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LETTERS TO THE EDITORS

ANOMALOUS DIVERSITY OF TROPICAL ICHNEUMONID
PARASITOIDS: A PREDATION HYPOTHESIS

Owen and Owen (1974) have recently presented data showing that species diversity and richness of Ichneumonidae (Hymenoptera), which are mainly parasitic on other insects, is no greater in tropical Africa than in temperate Europe, a result that runs counter to the prevalent trend of increasing species number in a taxon with decreasing latitude (see Fischer 1960). (Other exceptions include freshwater invertebrates and phytoplankton [Pianka 1974]). They note that this low tropical diversity cannot be the result of low host diversity, because host species such as Lepidoptera are considerably more diverse in the tropical areas. They conclude that, because ichneumonids tend to be niche specific rather than host specific, there are no more niches in tropical areas than in similar temperate areas.

Data from the New World tropics also show this trend of low parasitoid diversity. Janzen (1975) found that an English meadow had two to four times as many hymenopteran parasitoid species as a Costa Rican old field. The only Costa Rican sample that had a number of species similar to the English meadow was rain-forest understory, with twice as many species of potential prey insects (Janzen and Pond 1975). In a transect up the Venezuelan Andes, the numbers of hymenopteran parasitoid species were reduced proportionately less than other insect groups (Janzen et al. 1976). Janzen and coworkers attribute this at least partially to the increase in the number of potential prey individuals per species with increasing elevation. Janzen (1975) found that seed-eating bruchid beetles in Costa Rica supported only a few parasitoid species, and a number of bruchids were unparasitized. This contrasts strikingly with insects of temperate regions that commonly support 20–40 parasitoid species (e.g., Askew 1975; Price and Tripp 1972).

Janzen (1975) and Janzen and Pond (1975) have proposed that resource scarcity may account for the low diversity and species richness of parasitoids in the tropics. They reason that severe herbivore pressure leads to wide spacing of conspecific plants (Janzen 1970) and selection for chemical defenses and/or irregular flowering and fruiting. The chemical defenses necessitate specialization by the herbivores, which in turn may contain toxic chemicals requiring parasitoids to be highly specialized as well. Because of sparse and/or intermittent supplies of food, herbivore populations occur at low densities, and they become too scarce to be exploited by specialized parasitoids.

In this paper we present an additional explanation to account for this anomalous trend in parasitoid diversity. We hypothesize that predation is more

severe in the tropics and that parasitized hosts, with their parasitoids, will be highly selected against, because parasitized insects tend to be particularly susceptible to predation.

Parasitoids commonly cause their hosts to act abnormally or become sluggish, especially just before the parasitoid emerges. Host development time is also extended, resulting in greater exposure to predation (e.g., Führer 1968; Tripp 1960). Many insects show complex behaviors for predator avoidance, and, if this behavior becomes abnormal, they will be less likely to escape predation. Immature Lepidoptera are the most common hosts of both ichneumonid and braconid parasitoids (Matthews 1964; Owen and Owen 1974), and we will emphasize their behavior in our discussion, although we feel the hypothesis is applicable to other hosts and their parasitoids as well.

When lepidopteran caterpillars are threatened by predators, they may wriggle furiously, drop to the ground, present warning colors, regurgitate or secrete defensive chemicals, or mimic the appearance and movement of their host plant (Matthews 1974). Some lepidopteran larvae drop on a slender silken thread when approached (Gotwald 1972). Parasitism may seriously disrupt such escape behaviors, although information concerning such effects of parasitoids is sparse. That parasites do make hosts more vulnerable to predation has been shown by Holmes and Bethel (1972, and reference therein). One of the few studies on predator-parasitoid interactions has been done by Tostowaryk (1971), who demonstrated that parasitized sawfly larvae experienced more predation by pentatomid bugs than did unparasitized larvae.

Evidence suggests that predation is more severe in the tropics than in temperate regions (e.g., Elton 1973; Paine 1966; Pianka 1974), although good quantitative data are lacking. However, the major predator groups that exploit potential parasitoid hosts include birds, lizards, tree frogs, spiders, and ants, and each of these groups is more diverse in the tropics. Karr (1971, and personal communication) found that insectivorous birds show increased species diversity and tighter species packing in the tropics, suggesting that bird predation is more intense. Little information exists on the effects of lizards on the insect community, although they do eat substantial numbers of insects, including lepidopteran larvae (Schoener 1968; Stebbins 1954). Spiders are virtually unknown ecologically, although they are known to be effective insect predators in temperate areas (Moulder and Reichle 1972). Ants are much more diverse in the tropics (Wilson 1971), and they are significant insect predators in temperate areas (Kajak et al. 1972).

