

**IJEE SOAPBOX:  
THE UNRAVELING OF NATURE'S INFORMATION  
WEBS: THE NEXT DEPRESSING FRONTIER  
IN CONSERVATION?**



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After a lengthy transoceanic flight, you have arrived in a large city in a land that you have never visited, and even though it is late, you want to stretch your legs. After plotting an itinerary on the hotel tourist map, your walk first takes you through a lively, colorful, crowded urban environment. Then you turn a corner, and peer down a street, where no one is walking, as far as you can see, under the lonely streetlights. What do you do?

Well, I know what I would likely do, which is shift my itinerary, map or no map, and not go down that deserted lane. What I have done is use a kind of behavioral indicator—the presence or absence of my conspecifics at a particular place, when I know there are conspecifics nearby—as an indirect source of information about the local environment. Maybe there has been a recent unpleasant incident, or maybe the neighborhood just has a bad reputation for late-night shenanigans. Whatever it is, I do not want any part of it.

We humans do this all the time. The excellent set of papers in this special issue on behavioral indicators highlights how we as scientists can monitor the behaviors of individuals of other species to make inferences about the habitat quality they experience. By assuming that behavior is adaptive, and then recognizing that adaptation is always a joint function of the phenotype and the environment, we can carry out a kind of inverse optimality reasoning and make inferences about the environment from the behaviors we observe. And of course, if we can watch a swan bobbing its head and learn something about that swan's immediate environment (see Nolet et al., 2007, this issue), so can other swans, who doubtless on average watch each other more keenly and with greater perception than does even the most avid birder or skilled avian ecologist.

Information reduces uncertainty. From an evolutionary perspective, information also involves utility—it leads to actions that impact fitness (Dall et al., 2005). A broad and important emergent unifying theme at the interface of behavior and ecology is that animals use behavioral indicators provided by other animals to make decisions with fitness

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consequences. Such “public information” has many ramifying consequences, from mate choice, to the evolution of aggregation, to the creation of “traditional” sites for breeding colonies, to providing a template for cultural evolution (Danchin et al., 2004; Valone, 2007). In this essay, I reflect on some aspects of public information, and then briefly turn to conservation implications of the loss of such information.

I first became aware of this behavioral dimension of ecology when I was a graduate student at Harvard in the 1970s and became acquainted with a brilliant scientist, Ross Kiester, who at the time held a prestigious Junior Fellowship. In papers rarely cited today (e.g., Kiester, 1979), Ross explored an idea he called “cuing by conspecifics”. In experiments in lowland Panama, Ross permitted juvenile *Anolis* lizards to clamber up slender sticks, from which they could choose between nearby adjacent shrubs, which to Ross’s eye looked essentially identical. In one shrub, however, conspecifics would be present (by design), and conspicuous, but the alternative shrub would be empty. The juvenile anoles largely chose to move to the shrub already containing their conspecifics—even though lizards are fiercely territorial. As Ross noted, the mere presence of an active individual of one’s own kind in a habitat patch may contain information about the environmental conditions in that patch. One can reasonably infer that at least over the short run, abiotic conditions have not been too severe for the resident anoles, predators have not been too effective, and there is enough to eat. For these diurnal tropical lizards, many dangers, such as snakes and herp-snatching bats, may only emerge at night, with few cues to their presence in the daytime; and so, the presence of a conspecific means such dangers are not too sharply present. The fitness value of this information may outweigh the inconvenience of having to struggle for a territorial slot in a bush.

Returning to your nocturnal stroll, now that you are relieved to be back on a busy urban street, your stomach is growling, and you decide to grab a late meal. Three restaurants are lined up in a row. One is completely full, with a line outside. One is completely empty, and one is about half full. Where would you go? Knowing nothing else, I would certainly go to the half-empty one. There must be something off-putting about the empty restaurant, or surely someone would already be there. And there is no guarantee the crowd in one restaurant is there for the food; maybe it is just a popular hangout with the locals. Just like Ross’s lizards, I have used my conspecifics as cues for a habitat selection decision, and have also paid attention to potential density-dependent competition for space (a seat at a table) in deciding where to temporarily settle.

