CONSERVATION AND BIODIVERSITY

Insect Behavior and Ecology in Conservation: Preserving Functional Species Interactions

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ABSTRACT Conservationists are becoming increasingly aware of the value of insects and the need to include them in programs to preserve diversity. Most current endeavors emphasize individual species or specific taxa with little emphasis on preserving species interactions or processes. Insects exhibit spectacular and diverse behaviors and ecological interactions that should be preserved in their own right, and, more importantly, they provide essential processes for the long-term survival of populations and species assemblages in preserved landscapes. As habitats are increasingly fragmented and disturbed, vital insect-driven interactions may be disrupted, greatly diminishing the survival of the community. Research is needed to evaluate the effect of habitat change on insect interactions, in addition to the presence or absence of insects. The presence of a species does not indicate anything about its behavior; insect behavior is the key to participation in interactions, the lock binding communities together. Mutualisms such as pollination systems, and parasitisms such as bird-ectoparasite or parasitoid-herbivore systems, have been shown to be affected by fragmentation of habitats. Conservation management directed at ensuring the survival of functional flagship species interactions will preserve other codependent and coexisting species and interactions. Entomologists are the most competent at recognizing, understanding, and manipulating insect interactions and should apply this knowledge and these skills to the needs of conservation. Lessons from applied entomology, including integrated pest management, clearly show the importance of preserving interactions.

KEY WORDS biodiversity, conservation, habitat fragmentation, insect behavior, species interactions

So important are insects and other land-dwelling arthropods that if all were to disappear, humanity probably could not last more than a few months. Most of the amphibians, reptiles, birds, and mammals would crash to extinction about the same time. Next would go the bulk of the flowering plants and with them the physical structure of most forests and other terrestrial habitats of the world. The land surface would literally rot.

-E. O. Wilson, The Diversity of Life (1992)

WORLD-WIDE THERE ARE ≈10,000 known bird species, 4,000 mammal species, and 350,000 plant species, but insect species number in the tens of millions and probably constitute 75% of the animal life on Earth (Erwin 1988). Insects create the biological foundations for all ecosystems: they cycle nutrients, pollinate plants, disperse seeds, maintain soil structure and fertility, control populations of other organisms, and provide a major food source for other taxa (Majer 1987). Whether measured in terms of their biomass, or their numerical or ecological dominance, insects are a major constituent of terrestrial ecosystems and should be a critical component of conservation research and management programs.

Conservation efforts are directed at preserving what humans assess as valuable, from single species to entire ecosystems. Insects are receiving increased attention in conservation assessment and research because of a growing awareness of their importance as keystone species, as indicators of patterns of species richness, beta-diversity, and endemism, and as monitors of environmental change. Butterflies have received the greatest attention in insect conservation efforts and are most often used as subjects in singlespecies preservation programs of endangered or rare species, modeled after the "keystone" concept of vertebrate preservation (Arnold 1983, Murphy 1988, Murphy and Weiss 1988, New et al. 1995). Species richness of insect assemblages is used in conservation evaluation exercises to rank particular sites in relation to other sites in a region (Kremen 1992, Pearson and Cassola 1992, Kremen et al. 1993, Prendergast et al. 1993). As conservation tools, the presence or absence of insect species are used as monitors or indicators that measure environmental and biodiversity change or health (Disney 1986, Kremen 1992, Kremen et al. 1994).

In each of these conservation efforts (single species preservation, site ranking based on diversity patterns, monitoring of biodiversity) the presence or absence of insect species is the most important parameter that is

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measured. Attention to the vital role insects play in ecosystem processes is not considered. In this article, I draw attention to the significance of insect behavioral ecology and functional role in relation to conservation research and management. I specifically highlight the merit of conserving insects for the value of preserving unique and essential behaviors and ecological processes, the need for research on how environmental change affects insect behavior and ecological interaction, and the necessity of including species interactions in monitoring programs.

Preserving Insect Interactions

Preserving diversity is dependent on preserving interactions. Insects are living models of how complex organisms interact to produce larger collective communities. Insects are the "glue" that holds diversity together (Janzen 1987). It is not just the presence or absence of a species or habitat that is important in conservation, but whether or not the necessary insect-driven ecosystem interactions and processes are occurring.

Many insect species have experienced population extinctions in conserved ecosystems, where flora and vertebrates remained essentially unchanged (Thomas 1991). For example, 50 yr of conservation efforts directed at the lycaenid butterfly *Maculinea arion* L. failed, even though its apparent habitat and host plant were being protected (Thomas 1991). It was not until the interactions of the butterfly larvae with its obligate ant host were understood that conservation managers could develop a successful preservation strategy.

