Specialization: Species Property or Local Phenomenon?

L. R. Fox and P. A. Morrow

Summary. Many herbivorous insects have generalized diets over the species' entire geographical ranges but they function as specialists with restricted diets in local communities. Local feeding specialization can be produced by biochemical, behavioral, ecological, and evolutionary processes. Much evidence is incompatible with the widely held assumptions that diet breadth is a species characteristic and that specialization among herbivorous insects implies greater efficiency and less niche overlap.

Concepts of "specialization" and "generalization," which underlie many theories of ecology and evolution, have been applied to a broad array of processes at different biological levels (such as phenotypic characters of individuals, ecological properties of populations or species, adaptations associated with major phylogenetic radiations). The terminology itself is often extremely useful and even difficult to avoid, but the concepts and their assumptions are not necessarily identical in all the various usages.

In this article we emphasize mechanisms affecting ecological specializations at the population level and evaluate the concepts of specialization and generalization in the light of accumulating evidence from natural systems. We test some widely held assumptions about specialists by analyzing patterns of resource use in populations of herbivorous insects and discuss ways in which ecological specialization may arise. We conclude that there are many different mechanisms leading to dietary specializations and that, within overall phylogenetic constraints, specialization is often a flexible attribute of a population that is responding to features of its particular community, rather than an attribute of a species throughout its geographical range.

It is frequently assumed both that individuals from specialized species are more efficient (for example, metabolically, behaviorally) than individuals from generalized species and that these properties are possessed by species throughout their entire geographical ranges. These assumptions have the important corollary that specialists are more effective competitors than generalists, and hence they lead to predictions about patterns of resource use and competitive exclusion among species in a community. Slobodkin and Sanders (*1*) state, for instance, that a specialist exploits its particular environment better than do closely related generalists, and MacArthur (*2*) says that greater efficiency and the consequent division of labor is the "ultimate reason we have so many species." More recent work continues to assume greater efficiency and competitive ability of specialists (*3*).

These assumptions have been applied to herbivorous insects because of the high degree of chemical distinctiveness of many plant species used as food (*4–6*). The argument is that herbivores feeding on a variety of plants must be able to tolerate, detoxify, or possibly metabolize an array of qualitatively different chemicals that have potentially deleterious effects. Maintaining the metabolic machinery for dealing with such an array may involve biochemical and physiological costs that reduce the efficiency with which a generalized herbivore can process its food. Therefore, analysis of mechanisms affecting specialization and efficiency of food use by herbivorous insects provides a strong test of the assumed correlation between these characteristics. In a broader context, consideration of specialization as a local phenomenon affects the framing of questions about interactions between herbivores and their food. This applies to both ecological and evolutionary processes and their interpretations in terms of community organization and structure.

Definitions

Specialists and generalists intergrade in a continuum of patterns of resource use, and this is reflected in the diverse definitions of various authors. Specialization may mean simply that a species uses a relatively narrower portion of a resource spectrum than a generalist (*7*); Maynard-Smith (*8*) suggests that specialists use only one or "a few" resources, while Rosenzweig (*9*) distinguishes between specialists and "extreme" specialists. Kogan (*10*), Slansky (*11*), and Futuyma (*12*) define species of herbivorous insects as specialists if they consume plants within one species, one genus, or one family, respectively. These diverse and frequently vague definitions raise conceptual and methodological problems. Clear, consistent distinctions between the two groups are required to test predictions about the properties of generalists and specialists or about their roles in community dynamics.

We were forced to deal with definitions of specialization when we began comparing data that each of us had collected on phytophagous insects on *Eucalyptus*, the dominant genus of trees in Australia (*13*). On a continental scale the insects might be called specialists because they eat plants only within one genus. On the smaller scale of their geographical ranges, many species could be considered generalists because they feed on numerous eucalypt species (*14–17*). But when a local community is considered, many of these same species could be regarded as specialists because they feed only on a subset of the eucalypts available at that site (Table 1 and Fig. 1) (*18*). Thus, geographical scale as well as taxonomic level is important in identifying the degree of specialization and for making inferences about ecological properties of individuals, populations, or species.

Much of our recent work dealt with the question of whether herbivores selected among species of eucalypts locally and whether they functioned as specialists within each community. The definition of specialization that we use stresses the number of plant species that a herbivorous species eats locally. We define as local specialists herbivorous species that, over their entire geographical ranges, are generalized in the sense of

---

L. R. Fox is assistant professor of biology in the Biology Board of Studies, University of California, Santa Cruz 95064. P. A. Morrow is an associate professor of biology in the Department of Ecology and Behavorial Biology, University of Minnesota, Minneapolis 55455.

