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Ecological and Genetic Responses to Mycophagy in Drosophilidae (Diptera)

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Mushrooms present a paradoxical resource on which insects can feed. First, fungi possess an incredible diversity of chemical defenses. Whether by evolutionary design or fortuitous accident, many fungi manufacture one or more toxins that can have serious consequences for an unwise predator. The physical characteristics of fungi, which would be of considerable importance to tunneling insect larvae, are also diverse, including the delicate and deliquescing flesh of *Coprinus*, the spongy, fibrous, or waxy caps of Agaricales, the soft jelly matrix of the Tremellales, the brittle texture of many Clavarias, and the tough or even woody consistency of the polypores. One might hypothesize, therefore, that mycophagous insects would restrict their feeding niches to subsets of similar mushrooms for which they had evolved the means to avoid or detoxify any noxious compounds and adaptations for traversing and ingesting the mushroom context. Yet specialization can occur only if resources are sufficiently long lasting and predictable to be available throughout the feeding stages of an organism's life cycle. Mushrooms are generally considered to be ephemeral and unpredictable, so mushroom-feeding insects might be forced to be unselective in host choices. Thus, there are conflicting selection pressures on mycophagous insects: first toward specialization on a more homogeneous subset of a chemically and physically diverse class of resources, and then toward generalization on a variety of these unpredictable hosts.

For the past three years I have been studying the population biology of the mycophagous guild of Drosophilidae fruit flies in an attempt to

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learn how some species in this taxon respond ecologically and genetically to the challenges posed by a fungal-feeding niche. In the eastern United States there are about a dozen species of drosophilids that utilize mushrooms as both the larval and adult feeding sites, as follows:

genus *Drosophila*
  subgenus *Hirtodrosophila*
    duncani
    chagrinensis
  subgenus *Drosophila*
    ordinaria
    quinaria sp. group
      falleni
      recens
    testacea sp. group
      testacea
      putrida
    tripunctata sp. group
      tripunctata
genus *Mycodrosophila*
    dimidiata
    stalkeri
    claytonae
      species *A*
      species *B*

The adults of these species feed, court, mate, and oviposit on mushrooms. The eggs hatch in a few days, and the larvae begin tunneling through the mushroom context, feeding either on the mushroom itself or, more likely, on the associated microbiota of yeast and bacteria. After passing through three instar stages, each of one to two days duration, the larvae pupate on the mushroom or in the surrounding soil or leaf litter. They eclose about four days later as adults. The entire life cycle takes about fourteen days at a temperature of 22°C.

Within the family Drosophilidae there are fungus-feeding members of two genera in the eastern United States. The genus *Drosophila* contains a variety of fungus-feeding species that have received surprisingly little study relative to the much better known species used extensively in genetic research. The subgenus *Hirtodrosophila*, all species of which are thought to be mycophagous, contains one moderately common eastern species, *Drosophila duncani*, and several very rare species, *D. chagrinensis* being the only one I have encountered in my collections. Within the very large subgenus *Drosophila*, *D. ordinaria*

appears to be rather primitive morphologically and may be similar to the ancestral representatives of the subgenus from which the *Hirtodrosophila* diverged. *D. falleni* and *D. recens* are two fungus-feeders in the *quinaria* species group, most other species of which feed on decaying swamp vegetation. The fungus-feeder *D. tripunctata* is the only North American member of its species group, and *D. putrida* and *D. testacea* are the only New World species of the *testacea* group.

The *Mycodrosophila*, as the genus name indicates, are all fungus feeders. Three named species inhabit the United States: *M. dimidiata*, *M. stalkeri*, and *M. claytonae*. Electrophoretic analyses of genetic variation, however, quickly revealed that *claytonae* consists of two species (to which I will refer as *M. claytonae A* and *M. claytonae B*), sharing no alleles at six out of eighteen loci that I have examined. They do not interbreed, although they are found in close proximity, even on the same mushroom caps, and so would have ample opportunity to do so. I have yet to find any morphological characteristics by which they can be distinguished.

Among the mycophagous Drosophilidae, one finds two common distributional patterns. *D. duncani*, *D. falleni*, *D. tripunctata*, *D. putrida*, *M. dimidiata*, and *M. claytonae* range over much of the eastern half of the United States. The two *claytonae* species are both present in my collections from New York and Tennessee and presumably are broadly sympatric over much of the range ascribed to the named form. *M. stalkeri* is found from Ontario south to Texas, Mississippi, and Florida, but not along the eastern seaboard (Wheeler and Takada 1963).