Efforts to create riparian habitats in the Central Valley of California are aimed at restoring riparian vegetation and providing habitat for vertebrates, but may be destroying native insect communities. For example, native ants have narrowly escaped local extinction by the invasive Argentine ant, *Linepithema humile* (Mayr), in habitats that experience the natural summer drought. Summer flooding in artificial riparian habitats has facilitated the invasion of *L. humile* and the consequent extinction of native ants (Ward 1987).

The displacement of native ants by L. humile has been shown to affect community interactions and ecological processes. In the South African Cape fynbos. the Argentine ant has displaced the native, seed-dispersing ants, causing a significant reduction in seedling recruitment of endemic Proteaceae (Bond and Slingsby 1984). The continued invasion of the fynbos by L. humile may eventually lead to extinction of many endemic Proteaceae (Bond and Slingsby 1984). In Hawaii, the invasion of the Argentine ant is affecting native pollinators (Cole et al. 1992). The presence of L. humile was associated with a reduction of populations of major pollinators of native plants (Cole et al. 1992). The previous examples illustrate dramatic potential ecosystem-level consequences due to the presence and absence of species. Changes in community interactions, however, may more often result from

alterations of the behaviors of species that are present, rather than from the absence of these species.

Habitat Fragmentation

Fragmented habitats that appear healthy but are without the plant-insect and other ecological interactions necessary for long-term survival (Howe 1984, Saunders et al. 1991) can be termed homes of the "living dead" (Janzen 1986). Fragmentation of wild areas is a phenomenon that will only increase. Conservation biologists have studied how fragmentation has affected insect species composition (Powell and Powell 1987, Becker et al. 1991, Tscharntke 1992, Roland 1993), but few studies have investigated the effects on insect interactions in the community (Didham 1996).

Fragmentation of landscapes may affect insect parasitism in birds (Loye and Carroll 1995), insect pollination systems (Rathcke and Jules 1993), parasitism of insect herbivores (Kruess and Tscharntke 1994). predator-prey interactions (Roland 1993), or insect decomposers (Klein 1989). If seed set is pollinationlimited because of the lack of insect pollinators, or if bird nestling survivorship is reduced because of an increase in blood-feeding ectoparasites, the community may be sent on a cascade of interactions that slowly diminish the long-term survival of populations and the persistence of the community. As the process proceeds, fragmented habitats may become disproportionately rich in insect and plant species that lack complicated life cycles: plants that produce by asexual means, insects that have simple life histories. For example, nonmigratory insects whose larvae and adults feed on the same host plant will be favored over migratory insects that require different obligate host plants for each life stage.

The effect of fragmentation on pollination systems and plant reproductive success has been investigated in bee-pollinated trees in chaco dry forest in Argentina (Aizen and Feinsinger 1994a, b) and in butterflypollinated herbs in Sweden (Jennersten 1988). In each of these studies, the vital, mutualistic interactions in the fragmented habitats suffered in comparison with that of continuous habitats. Aizen and Feinsinger (1994a) found a reduction in the number of native bees visiting 2 dominant tree species in forest fragments than in continuous forests. They also found declines in pollen tube number per flowers, in fruit set, and in seed set for species in forest fragments (Aizen and Feinsinger 1994b). Jennersten (1988) found a lower abundance and diversity of flower-visiting insects and higher pollinator-limited seed set in meadow fragments than in continuous habitat. We must understand how pollination behavior is affected by the shape and form of the landscape in order to preserve interactions that will ensure the long-term stability of the communities.

Efforts to restore threatened habitats often produce new island fragments. Vernal pool, prairie, or riparian restoration concentrate on the restoration of vegetation assemblages, but little attention is given to ensuring that habitat specific insect interactions are restored (Thorp and Leong 1995). Monitoring of restored habitats should include an evaluation of the functioning of species interactions such as pollination.

Higher level interactions such as the parasitism of herbivores by parasitoids may be more susceptible to the effects of fragmentation (Kruess and Tscharntke 1994). Parasitoids or other insects that are characterized by small and highly variable populations may not successfully colonize isolated habitats. Lessons learned from biological control of insects should be applied to understanding how to ensure the preservation of higher tropic interactions in fragmented natural habitats.

Scale

Our notion of landscape patterns is dominated by the spatial and temporal distributions of terrestrial vertebrates and needs to be redefined once insects and their interactions are considered. On a larger scale, landscapes are often fragmented and include elements such as matrices, patches, and corridors (Forman and Godron 1986). This interpretation of the landscape may be appropriate for some plants and vertebrates, but for preserving insect interactions, it may not be helpful. The spatial and temporal distributions of insect dynamics involved in pollination or parasitism may not coincide at all with the borders of patches, corridors, or a matrix.

The boundaries of insect habitats, both physical and behavioral, cannot often be defined. For example, many small populations of insects may exhibit "shifting mosaic" metapopulation dynamics, and be highly vulnerable to extinction by stochastic changes in population density or environmental accidents (Harrison et al. 1988). For these populations, occasional recolonization from other habitat patches after local extinction is necessary for the persistence of the species. The effect of aberrant weather patterns on the species life cycle and behavior, and the patchy distribution of suitable habitat patches, make it difficult to define the exact habitat boundaries to safeguard the persistence of the species and their interactions.

