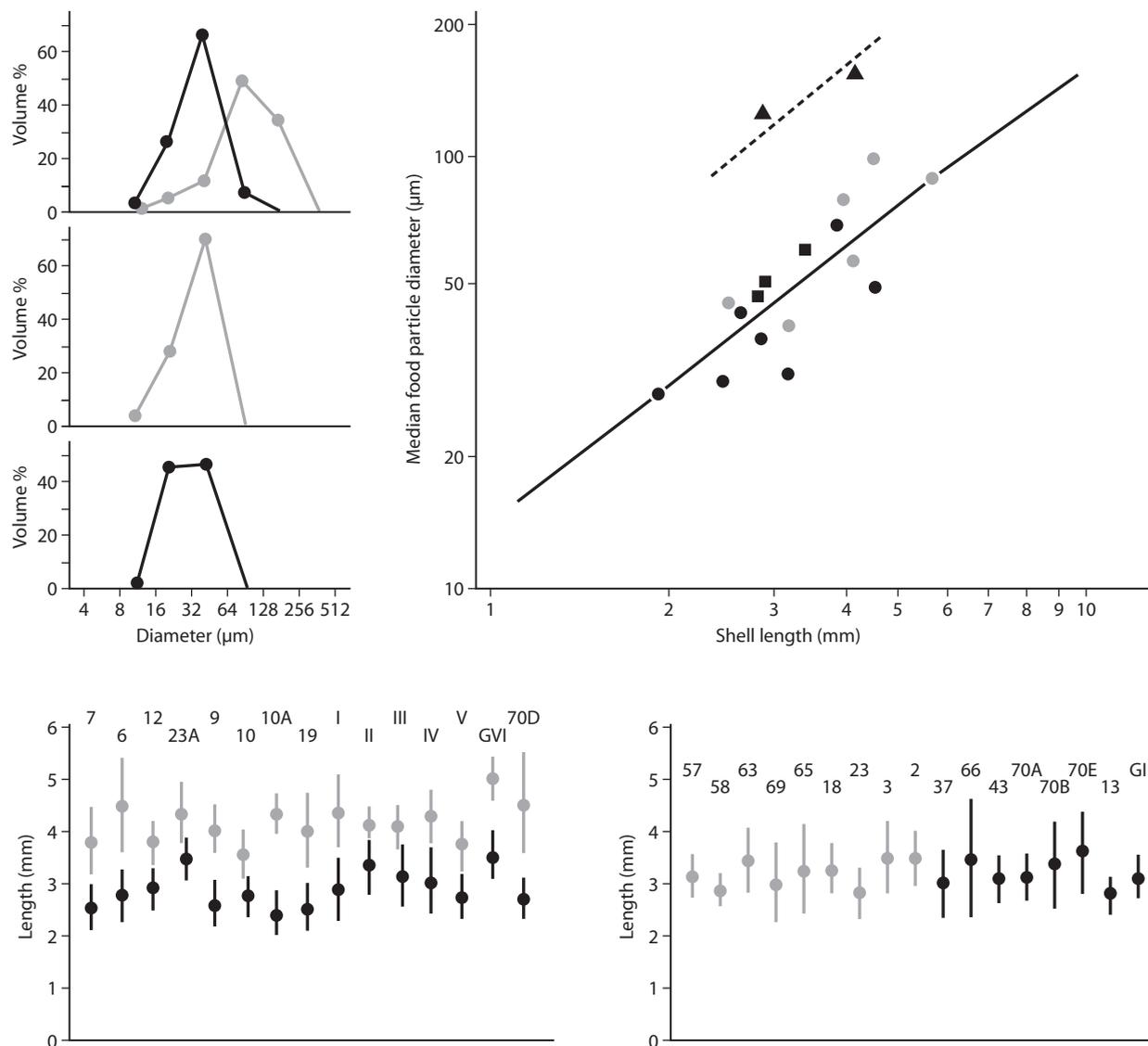
specialist (figure 9, middle), in either case producing the same utilization for all individuals combined (figure 9, right). What difference does it make which of the two situations one has? A series of specialist individuals may eventually allow the population as a whole to be more generalized in the absence of competing species, and this “polymorphism” might even lead to speciation (see chapter I.18). Such polymorphism, when measured in terms of those morphological characters corresponding to position on the niche axis (e.g., shell size corresponding to mean food-particle size), was uncommon in the literature at the time of Taper and Case’s paper, and this was consistent with their theoretical model in which the proportion of different kinds of individual niches evolves once the competing species meet geographically. Recently, however, Bolnick, Svänback, Arágo, and Persson looked at the resource-utilization niches themselves rather than the morphological characters that reflect them. They found that the bigger the  $w$  for the total population, the bigger the between-phenotype niche width, measured as the standard deviation of the  $d$ ’s of the niches of the component individuals. It remains to be seen exactly how these apparently somewhat contradictory trends will be reconciled.

