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RESOURCE PREDICTABILITY AND NICHE BREADTH IN THE *DROSOPHILA QUINARIA* SPECIES GROUP

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Levins and MacArthur (1969) have modeled the conditions under which an insect ought to increase the variety of plants on which it oviposits. They assume that an insect's reproductive success is a multiplicative function of the probability of its finding an acceptable host plant, and the number of young produced if such a plant is found. The number of young produced depends on the suitability (presence or absence of competitors, toxicity, etc.) of the plant. Qualitatively, they predict that an insect should increase the number of plant species on which it will oviposit if the probability of finding one of its host plants is low, or if the array of new plants utilized does not include too many unsuitable species. Some unsuitable species may be used because the insect does not possess the neurosensory ability to distinguish them from those that are suitable. This note relates these considerations to the observed host-plant ranges of two members of the *Drosophila quinaria* species group, *D. quinaria* and *D. falleni*.

Suspected larval resources (fungi, slime fluxes, oozing sap flows, fruits, flowers, and decaying leaves, bark, and wood) were collected from various localities in Maine and New York State. They were placed on a layer of wet sand in 350 ml plastic cups, which were sealed with plastic wrap, perforated for ventilation. Cultures were incubated at 20 ± 1 C. *Drosophila* species were identified when they emerged as adults.

The only resource from which *D. quinaria* emerged is the skunk cabbage, *Symplocarpus foetidus* (Araceae) (Table 1). The only other drosophilid reared from these plants is *Scaptomyza borealis*, which was not bred from any other potential resource. In the spring, *D. quinaria* breeds in the flowers, spathes, and spadices of these plants, whereas in late summer and fall, it utilizes the decaying leaves and petioles. This finding and the fact that the ranges of *D. quinaria* and *S. foetidus* are nearly coextensive (Sturtevant, 1921; Patterson and Wagner, 1943; Rickett, 1966) suggest that the former is a monophagous species. This is easy to understand in terms of the Levins-MacArthur hypothesis. Because skunk cabbages appear in the same localities, at approximately the same time, year after year (Fernald, 1950), individuals of *D. quinaria* have a high probability of finding a resource upon which to oviposit. An individual that accepted more species as host plants would have only a slightly greater chance of finding one of them, while it would incur a potentially serious risk—the inclusion of unsuitable species among those accepted. Other host plants may be unsuitable because of competition with other insect groups (see below). Selection favors monophagy.

Wheeler (1954) has found that the closely related *D. magnaquinaria* breeds in a related skunk cabbage, *Lysichiton americanum*, in the Pacific Northwest. Both species of skunk cabbages, and members of the Araceae in general, are extensively riddled with raphides of calcium oxalate, which render the plants nearly immune to attack by insects (B. J. D. Meeuse, pers. comm.). These two *Drosophila* species must have some adaptation, probably derived from a common ancestor, that has facilitated use of and coevolution with these Araceae (Ehrlich and Raven, 1964). It is conceivable that monophagy in these species is enforced by their dependence on skunk cabbages for specific nutrients [cf. *D. pachea* (Heed and Kircher, 1965)]. However, this idea is unlikely, as both species can be maintained in the laboratory on standard media (Sturtevant, 1921; Wheeler, 1954). In any event, such obligate dependence on one host species would most likely be a result of monophagy, not a primary cause of it.

Carson (1971) suggests that the widespread use of decaying leaves by Hawaiian *Drosophila* evolved in the absence of competition from other insect groups. On the North American continent, preemption of this niche by these other groups presumably prevents its use by *Drosophila* (McDonald et al., 1974). As reported here, *D. quinaria* breeds in the decaying leaves of *Symplocarpus foetidus* in eastern North America. I suggest that the absence of competitors, which is due to the presence of calcium oxalate, has allowed *D. quinaria*, and probably *D. magnaquinaria* to evolve an adaptation for breeding in the decaying leaves of these Araceae.

