Hawaii: A World Without Social Insects

EDWARD O. WILSON
(Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA)

Editors' note: This essay originally appeared as a chapter within E.O. Wilson's 1990 book *Success and dominance in ecosystems: The case of the social insects*, published by the Ecology Institute following the presentation of the *Ecology Institute Prize 1987 in Terrestrial Ecology* to Professor Wilson. Because of the importance of this essay, we reprint it here to make it more widely available in Hawaii and the Pacific. The essay provides many ideas that should stimulate research in ecology and conservation biology. Much remains to be learned about the pervasive ecological interactions of ants in Hawaii. Since this paper was written, several papers have appeared that complement this essay: Bach (1991), Cole *et al.* (1992), Gillespie and Reimer (1993), and Reimer (1994). We thank Professor Wilson and Professor Otto Kinne of the Ecology Institute, Oldendorf/Luhe, Germany, for their permission to reprint this essay.

In order to assess the impact of a dominant group of organisms, it would be extremely useful to have biotas free of the dominant group that can serve as evolutionary controls. This baseline is not easily found, because dominant groups are also as a rule very geographically widespread. The eusocial insects in particular have almost completely filled the terrestrial world. But there is one place to look. They did not, prior to the coming of man inhabit the easternmost archipelagoes of the Pacific. In particular, they did not reach Hawaii. This most isolated of all archipelagoes evolved a rich endemic fauna and flora in the absence of termites, ants, and eusocial bees and wasps (Zimmerman 1948, Wilson & Taylor 1967, Williamson 1981).

The massive weight of the social insects was therefore lifted from the plants and animals that departed from their midst and colonized Hawaii. Insects and other arthropods were freed from predation by ants and social wasps. Conversely, predators and scavengers did not have to compete with ants and social wasps; and invertebrate decomposers of wood did not have to contend with termites in the rotting logs and stumps. On the negative side, plants were deprived of the protection of ants and the pollination services of social bees.

How did the Hawaiian biota respond to this release? Unfortunately, we cannot directly read off the results, because there is an additional force working in Hawaii that is easily conflated with the absence of social insects: the disharmonic nature of the biota as a whole. The Hawaiian biota, as expected from its extreme remoteness, has evolved from a limited number of stocks, which have radiated extensively thereafter. By 1980, 6500 endemic insect species had been described, and these are believed to have evolved from about 250 original immigrant species (Williamson 1981). A typical case is the oecanthine tree crickets, comprising 3 genera and 54 species, or 43% of the entire known oecanthine fauna of the world, all derived from a single species that colonized the islands no more than 2.5 million years ago (Otte 1989). Disharmony of this kind means that not just social insects but many other major stocks of invertebrates are absent in the native fauna. Their absence as predators, herbivores, and decomposers must also be taken into account when assessing the histories of the sweepstakes winners.

The problem, while not readily soluble, is nevertheless tractable. Given the great ecological importance of social insects and the general significance of dominance in community evolution, the Hawaiian biota deserves a new look with social insects in mind. It is entirely possible that certain traits of the Hawaiian fauna usually ascribed to disharmony and reduced dispersal opportunity, such as extreme local abundance and flightlessness, are due at least in part to the lack of pressure from social insects, especially ants. What I offer now as a first analysis is a set of properties of biotas expected from the absence of social insects, without the attempt (or even the capacity, given the present scarcity of ecological knowledge) of disentangling the effects from those due to the absence of other, ecologically equivalent invertebrate groups as a reflection of disharmony in the fauna.

Scale insects and other honeydew producing insects protected by ants elsewhere will be scarcer relative to related groups. This prediction is confirmed but vitiated by the disharmonic nature of the fauna. There are no native coccids, fulgorids, or aphids, among the groups most avidly attended by ants elsewhere. Their absence could be ascribed either to the absence of ant protectors or bad luck in the dispersal sweepstakes. The latter hypothesis seems somewhat less likely in view of the fact that aphids are excellent dispersers. There is only one butterfly species belonging to the Lycaenidae, a family whose caterpillars are heavily attended by ants, but the native butterfly fauna of Hawaii is, inexplicably, very small overall. Mealybugs (Pseudococcidae), also much favored by ants, are represented by 3 endemic genera and 14 species, but are heavily outweighed in diversity by the homopterous families Cixiidae, Delphacidae, and Psyllidae, which are not attended by ants (Zimmerman 1948).

Both herbivores and predaceous insects will occur in denser, less protected populations. This prediction is dramatically confirmed. A very high percentage of the endemic insect species are flightless, and also generally "sluggish," to use Perkins' (1913) term, with populations persisting on the same tree or bush for years. Otte (personal communication) has referred to the conspicuous abundance of endemic crickets and their "lackadaisical" behavior. Many of the species walk about in the open where they can be easily picked up with the fingers, in sharp contrast to the cryptic, fast-moving species that occur in other faunas. Caterpillars such as those of the pyraustid moth genera *Margaronia* [now *Glyphodes* and *Stemorrhages*] and *Omiodes*, the extremely diverse drosophilid flies, and a few other dominant groups are comparably abundant and accessible, or at least were so in the last century in the less disturbed habitats. These are the kinds of insects most vulnerable to ant predation. No fewer than 36 ant species have been introduced by man, including the notorious omnivore and pest species *Pheidole megacephala*. The widespread destruction of native Hawaiian insects by ants is well known. Zimmerman (1948) states that "the introduction of a single species of ant, the voracious *Pheidole megacephala*, alone has accounted for untold slaughter. One can find few endemic insects within that scourge of native insect life. It is almost ubiquitous from the seashore to the beginnings of damp forest." Otte has observed the same displacement in the case of native crickets on Hawaii and the Society Islands, which also lacked ants before they were introduced by human commerce. There are other major causes of extinction of Hawaiian native insects, including habitat destruction and the incursion of alien parasites and diseases. But the important point with reference to the question of social insect dominance is the documented extreme vulnerability of the native insects to introduced ants in both disturbed and undisturbed habitats, which is consistent with observations in other parts of the world where ants are native. (Ants may also have played a key role in the retreat of the rich and abundant Hawaiian land snail fauna, comprising over a thousand species, although I am not aware of studies addressing this possibility.) The converse conclusion is equally important: the local abundance of behaviorally vulnerable, epigaeic insects is consistent with the absence of native ants, whether or not it explains the phenomenon entirely.