D. ordinaria, *D. testacea*, and *D. recens* have distributions extending across the northern states and southern Canada and then down the Appalachians at least as far as Tennessee and North Carolina. *D. testacea* is found also in northern Europe and Asia. *D. chagrinensis* is known previously from only a few specimens collected in Ohio, Wisconsin, and Iowa (Strickberger 1962), while I reared a single female from a *Tremella* sp. of jelly fungus in Ithaca, New York (Lacy 1981).

Populations of these mycophagous drosophilid species were sampled in the Ithaca, New York, area and on the Tennessee side of the Great Smoky Mountains National Park. The Ithaca collecting sites, sampled from June to October of 1978 and in May, June, September, and October of 1979, 1980, and 1981, included an uplands pine forest, two mixed deciduous-hemlock forests, two deciduous forests, and an elm swamp. Nine sites in the Smokies, sampled in July and August of 1979, 1980, and 1981, ranged from lowland (1500 feet) streambank forests through mid-elevation (3000 feet) hardwood forests to high-elevation (6000 feet) spruce-fir stands. Detailed descriptions of all collecting sites

are given in Lacy (1982a). Adult flies were aspirated directly off any mushrooms encountered during periodic (approximately weekly) searches of each collecting site; mushrooms were brought back to a lab and placed in half-pint bottles over Instant *Drosophila* Medium (Carolina Biological Supply) in order to rear flies from the eggs, larvae, and pupae present in the mushrooms when picked. Only a few specimens of *M. stalkeri* and *D. chagrinensis* were collected, in Tennessee and New York, respectively. Otherwise, all species listed above were collected in both geographic regions.

The trophic resources of adults and larvae are quite distinct in many insects, which presumably decreases competition among life stages. When I compare the host preferences of feeding adult drosophilids to the larval resource use, I find little evidence for niche separation with respect to host selection. Although the larvae and adults feed on the same mushroom species, niche separation is imposed on a smaller spatial scale, since the larvae tunnel through the fungal tissue, while adults are restricted to feeding at the surface.

Table 12.1 lists for each fly species the host mushroom genera which account for at least 1 percent of the collections in the Smoky Mountains. Data on both larval and adult feeding sites are pooled in this table. In the table are noted the total numbers of flies collected or reared from mushrooms and the percentage of these flies found on each host genus. Host utilization lists such as these are informative but do not necessarily reflect the host preferences of the fly species, because availability as a resource is very unevenly distributed among these mushroom genera. During field collections, *D. falleni*, *D. recens*, *D. tripunctata*, *D. putrida*, and *D. testacea* appeared to use species of basidiomycete mushrooms in a fairly indiscriminate fashion. *D. falleni* and *D. testacea* seem especially attracted to *Tricholomopsis platyphylla*, *D. testacea* uses fleshier polypores more than the other flies, and occasionally flies can be found on Ascomycetes; but otherwise these species use a similar variety of gilled and boletoid mushrooms. The state of decay of a mushroom has much more effect on fly abundance than does its species. Even the small differences in the host utilization lists of the fly species may be due more to differences in the elevational distributions of the flies than to host selectivity. *D. recens* and *D. testacea* are more common at the higher elevations in the Smokies, while *D. putrida* is most abundant at the lowest elevations. The host lists of *D. falleni*, *D. recens*, *D. tripunctata*, *D. putrida*, and *D. testacea* represent well the mushroom availability at the sites where they were collected.

The other mycophagous drosophilids are more selective in host

Table 12.1 Common Fungal Host Genera of Mycophagous Drosophilidae in the Great Smoky Mountains and Percentage of Collection Made from Each Mushroom Genus