0036-8075/81/0227-0887$01.75/0

Table 1. Distribution of herbivorous insects among three species of codominant *Eucalyptus* in the Snowy Mountains, New South Wales (*22*), expressed as percentage of insect species and percentage of insect individuals in each category. Two operational definitions of "specialists" are (i) ≥ 90 percent of individuals on one host species, which includes the most extreme possible definition of (ii) 100 percent of individuals on one host. The latter group consists mainly of rare species. Both definitions are presented in this table. While neither the geographic nor host ranges of most of these insects are known, available data suggest that many common insects at this site utilize other *Eucalyptus* spp. elsewhere. "Generalists" were defined as those species roughly randomly distributed among the three potential hosts (≤ 70 percent of individuals on one host with no obvious preferences among the other *Eucalyptus*). Half of the trees present were *E. pauciflora*, with approximately 25 percent in each of the other species. Only those herbivorous species encountered at least four times during the survey are included. An additional category, not included, are those herbivores with relatively large populations on two hosts: these represented 35 percent of the species and 47 percent of the individuals collected. Note that *E. stellulata* is used by more "local specialists" than the other *Eucalyptus*.

Species of host plant	Insect species (No.)	Percent of species that are			Insects collected (No.)	Percent of individuals in species that are		
		Local specialists		Local generalists		Local specialists		Local generalists
		≥ 90 percent	100 percent			≥ 90* percent	100 percent	
E. pauciflora	41	15	10	27	1057	8	3	21
E. perriniana	31	32	19	35	1044	48	8	10
E. stellulata	49	51	29	22	1701	50	8	10
Total number	80	41	24	11	3802	1429	253	490
Percent of total		51	30	14		38	7	13

*Does not include the few individuals on other *Eucalyptus* spp.

feeding on a variety of plant species, but which have much more restricted diets within particular communities. Our objective is not to define a new category of specialists but to emphasize the importance of scale. Indeed, it is likely that local specialization is a common property of generalized herbivores. Other concepts such as "choosey generalists" (*19*) and "ecological monophages" (*20, 21*) are similar to local specialists but do not emphasize how herbivores function in communities.

Local Specialization

For any population, factors leading to "local specialization" (Table 2) need not be mutually exclusive, and interactions between factors are quite likely. Further, separate populations of a herbivorous species may be "local specialists" for very different reasons.

It is often difficult to tell from the available descriptions which mechanisms influence selection of host plants in a particular situation, either because all possible alternative mechanisms are not examined or because data are not presented in ways that allow mechanisms to be recognized (for example, potential host plants that are rare or not used locally are not mentioned). Local specialization can most easily be detected by observations of variation in spatial or temporal patterns in the use of host plants. However, recognition of these patterns of local variation usually depends on extensive knowledge of the herbivore's diet in other parts of the species' range, and in different seasons.

Restricted Number of Usable Plants

Spatial variation. A list of host plants compiled for an insect species over its geographical range may be long, but locally only one or a few host species may be present. For example, the lycaenid butterfly *Plebejus icarioides* occurs broadly over the region west of the Great Plains of North America, while the geographical ranges of most of its 28 host lupines are much smaller (*22*). Similar patterns are found for some of the chrysomelid beetles and sawflies eating *Eucalyptus* in Australia (*14, 16, 18*), *Heliconius* butterflies feeding on *Passiflora* species (*20, 23*), and bruchid beetles using legumes in Central America (*24, 25*), aphids feeding on goldenrods (*Solidago*) in Canada (*26*), and potato beetles on solanaceous plants in North and Central America (*27*).

Even in one geographical area, a herbivore may occur in more habitats than any particular food plant species and so, within any one habitat, may be more specialized than a list of all potential food plants in the area would indicate. For instance, in Guanacaste Province, Costa Rica, one bruchid beetle species uses one legume on ocean dunes and another in freshwater marshes (*25*).

Temporal variation. At any site, relative food availability may change seasonally because plants develop at different rates; hemipterans, such as *Lygaeus equestris* and some mirids (*28*), feed on a variety of host plants each year, but only on one or a few species at a time since the plants are not all available simultaneously. In addition, population dynamics and phenology of the herbivores often varies among sites because of local patterns of plant availability. A good example is oviposition in the checkerspot butterfly *Euphydryas editha*. The quality of host plants varies among sites during the flight season. At one site more eggs were laid on *Orthocarpus densifloras*, which had younger tissue, than on senescing plants of *Plantago erecta*; at a nearby site, females avoided the flowering *Orthocarpus* and laid 98 percent of their eggs on *Plantago*. Larvae could complete development successfully on either host (*29–31*).

Temporal variation in host plant availability is sometimes caused by the herbivores themselves. Very polyphagous species, such as the gypsy moth and some grasshoppers and locusts (*32*), have distinct food plant preferences but may feed on less preferred plants after they destroy primary host species. *Locusta migratoria*, for instance, has distinct preferences among grasses and strongly prefers grasses to dicots, but eats dicots in nature after consuming the available grasses (*33*).

Local availability also may change over longer time spans, due to succession, introduction and extinction of species, variation in relative abundance between years, and human interference. Data on altered food habits after intentional or accidental introduction of plants indicate how food usage can be modified when new usable species become available. Native insects use introduced plants such as cacao and sugarcane in tropical areas, *Pinus radiata* and *Hypericum perforatum* in Australia, and *Eucalyptus* in Costa Rica and Brazil (*20, 34*). If such rapid changes in host plant use follow human interference, presumably similar changes can occur under natural conditions.

