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## EVOLUTIONARY IMPORTANCE OF OVERSPECIALIZATION: INSECT PARASITOIDS AS AN EXAMPLE

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Gould (1982) reviewed evolutionary mechanisms that can operate at different hierarchical levels: gene, individual, deme, population, and species. He suggested that interactions between these levels can modulate evolutionary outcomes. One such possible interaction, overspecialization, has been described as the evolution of highly complex and ecologically constraining traits that convey a selective advantage to individuals, but lead to a higher probability of extinction of the species by restricting the ability of the species to withstand environmental change (Simpson 1953; Cifelli 1969; Valentine 1969, 1973; Bretsky and Lorenz 1970; Thompson 1976; Gould 1982). Some effects of environmental fluctuations on the extinction of species of differing sensitivity to environmental change have been modeled by Leigh (1981).

Observing that overspecialization is a process operating between two levels, individual and species, Gould suggested that overspecialization may be "a central evolutionary phenomenon that has failed to gain the attention it deserves" (1982, p. 385). As he remarked, it is usually dismissed as a minor and unusual phenomenon. Here we discuss the relationship between complexity and ecological specialization, provide an operational definition of overspecialization, and place this concept in the context of evolutionary theory. Also, since no widespread and important examples of extant organisms affected by overspecialization appear to have been identified, we suggest an example that could provide a system for the study of this phenomenon.

The presence of complex morphology (or physiology, behavior) does not predict the ecological breadth of a species or its evolutionary longevity. Complexity may lead to an evolutionary cul-de-sac or open new adaptive zones (Simpson 1953). Examples from the paleontological literature support both alternatives. Evidence supporting the first alternative includes the observation that during periods of mass extinction Paleozoic bryozoan genera with complex morphologies had a higher extinction rate than simpler forms (Anstey 1978). Complex genera survived better than simple genera, however, outside these periods of mass extinction. As evidence supporting the second alternative, the increased complexity of limb pairs in orders of free-living aquatic arthropods was not correlated with

TABLE 1  
RELATIONSHIP BETWEEN SELECTION ON THE INDIVIDUAL AND THE POPULATION CONSEQUENCES  
OF SUCH SELECTION

CONSEQUENCES FOR POPULATION IF TRAIT BECOMES WIDESPREAD	SELECTION FOR TRAIT AT THE INDIVIDUAL LEVEL	
	Yes	No
Increase or no effect on size	Individual selection, kin selection	Group selection
Decrease in size	Overspecialization	Maladaptation

evolutionary longevity (Flessa et al. 1975). We suggest that the increased complexity in arthropods (with a presumed specialization of function) appeared to affect only a few of the repetitive limb pairs at a time and that the unaffected limb pairs retained a simple morphology (and presumably generalized functions). In this case, arthropods may have acquired specialized limbs without sacrificing generalized functions.

#### ESSENCE OF OVERSPECIALIZATION

Problems with determining complexity, specialization, and ecological constraint sharply limit the usefulness of a definition of overspecialization employing such terms. We propose that the essence of overspecialization is the consequence for the population of an adaptation. Overspecialization occurs when the effect of a trait is selectively advantageous to an individual but disadvantageous to the population because it results in a decrease in population.

Table 1 outlines the logical relationship between individual selection, group selection, overspecialization, and maladaptation. Kin selection, wherein the fitness of an individual is increased by actions that promote the fitness of genetically related individuals, is similar to individual selection (E. O. Wilson 1975, p. 117). Group selection may explain the evolution of traits that do not necessarily benefit the individual when individuals are organized into small, isolated populations. In these structured demes, selection between populations may override selection within a population (Wright 1969; D. S. Wilson 1980, p. 38; Leigh 1983).

We distinguish overspecialization from other forms of individual selection on the basis of its consequences. Because the consequences of individual selection for populations have generally been ignored, overspecialization has not been examined closely. Since overspecialized traits are selectively advantageous to the individual, overspecialization is distinct from a frank maladaptation. In the table, sexual selection would be similar to either individual selection or overspecialization depending on the population consequences of such selection.