Increased predator diversity would not necessarily cause increased predation pressure, because this would also depend upon predator densities and prey utilization, which are generally unknown. Ants, however, are one predator group that do appear to be much more dominant and abundant in the tropics (Elton 1973; Wilson 1971), and they may be the major predators of parasitized insects. Lepidopteran larvae can constitute up to 60% of the prey items collected by driver ants (Gotwald 1974). The intense foraging behavior exhibited by driver ants and army ants is largely a tropical phenomenon (Wilson 1971), and the workers of many other species are omnivorous scavengers that readily capture insects that are sessile, injured, or dead (Carroll and Janzen 1973). The

relative lack of sessile insects such as aphids and coccids in the tropics has been partially attributed to increased ant predation (Eastop 1972) and to increased predation in general (Janzen 1973).

If predation is a major factor in reducing parasitoid-species diversity in the tropics, a number of predictions can be made:

1. Injured, parasitized, or exposed insects should be more quickly discovered and captured in the tropics than in temperate regions by foraging predators such as ants. Culver (1974) found twice as many mobilizations of ants per hour in Puerto Rico as in West Virginia, suggesting that this prediction may be supported, although data are needed from the continental tropics.

2. A greater proportion of tropical parasitoids should exploit insect stages that are least susceptible to predation, such as pupae, which have hard protective coverings and are often well hidden, less abundant, and more randomly dispersed than earlier developmental stages. Or they should exploit hosts which live in well-protected habitats such as roots or stems, rather than exposed habitats such as leaf surfaces.

3. Our second prediction can be examined indirectly, because Price (1972) has demonstrated that long ovipositors are adaptive for reaching well-concealed hosts; therefore, tropical species should have proportionately longer ovipositors on the average than temperate species. In addition, if the hosts experience little predation, their parasitoids have a better chance of surviving than do parasitoids of more vulnerable hosts, and they tend to be K-strategists (Price 1973). We predict that more tropical parasitoids than temperate species will exhibit the K-strategy of having relatively few ovarioles and laying few eggs.

4. Parasitoids that do attack susceptible stages, such as leaf-feeding caterpillars, should affect their host's behavior less and for a shorter time than their temperate counterparts. Or they should cause the larvae to adopt a hiding behavior before their normal escape behavior becomes impaired. One possible strategy would be for the parasitoids to develop quickly, which could result in tropical parasitoids being smaller in size than their temperate relatives.

5. In addition to tropical-temperate comparisons, the relationship between parasitoid and ant diversity in other contrasting habitats could be examined. For example, tropical Hawaii, which has no endemic ant fauna (Wilson 1971), appears to have a relatively well-developed hymenopteran parasitoid fauna. The parasitoid hymenoptera:lepidoptera species ratio is approximately 1:2, which is similar to that for North America (calculated from Borror and DeLong [1964] and Zimmerman [1948]) and much higher than the ratio of 1:20 estimated by Owen and Owen (1974) for their collections from the African tropics.

6. Since some families of parasitoid insects contain species groups that exploit plants instead of insects, these can provide a control by which to examine the reduction of parasitoids. The plant parasitoids which live protected within plants should not be affected by predation to the same degree as the insect parasitoids. Some families that could be studied in this way are Cynipidae, Eurytomidae, and Tormyidae.

Increased predation has been postulated as a major cause of higher species diversity in the tropics (Janzen 1970; Paine 1966; Pianka 1974); our hypothesis suggests that increased predation would have the opposite effect on parasitoid

diversity. The parasitoids may be an especially amenable group for examining predation and diversity trends. We recognize that other factors are probably also important and may produce results similar to our predictions for other reasons, but we hope that a consideration of our predictions will focus research on a number of biological phenomena which may otherwise be overlooked. The interactions between parasitized hosts and predators could have significant influences on the population abundances and fluctuations of both parasitoids and hosts. This possibility would be important to consider in biological control programs and in estimating parasitism levels in the field (e.g., Tostowaryk 1971). The defenses of insects against other small arthropod predators have largely been ignored (Matthews 1974), and little quantitative data exist concerning the impact of different types of predators on the insect community. The coevolution of parasitoids and their prey offers situations parallel to those being recognized for herbivores and plants (Ehrlich 1970), but few studies have taken this approach. It should be noted that our predation hypothesis should apply to other major taxa of parasitoids as well, notably Tachinidae, Braconidae, and Chalcidoidea. Studies of several families could be made to determine the validity and generality of this hypothesis.

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