## 5. ENVIRONMENTAL NICHE MODELING AND ANALYZING NICHE ON A MACROSCALE

A recent set of techniques, called environmental niche modeling (ENM), combines elements of all three niche

concepts. The method characterizes the macrohabitat niche of a species by quantitatively summarizing geographic-information-system (GIS) information on climatic and similar variables at stations throughout the species’ geographic range. Such macrohabitat niche information is then used to predict the potential geographic range of the subject species. Because of its focus on macrohabitat, the scale is similar to Hutchinson’s version of the population-persistence niche. However, the method specifies the “empty niches” of Grinnell’s recess/role niche as those localities having the niche characteristics of the subject species but where that species does not, in fact, occur. Finally, it allows quantification of niche similarity between species via measures of niche overlap used for the typically finer scale of resource-utilization niches of MacArthur and Levins.

One of the most successful applications of ENM so far examines the question of whether the more closely related species are, the more similar are their niches. The question is important because if the answer is yes, evolutionary history must have a major influence in determining niche characteristics relative to the influence of the community in which the species now occurs. A study by Knouft, Losos, Glor, and Kolbe on the 11 species of the *Anolis sagrei* group in Cuba found no evidence that niches were more similar, the more closely related the species (evolutionary relatedness is assessed using molecular genetics). A second study, by Warren, Glor, and Turelli showed along with the previous study that the most recently diverged species



**Figure 8.** (top left) Resource-utilization niches for prey size among two species of gastropods (*Hydrobia ulvae*, gray circles; *H. ventrosa*, black circles) where the species overlap (top), where *H. ulvae* is alone (middle), and where *H. ventrosa* is alone (bottom). (top right) Median diameters of ingested food particles of four species of *Hydrobia* plotted against shell length. (bottom) Average lengths of

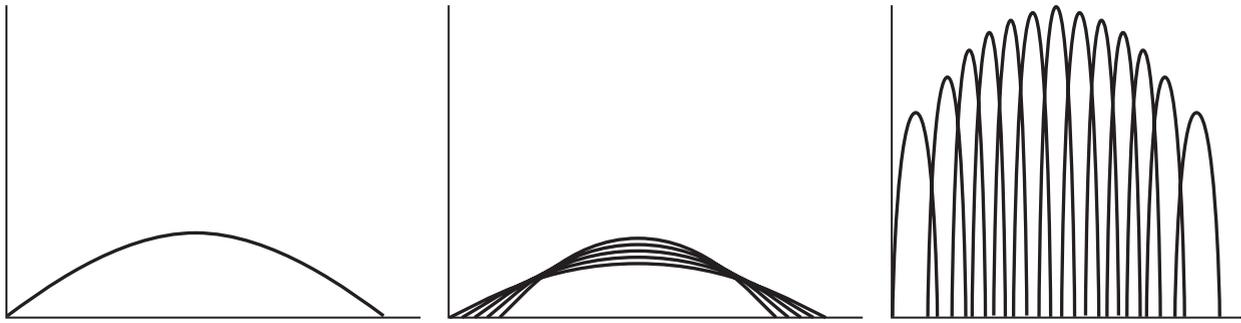
*Hydrobia ulvae* (gray circles) and *H. ventrosa* (black circles) from 15 localities where the species co-occur (left) and 17 localities where one of the two species occurs alone. All samples from the Limfjord during summer 1974. [Redrawn from Fenchel, T. 1975. Character displacement and coexistence in mud snails (Hydrobiidae). *Oecologia* 20: 19–32]

had the greatest climatic-niche differences. The second study, however, gave somewhat more support for the hypothesis in general, in that niche similarity between closely related species of birds, butterflies, and mammals separated by the Isthmus of Panama was greater than expected by chance. However, somewhat contrary to the founding ENM study by Peterson, Soberon, and Sacherz, niches were rarely identical, so the