Thus, there may be valuable information that can be gleaned about the environment, given by the mere presence or absence of conspecifics. Of course, the value and reliability of such information strongly depends upon many details in the local environment. For instance, there are sampling considerations. If a single lizard is seen in one bush, and none in the other, what is the chance that lizards in the latter bush are actually present, but just missed by chance? So the more individual lizards that are present in the occupied bush, the more certain the newcomer will be that it is a good spot for lizards to live (relative to the empty bush). But if there are too many lizards already present, relative to the size of the bush, negative density dependence is likely. If one bush has a few individuals, and the other a lot, and the a priori expectation is that the population is at demographic

equilibrium, and if territoriality is weak, then habitat selection theory (Fretwell, 1972) suggests that fitnesses should be equilibrated across the two habitats. The juvenile lizard should in this case be indifferent in its choice of where to move (but it should still avoid empty bushes). If lizards were annuals with synchronous generations, emerging all at the same time, the presence of conspecifics would reflect conditions only over a very short time period; the other lizards are themselves young, so presumably moved into the bush only a short while ago, and hence provide an unreliable cue as to habitat quality. If habitat quality is highly variable through time, the presence of a conspecific may actually reflect good times in the past, rather than good times in the present. And so forth. Yet despite these complications and caveats, in many circumstances it is adaptive to use conspecifics as cues, to reduce search costs during habitat selection, and to increase the accuracy of behavioral decisions (Fletcher, 2006).

Beyond the information that is implicit in the mere fact of existence, organisms give off many cues as to their internal states, which again can provide valuable information about the environment to other organisms. Sometimes these cues are provided by direct phenotypic traits—the sleekness of coat or plumage, the fatness of a profile, or the skittishness of a forager all can provide hints as to the quality of the local environment. Animals can watch each other, and change habitats to track the decisions of successful foragers (e.g., starlings; Templeton and Giraldeau, 1996). The state of immigrant lizards can provide information useful for residents in making decisions about emigration (Cote and Clobert, 2007). Cues about environmental quality are often left behind by animals. For instance, snakes have refined chemosensory systems that are used in seeking out communal hibernacula (Greene, 1997). Recently Clark (2007) found that timber rattlesnakes, which are solitary sit-and-wait predators, can use conspecific chemical cues to make choices about where to lurk; they are more likely to choose paths following the chemical trails of conspecifics than to move across a blank space. Moreover, after moving, the rattlers are more likely to spend time coiled, waiting hopefully for an opportunity to strike, when the conspecific that left the trail had recently fed, than when it had not. Male garter snakes use skin lipids to judge the length and body condition of potential mates (Shine et al., 2003), and similar abilities are likely widespread among serpents. Chemical cues that may have evolved in the context of mate choice could then be co-opted by snakes making foraging decisions. These lipids are long-lived, and so provide an informational cue that might linger long after the snake itself has wandered away.

Just by existing, and consuming, and annoying the neighbors, and exuding waste products, and attracting predators, and indeed modifying the physical and biotic environment in a whole panoply of ways, organisms necessarily leave a transient echo of themselves in the world, wherever they have passed. This echo is implicitly charged with different kinds of information, each of which decays over time and reflects a sampling of the world over some temporal and spatial scale, with differing degrees of reliability. The giving-up density (GUD) of a foraging patch, for instance, provides an integrated assessment of local habitat quality, including risks of predation (Brown, 1992; Brown et al., 1999; Brown and Kotler, 2004). As discussed by several papers in this issue (Morris and Mukherjee, 2007; Nolet et al., 2007; Olsson and Molokwu, 2007; Persson and Nilsson,

2007; Schmidt and Schaubert, 2007; Whelan and Jedlicka, 2007), behavioral ecologists can use GUDs to assess in a refined manner how an organism perceives spatial heterogeneity in, for instance, predation risk. In like manner, a wandering individual entering a new area could use variation in food density as an indirect assay of how conspecific residents have recently perceived risk in their environment.

