BEHAVIORAL INDICATORS AND CONSERVATION: WIELDING "THE BIOLOGIST'S TRICORDER"

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The adaptive behavior of organisms has been dubbed "The Biologist's Tricorder" (Rosenzweig, 2001). In the science fiction television show "Star Trek", the tricorder gave crewmembers astounding diagnoses on medical and scientific concerns, and this information somehow managed to be precisely relevant and needed. Likewise, behavior can provide astounding information on the status of individuals and populations in diverse ecological situations. This includes insights into the internal state of individuals, the richness of the environments in which they live, the suitability of their habitats, the extent to which they face danger from predators (and therefore the wellbeing of the predator populations), the carrying capacity of the population, interactions with their competitors and predators, and more. And foraging behavior often yields the most far-reaching insight.

Foraging behavior tells us about adaptations sculpted by natural selection, about population dynamics, about competition and predation, and about community structure. Let's start with the foraging process. When a forager begins to look for food, the energy and nutrients it obtains contributes to its ability to maintain its body and state, and if it is sufficiently successful, it will have enough left over for reproduction. Thus, foraging decisions have contributed to its survivorship and fecundity, the two major components of fitness. Furthermore, if the individual is extremely unlucky, it may encounter a predator and, instead of finding food, it may become food itself. Again, its foraging choices contribute to survivorship, and hence fitness. Thus, we can expect that behaviors in general, and especially behaviors linked to foraging, represent adaptive responses balancing the risks of mortality with the rewards of reproduction to maximize fitness. Insofar as foraging choices represent responses to fitness opportunities and hazards, they can serve as indicators of these ecological circumstances. Behavioral indicators can reveal such vital information as the best food types, the richest patches, the best habitats, and optimal movement patterns—knowledge that can be most useful in conservation and management.

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Behavioral indicators can also inform us about population biology. We start with fitness. Of the many definitions, the most useful may be that fitness is the per capita population growth rate for a class of individuals that share an evolutionary strategy. Strategies yield shared behaviors, and necessarily a common response to the effects of density. So it may be possible, once the mapping of behaviors to fitness has been measured, to use behavior alone to infer the dynamics of populations. That is, behavioral decisions should reflect fitness consequences and therefore reflect short-term population dynamics.

Beyond that, behavior can also yield insights into ecological communities. Often, the two most important classes of species interactions for structuring ecological communities are competition and predation. Resource competition arises when two species share a common resource. The decisions that individuals of one species make regarding where to look for food, when and where to be active, and what to eat, will affect the distribution and abundance of resources left behind and available for competitors. The distributions of resources that we see and measure are the consequences of foraging decisions that create a kind of "patch topiary." That is, the world is like a collection of shrubs in a formal garden in which their sizes and shapes, however fantastic they may be, are the results of careful trimming, pruning, and harvesting. In the case of a topiary garden, the shrubs come to resemble animals, people, objects, and geometric shapes by a combination of the growth of the plants and the trimming by the gardener according to the gardener's aesthetic vision.

In the natural world, the distribution of resources is sculpted by renewal rates of the resources via the population and individual growth of the resources themselves, or some other sort of renewal process, and the profitable opportunities that the distribution and abundance of the resources present to the foragers. Individuals forage when and where it is most profitable according to their aptitudes, and leave behind for others patches and resources of lower value according to their inaptitudes. Factors affecting foraging profitability necessarily affect what gets left behind for the competitor and therefore signal the intensity of competition. Likewise, predation is the outcome of the foraging decisions by the predator as it attempts to encounter prey and of the foraging decisions of potential victims as they attempt to balance the conflicting demands of food and safety. Decisions made by each will determine the intensity and rate of predation. And the decisions made define the indirect effects of predators on their prey. The foraging decisions of predators and competitors with varying aptitudes create strong frequency dependence such that the opportunities available to an individual depend on the densities and the aptitudes of its competitors and predators. A judicious study of foraging behavior can therefore reveal the frequency dependence and the mechanisms by which species coexist, and pinpoint those salient features of the environment and of the organisms most germane to promoting biodiversity. More than that, those same decisions can affect the intensity of competition between competitors and even other predators and prey. Thus foraging behavior also tells us about higher-order species interactions.

Finally, behavioral indicators often can provide the most appropriate information for managers in the timeliest manner. Behavioral decisions occur at the margin. That is, organisms should perform a behavior such as exploiting a resource patch until the

marginal benefits fall to equal the marginal costs. At that point, it is no longer profitable to continue the activity, and the organism should quit and seek another opportunity or another activity. It should adjust its time across activities such that the marginal value of each is the same for all. At this point, it is maximizing its profit. Thus the decisions of an individual will reveal the magnitude of foraging profit. When profit is high, individuals invest in reproduction and populations thrive. But when profits begin to fall, then populations may be threatened, and management intervention may be appropriate. In this manner, behavioral indicators can serve as leading indicators of habitat change, alerting managers to incipient disasters even before population sizes have declined.