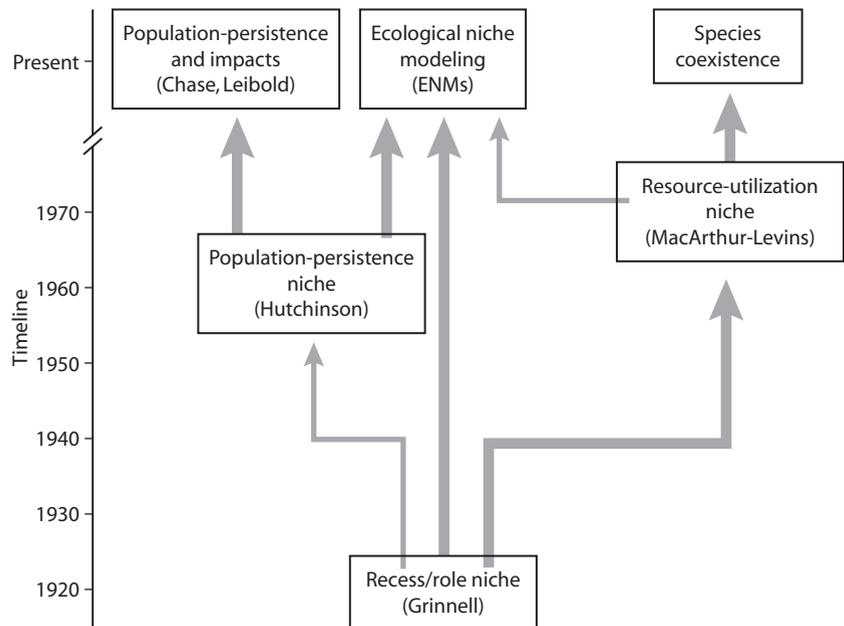
overall answer is in fact mixed, as is so often the case in ecology.

## 6. CONCLUSION

The research trends discussed in relation to the three niche concepts are summarized as an evolutionary tree in figure 10. In this diagram, the thicker arrows



**Figure 9.** (left) Resource-utilization niche of a species population. (middle) Population of generalist individuals whose niches sum to the curve at top. (right) Population of specialist individuals whose niches sum to the curve at top. (After Klopfer, Peter H. 1962. Behavioral Aspects of Ecology. Princeton, NJ: Princeton University Press)



**Figure 10.** Timeline showing the development of niche concepts and the research programs stemming from them.

indicate a greater influence of one concept or research program on the next. Note that all three niche concepts, despite sometimes rather early beginnings, have stimulated research that is being actively pursued at the present time.

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# I.2

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## Physiological Ecology: Animals

Martin Wikelski

### OUTLINE

1. Guiding concept: Trade-offs
2. Guiding concept: Performance as integrative measure of individual fitness
3. Process I: Acquisition of environmental information
4. Process II: Internal communication and regulation of physiological function
5. Process III: Energy expenditure as one central hub for trade-offs
6. Process IV: Key innovations
7. Process V: Self-defense: Immunoecology
8. Application: Conservation physiology
9. Future challenges

Physiological ecologists study how animals live and function within environments that are constantly changing. Key guiding concepts in physiological ecology are that (1) individual animals are subject to trade-offs such that all (physiological) actions cannot be performed maximally at the same time. Trade-offs underlie the fact that “a jack of all physiological trades is a master of none,” which in turn is the basis of the generalist-specialist continuum that brings about much of the niche differentiation in ecology. (2) A second guiding concept is that whole-organism performance provides an integrative measure of individual success in life. Quantifying individual performance allows physiological ecologists to assess the integration of traits within an organism and to determine how natural selection orchestrates not just one but all characteristics of an organism at the same time. Whereas in the past, physiological ecologists have also often studied animals in laboratory situations, technological advances now allow researchers to “go wild” and address individual physiological functions in the very environment where such functions have evolved. The importance of studying animal function in the wild cannot be overestimated because many organismal trade-offs are expressed only when food is scarce or predators are abundant.

### GLOSSARY

**constraints.** These can absolutely limit certain actions of an organism. Even if all efforts in a trade-off scenario are devoted toward a particular action, this action is not sufficient to satisfy an organism’s current needs.

**energy.** In biology, energy, which is essential for life, is gathered from the breaking of chemical bonds during metabolic processes. Energy is often stored by cells in the form of substances such as carbohydrate molecules (including sugars) and lipids, which release energy when reacting with oxygen.