D. falleni		*D. recens*		*D. tripunctata*		*D. putrida*	
N = 2955		N = 624		N = 2270		N = 3585	
Russula	36	*Russula*	62	*Russula*	60	*Russula*	44
Tricholomopsis	18	*Hygrophorus*	11	*Boletus*	8	*Boletus*	27
Boletus	17	*Amanita*	9	*Lactarius*	8	*Lactarius*	12
Amanita	8	*Boletus*	2	*Amanita*	7	*Amanita*	6
Lactarius	7	*Tricholomopsis*	2	*Suillus*	3	*Tricholomopsis*	5
Hygrophorus	4	*Sparassis*	2	*Hygrophorus*	3	*Suillus*	1
Suillus	2	*Lactarius*	2	*Tricholomopsis*	2	*Cortinarius*	1
Cortinarius	1	*Gyroporus*	2	*Collybia*	2	*Clitocybe*	1
Entoloma	1	*Cortinarius*	1	*Entoloma*	2	*Gyrodon*	1
Clitocybe	1	*Collybia*	1	*Cortinarius*	1	*Tremellodendron*	1
Omphalina	1	*Xeromphalina*	1	*Peziza*	1		
Collybia	1	*Hydnum*	1				

D. testacea		*D. ordinaria*		*M. dimidiata*	
N = 2009		N = 1320		N = 293	
Russula	51	*Russula*	52	*Clavulina*	18
Tricholomopsis	13	*Cerrena*	17	*Tremellodendron*	15
Lactarius	9	*Collybia*	7	*Cantharellus*	15
Boletus	8	*Tricholomopsis*	7	*Russula*	14
Amanita	5	*Cortinarius*	3	*Lactarius*	8
Cortinarius	5	*Hygrophorus*	1	*Peziza*	7
Collybia	2	*Amanita*	1	*Gomphidius*	5
Suillus	2	*Lactarius*	1	*Polyporus*	4
Laetiporus	2	*Boletus*	1	*Hydnum*	3
Cerrena	2	*Entoloma*	1	*Ramaria*	2
				Clavulinopsis	2
				Boletus	2
				Entoloma	1
				Collybia	1
				Laccaria	1

D. duncani		*M. claytonae A*		*M. claytonae B*	
N = 138		N = 50		N = 10	
Tyromyces	63	*Tyromyces*	78	*Ganoderma*	100
Laetiporus	21	*Polyporus*	10		
Pleurotus	14	*Boletus*	8		
Boletus	2	*Tricholomopsis*	2		
		Pleurotus	2		

Note: N = number of flies collected. Percentages do not all add to 100 because of rounding error and because a few mushrooms were not identifiable as to genus.

choice. *D. ordinaria* is found only at the higher elevations in the mountains (above 3000 feet) and utilizes a subset of the mushrooms encountered there. For example, such dissimilar mushrooms as *Cerrena* and *Collybia* are preferred by *D. ordinaria* over the more abundant Amanitas. *D. duncani* is a host specialist found predominantly on some of the fleshier Polyporaceae species, even though the gilled mushrooms (Agaricales) and the boletes (Boletaceae) are many times more abundant in the Smoky Mountains. One gilled mushroom, *Pleurotus ostreatus*, is included in the preferred diet of *D. duncani*. The two *Mycodrosophila claytonae* species also feed almost exclusively on polypores, using even the woody forms such as *Ganoderma applanatum*. The polypores are relatively uncommon in the Smokies, and so their associated fauna is also sparsely and patchily distributed. Finally, *M. dimidiata* uses a variety of fungi, including some agarics and polypores and also coral fungi (Clavariaceae), Heterobasidiomycetes, chanterelles (Cantharellaceae), and Ascomycetes that are not commonly utilized by any other drosophilids.

In contrast to their rarity in the Smokies, polypores are abundant around Ithaca, New York. One species in particular, *Polyporus squamosus*, is almost ubiquitous throughout the breeding season of the flies, from May through September. The host use observed in Ithaca fly populations (table 12.2) reflects this preponderance of *Polyporus*. Again *D. falleni* is fairly nondiscriminating in host choice, and its host list reflects the availability of mushrooms in the Ithaca study sites. *D. putrida* and *D. testacea* tend to be more seasonal breeders, with *D. putrida* common in midsummer and *D. testacea* common in spring and fall. They rather indiscriminately exploit the mushrooms available at those times, although as in the Smokies, *D. testacea* shows a greater reliance on polypores. *D. tripunctata* and *D. recens* are both very rare in Ithaca, so the wide diversity of mushrooms on which they likely feed may not be well represented in my limited samples of these species. *D. ordinaria*, also much less common in Ithaca than in the Smokies, uses a broad spectrum of mushrooms. *D. duncani* and the sibling species of *M. claytonae* are polypore specialists, as they are in the Smokies. Again, gilled mushrooms (*Pleurotus* and *Crepidotus*) with a growth form resembling that of the bracket fungi show up in the diet of flies that are otherwise restricted to polypores. *M. dimidiata* feeds on some polypores and agarics in Ithaca, while the coral fungi and chanterelles it uses in the Smokies are not sufficiently common in Ithaca to be a major component of its diet.