Restricted Use of Several Potential Host Species

In contrast to the previous examples, several potential host plant species may be available simultaneously within a community, yet the herbivores do not eat them all. Proximal mechanisms of insect choice, such as the secondary chemistry or nutrient content of individual plants, have been extensively described (*35*). However, responses of individual insects may be greatly modified by characteristics of the community such as the relative and absolute densities of host and nonhost plants, the dispersal patterns of the insects, the presence of other herbivores, or the effects of abiotic factors (*36*–*38*). Use of particular plant species may differ even among communities with identical lists of potential hosts. In this section we discuss ways that diets vary, whether the insects' preferences are fixed so that flexibility in food choice is eliminated, or whether preferences depend on properties of the local community.

Fixed preferences. If inherent preferences for food depend solely on characteristics of host plant species and are not modified in the context of local communities, then there should be a consistent rank order of choices made among plants in different local communities, provided that there is no local genetic differentiation of the herbivores or geographical variation in host plant traits. Such a mechanism of host selection might be recognized if one plant species is used whenever it is available, while another is used only in the absence of other acceptable hosts. Examples of inflexible preference may be the butterflies *Plebejus icarioides* and *Glaucopsyche lygdamus*, which deposit eggs on lupines depending on the relative density of pubescence; *Plebejus* selects the most pubescent of the locally available lupine species, whereas *Glaucopsyche* selects the least pubescent lupines (*22*, *39*). In cases such as these, the characteristics of the rest of the community can be ignored.

Changing preferences. We found many examples where the preference ranking of different food species changed locally, and depended on the local population or community context. Some general sources of variation in food plant selection (Table 2) are as follows.

1) Behavioral patterns of herbivores may explain modifications of host plant use. One commonly suggested behavioral pattern called the "Hopkins Host-Selection Principle," proposes that females preferentially lay eggs on the plant species on which they themselves developed (*40*, *41*). We found no clear examples to support this hypothesis; on the contrary, experiments showed that adult beetles of *Leptinotarsa decemlineata* and *Chrysophtharta m-fuscum*, and adult butterflies of *Papilio machaon* and *Euphydryas editha* are not influenced by larval food (*17*, *29*, *42*). However, some lepidopteran larvae select food species which they ate during earlier instars (*43*–*46*).

2) Selection of a host plant may have a strong genetic basis controlled by only one locus or polygenic region, so that shifts in preferences for particular host plants can be very rapid. This has been shown for *Rhagoletis pomonella*, a tephritid fruit fly whose feeding patterns have altered to include introduced apples and cherries (*47*, *48*). Populations on these new host plants appear to be "sibling species" that do not interbreed with the parent population and now have morphological differences that distinguish them from forms on the original host plants. These changes occurred within one or a few generations and seem irreversible, reflecting intense natural selection for different demographic characteristics and patterns of oviposition associated with temporal differences in fruiting between the original and new host plants (*48*). Local populations of *Euphydryas editha* show different oviposition preferences in the field, apparently as adaptations to local patterns of predation and of relative abundances, quality, morphology, and phenology of the plants (*29*, *49*).