**hormones.** These substances are chemical messengers that carry information from one part of the organism (e.g., the brain) to another (e.g., the gonads) often via the blood transport system. Hormones bind to receptors on target cells and thus regulate the function of their targets. Various factors influence the effects of a hormone, including its pattern of secretion, transport processes, the response of the receiving tissue, and the speed with which the hormone is degraded.

**metabolic rate.** Energy expenditure per unit time. Metabolic rate is normally expressed in terms of rate of heat production (kilojoules per time).

**performance.** This refers to whole-organism performance capabilities (e.g., how fast an organism can sprint) that are determined by physiological traits (e.g., composition of muscle fibers).

**trade-offs.** These attributes refer to the loss of one quality or aspect of something in return for gaining another quality or aspect.

Physiological ecology occupies a central role in the biological sciences and has a long tradition of integrating other biological disciplines. Physiological systems provide the interface between genomics at the lowest mechanistic level to organismal life history and evolution at the highest level of biological integration.

Every biological process linking genes to behavior will ultimately have to be understood mechanistically on the physiological level to truly provide a picture of how organisms function.

There are many levels at which physiological ecologists attempt to discern how organisms work. On the lowest level, physiological ecology meets genomics and proteomics. For example, Chi-Hing Chris Cheng and Art DeVries from the University of Illinois, working on the antifreeze protein in Antarctic fish, discovered that the protein is coded by a simple but frequent DNA repeat derived from a snippet in a trypsinogen-like protein gene, initially presumably by chance. This protein appeared to have just the right structure to recognize the surface structure of ice crystals that enter into the blood of the fish. Working up the physiological levels, because ice that enters into the fish's circulation always end up in the spleen, Cheng and DeVries hypothesized that the immune system, perhaps macrophages, of these fish living at subfreezing temperatures would take care of the nascent ice crystals encapsulated or presented by the antifreeze protein. Perhaps not unlike a pathogen, the immune system then either "kills" or lyses or excretes the nasty foreign body—a spiny ice crystal that would otherwise serve as a crystallization hotbed for more ice. What followed showed the true heuristic power of the physiological ecology approach. When Cheng and DeVries compared different antifreeze proteins among unrelated species of Antarctic and Arctic fish, they found that all of them use the same mechanism to deal with nascent ice in their blood and body fluids. It turned out that most fish can survive within the subfreezing, icy polar waters only if they have enough "antifreeze" in their circulation. Thus, Cheng and DeVries were able to integrate from a simple physiological innovation to explain a major ecological question: why there exist almost exclusively notothenioid, antifreeze fish around the Antarctic continent. Moreover, Cheng recently discovered that an unrelated innovation provides Arctic cod fishes with a near-identical antifreeze protein as the Antarctic notothenioids to brave the cold in the North.

However, organismal innovations rarely if ever come without a cost. It is not entirely clear what the cost is for Antarctic fish to have antifreeze protein, but we may soon find out if the Antarctic ocean circulation changes with global warming and the waters around the icy continent warm up. Such conditions could allow other, "nonantifreeze" fish to invade and challenge the old survivors, perhaps by bringing pathogens into a system that is not optimized to deal with anything else invading cells but ice crystals. If so, we may yet again see how physiological trade-offs govern ecological processes.

## 1. GUIDING CONCEPT: TRADE-OFFS

Physiological trade-offs are truly ubiquitous in nature. Everybody can immediately and intuitively understand them. If an organism puts too much energy into detoxifying ice crystals, other functions—perhaps predator defense, pathogen killing, or sperm maturation—lag behind (in fact, many notothenioid fish species are infested, often heavily, by parasites). Ecologists have discovered many pervasive life history trade-offs whose physiological underpinnings are currently under intensive investigation. For example, the more an animal reproduces, the more likely it is to lead a shorter life. The faster an animal grows, the more resources it needs, and again the more likely it is to lead a shorter life. However, there are circumstances when such trade-offs are not observed. In one, animals come in different qualities, with high-quality individuals within a species sometimes "living harder and dying older" than low-quality individuals. Such exceptions to the trade-off rule present considerable challenges and research opportunities for physiological ecologists. What mechanism(s) allow—at least in the short run of one or several generations—one individual to be more likely to survive or to live longer than others? Another challenge to the trade-off rule is presented by laboratory, domestication, and generally captive conditions. Under such circumstances, animals often appear to escape trade-offs. Again, it is yet unclear how animals can become "masters of all trades." The most likely physiological scenario is that the abundance of energy and nutrients provided in captivity allows individuals to obtain everything they need and thus to override physiological trade-offs. If confirmed and analyzed on the mechanistic level, this important distinction between feast and famine in the wild and almost pure feast in the laboratory could shed significant light onto one of the most pervasive principles in physiological ecology.