In this issue, we present 13 articles that apply behavioral indicators to conservation issues and animals with high conservation value. These contributions highlight the scope of the approaches, issues, and organisms that can be dealt with using behavioral indicators. The articles illustrate the efficacy of behavioral indicators in current use and hint at the untapped potential for new applications yet to come. We highlight below the various contributions of this compendium.

Western sandpipers have become seemingly less abundant at stopover sites in recent years. This has caused concern. In fact, sandpiper numbers have not changed, but rather their behavior at stopover sites has made them harder to count, at least at some sites. The agent for this behavioral change is the recovery of populations of peregrine falcons and merlins along the migration route, rendering smaller sites especially dangerous. Sandpipers spend less time at those sites and feed farther from shore while there. Taylor et al. (2007) use individual-based modeling and genetic algorithms to derive behavioral indicators for changes in risk of predation and food availability along the migratory route. They start with the premise that birds are selected for behavior that promotes early arrival time at breeding sites and high energy reserves upon arrival. They also assume that migratory timing and routing is flexible, but that changes at one site must be compensated for at other sites. They examine usage of stopover sites that differ in risk, the rate at which birds feed, and the rate at which birds accumulate food. Foraging intensity along the migratory route provides an indicator of food availability while the ratio of usage of larger, safer, less resource-rich sites relative to smaller, riskier, higher resource-rich sites provides an indicator for risk of predation. Such behavioral indicators can allow for better knowledge of population wellbeing and management of the flyway.

To what extent can giving-up densities (GUDs, the amount of food left behind in a resource patch following exploitation) and patch use be used to estimate habitat quality? In the quest to model patch use and how it may reveal environmental quality, the Olsson and Molokwu (2007) contribution is likely the most successful and applicable. It has always been tempting to see environmental quality tied up in the missed opportunity cost of foraging, MOC. However, it was also easier to establish its connection with the predation cost of foraging, P. But, simply using P to assess habitat quality poses a double bind. Were GUDs high because of high risk or high environmental quality? MOC was thought to play a lesser role, particularly in animals that run out of useful things to do. Olsson and Molokwu (2007) conceptually dissect the effects of changing risks and opportunities on both MOC and P, simultaneously. They begin with a clear exposé on what

can change P, but not MOC. Within-home-range variation in predation risk manifests in P, but not in MOC. Within-home-range variation in patch quality influences neither. But change the overall quality patches within a home range, or overall mix of risky and safe patches, and then both P and MOC change. The changes are predictable. Increase overall food availability and the MOC rises linearly, with less pronounced changes in P. When productivity increases through simply having more food patches, both P and MOC rise, and the spread between safe and risky patches expands dramatically. Reduce predation risk, and P falls linearly even as MOC rises slightly. These effects and more become useful and transparent. This paper provides a welcome and needed extension of patch use theory to applied and research ecologists alike.

Where Olsson and Molokwu extend patch use to conservation, Whelan and Jedlicka (2007) show how patch use can and should be integrated into monitoring programs. It is the empirical and practical complement to the modeling of Olsson and Molokwu. In restoration or conservation projects, goals may include maintaining viable populations of valued species. Census data such as those on the birds of Midewin National Tallgrass Prairie provide a standard feature of monitoring programs. But, this monitoring may be incomplete. By the time a statistically defensible decline has occurred, it is already too late to avert the catastrophe. Furthermore, census data alone do not answer why a population is trending up or down. Whelan and Jedlicka urge patch use as an additional monitoring tool. The authors draw from their own research and from others to show how squirrels, woodpeckers, starlings, fish, and other species have revealed habitat quality through their patch use behaviors. A compelling link is made between these studies and the use of foraging behaviors as leading indicators of habitat change. Foraging behaviors may predict future trends in population size, and explain current and past trends. Whelan and Jedlicka's prose provides details and a convincing rationale for connecting census data and behavioral indicators into a more successful monitoring program. But, it is their Table 1 that is truly valuable. It provides a Rosetta Stone for translating population trends and giving-up densities (in safe and risky microhabitats) into specific conclusions regarding the environmental prospects for the species.

Kate Searle and coauthors (Searle et al., 2007) show us that many different foraging behaviors can be used to address two of the most demanding problems of our time, carbon dioxide enrichment and landscape change. And while they do that, they also illustrate how classical estimates of landscape condition can mislead our efforts at conservation and management. Natural selection's landscaping is perceived differently by different species. So, simple measures of biomass and structure cannot capture the true value of resources for all of the species that tend and prune the garden. Searle et al. recommend a radical change: Measure the foodscape, not the landscape. How do you do that? Like a fine clothier tailoring fabric, fashion, and style to match clients' tastes, you choose those foraging behaviors that give the best fit with climate, habitat, and landscape change. Browse the table of candidate behaviors provided by Searle et al. to find one that suits you.