These cues cut across species lines. Moller (1992) used song playbacks to show that birds from a wide range of species increase their rate of singing in response to vocalization by birds of species other than their own. He suggests that this responsiveness reflects a kind of social facilitation—a singing bird is one that is momentarily acting as if predators are not present. So if a cardinal is lustily calling, a chickadee may feel more confident that a sharp-shinned hawk is not lurking nearby, and so call out more itself. Monkkonen et al. (1996) found similar effects for birds responding to various species of titmice (*Parus* spp.). Mixed species flocks emerge from species actively seeking out each other, suggesting a widespread dimension of interspecific facilitation in many guilds in which species as judged from their diets are expected to compete for resources. The direct negative effect of a competitor on fitness may at times be outweighed by its indirect positive effect as an indicator of habitat quality. Seppanen et al. (2007) have recently reviewed numerous examples of heterospecific sharing of information for a wide range of taxa. They point out that for many species in many communities, there are considerably more heterospecifics around than there are conspecifics, and this makes it likely that cross-species information gleaning is ubiquitous. The ability to exploit cues from heterospecifics may lead to a kind of diffuse facilitation within resource guilds. Or, some species may be keystone information sources, relied upon by suites of other species in going about their business, much like a village gossip may be the most reliable source about local news. Quantifying the pathways and strengths of these links in information webs is an important challenge.

Heterospecific cuing also influences predator–prey interactions, sometimes in surprising ways. Prey may be paradoxically attracted by the presence of predators. Raimondi (1988) showed that larval barnacles in the species *Chthamalus anispoma* settled preferentially on rocks with mucous trails put down by the snail *Acanthina angelica*. Yet the snail is a major predator on the barnacle. The larval barnacles would seem to have suicidal impulses! The explanation is that the larval barnacles can only survive in a narrow zone of the intertidal, and they have a poor innate capacity for discerning where that zone is. The snail mainly occurs within the particular intertidal zone that the barnacle can tolerate. So, by using its predator's mucous trail as a cue, the larval barnacle avoids the near-certain mortality it would face by settling in the wrong zones, at the risk of providing a meal for the predator later in life. Stamps and Krishnan (2005) provide a formal model for when one might expect to observe this at-first-glance paradoxical behavior.

As noted for snakes above, intraspecific signaling systems are ubiquitous because they are useful for finding and selecting mates, but once such systems exist, they then can be exploited by other taxa. Many examples could be cited, but just to mention one, Dicke (2006) notes that conspecific organisms often interact via pheromones, and these pheromones can be tapped as cues to tasty meals by their natural enemies. Male *Pieris*

*brassicae* butterflies, while mating, anoint females with an anti-aphrodisiac pheromone, thus reducing sperm competition with other males. Unfortunately, this pheromone is used as a cue by an egg parasitoid wasp, *Trichogramma brassicae*, which lands on the mated female and rides her until she deposits some eggs, which are then attacked by the wasp (Fatouros et al., 2005).

Even plants can take cues from each other (Calloway, 2002). For instance, plant resource allocation may be sensitive to the presence of neighboring competitors. Gersani et al. (2001) used an ingenious split-rootlet experimental design to show that in soybeans, the presence of a neighbor could lead to a proliferation of rootlet growth by an individual. They suggested that this behavior reflects a “tragedy of the commons”, where a given plant scrambles to extract resources more quickly than it might do when alone—because if it does not utilize them quickly, the neighbors will. There are indeed increasing numbers of examples of “communication” between plants outside the typical realm of shared depletion of limiting resources. Plants can influence higher trophic levels via infochemicals, and thus manipulate their herbivore load. Carnivorous arthropods use plant-produced volatiles induced by herbivores for finding their prey. Damage by herbivory can induce a plant to increase its investment in defensive compounds, many of which are volatile and provide cues that attract natural enemies of those herbivores. There is increasing evidence that this tritrophic interaction can in turn trigger greater investment in defenses by neighboring plants, which thus more effectively ward off herbivores (Arimura et al., 2000; Dicke et al., 2003a). If investments are costly, this presumably comes at the expense of resource acquisition, and so there could be an emergent complex intertwining of plant competitive interactions, herbivory, and top-down control, mediated by how plants communicate chemically among themselves and with higher trophic levels.