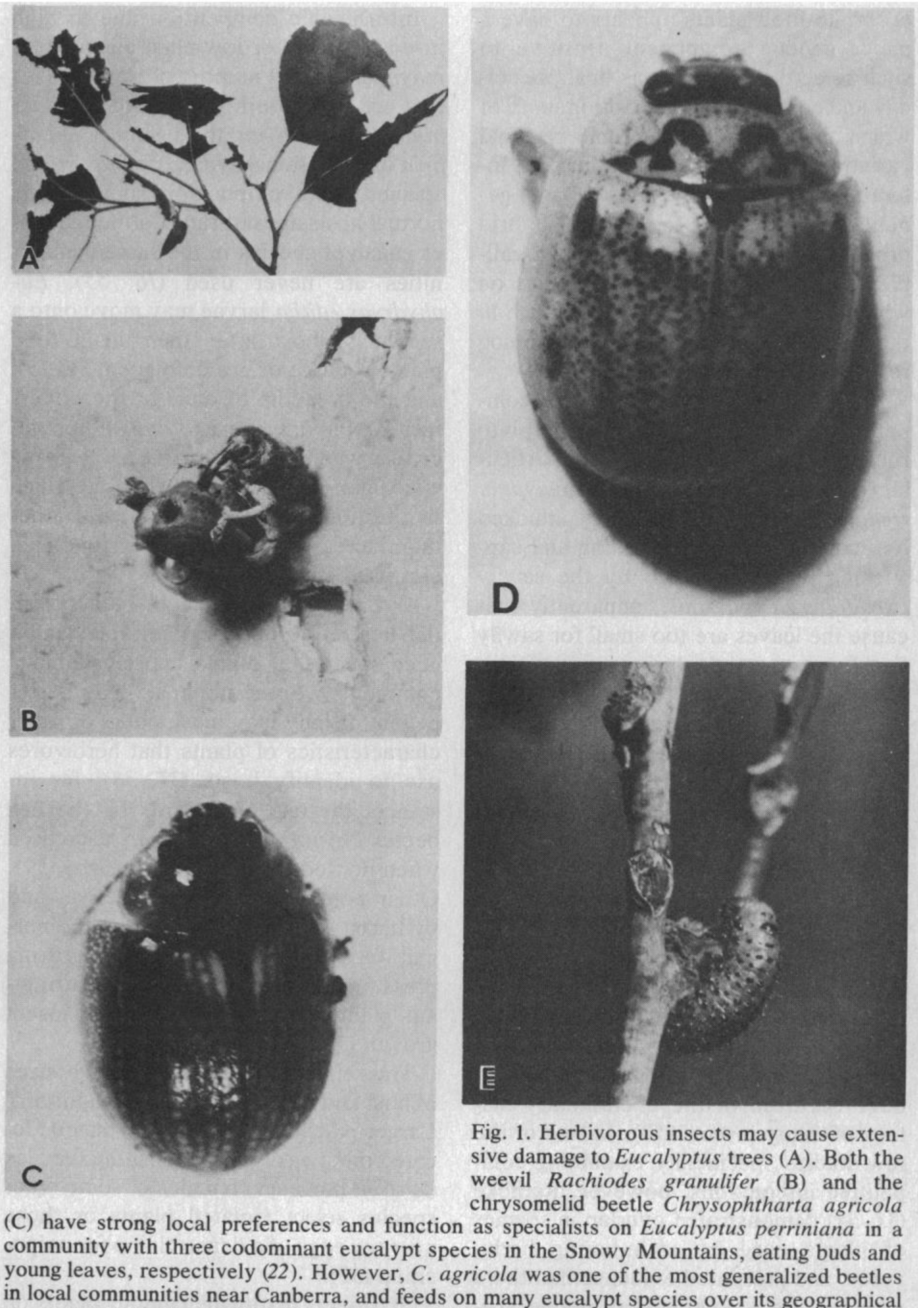

Fig. 1. Herbivorous insects may cause extensive damage to *Eucalyptus* trees (A). Both the weevil *Rachiodes granulifer* (B) and the chrysomelid beetle *Chrysophtharta agricola* (C) have strong local preferences and function as specialists on *Eucalyptus perriniana* in a community with three codominant eucalypt species in the Snowy Mountains, eating buds and young leaves, respectively (*22*). However, *C. agricola* was one of the most generalized beetles in local communities near Canberra, and feeds on many eucalypt species over its geographical range (*18*, *21*). *Chrysophtharta m-fuscum* (D) uses relatively few eucalypts both locally and throughout its range, concentrating on species with a particular leaf morphology (*21*). For many beetles, most damage is done by larvae, such as the unidentified chrysomelid (E) feeding on leaves and buds of *E. pauciflora*.

In laboratory experiments, females from different populations preferentially laid eggs on the main host plant used for oviposition where they were collected, reflecting microevolutionary differentiation among populations (*29*).

Differences in the abilities of local populations to use particular food plants also may be genetically based. In Australia, larvae of the butterfly *Papilio demoleus* from New South Wales develop successfully on *Citrus*, whereas the same plants are toxic to larvae from populations in Queensland (*50*). Hsiao also has recently demonstrated differentiation in populations of potato beetles (*27*).

In some systems, then, choice of appropriate food plants appears to have a major genetic component sensitive to such selective pressures as host phenology and community composition, both of which may have considerable regional variation. In addition, there may be interactions between behavioral and genetic responses to food since hybrid progeny of monophagous tephritid gallflies oviposited on the plant species on which they had been reared, although in the following generation the conditioning response was much weaker (*47*).

3) Direct or indirect effects of competitive interactions with other herbivorous insects may alter the use of particular food plants. For example, *Euclayptus stellulata* is normally severely attacked by many species of leaf-eating and sap-sucking insects but not by the sawfly *Pseudoperga guerinii*, apparently because the leaves are too small for sawfly females to grasp during oviposition. However, when competition by other insects was reduced by applying a contact insecticide, the leaf size of *E. stellulata* increased (possibly because the numerous phloem feeders no longer interfered with leaf development), and *P. guerinii* readily oviposited on them (*51*). *Pseudoperaga guerinii* normally oviposited on young leaves of *E. pauciflora* that are 17.5 ± 4.4 (± standard deviation) millimeters wide (Fig. 2) (*51*). Changes in the use of host plant species due to interspecific interactions have seldom been studied intensively, but are assumed to have occurred in the evolutionary history of many insects (*52*). In one of the few studies specifically examining competitive interactions, however, Rathcke (*53, 54*) demonstrated overlap in species of plants used by stem-boring herbivores, and presented evidence that there was no direct competition among species; the one instance of competition was by aggression, rather than exploitation of the same food.

Table 2. Factors influencing "local specialization" of herbivorous insects.

- *Number of usable plants restricted locally*
  - In space
  - In time
- *Several potentially acceptable plants available; herbivores do not use all of them*
  - Preferences fixed
  - Preferences change locally
    - Herbivore behavior
    - Genetic variation among herbivores
    - Competition among herbivores—interspecific or intraspecific
    - Changes in abundances of host and nonhost plants
    - Changes in plant quality—phenotypic or genotypic (or both)
    - Others

Intraspecific competition due to high insect densities or low plant abundances may increase the number of plant species that are used. Both the psyllid *Cardiaspina albitextura* and the sawfly *Perga affinis* use additional sympatric *Eucalyptus* species when oviposition sites on the normal hosts are saturated, although other eucalypt species in the same communities are never used (*16, 55*). *Euphydryas editha* larvae may move onto a secondary host after their main food plants senesce or are defoliated (*30, 56*), and the breadths of diets of the butterflies *Papilio indra* and *P. rudkini* both increase when food is scarce (*57*). However, many insect species migrate when oviposition sites are saturated, rather than increasing the number of food species used locally (*31, 58*).