The usual examples of overspecialization have tended to focus on the seemingly bizarre traits that characterize the peacock, saber-toothed tiger, Irish elk, and others. In these cases there is no evidence that a fancy tail, big canines, or big antlers (no larger than expected for an animal of its size; Gould 1974) would be ecologically constraining or necessarily result in smaller population sizes.

By focusing on environmental change, the traditional scenario for overspecialization tends to reduce the concept to a truism. Ultimately, all environments change. Thus, in the long run, any trait may sooner or later become maladaptive or appear overspecialized (R. R. Warner, *in littera*). Such formerly useful traits, now maladaptations following environmental change, are distinct from overspecialization as defined here. The negative population consequences of overspecialization are intrinsic, at times resulting automatically from the action of an overspecialized trait.

#### AN EXAMPLE

A parasitoid may be defined as a consumer that kills one and only one host (prey) during a life history stage (Kuris 1974). Most examples are found among the hymenopterous insects. Typically, an adult female wasp locates a host insect and lays one or a few eggs on or in the host. After hatching, the larval parasitoid slowly consumes the host insect. Following the death of the host, the parasitoid pupates and then emerges as an adult wasp. Physiologically, parasitoids resemble parasites; ecologically, their impact is akin to predation. The consequences of host-location behavior by parasitoid insects show that in an ecologically significant group of organisms composed of many species, overspecialization is an important evolutionary mechanism. Female parasitoid insects have evolved complex searching mechanisms to locate suitable hosts, traits that are obviously critical to female reproductive success. Depending on the particular type of host, such locating behaviors may involve visual, olfactory, tactile, and auditory cues in various combinations (Askew 1971; Cade 1975).

Parasitoids are often highly efficient searchers. The ability of many parasitoid species to drive host populations to low levels and then to continue to locate hosts at the subsequent low densities is well documented (DeBach and Sundby 1963; Flanders 1966; Hassell and Varley 1969; Huffaker et al. 1971; Kuris 1973; but see Murdoch et al. 1984). Because of this capability they are frequently used as biological control agents for host insects that are agricultural pests (Huffaker et al. 1971; Kuris 1973). But, therein lies the rub. Ultimately, however, the selection for efficient searching behavior, so necessary for the success of the individual insect, causes a dramatic and often persistent depletion of the host resource. The parasitoid population is thereby also reduced. That many host insects are plentiful where they have been introduced but are rare in their native lands supports the conclusion that this is a widespread phenomenon (Kuris 1973; DeBach 1974). When native host populations are examined, a high prevalence of parasitoids is often recorded (Huffaker 1971; DeBach 1974).

Presumably, low-density host populations are more likely to undergo local extinction than high-density populations (see Murdoch et al. 1984 for evidence of local extinction from parasitoid activity). This would result in the concomitant disappearance of the resident parasitoid population. Thus, selection for highly efficient host-location behaviors appears to lead inevitably to an increased likelihood of at least local extinction of such parasitoids. Finally, a logical consequence of this causal chain is that the increased frequency of an efficient searching genotype is accompanied by a decrease in the total abundance of this genotype.

Some evolutionary processes may counterbalance the selection of overspecialized traits. As conditions approach local population extinction, selection for traits that promote the use of alternative host species should occur. Under these conditions founder effects and bottlenecks may intensify selection and provide a hospitable milieu for genetic changes enabling adaptation to a new host. To the extent that such countering forces operate, the overspecialization process does not necessarily lead to global extinction.

## SUMMARY

The use of parasitoids as an example of overspecialization permits this evolutionary mechanism to be studied more readily. Parasitoids are widespread, are readily cultured in laboratories, have short generation times, and lend themselves to comparative studies. Several important questions can be explored. Are highly host-specific parasitoids more likely to cause local extinction of host populations than parasitoids that exhibit low host specificity? What kinds of environmental fluctuations endanger such specialists? What factors limit overspecialization?

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