One of the most familiar conceptual models in ecology is the food web—a diagram of boxes and arrows, nodes and links, tying together the eaters and the eaten. Food webs embody much more biology than just flows of energy and nutrients, and indeed it is becoming increasingly clear that “food webs interact with infochemical webs that modulate direct and indirect interactions” (Dicke et al., 2003b). Given that behaviors are always to a degree plastic, the way organisms extract information from their environments has a large effect on defining the structure of food webs (who eats whom), and the quantitative flows of energy and materials through these webs (how much gets eaten in any given link). Dicke (2006) notes that “each infochemical may mediate many interactions... [so] the infochemical web is more complex than the food web”. Elucidating the information dimensions of food webs is an important and largely untouched challenge, one that provides a natural linkage among behavioral ecology, cognitive ecology, and community ecology.

The existence of such information webs means that humans can disrupt natural ecosystems not merely through the familiar routes of habitat destruction, harvesting, poisoning, species introductions, and so forth, but more indirectly by the degradation of the subtle information tapestries that organisms rely on in crafting their lives and maintaining their Darwinian fitness. If conspecific cues guide habitat choice and other

behavioral decisions, a reduction in density may make it harder to come by reliable cues. As Dukas (1998, p. 158) notes in a discussion of the relationship between sociality and learning, “a larger quantity and better quality of information may be generated and transmitted within and between generations in larger social groups”. Thus, a hidden cost of cuing by conspecifics is that an Allee effect emerges at low numbers, because there is less and lower-quality information. This makes it harder for populations for instance to rebound from disturbance, or aggravates the demographic risks of over-harvesting. Many translocation programs in conservation fail (Stamps and Swaisgood, 2007), and this may in part reflect a kind of Catch-22; by definition, translocation will be into an empty habitat, where the introduced organisms cannot benefit from cues supplied by residents and so are more likely to make poor behavioral choices. When humans modify landscapes, they disrupt crucial cues that dispersers use in optimally moving from one place to another (Fahrig, 2007). In like manner, even if the landscape superficially stays the same, if humans impact the abundance and distribution of species, this may make it harder for the organisms that are left to glean from the environment information needed to maintain fitness.

Modern humans also are noisy, flood the air and water with strange and noxious chemicals, and cut the darkness of night with the glare of electric lights. These direct impacts on the information environment are bound to distort preexisting webs of information that organisms historically depended upon in a variety of ways. For instance, cars and trucks are pervasive sound-producers in settled landscapes. In a review of impacts of roads upon wildlife populations, Forman et al. (2003, p. 274) note that “Many song bird populations appear to be inhibited by remarkably low noise levels....The noise levels [above which these effects occur]... are similar to those in a typical library reading room”. The effects were substantial even at distances of more than 1 km from roads.

In the early 1980s, I was lucky to be able to spend a month camping in a tent in the middle of beautiful rainforest, at Cocha Cashu in the middle of Manu National Park, Peru. We were a great distance from any settlement, with the only use of machinery the occasional sputtering of a small generator to recharge batteries. I remember waking up in the middle of the night, the first few nights I was there, listening to the mysterious night sounds, and thinking that something, I knew not what, was wrong. It finally dawned on me that my subconscious was expecting the low hum of the mechanized world—the distant roar of trucks on the highways, the purring of heaters or air conditioners, the droan of transformers, and so on—that nearly always surrounds us in a blanket of ever-present sound, even though we are conditioned to tune it out. The absence of these sounds was a palpable void in the jungle night. The flip side of this observation is that the presence of these noises must constantly muffle signals that the world would otherwise be whispering to its denizens, which then suffer because of this degradation in their sensory environment.

I think this deterioration in the information web that species utilize is potentially a serious issue, and needs more attention by conservation biologists. As an aside, we too suffer this degradation. One of the sad consequences of environmental destruction, I feel, is that we are the victims of a kind of sensory deprivation in the modern world, with a diminution in the range of natural visual experiences, fragrances, sounds, and

textures that our ancestors surely knew. There is a sensuous dimension to biophilia (Wilson, 1984), which may be needed to motivate people to care about saving nature. We are in danger of losing the dimension of the world that permits the poets of the world to experience it, and then write lines like “The palm at the end of the mind, beyond the last thought, rises in the bronze décor, a gold-feathered bird sings in the palm... the wind moves slowly in the branches. The bird’s fire-fangled feathers dangle down.” (Stevens, 1971). With this loss, we lose in part the world, and an essential part of who we are.

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