The non-formicid predators in the mesofauna (0.2 to 2.0 mm body length range), especially carabid beetles and spiders, should be more diverse and abundant. Also, predators should have evolved in mesofaunal arthropod groups that are not predaceous in other parts of the world. I call attention here especially to carabid beetles and spiders, because it is my experience in many other parts of the world that large numbers of species belonging to these two predatory groups have similar microhabitat preferences to ants. They occur abundantly in the litter and soil and especially under rocks not yet colonized by ants. In the summit forest of Mt. Mitchell in North Carolina, USA, where ants are very scarce, I found carabids and spiders to be more abundant, or at least more conspicuous, than at lower elevations. Darlington (1971) and Cherix (1980) present evidence that ants generally reduce the abundance of ground-dwelling carabids and spiders in both the tropics and temperate zones, especially those species specialized to live in soil and rotting vegetation. And as expected, carabids and spiders are both very diverse and abundant in the native forests of Hawaii. Other mesofaunal predatory groups that have radiated include the nabid bugs, staphylinid beetles, dolichopodid flies, and muscid flies of the genus *Lispocephala*. Groups that have moved into the ant predator zone include the geometrid moth *Eupithecia*, whose caterpillars ambush insects like praying mantises, and the damselfly *Megalagrion*, whose predator nymphs have left the aquatic environment entirely to hunt on the ground, especially under clumps of ferns. As I have stressed, these adaptive radiations and major ecological shifts may have been favored by the absence of competing predators in addition to ants, due to the general disharmonic nature of the fauna. Yet it is hard to imagine their occurring at all if a well-developed ant fauna had been present.

Non-formicid scavengers should be diverse and prominent relative to those in ecologically otherwise comparable faunas. Ants are strongly dominant as the scavengers of small arthropod corpses in most parts of the world. It is to be expected that this largely empty niche was filled by other groups on Hawaii, perhaps (at a guess) staphylinid and histerid beetles, but I know of no studies addressing the matter. Wood borers other than termites should be very prominent. In the absence of termites, we should expect to find a greater diversity and abundance of insects that bore through dead wood, especially the softer, rotting "wet" wood favored by so many termite species elsewhere in the world. Again, studies appear not to have been directed specifically to this hypothesis. Candidate groups include beetles of the families Anobiidae, Cerambycidae, Curculionidae, Elateridae, and Eucnemidae, which have in fact radiated extensively on Hawaii.

Solitary wasps and bees should be relatively diverse and very abundant. The solitary eumenid wasp genus *Odynerus* is represented by over 100 endemic species on Hawaii and, until the last century at least, was extremely abundant. The solitary hylaeid bee genus *Hylaeus* contains at least 50 endemic species, all derived from a single ancestor. The relation of these minor evolutionary explosions to the absence of social wasps and bees is an intriguing possibility but has not yet been explored.

Extrafloral nectaries and elaiosomes will be reduced or absent in the native flora. In general, extrafloral nectaries serve to attract ants, which in turn protect the plants from herbivores. Extrafloral nectaries are substantially scarcer in the Hawaiian flora than elsewhere, in agreement with the prediction (Keeler 1985). Eleven endemic species and 6 indigenous species do have the nectaries, which may be attended by protector arthropods other than ants or simply reflect phylogenetic inertia. Significantly, three other indigenous (but not endemic) species having extrafloral nectaries elsewhere lack them on Hawaii, again supporting the prediction. Elaiosomes are seed appendages attractive to ants that induce the ants to disperse the seeds. No study has been made to my knowledge of their relative abundance on Hawaii.

To conclude, Hawaii has long fascinated biologists for its superb adaptive radiations, and depressed conservationists for the continuing destruction of those same evolutionary wonders. I suggest that the value of the biota is enhanced still further by the realization that it is a natural laboratory, the unique site of an experimental control, for the assessment of the impact of social insects on the environment. These insects are so dominant in almost all other parts of the world that their absence in the original, native Hawaiian fauna and flora provides an exceptional opportunity to study the effects of ecological release on the part of taxa that would otherwise have interacted with them most strongly. At the very least, the absence of social insects should be taken into more explicit consideration in future studies of the biota. What is clearly needed are deeper studies of the life cycles of native Hawaiian taxa in comparison with sister taxa elsewhere, and especially on other islands with and without key elements such as social insects.

Hawaii, the most remote archipelago in the world and home of a rich endemic fauna and flora, was evidently never colonized by social insects before the coming of man. The absence of these dominant elements means that the Hawaiian native biota is a controlled experiment in which we can observe the effects of freedom from social insects, especially ants and termites. It seems probable that the circumstance was a major contributor to some of the tendencies characterizing the Hawaiian biota as a whole, including flightlessness, lack of evasive behavior, increased abundance and diversity of carabid beetles and spiders, adaptive shift to predation in some terrestrial insect groups, and the loss of extrafloral nectaries in flowering plants.

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