Migratory birds provide the subjects for three papers in this compendium (Nolet et al., 2007; Taylor et al., 2007; van Gils et al., 2007), and foragers that dive for their prey

provide the subjects for another three (Mori et al., 2007; Nolet et al., 2007; van Gils et al., 2007). The paper by Nolet et al. (2007) does both by examining the foraging behavior of migratory tundra swans. But these swans do not exactly dive. Rather, they feed on starch-rich tubers of aquatic plants buried in the muddy bottoms of the shallows of lakes found along the migration route. To do so, they must trample spots in the mud to free up the tubers. Then, they can dip their heads to retrieve the food. In this case, the time spent trampling for swans is equivalent to the time diving down to the food patch for seals (Mori et al., 2007), and similar models apply. Nolet et al. (2007) modify previous models for optimal diving time to calculate optimal head dipping and optimal surface times as functions of habitat quality. This infers that head dipping rates provide behavioral indicators of habitat quality. Then, from field data they demonstrate that foraging behavior accurately revealed habitat quality and even allowed accurate estimations of gain rate while feeding and daily energy gain at spring staging sites.

The tactics and natural history of diving mammals and birds both fascinate and elude us humans who rarely hold our breath for more than a minute. The idea of a sperm whale submerging for 30–45 min to depths of 400 m or more seems like physiological magic. Yet this is simply a particular form of foraging where patches reside below the water's surface, and the forager begins and ends on the surface of the water. This challenge of how to study the foraging behavior of diving animals as they disappear beneath the water poses methodological challenges, and as Mori et al. (2007) demonstrate, methodological opportunities. In their previous work, they have developed sophisticated indices for assessing habitat quality and using diving behavior as an indicator. Here, they develop a simpler index to use as a behavioral indicator that takes advantage of a physiological reality of air-breathing diving animals. Following a dive, the foragers must have a latency period during which they regain their breath. This means that given the diving depth, there is some "standard time" at a depth that maximizes the fraction of time spent within a feeding "patch". The ratio of actual time to this standard time should increase with patch quality. And indeed it does. Their successful applications of foraging theory and patch use theory to diving behavior shows how novel behavioral indicators can be developed for animals with otherwise recalcitrant natural histories. Thanks to their index, Weddell seals can be the subject for behavioral indicators of habitat quality.

We see the value of behavioral indicators clearly in Mike Heithaus and coworkers' application of habitat-selection theory to a World-Heritage marine seagrass ecosystem (Heithaus et al., 2007). Dugongs (as well as piscivorous dolphins and cormorants) in Western Australia's Shark Bay balance risk and reward in their choice of habitat. When predatory tiger sharks are sparse, all three species are distributed equally across shallow and deep-water habitats. But when sharks are abundant, they shift to deeper water. And counter to intuition, dugongs preferentially use areas with the greatest shark density. It turns out that seagrass beds with the lowest abundance of sharks are also the most dangerous. They lack escape routes to deeper water. So the amount of safe habitat (edge) is a better predictor of dugong abundance when sharks are abundant than is the area available for foraging. Conservation of dugongs may depend less on how "much" habitat we preserve, and more on preserving the correct matrix of habitats.

Calidris canutus islandica, an exquisite shorebird that breeds in the high Arctic and overwinters in Europe, walks a physiological and behavioral tightrope. Like seasoned human frequent flyers, knots travel light. They fly southeast in the fall from Canada and Greenland to the Netherlands with small gizzards. Paradoxically their thrifty packing, so crucial to successful migration, comes at great cost. The Wadden Sea provides none of the high-quality, easily digested arthropods that provided summertime fare for their chicks. Instead, they must now subsist on a low-quality diet of mollusks, shell and all. Their gizzards are not up to the job, and for the first days and weeks, knots often face a negative energy balance. Jan van Gils et al. (2007) show us how knots overcome the disadvantage. The knots forage as long as possible until their gizzards expand to deal with the shell mass of the bivalves. Then, because foraging is dangerous, knots adjust foraging time to minimize risk. Since the relative abundances of more fleshy and less fleshy bivalves differ among years, so too does the optimum gizzard size. It grows to match the availability of prey. But gizzard size alone is an incomplete measure of prey quality because the optimum size also depends on foraging time.