4) The co-occurrence of both potential host and nonhost plants may influence species of plants chosen within a community. Some nonhosts may be repellent or they may mask odors or other characteristics of plants that herbivores use to identify hosts (*37, 38*); for instance, the use of collards by the flea beetle *Phyllotreta cruciferae* decreased when nonfood species grew nearby (*59*). Other nonhosts may be attractive, and by luring herbivores away from the normal food species may reduce grazing pressures on the host plants; the attractant plants often do not support insect growth (*37*).

The relative densities and patch sizes of host and nonhost plants are important. Larger patches of food plants may be located more easily by ovipositing females (*59–61*); however, females of some other species select isolated plants or those near the edge of a dense clump for oviposition (*62*).

5) Insects distinguish among plants on the basis of qualitative differences in traits such as secondary chemistry, phenology, nutritional and morphological features (for example, plant size or leaf shape), as well as site conditions such as temperature, humidity, and shade. Damaged or diseased trees are more attractive to pine bark beetles than are healthy trees (*63*), while eruptions of psyllids on eucalypts and spruce budworm on spruce may in part be responses to changes in leaf amino acids in drought-stressed or old leaves, respectively (*64*). Recently, Edmonds and Alstad (*65*) presented data suggesting rapid selection for demes of scale insects on individual pine trees, probably in response to differences in terpenoid chemistry.

6) Several other factors have been shown to influence usage of host species, but to date have received less attention than those mentioned above. This does not mean that they will be less important in determining local specialization. For example, the presence of nonherbivorous animals—predators, parasitoids, mutualistic species—may determine not only abundance but also species of host used. Predators may occur only on certain plant species [possibly because of attraction to plants with extrafloral nectaries (*66*)], or on plants growing in a restricted portion of the habitat, such as ants on *Pedicularis* in the shade (*29*). Ants also may transfer eggs or larvae from one plant species to another and increase the numbers of host species used by larvae (*22, 23, 67*).

Finally, diet breadth may be related to predictability of abundances or distributions of potential hosts, often reflecting differences in climatic predictability. Several species of butterflies, grasshoppers, and *Drosophila*, for instance, use fewer hosts in more predictable habitats (*54, 68*), which agrees with some common predictions of foraging theory (*1, 69, 70*). However, acridid grasshoppers living on spatially unpredictable plants in a tropical rain forest were very specialized (*71*).

Discussion

Community implications. Over their entire geographical ranges some herbivorous insect species include more host taxa in their diets than others. Herbivorous species restricted to a single host plant species [true monophages (*72–74*)] are found in all major groups (*75, 76*), but the majority of species studied do not have such restricted diets (*4, 5, 10–12, 34, 73*). The evidence presented in this article shows that, for many species, the observed breadth of diet is not a consistent property of the species over its whole

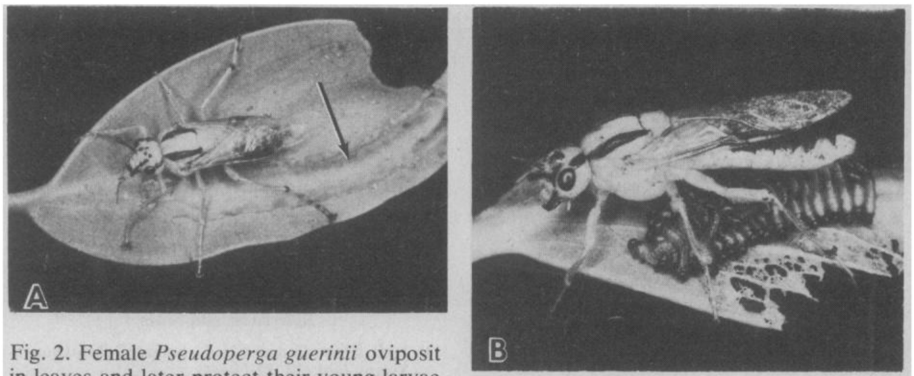

Fig. 2. Female *Pseudoperga guerinii* oviposit in leaves and later protect their young larvae from predators. Leaf width is critical for oviposition because females grasp leaf margins as they lay eggs (*20*). (A) The female is positioned above a completed egg pod (see arrow); (B) defensive posture of a female over young larvae.

range, but instead local restrictions on resource use may be caused by a variety of ecological, chemical, morphological, or genetic factors acting in the context of local communities. Consequently, an individual's proximal physiological responses to plant characteristics are not sufficient to predict resource use in the field.