In contrast to *D. quinaria, D. falleni* is polyphagous, breeding in many taxonomically diverse species of fleshy fungi (Table 1). Other drosophilids reared from these fungi include *D. busckii, D. putrida, D. testacea, Leucophenga varia*, and *Mycodrosophila dimidiata*, none of which is monophagous. *D. falleni* does not utilize fungi that do not deliquesce (e.g., *Fomes*) nor those that are very small (e.g., *Marasmius*). The mushrooms in which it does breed contain a variety of potentially toxic principles. For example, *D. falleni* has been reared from *Amanita muscaria*, which contains a number of alkaloid neurotoxins, very high concentrations of vanadium (Bertrand, 1950), and which is a renowned flykiller. It also utilizes *A. bisporigera* and *A. virosa*, both of which contain highly toxic amanitins, short-chain cyclic polypeptides that damage cell membranes and disrupt RNA synthesis (Wieland, 1968). *D. falleni* may cope with this spectrum of potential toxins in a number of ways. On the one hand, it may possess an arsenal of enzymes, each specifically selected to detoxify a given poison (e.g., Teas, 1967). Alternatively, or in addition, it may have high activity levels of mixed-function microsomal oxidases, or other general-purpose enzymes, which are thought to detoxify a variety of poisons (Krieger et al., 1971). In any case, as *D. falleni* appears unaffected by these potentially toxic compounds, the proportion of mushroom species that are unsuitable probably is small. Acceptance of a broader range of fungi on which to oviposit would include a relatively insignificant number of unsuitable species.

TABLE 1. *Breeding sites of* D. quinaria *and* D. falleni.

		Adults reared	
Substrate	*N*	*D. falleni*	*D. quinaria*
Symplocarpus foetidus			
flowers	70		262
leaves and petioles	9		19
Clavulina cinerea	6	1	
Suillus tomentosus	16	2	
Boletus chrysenteron	25	19	
Pluteus cervinus	2	26	
Lactarius lignyotus	2	6	
Russula emetica	15	8	
subfoetans	60	89	
Amanita bisporigera	4	51	
flavoconia	16	59	
flavorubescens	16	169	
gemmata	16	19	
inaurata	8	46	
muscaria	25	557	
rubescens	13	353	
virosa	10	207	

Individual mushroom species are an unpredictable resource in both space and time (Kauffman, 1918; Orlos, 1975), making the probability of finding a given species on which to oviposit very low. Because of this, and because the inclusion of more host species is unlikely to expose offspring of *D. falleni* to potential toxins that they cannot tolerate, selection will favor an increase in the variety of acceptable host plants. *D. falleni* probably breeds in a large number of mushroom species.

Additional support for the Levins-MacArthur hypothesis comes from the rich drosophilid fauna of Hawaii (Heed, 1968). Here, many of the species are monophagous, breeding in the fermenting parts of abundant tree species. These resources must be highly predictable in occurrence. The polyphagous species tend to breed in less predictable resources, e.g., fungi. However, in contrast to *D. quinaria* and *D. falleni*, larval habitats and taxonomic affinity are closely correlated in the Hawaiian Drosophilidae (Heed, 1968; 1971).

Finally, consider the relation between host-plant predictability and defensive chemistry. Recent studies (Feeny, 1975; 1976; Rhoades and Cates, 1976) suggest that host plants and parts thereof that are predictable in occurrence should contain relatively high concentrations of compounds that are difficult to render harmless. Different plant species that are predictable should converge on a common strategy. Skunk cabbages and other Araceae have adopted this strategy by laying down high concentrations of calcium oxalate crystals, which are not readily detoxified. On the other hand, plant species or parts whose occurrence is unpredictable should employ a wide variety of compounds that are effective in small concentrations. However, an animal that has counteradapted to these compounds may detoxify them at a low metabolic cost. Mushrooms appear to be so defended. Thus, some lethal amanitins, which are present in very low concentrations (.014% wet weight), are rendered thoroughly non-toxic by a simple dehydroxylation (Wieland, 1968). Their unpredictability makes the probability of counteradaptation rather slim. However, for *D. quinaria* and *D. falleni*, it appears that the predictability of occurrence has been of greater selective importance than the chemical diversity of larval resources in the evolution of monophagy and polyphagy.

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