The question of how trade-offs come about immediately leads us to question how a multitude of organismal functions can be integrated and optimized. Physiological ecologists have found a simple, perhaps ingenious, way to ascertain how individual animals can deal with their environment.

## 2. GUIDING CONCEPT: PERFORMANCE AS INTEGRATIVE MEASURE OF INDIVIDUAL FITNESS

Instead of analyzing each physiological trait on its own in isolation, physiological ecologists resort to quantifying whole-organism function. Imagine the different ways in which one could answer whether lizard muscle fibers work well at low or at high temperatures. A valid reductionist approach could be to isolate each muscle

fiber type, cultivate them all in vitro, expose the fibers to different temperatures, stimulate them electrically, and measure their energy expenditure and contraction rate and speed.

However, what matters for individual animals is how they use their entire complement of muscles to perform certain common tasks such as fast running. Maximum running speed may be related to male fighting ability, female nest-digging ability, insect-catching capacity, and agility to escape predators. Thus, all individuals in a lizard population are expected to rely on fast sprint speed. Ray Huey of the University of Washington made use of this experimental paradigm and showed in comparative studies of individual whole-body performance that most ectotherms are able to cope with a large range of low environmental temperatures. However, as individual performance reaches its maximum, it rapidly drops off toward even higher ambient temperatures. The physiological basis for this performance asymmetry is presumably found in temperature sensitivities of physiological or molecular processes.

Interestingly, individual performance is also subject to strong trade-offs. For example, although some species of ectotherms have large temperature ranges under which they can perform well, others have very narrow performance breadths (see below).

### 3. PROCESS I: ACQUISITION OF ENVIRONMENTAL INFORMATION

One of the most survival-relevant tasks of animals is to gather environmental information. Again, this task is subject to physiological trade-offs. Physiological ecologists working on bat echolocation determined that producing the ultrasound that bounces back from objects, i.e., provides bats with environmental information, is costly both in immediate energetic costs and in associated physiological costs. In addition to energetic costs, bats face the costs of producing organs and brain structures that enable them to expend energy on echolocation calls in the first place. Biologists actually exploit the fact that environmental information gathering is expensive. Bats spare the costs of echolocation when flying in known habitat and often do not echolocate there, allowing researchers to trap them with fine nylon nets.

High physiological costs of maintaining functioning tissue may also explain why juvenile migratory songbirds start out with a small hippocampus, a brain area involved in spatial memory and thus long-term information gathering. As individuals conduct their first transcontinental journeys, they add additional cells and

connect their cells in more complex ways. However, because space in the brain capsule is presumably limited, the physically and physiologically expanded spatial memory for a life on the move may again be traded off against other brain functions that in turn deteriorate.

Energetic trade-offs between form and physiological function are particularly prominent in long-distance migratory songbirds that had to evolve streamlined foreheads for aerodynamic reasons, compared with their short-distance migrating relatives. Physiological ecologist Melissa Bowlin recently learned by studying heart rate in naturally migrating New World thrushes (songbirds) that even small morphological differences significantly affect costs of transport in the air.

### 4. PROCESS II: INTERNAL COMMUNICATION AND REGULATION OF PHYSIOLOGICAL FUNCTION

Once environmental information is gathered, it needs to be communicated most efficiently throughout the organism. Again it appears that cost minimization and trade-offs are key guiding physiological principles. Quick, practically immediate transfer of environmental information is achieved by costly electrical (neuronal) connections. However, for many types of information that either need to be communicated continuously or at least on the long term, electrical connections are by far too costly. Instead, animals use small and “cheap to produce” messenger chemicals (hormones) that bind to receptors in target tissues. The main advantage of a hormonal communication system is that it is inherently flexible at many levels, i.e., rates of physiological processes can be altered at production, at the chemically supported transport of hormones to target tissues, at the possible breakdown of messenger chemicals, and with respect to the number of receptors expressed at and by target tissues. Thus, for example, if a cell does not need (much) stimulation, it can degrade particular types of incoming hormone molecules (indicating particular, general environmental messages) in its periphery and/or provide only very few receptor sites as “mailboxes.” Cells can also destroy the “mail” immediately so that it has no long-lasting effect.