Table 12.2. Common Fungal Host Genera of Mycophagous Drosophilidae in Ithaca, New York, and Percentage of the Collection Made from Each Mushroom Genus

D. falleni		*D. recens*		*D. tripunctata*		*D. putrida*	
N = 15193		N = 130		N = 42		N = 2028	
Polyporus	57	*Lactarius*	31	*Gyrodon*	36	*Polyporus*	61
Psathyrella	8	*Polyporus*	25	*Coprinus*	33	*Psathyrella*	9
Pluteus	7	*Pluteus*	16	*Polyporus*	17	*Coprinus*	6
Coprinus	6	*Cortinarius*	12	*Russula*	5	*Agaricus*	6
Collybia	3	*Tricholomopsis*	6	*Lactarius*	2	*Amanita*	5
Amanita	3	*Coprinus*	5	*Mycena*	2	*Pluteus*	3
Crepidotus	3	*Gyrodon*	2	*Psathyrella*	2	*Gyrodon*	2
Gyrodon	2	*Collybia*	1	*Tyromyces*	2	*Tricholomopsis*	1
Pleurotus	2					*Lactarius*	1
Lactarius	2					*Tyromyces*	1
Russula	1					*Russula*	1
Tricholomopsis	1					*Pleurotus*	1
						Daedalea	1
						Crepidotus	1

D. testacea		*D. ordinaria*		*M. dimidiata*	
N = 1798		N = 200		N = 284	
Polyporus	79	*Polyporus*	60	*Crepidotus*	56
Amanita	5	*Pluteus*	17	*Polyporus*	31
Coprinus	3	*Collybia*	7	*Pluteus*	4
Pluteus	3	*Amanita*	5	*Hygrophorus*	3
Gyrodon	2	*Laetiporus*	2	*Clitocybe*	2
Psathyrella	2	*Tricholomopsis*	2	*Pleurotus*	1
Pleurotus	1	*Gyrodon*	2	*Psathyrella*	1
Russula	1	*Hericium*	2		
Cortinarius	1	*Tyromyces*	1		
Lactarius	1	*Gymnopilus*	1		
		Pleurotus	1		
		Lactarius	1		
		Psathyrella	1		
		Cortinarius	1		

D. duncani		*M. claytonae A*		*M. claytonae B*	
N = 122		N = 138		N = 97	
Grifola	74	*Polyporus*	80	*Polyporus*	87
Laetiporus	15	*Crepidotus*	13	*Ganoderma*	10
Polyporus	9	*Ganoderma*	6	*Pleurotus*	3
Tyromyces	2	*Grifola*	1		

Note: N = number of flies collected. Percentages do not all add to 100 because of rounding error and because a few mushrooms were not identifiable as to genus.

Ecological Responses to Mycophagy

With these host lists we can consider how the mycophagous drosophilids respond to conflicting selection pressures toward specialization and generalization. First note that not all species have adapted to mycophagy in identical ways. Some species feed on a variety of mushrooms, including many that are toxic to other animals and even other Diptera, as is the fly agaric, *Amanita muscaria*. Thus the diversity of mushroom chemistry does not invariably lead to specialization on just a few hosts. In fact it is the host specialists that use chemically benign, though perhaps physically harsh, microhabitats, while the generalist species feed on many toxin-producing mushrooms.

To consider the role of host predictability on the ecological specialization or generalization of the drosophilids, a quantitative measure of the duration of mushroom caps is needed. While any mycologist, or even casual mushroom collector, would assert that *Coprinus* are more ephemeral than *Russula* and *Russula* more so than the Polyporaceae, I have been unable to locate any studies in which the durations of individual fruiting bodies of fungi were measured. To collect such data, I marked mushroom caps as they emerged from the ground or appeared on rotting wood in a study site along the Little River, at an elevation of 2100 feet in the Smoky Mountains. The area was searched daily, any new mushrooms were marked with plastic stakes, and the conditions of all earlier caps were recorded. Although mushroom duration was highly variable, depending on weather, microhabitat, and visitation by fungivores, the fates of 426 mushrooms in 19 genera were recorded during July and August of 1979 and 1980, providing preliminary quantification of the ephemeral nature of these mushroom genera.