Discussions of chemical coevolution between plants and herbivores have emphasized the usefulness of defining specialization in terms of higher taxonomic categories (usually families) that an insect species uses over its entire geographical range, since taxonomic affinity can be a good predictor of general patterns of host use (*3, 4, 10–12, 77*). However, knowledge of the numbers of species, genera, or families of plants used by a herbivorous species as a whole may provide little information about local use of food or effects of the herbivore on the plant community. The ecological effects of a herbivore eating a number of plant species from several families may be no different, in terms of community dynamics, from the effects of a species eating the same number of closely related plants. The species of host plants respond independently to grazing pressures because they belong to different, noninterbreeding gene pools. The degree of relatedness between the plants does not influence the dynamics of the outcome per se.

Population dynamics of strictly monophagous species and of those herbivores that are locally monophagous because only one potential host species is available are very sensitive to changes in the abundance of their food plants. The dynamics of local specialists that have the opportunity to consume more than one type of host will be more buffered: for example, herbivores could switch to other potential food species if their preferred items become scarce. Depending on the competitive interactions among the hosts and the impact of grazing on the plants' fitnesses, feeding patterns could influence community diversity. Community consequences of feeding preferences among herbivorous insects, such as changes in plant species composition, have been demonstrated in such natural communities as subalpine *Eucalyptus* forests (*78*), and by the introduction of herbivores for biological control of weeds (*79*): analogous consequences have been dealt with extensively in studies of predator-prey interactions (*80*).

Feeding efficiency. Since there are many reasons for restriction of diet, we question the assumption that the major evolutionary reason for the existence of specialization among herbivores is an increase in feeding efficiency (*4, 6, 41, 81, 82*). For herbivores, efficiency often refers to an animal's ability to digest and assimilate food. Species that feed on taxonomically diverse host plants (family generalists) encounter a broader range of defensive compounds than those feeding within one family (family specialists) since related plants typically contain similar chemicals (*4, 6, 83*). It is commonly assumed that a herbivore must commit more of its resources for tolerance or detoxification if it encounters a variety of very different defensive compounds, so that herbivores using diverse arrays, or greater numbers, of host species are relatively less efficient at converting plant biomass to animal tissue than are herbivorous species using smaller arrays (*4, 12, 61, 77*).

These predictions have been tested by comparing related herbivorous species feeding on different numbers of related plants. However, the predictions are not supported by the data, which show no consistent differences in efficiency (*44, 84, 85*). The predictions have also been tested for herbivore species feeding on different numbers of plant families, and initially were supported by evidence that lepidopterous larvae of species which feed on many plant families have higher levels of general-purpose detoxification enzymes in their midguts than larvae of species feeding only on one family (*82*). However, larvae of the armyworm *Spodoptera eridania*, a species using plants from many families, grew as well as larvae of the more specialized cabbage butterfly *Pieris rapae* (restricted to crucifers), when they were both fed leaves with concentrations of sinigrin typically found in crucifers (*45*). This result is consistent with the observation that detoxification enzymes are inducible and dose-dependent (*86*). Auerbach and Strong (*87*) found that beetles restricted to *Heliconia* species were more efficient at digesting their food than polyphagous lepidopterans feeding on the same plants, but a recent survey of a large number of lepidopteran species demonstrated no consistent differences in digestive efficiency between family specialists and family generalists, even those feeding on plants containing compounds that reduce digestibility (*85*). Thus, to the extent that unrelated species can be validly compared (*88*), these studies show that reduced breadth of diet is not necessarily correlated with increased efficiency of feeding.

Other data comparing feeding of herbivores on a variety of plants also do not support the hypothesis that efficiency of resource use is inversely related to the variety of defenses encountered. On the contrary, differences in feeding and growth of the insects seem to depend more on the nutritional value of the plants, especially water and nitrogen contents, than on the taxonomic range of plants used by the herbivore (*46, 85, 89*). Thus, while different species of herbivorous insects may show differences in metabolic efficiency, this need not be linked to the range of food plants that is used. This does not imply that individuals within a species have equal feeding efficiencies on all their food plants [there is much evidence to the contrary (*85, 90*)], but only that the length of a species' host list is not a good predictor of its efficiency on acceptable plants.

Conclusions

The ecological factors affecting the use of different numbers of host plant species are presumably also important in the evolution of these traits. We have discussed several in this article. Additional mechanisms exist. As examples, chance local events may eliminate genetic information necessary for recognition or use of host plants, and selection for escape from predators through mimicry or crypsis may reduce the variety of host species that is used. Most of these mechanisms require no assumptions about efficiency or competitive ability.

Because of the diversity of mechanisms leading to different patterns of host use in local communities, there is no a priori reason to predict that specialists will have greater efficiencies or competitive advantages. This is supported by detailed studies testing for differences in metabolic efficiency among herbivores feeding on varying numbers of species (or even families) of plants. Nor does the corollary necessarily follow that species with more restricted diets will have safer niches with less overlap by other species, while those using a greater variety of host plants are exposed to more competitors (*91*). At least among herbivorous insects, species using radically different numbers of plant species may be found feeding and ovipositing on the same plants—for example, on *Eucalyptus* spp., ragweed, Klamath weed, and bracken fern (*17, 18, 34, 73, 74*). In fact, among the most extremely host restricted group of herbivores yet described, 116 species of leaf miners shared 18 species of oak, often with several species of miners present on the same tree or same leaf (*92*); in another study of the distribution of lepidopterans within one forest, there was a larger proportion of local specialists on tree species with a higher faunal load (diversity and abundance) than on tree species supporting fewer herbivores (*76*).