Physiological ecologist John Wingfield showed that this cheap hormonal messenger system conveys both long-term and short-term environmental information and prepares the individual organism for certain activities. Many animals reproduce seasonally and grow reproductive organs in response to changes in day length, often mediated by the light-sensitive hormone melatonin. Because of physiological trade-offs, individuals do not allocate maximum efforts toward certain

reproductive activities such as territorial defense from the outset. Instead, organisms often use behavior–physiology feedback loops to allow them to carefully regulate their efforts in response to environmental factors, in this case the actions of other members of the population. Thus, if population density is high in songbirds, individuals interact with others of the same species more often. Wingfield showed that individuals can ramp up reproductive hormones such as testosterone in response to a social, particularly reproductive, challenge. It is yet unclear whether this feedback is via increased physical activity (i.e., energy expenditure), increased neuronal stimulation (e.g., visual density), or a combination. In any case, it is clear that animals use hormones as a cheap means to communicate environmental information throughout the body.

### 5. PROCESS III: ENERGY EXPENDITURE AS ONE CENTRAL HUB FOR TRADE-OFFS

All along it has become obvious that organismal trade-offs can be expressed to a significant extent in terms of allocations in energy turnover. Energy is probably one of the physiological factors that are most limited under natural circumstances. It is thus not astonishing that physiological ecologists cast many of their discussions in energetic terms and consider energy as the central hub for physiological trade-offs.

Life follows the laws of thermodynamics, i.e., energy can neither be created nor destroyed (First Law). Furthermore, the disorder of a system (its entropy) increases over time as its energy content degrades to unusable heat. The only way animals can compensate for ever-increasing entropy is by constantly acquiring energy via food. However, foraging is again costly as well as time consuming, i.e., poses opportunity costs and is risky. The food then has to be broken down into chemicals usable by the organism, again a costly, damaging, time-consuming process.

Because animals will do anything to minimize costs, it should be obvious that environmental temperature is one of the most important habitat factors. Temperature has a hump-shaped influence on molecular processes such as enzyme activity. Coming from the low side, increasing temperatures enhance the rate of physiological processes and thus energy expenditure. Higher-than-optimum temperatures often show destructive effects and can result in serious structural damage.

Organisms incur costs at low environmental temperatures either because they are less agile (many ectotherms) or because they have to produce more internal heat (endotherms). Some animals have special tissues that help them produce heat very efficiently,

such as brown fat in bats, which produces heat without shivering. Higher-than-optimum temperatures often become dangerous because organisms very rapidly lose performance and expend much energy in thermoregulatory activities, both behaviorally and physiologically (panting, activation of heat shock proteins).

Although most animals attempt to minimize energy expenditure for nonessential tasks, it has become clear that, across various types of animals, high energy expenditure has evolutionary benefits. Increased energy expenditure involving constantly high body temperatures with an associated constant interior milieu has perhaps been one of the key innovations in physiology.

### 6. PROCESS IV: KEY INNOVATIONS

Evolutionary key innovations give organisms access to new resources and cause rapid, sometimes spectacular adaptive radiation, as seen above in the case of antifreeze proteins. It has been postulated that a long sequence of key physiological innovations is responsible for the diversity of life forms present today.

For example, Michael Berenbrink and colleagues discovered that a key physiological innovation underlies the large adaptive radiation of fish. It is the unique ability of fish to secrete molecular oxygen into the swimbladder—a seemingly simple physiological process that had already been invented some 100 million years earlier in the eye. However, because certain fish were later able to regulate swimming behavior very cheaply using their new oxygen-filled swimbladders, they diversified hugely in form and function. The physiological key in this process was a change in the  $\text{Na}^+/\text{H}^+$  exchange activity of red blood cells and a change in the content of surface histidine of hemoglobin (histidine is one of the 20 most common amino acids).

Another common key innovation—and again a highly efficient way of organisms to economize on physiological expenses—is to use special chemical components of other organisms. May Berenbaum demonstrated such a system very nicely in the interaction between the parsnip webworm and wild parsnips. Throughout the parsnip plant there exist a group of toxic chemicals called furanocoumarins that are the favorite food of the parsnip webworm. Furanocoumarins are so toxic that only very few herbivores can deal with them. However, webworms possess a highly efficient detoxification system involving cytochrome P450s, a very large and diverse superfamily of hemoproteins (iron-containing proteins) that simply insert one atom of oxygen into an organic substrate. Webworms use the toxic furanocoumarins to strongly deter predators from eating them.