Table 12.3 gives, for each of the genera at this study site, the mean duration in days from the first emergence of a cap to the time that the mushroom had either disappeared, thoroughly dried, or so totally rotted away that I judged any remaining mushroom tissue to be incapable of supporting a drosophilid larva. In the first column of the table are the mean durations averaged over all mushroom caps recorded. Many of these mushrooms, however, had the duration of fruiting suddenly ended by vertebrate fungivores (rodents, skunks, and deer were common at the site) or by voracious snails. The second column in table 12.3 lists the durations averaged over only those mushrooms that were not consumed by anything larger than tunneling insect larvae. While these data are subject to much error, they do reflect the relative

Table 12.3. Duration of Mushroom Caps

	All Caps		Caps Not Eaten by Vertebrates or Snails	
	$\bar{X}$	N	$\bar{X}$	N
Coprinus	3.0	1	3.0	1
Marasmius	3.8	4	3.3	3
Pluteus	4.4	5	3.5	4
Entoloma	5.2	19	5.4	14
Crepidotus	4.0	3	6.0	1
Pholiota	6.0	3	6.0	3
Collybia	5.9	11	6.2	9
Lepiota	6.0	6	6.7	3
Tremellodendron	6.7	3	6.7	3
Hygrophorus	6.0	32	7.0	19
Tricholomopsis	7.0	1	7.0	1
Amanita	4.7	117	7.2	38
Russula	7.3	94	10.4	47
Boletus	6.7	52	10.6	22
Cantharellus	10.8	6	10.8	5
Suillus	9.0	18	12.0	11
Leccinum	13.0	2	13.0	2
Lactarius	8.4	39	13.7	15
Clavaria	18.6	9	18.6	9

NOTE: $\bar{X}$ = mean duration in days of individual mushroom caps, from first appearance until the cap had rotted away, thoroughly dried, or been entirely consumed; N = number of caps observed.

longevities as I might subjectively estimate them from my experiences in the field.

The distributions of host fungus use for some of the populations of drosophilids in the Smoky Mountains were plotted with respect to average mushroom duration (figure 12.1). Across the *x*-axis are located the more commonly used host genera at positions indicating their mean durations from the second column of table 12.3. While I have no duration data on the polypore fungi, I guessed that the fleshier Polyporaceae last on the order of one month and so placed the polypores at thirty days' duration in the figure. Some polypores last much longer, even years, but few would be as ephemeral as any of the Agaricales or Boletaceae. The heights of the bars in the figure indicate the percentage of each species (from table 12.1) found on host genera with the indicated durations.

Thus, figure 12.1 illustrates the variation among fly species in the nature of the hosts they exploit. Some are found on long-lasting polypores which fruit year after year at the same locations and so are