Because harvest rate of resources from patches depends on resource density, the giving-up density provides an estimate of quitting harvest rates and hence reflects the costs and benefits of patch use. Morris and Mukherjee (2007) have previously taken advantage of this to use GUDs and the manner in which they change with population density to reveal carrying capacity. Here, they demonstrate density-dependent patch use behavior for red-backed voles in boreal forests. But interestingly, this density dependence is manifested in only one of the two years of their study. Rather, GUDs and quitting harvest rates are higher in the second year, the year in which there was no obvious density-dependent patch use. That year was one of exceptional rainfall and productivity that allowed foragers to cream-skim each patch. Thus, optimal behavior along with an appropriately effective experimental design revealed spatial and temporal variation in habitat quality as well as density-dependent foraging.

Intermediate predators such as raccoons and foxes and even insectivorous rodents may have to worry about their own safety when they, in turn, face their own predators. This may have consequences for their use of time and space and may create predator-free space and, therefore, opportunities for their prey. These opportunities can be revealed by measuring giving-up densities for the predator. Use of space by foraging predators as revealed by live trapping, tracking, and rates of removal of single food items (activity density) provides a further behavioral indicator. Knowledge of predator-free space can aid in managing the prey species. Schmidt and Schauber (2007) discuss the theory underlying the concept of predator-free space and its implications for incidental prey. They then review case studies of behavioral indicators of predator-free space left behind by white-footed mice, eastern chipmunks, and raccoons preying on nests of passerine birds and for various small mammals preying on gypsy moth larvae. The behavioral indicators often prove to be better indicators of rates of predation than even measures of the densities of the predators themselves.

Shallow lakes may exhibit alternative, stable states that differ in turbidity. One state has clear water, low standing crop of phytoplankton, and low concentrations of sus-

pended materials. The other has high production of phytoplankton and high rates of resuspension of sediment that cuts light levels for aquatic macrophytes. Humans prefer the clear state. The turbid state favors planktivorous and benthivorous fish that contribute to resuspension and reduce the pelagic hunting ability of piscivorous fish. The clear state favors large, rooted aquatic plants that promote sedimentation and provide protection for young piscivores at the expense of the planktivores and benthivores. Persson and Nilsson (2007) show how behavioral indicators can be used to assess the state of a lake and its resilience to change. By measuring giving-up densities of the benthivores and the density of benthic resources, one can estimate both ecosystem productivity and maximum benthivore size. When both are high, the system is highly resilient. The manner in which fish balance short-term gains and long-term future prospects, and the differences in giving-up densities in safe versus risky habitats, can indicate whether the ecosytem is stable, improving in quality, or deteriorating. Based on these, managers can decide when actions such as benthivore removal may be necessary for maintaining lake water quality.

Norman Owen-Smith and James Cain (Owen-Smith and Cain, 2007) illustrate how one of those behaviors, home-range use, can inform and guide conservation of African antelopes. Sable antelope, arguably the family's most elegant and statuesque species, were counted by the thousands in Kruger National Park in the 1980s. Now their numbers have dwindled to a few hundred. Successful management and recovery depends on our ability to understand such fundamentals as herd behavior, habitat use, and seasonal movements. Owen-Smith and Cain show us how to glean many of these insights by merging GPS technologies with home-range analysis. Sable antelope maintain large home ranges in order to access critical resources. But core-use areas are small and travel costs are high. Nevertheless, Owen-Smith and Cain now know which areas sable prefer and when they are most likely to use them. Managers can begin to assess resource quality in those sites, devise mechanisms to improve others and, with luck, hasten recovery.

World-class zoos employ behavioral endocrinologists as researchers and professionals contributing to animal welfare. Feces provide a non-invasive and inexpensive means for monitoring stress hormones, reproductive hormones, and more. Insofar as stress hormone levels represent responses to environmental circumstances, these techniques hold great promise as indicators for wild populations. Not surprisingly, their application to wild populations is growing beyond the mode-controlled and circumscribed world of captive animals. A lot of things can happen between the hormones in the blood and their metabolites in the feces. Also, a lot of things can happen between the collection of the feces in the field and the measurements taken in the lab. Wielebnowski and Watters (2007) provide a tour-de-force of opportunities, issues, and problems that may arise in using fecal endocrines as behavioral indicators. The paper provides a step-by-step catalog of problems and solutions for collecting samples, storing material, processing, and then finally interpreting results. This should be a valuable source of material and ideas for those currently using or planning to use these techniques and for those that want to fully understand the results of fecal endocrine studies. Attention to the perspective and advice of this paper should enhance and expand the application of fecal hormones as behavioral indicators.

The papers of this compendium illustrate some of the many possible behavioral indicators, what they mean, and how they can be used. In particular, we have seen how behavioral indicators can provide essential information not easily accessible through other means. We hope that others will find inspiration in these examples and apply them to their own work and even develop new and perhaps better behavioral indicators and new and perhaps better uses. We have just now only begun to wield "The Biologist's Tricorder". It is powerful and often simple and inexpensive to operate. We envisage it soon becoming a standard tool in the toolboxes of all conservation biologists and managers.

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