Conservation research and management need a clear picture of these interactions and the spatial scale of these features. Food plants, nesting habitats, and oviposition sites may be highly localized, whereas flight paths may be over many kilometers.

Saving Species Interactions Versus Habitat

Generalizing about insects—a group that contains 10–100 million species—is difficult. In addition to demonstrating vast variation in morphology, insects vary greatly in behavior and role in ecological interactions— even within the life stages of the same species. Therefore, insects may be excessively species rich and behaviorally diverse for a species by species conservation approach, and perhaps a habitat based conservation approach that emphasizes ecosystem functioning and flagship species interactions is more

appropriate. This model assumes that by preserving flagship species interactions, coexisting and codependent species and their interactions will be saved. A habitat conservation approach that includes species-interaction management are complementary efforts. For example, when the interactions between the host ant and the lycaenid *M. arion* was restored and managed, other endangered species and vulnerable species of terrestrial invertebrates found in that habitat also made a resurgence (New et al. 1995).

Although all behaviors and interactions are interesting and necessary at one level, certain species exhibit life histories that are so unique and spectacular that they make excellent flagship species for preserving habitat and ecological interactions. For example, in tropical systems, euglossine bees are one of the more intensively studied group of insects. They are taxonomically well known, and have provided contributions to the understanding of complex interactions, including plant-pollinator coevolution, chemical ecology, population dynamics, mimicry, parasite-host relationships, and competition (Roubik 1989). With the help of chemical attractants, the mutual dependence between orchids and their male euglossine pollinators can be addressed at the level of community assemblages. The wealth of information and their ecological importance make euglossine bees a model tropical system for investigating the effect of fragmentation and other forms of habitat change on insect interactions. The ground work for this research is provided in studies of bee abundance and species richness in forest fragments (Powell and Powell 1987, Becker et al. 1991).

In conclusion, if protected areas are to be more than just preserves of the "living dead," then their ecosystem interactions must also be salvaged. That is, insect assemblages and behavioral interactions must be protected. To accomplish this, we must understand how insect behavior and function are affected by the changes in species assemblages and the shape and form of landscapes. For most insects, however, there is no knowledge of their behavior and ecological interactions and the scale at which these factors are important. This lack of information means that we must rely on saving known interactions as flagships for preserving other coexisting and codependent taxa. Because entomologists are the best source of information on insect interactions, they must direct this knowledge to integrate behavior with conservation research and planning.

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Editors' Note

Annals Initiates New Section

THE FOLLOWING set of two papers, the Annals opens a new Section, Consertation and Biodiversity. This Section welcomes Invited, Forum, and regular papers on the entomological aspects and implications of these topics. The Section is open to empirical and theoretical papers on entomological biodiversity (the measuring and analysis thereof, and the results), extinction (local, global), endangered species, endangered habitats, conservation of these, and so on. The list could be extended to the limits of the readers' ingenuity. And we hope it will be.

Carl W. Schaefer Leo E. LaChance Editors, Annals of the Entomological Society of America

AUTHORS' NOTE

Importance of Insect Behavior in Conservation

ONSERVATION ISSUES REVOLVE around the preservation of species in a world of unprecedented habitat change (Soule 1986, Hagen and Johnston 1992, Dingle et al. 1997). One tool for evaluation of habitat condition that is becoming increasingly useful in broad-scale ecological studies is the characterizing of insect biodiversity (Gaston et al. 1993). But a prerequisite to understand or even to sample biodiversity is knowledge of the behavior of insects. In this forum, we address insect behavior as a changing aspect of insect biodiversity that can have important conservation repercussions.

Just as the immune system allows the physiology of an organism to evaluate and respond to internal environmental change, so behavior is the first aspect of an organism to respond to changes in the larger environment (Slobodkin and Rapoport 1974, Loye and Carroll 1995, Dingle et al. 1997). The behavioral response of an organism to exploit or avoid change will often be under strong selection. Thus, the response to environmental change may alter resource availability in ways that drive evolution to new directions. These new directions can have repercussions on community structure and on conservation attempts.

Here, our approach is to present two issues that focus on arthropod behavior in conservation research and management. The first issue is the importance of insect behavior in biodiversity evaluation. The second is the role of ectoparasite behavior (e.g., host-finding success in changing environments) as a potential problem in vertebrate conservation. The models used in the second paper are the arthropod ectoparasites of birds and their effects on nesting behavior.

The use of insects for evaluation of changing patterns of biodiversity is well known. However, without more knowledge of the behavioral biology of arthropods, preservation and management of entire communities of associated organisms may be compromised.

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