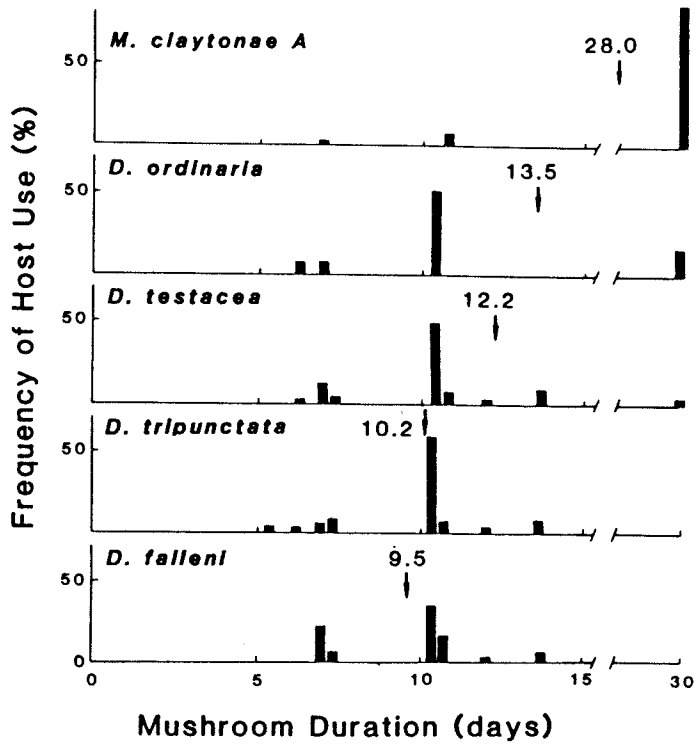

Figure 12.1. Distributions of host utilization by some mycophagous Drosophilidae in the Great Smoky Mountains, Tennessee. The location of each bar along the *x*-axis indicates the mean duration of caps of a host mushroom genus (from table 12.3). The height of each bar shows the percentage of flies collected from that genus (from table 12.1). The mean of the host distribution for each fly species is indicated by an arrow.

quite stable and predictable trophic resources. Other flies use a variety of short-lived and presumably unpredictable agarics and boletes. Even *Coprinus* can be an oviposition site, although later stages of larval development must take place in the soil moistened by deliquesced mushroom remains. Not so obvious from the figure is the finding that the drosophilids which feed on more predictable mushrooms tend to be trophic resource specialists, while those using unpredictable mushrooms are much broader generalists with respect to the diversity of mushroom species consumed. This trend is shown in figure 12.2 for all ten species of mycophagous drosophilids in the Smokies and in Ithaca. The diversity of host species used by each fly species was measured by the Shannon Diversity Index (Shannon and Weaver 1949):

$$H' = -\sum p_i \log_e p_i.$$

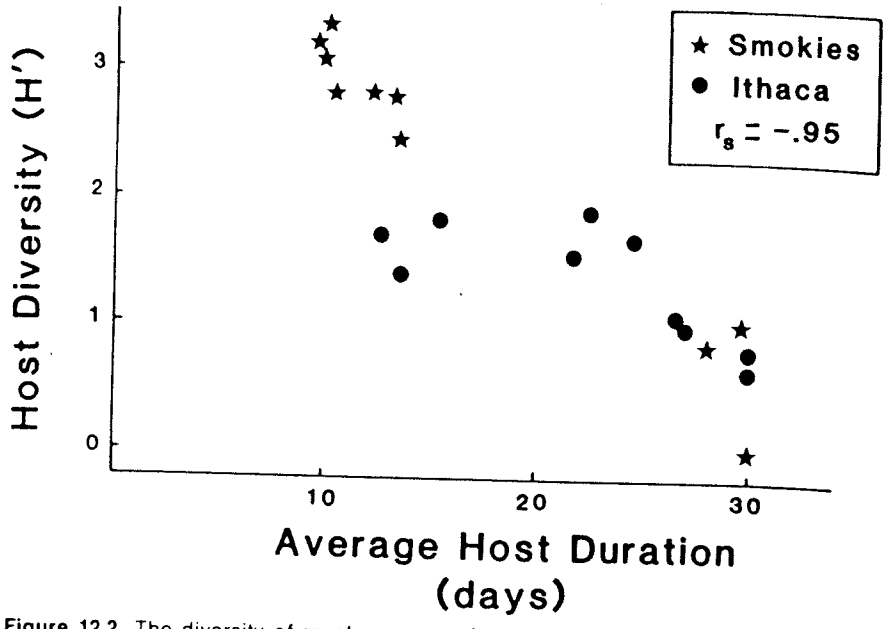

Figure 12.2. The diversity of mushroom species used as hosts, as measured by the Shannon Diversity Index, plotted against the mean durations of the hosts utilized by each of 10 species of mycophagous Drosophilidae sampled in the Great Smoky Mountains, Tennessee, and in Ithaca, New York. The Spearman rank correlation (r_s) was calculated from the combined data set of 20 points, and is significant at $P < 0.001$.

in which p_i is the proportion of flies collected from mushroom species i. This host diversity is plotted against the mean duration of the host mushrooms used by each fly population (calculated as in fig. 12.1). The negative association between host duration and host diversity is highly significant (Spearman rank correlation, $r = -.95$, $P < .001$). Similar correlations are obtained for the data on Ithaca populations and on the Smoky Mountains populations when they are analyzed separately. In summary, I found that predictable fungal resources allow some Drosophilidae species to be host specialists. Other species are generalists, feeding on unpredictable resources and perhaps thereby avoiding strong competition with the polypore specialists.