The local context for specialization in the use of resources has important implications for understanding not only the evolution and dynamics of populations of herbivores and their host plants, but also the dynamics of the whole community. Recent ecological and evolutionary theories link arguments about efficiency and resource allocation of individuals to both optimal selection of resources and to the way species are packed into communities. However, the evidence for local specialization predicts that the outcome of competitive interactions and the ability of a species to invade or remain within a community are not necessarily related in any simple way to how individuals use their resources.

The extent to which these conclusions apply to other systems (*93*), to other phenotypic characteristics of organisms, and at other biological levels will depend on the context in each case. All arguments depending on a priori assumptions about the properties of specialists should be carefully examined to ensure that the usage of concepts of specialization at any ecological and evolutionary level is compatible with appropriate selective mechanisms operating within local populations.

References and Notes

1. L. B. Slobodkin and H. L. Sanders, *Brookhaven Symp. Biol.* **22**, 82 (1969).
2. R. H. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972), p. 61.
3. D. S. Wilson, *The Natural Selection of Populations and Communities* (Benjamin/Cummings, Menlo Park, Calif., 1980), p. 127.
4. P. Feeny, in *Coevolution of Animals and Plants*, L. E. Gilbert and P. H. Raven, Eds. (Univ. of Texas Press, Austin, 1975), p. 3.
5. P. R. Ehrlich and P. H. Raven, *Evolution* **18**, 586 (1964).
6. D. H. Janzen, in *Biochemical Aspects of Plant and Animal Coevolution*, J. B. Harborne, Ed. (Academic Press, New York, 1978), p. 163.
7. M. L. Cody, *Competition and the Structure of Bird Communities* (Princeton Univ. Press, Princeton, N.J., 1974).
8. J. Maynard-Smith, *Models in Ecology* (Cambridge Univ. Press, London, 1974).
9. M. L. Rosenzweig, in *Proceedings of the First International Congress of Ecology*, W. H. van Dobben and R. H. Lowe-McConnell, Eds. (The Hague, 1974), p. 401.
10. M. Kogan, *Proceedings of the 15th International Congress of Entomology* (1976), p. 211.
11. F. Slansky, *J. N.Y. Entomol. Soc.* **84**, 91 (1976).
12. D. J. Futuyma, *Am. Nat.* **110**, 285 (1976).
13. L. D. Pryor and L. A. S. Johnson, *A Classification of the Eucalypts* (Australian National Univ. Press, Canberra, 1971).
14. J. J. Burdon and G. A. Chilvers, *Aust. J. Bot.* **22**, 103 (1974).
15. P. B. Carne, *Aust. J. Zool.* **14**, 647 (1966); P. A. Morrow, in *The Role of Arthropods in Forest Ecosystems*, W. J. Mattson, Ed. (Springer, New York, 1977), p. 19.
16. P. B. Carne, *Aust. J. Zool.* **13**, 593 (1965).
17. L. R. Fox, in preparation.
18. P. A. Morrow, *Aust. J. Ecol.* **2**, 89 (1977).
19. J. L. Harper, *Brookhaven Symp. Biol.* **22**, 48 (1969).
20. L. E. Gilbert, in *Analysis of Ecological Systems*, D. J. Horn, R. D. Mitchell, G. R. Stairs, Eds. (Ohio State Univ. Press, Columbus, 1978), p. 117. Gilbert distinguishes between ecological monophagy and coevolved monophagy. Monophagy is too restrictive to use in all cases of local diet restriction, and ecological causes of local specialization may also be coevolved between herbivores and their hosts.
21. L. E. Gilbert and J. T. Smiley, in *Diversity of Insect Faunas*, L. A. Mound and N. Waloff, Eds. (Blackwell, Oxford, 1978), p. 89.
22. J. C. Downey, *Syst. Zool.* **11**, 150 (1962); ——— and D. B. Dunn, *Ecology* **45**, 172 (1964).
23. L. E. Gilbert and M. C. Singer, *Annu. Rev. Ecol. Syst.* **6**, 365 (1975).
24. D. H. Janzen, *ibid.* **2**, 465 (1971); *Ecology* **52**, 964 (1971); in *Taxonomy and Ecology*, V. H. Heywood, Ed. (Academic Press, London, 1973), p. 201; *Ecology of Plants in the Tropics* (Arnold, London, 1975).
25. D. H. Janzen, in *Evolutionary Strategies of Parasitic Insects and Mites*, P. W. Price, Ed. (Plenum, New York, 1975), p. 154.
26. E. C. Pielou, *Ecology* **55**, 1359 (1974).
27. T. H. Hsiao, *Entomol. Exp. Appl.* **24**, 437 (1978).
28. O. Kugelberg, *Entomol. Scand.* **5**, 49 (1974); C. Solbreck and O. Kugelberg, *ibid.* **3**, 189 (1972); C. W. D. Gibson, *Oecologia (Berlin)* **25**, 55 (1976).