Although animals can engage the help of others, perhaps through their chemicals, to defend themselves against predators, there are also more direct ways to fight pathogens and parasites.

## 7. PROCESS V: SELF-DEFENSE: IMMUNOECOLOGY

The study of the physiological ecology of immune reactions is a relatively new but fast growing and highly important field. In the past, immune biology has largely focused on very specific, fine-scale mechanisms of the immune defense. Immunoeology adds the systemic component to such detailed studies by addressing the integration of various immune responses on the individual level. In a key contribution, Kelly Lee and Kirk Klasing showed that the relative immune defense effort spent on either the innate or the adaptive arm of the immune system may be ecologically important. For example, such a differential allocation of efforts into different arms of the immune system may distinguish highly from poorly invasive species, such as the house sparrow and the tree sparrow, respectively.

Along the idea of whole-organism performance tests (see above), immunoeologists assess the reaction of individuals toward various immunological challenges simultaneously and as a composite measure. Physiological immune responses can be mediated by essentially two arms, the innate and the adaptive part of immune systems. The first line of defense is usually the innate arm. Specialized cells patrol tissues and have a superb ability to recognize an invader as foreign. As soon as the foreigner-recognition process starts, the first innate cells release signal molecules (cytokines) attracting bacteria- and virus-eating cells (scavenger macrophages, natural killer cells). Subsequently, the cells of the innate immune system send specialized signal molecules to the second (adaptive) arm of the immune system. The adaptive part of the immune system activates its machinery to produce antibodies that bind to and neutralize the foreign invaders. Whereas the innate system is costly to maintain and to activate, the adaptive system is costly to grow in the first place—once it is established, it appears fairly cheap to maintain.

It is important to note that organisms differ strongly in how much emphasis they put on the two arms of the system. Again it appears that because of omnipresent trade-offs, a jack of all immunological traits is a master of none. It is important to note in this context that some biomedical experimental subjects such as the house mouse do not necessarily provide systems that reflect the immune allocation in humans. Whereas humans are long-lived and invest heavily in the adaptive arm of the immune response (costly to develop but

cheap to run), house mice are generally so short-lived and dependent on fighting each disease immediately that they invest much more strongly in the innate arm of the immune response. It will remain a challenge in physiological ecology to understand exactly how organisms allocate resources toward immune responses.

## 8. APPLICATION: CONSERVATION PHYSIOLOGY

Animals have always been sentinels for environmental changes and catastrophes. For example, when the causal (reproductive) effects of dichloro-diphenyl-trichloroethane (DDT) on top predators became clear, DDT-like substances were prohibited in large parts of the world. For conservation strategies to be successful, it is important to understand the physiological responses of organisms to their changed environment. Perhaps one of the most useful tools in conservation physiology is the rapid assessment of environmental stress via the measurement of glucocorticoid “stress” hormones. These steroid hormones are ubiquitous in vertebrates and occur at low (baseline) levels in all individuals. In many cases when individuals are experiencing increased environmental demands such as inclement weather or predation, glucocorticoids increase in the circulation and, subsequently, in the feces. Conservation physiologists often experimentally induce mild stress (capture and handling) to assess the capacity of an individual to react to environmental stress. The usefulness of conservation physiology is that it can reduce the complexity of conservation problems to highlighting a single set or small number of the most important stressors for organisms. New physiological techniques can enable a rapid assessment of the causes of conservation problems and the consequences of conservation actions.

## 9. FUTURE CHALLENGES

The biggest challenges in the future of physiological ecology will be to monitor, understand, and ultimately predict what animals do during their often long lives. Advanced biologging techniques of physiological parameters are at the brink of enabling field researchers to conduct studies that a few years ago were possible only in a laboratory situation. Furthermore, even small animals can perhaps soon be followed over large temporal and spatial scales in the wild. Such new data on physiological state and overall individual space use may ultimately allow researchers to understand the animal mind. Once we know in (almost) real time how individuals process environmental information (via hormonal mechanisms), and we know the environmental conditions in the vicinity of an individual (via

animal-borne location loggers) in combination with the individual's physiological state, we may be able to predict decisions of animals mechanistically.

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