Genetic Responses to Mycophagy

As the unpredictability of fungal trophic resources forces the inclusion of a wide diversity of mushrooms in the diets of some insects, this diversity in turn can affect the genetic structure of mycophagous

populations. Organisms whose populations inhabit a range of environments, and exploit a variety of resources, will be subjected to selective forces that vary both temporally and spatially. Each larva of the fungus-feeding drosophilids is restricted to the relatively homogeneous microhabitat of a single mushroom cap, and yet other larvae perhaps only meters away, or of subsequent generations, may find themselves tunneling through very different fungal media. Many theoretical treatments, first by Ludwig (1950) and then by Levene (1953), Dempster (1955), Haldane and Jayakar (1963), and others have shown that such temporal and spatial variation in selection can maintain genetic polymorphisms that could not be preserved in a constant selection regime. Extending this concept of "multiple niche polymorphism," DaCunha, Burla, and Dobzhansky (DaCunha et al. 1950; Dobzhansky et al. 1950; DaCunha and Dobzhansky 1954), and later Van Valen (1965), developed the "niche-variation hypothesis," asserting that broad-niched species (those using a variety of resources) would be more variable both genetically and morphologically than would populations of more specialized, or narrow-niched, species.

Ever since the selectionist-neutralist controversy was triggered by the discoveries of surprisingly high levels of genetic variation in natural populations (Kimura and Ohta 1971; Nei 1975; Lewontin 1974), the niche-variation hypothesis has been the focus of much debate. Levels of genetic variation measured by techniques such as electrophoresis might correlate with habitat heterogeneity if the variation we observe is subject to, and maintained by, natural selection (the "selectionist" viewpoint). However, if many genetic alleles are effectively neutral (equal in their phenotypic effects and selective advantages), then only the balance between mutation and random genetic drift would affect genetic polymorphisms (the "neutralist" viewpoint). Assuming that mutation rates are relatively constant among similar species, effective breeding population sizes would be the only direct correlate of genetic variation if the neutralist school is correct.

The mycophagous Drosophilidae, ranging from generalists to extreme specialists, offer an ideal opportunity to test the niche-variation and the neutralist hypotheses. As explained above, the niche breadth of these drosophilid species can be assessed by the Shannon Index of the diversity of mushroom species used as hosts by the larvae and adult flies. Genetic variation has been measured by horizontal starch gel electrophoresis, on which I can resolve enzyme variation (or lack of variation) at from twelve to twenty-eight genetic loci in the fly populations (Lacy 1982a, 1982b). For each locus genetic diversity is quantified

by the same Shannon Index used for host diversity, but with p_i set equal to the frequency of each electrophoretically detectable allele (electromorph) in the population. Since some loci are characteristically variable or characteristically monomorphic across similar taxa (Johnson 1976; Selander 1976), between-species comparisons of genetic variation should be made only on sets of loci that are scored in both species. To compare genetic variation among any two fly species, therefore, I averaged the Shannon diversity measurements for each species across the loci for which both species were scored. Ordered pairings were determined from such two-species comparisons and then combined to form a single ranking of species from the most polymorphic to the least. The niche-variation hypothesis was tested by calculating the Spearman rank correlation between this ranking of genetic variation and the ranks of host diversity.

To test the prediction of the neutralist theory, ideally one would first determine the effective breeding population sizes. Unfortunately, the necessary parameters of migration, population fluctuations, and variance in reproductive success are difficult, if not impossible, to measure. The abundances of the species of mycophagous drosophilids vary over several orders of magnitude (see tables 12.1 and 12.2), however, and vast differences in migration rates or other parameters would therefore be necessary for the abundances to be unrepresentative of effective population sizes. I therefore estimate relative population sizes by the proportion of each fly species in my collections.

Figure 12.3 shows the relationships among host diversity, genetic variation, and abundance of the mycophagous flies. There is a significant rank correlation between the diversity of host mushroom species and the amount of genetic variation in the Smoky Mountains populations, as is predicted by the niche-variation hypothesis. Of almost equal magnitude, however, is the correlation between abundance and genetic variation expected if stochastic variation in gene frequencies, and not selection, determines the amount of genetic polymorphism. In the Smoky Mountains populations, the generalist species of flies are more abundant than are the specialists which feed on uncommon polypore fungi, resulting in a significant correlation between host diversity and abundance as well. Unfortunately, these associations among all three factors (host diversity, genetic variation, and abundance) confound any attempt at a conclusive test of either the niche-variation or the neutralist hypothesis. A strict selectionist can argue that the host diversity–genetic variation correlation reflects the role of heterogeneous host use in the maintenance of variation, while the abundance–genetic variation correlation could be a secondary one due only to the fact that abundances are correlated with host diversities. A neutralist, on the other hand, can argue the opposite cause-effect relationships: The abundance–genetic variation association may be the relevant one, while the correlation of host diversity with genetic variation could be indirect, via the correlation of abundance and host diversity. Since there are no nonparametric methods for separating independent effects among multiple correlations, neither of these alternative explanations can be discounted in this case.

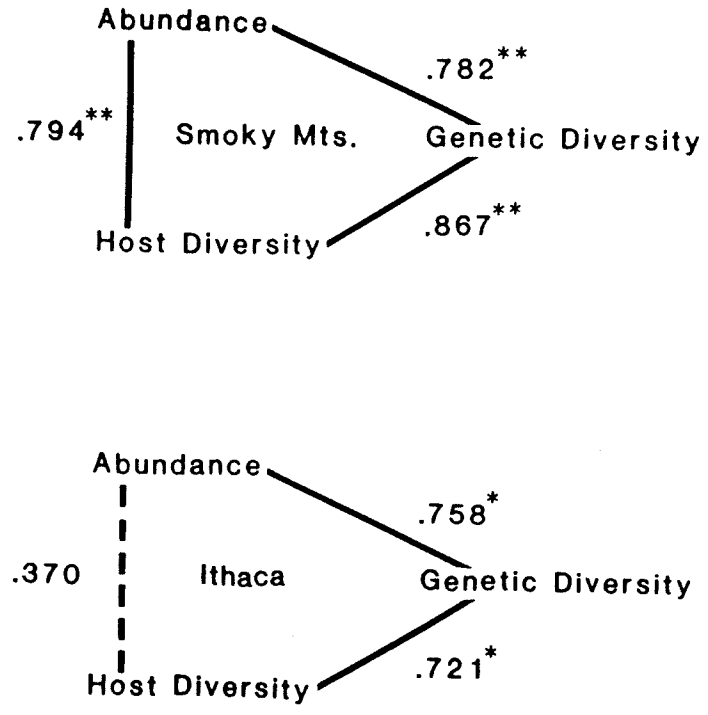

Figure 12.3. Associations between abundance, genetic diversity, and the diversity of host mushroom species among mycophagous Drosophilidae in the Great Smoky Mountains, Tennessee, and in Ithaca, New York. Values shown are Spearman rank correlations, with two, one, and no asterisks indicating statistical significance levels of $P < .01$, $P < .05$, and $P > .05$, respectively.

In Ithaca, however, there are some rare generalist fly species (*D. tripunctata, D. recens*), and so we find no association between abundance and host diversity. Yet, as in the Smoky Mountains populations, both host diversity and abundance correlate strongly with genetic variation. Lacking possible indirect explanations for either significant association, we must conclude that the diversities of host mushrooms exploited, and

the population sizes, separately affect the levels of genetic variation in these species. It would seem, then, that natural selection can maintain high levels of genetic variation by favoring alternative genetic alleles on different mushroom hosts or in different microhabitats, but that some of this variation may be lost in small populations due to stochastic genetic drift (Lacy 1982b).

Summary

Since they inhabit diverse but discrete microhabitats, the mycophagous insects present us with a fertile testing ground for theories concerning the effects of resource distribution on foraging patterns and the nature of genetic variation. The mycophagous drosophilid flies in eastern North America display a range of ecological and genetic responses to their fungal trophic resources. Some specialize on the very long lasting, predictable bracket fungi. Populations of these species have less genetic variability than do most drosophilids. Other species are broad generalists, nonselectively consuming a diverse array of basidiomycete mushrooms, including many very ephemeral, unpredictable host fungi not inhabited by the specialists. The heterogeneous niches of the generalist species seem to maintain high levels of polymorphism, though there is evidence that variation in the rarer of these species may be decreased by genetic drift. Many other groups of organisms need to be studied, however, before we can generalize about the relationships among host predictability, host diversity, and genetic variation found in the mycophagous Drosophilidae.

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