29. M. C. Singer, *Evolution* **35**, 383 (1971). Recent breeding and choice experiments have demonstrated that Hopkins host selection is not involved in females' choices of plants for oviposition (M. C. Singer, personal communication).
30. M. C. Singer, *Science* **176**, 75 (1972).
31. L. E. Gilbert and M. C. Singer, *Am. Nat.* **107**, 58 (1973).
32. H. A. Bess, *Conn. Agric. Exp. Sta. New Haven Bull.* **646**, 1 (1961); ———, S. H. Spurr, E. W. Littlefield, *Harv. For. Bull.* **22**, 1 (1947); D. E. Leonard, *Annu. Rev. Entomol.* **19**, 197 (1974); E. A. Bernays, R. F. Chapman, J. Horsey, E. M. Leather, *Bull. Entomol. Res.* **64**, 413 (1974).
33. E. A. Bernays, R. F. Chapman, J. MacDonald, J. E. R. Slater, *Ecol. Entomol.* **1**, 223 (1976).
34. D. R. Strong, Jr., *Science* **185**, 1064 (1974); ———, E. D. McCoy, J. R. Rey, *Ecology* **58**, 167 (1977); K. M. Moore, *Proc. Linn. Soc. N.S.W.* **88**, 340 (1963); F. Wilson, *CSIRO Bull.* **1**, 169 (1943); D. R. Strong, Jr., *Annu. Rev. Entomol.* **24**, 89 (1979).
35. Reviewed in H. F. Van Emden, Ed., *Insect/Plant Relationships* (Blackwell, Oxford, 1972); J. B. Harborne, Ed., *Introduction to Ecological Biochemistry* (Academic Press, New York, 1977).
36. We discuss community characteristics affecting grazing at length in this article. General discussions and more references are in D. Pimentel, *Ann. Entomol. Soc. Am.* **54**, 61 (1961); R. B. Root, *Oecologia (Berlin)* **10**, 321 (1972).
37. P. R. Atsatt and D. J. O'Dowd, *Science* **193**, 24 (1976).
38. R. B. Root, *Ecol. Monogr.* **43**, 95 (1973).
39. D. E. Breedlove and P. R. Ehrlich, *Oecologia (Berlin)* **10**, 99 (1972).
40. F. C. Craighead, *J. Agric. Res.* **22**, 189 (1921); W. H. Thorpe, *Biol. Rev. Cambridge Philos. Soc.* **5**, 175 (1930). This concept recently has been reviewed by M. A. Smith and H. V. Cornell, *Anim. Behav.* **27**, 365 (1979).
41. V. G. Dethier, *Evolution* **8**, 33 (1954).
42. W. Bongers, *Meded. Landbouwhogesch. Opzoekingsstn. Staat Gent.* **30**, 1516 (1965); C. Wicklund, *Entomol. Exp. Appl.* **17**, 189 (1974).
43. T. Jermy, F. E. Hanson, V. G. Dethier, *Entomol. Exp. Appl.* **11**, 211 (1968); C. Wicklund, *ibid.* **16**, 232 (1973). The tendency of some immatures to select food they previously ate may be advantageous because feeding rate or efficiency (or both) declines when they change food plant species, or even if they are placed on different individuals of the same host, perhaps because of time needed for induction of new or more digestive enzymes; L. M. Schoonhoven and J. Meerman, *Entomol. Exp. Appl.* **24**, 689 (1978).
44. J. M. Scriber, *Entomol. Exp. Appl.* **25**, 203 (1979). The butterfly *Papilio glaucus* was both more polyphagous and less efficient than *P. troilus*, but direct comparisons are difficult because in one experiment larvae of both species were reared on different plants and in another, plant species were changed during development.
45. P. A. Blau, P. Feeny, L. Contardo, D. S. Robson, *Science* **200**, 1296 (1978).
46. P. A. Morrow and L. R. Fox, *Oecologia (Berlin)* **45**, 208 (1980).
47. M. D. Huettel and G. L. Bush, *Entomol. Exp. Appl.* **15**, 456 (1972).
48. G. L. Bush, *Evolution* **23**, 237 (1969); *Annu. Rev. Ecol. Syst.* **6**, 339 (1975); in *Evolutionary Strategies of Parasitic Insects and Mites*, P. W. Price, Ed. (Plenum, New York, 1975), p. 187.
49. R. R. White and M. C. Singer, *J. Lepid. Soc.* **28**, 103 (1974).
50. R. Straatman, *ibid.* **16**, 99 (1962).
51. P. A. Morrow and V. C. LaMarche, Jr., *Science* **201**, 1244 (1978); P. A. Morrow, unpublished observations.
52. K. L. Hicks and J. O. Tahvanainen, *Am. Midl. Nat.* **91**, 406 (1974).
53. B. J. Rathcke, *Ecology* **57**, 76 (1976). Aggressive interactions between bees competing for floral resources prevent the less aggressive species from using the presumably more desirable clumped floral resources [S. P. Hubbell and L. K. Johnson, *Ecology* **58**, 949 (1977)]. Gilbert and Singer (*23*) review examples where competition among butterflies for the use of host species may be inferred from species lists in allopatric and sympatric situations.
54. W. W. Benson, *Evolution* **32**, 493 (1978).
55. L. R. Clark, *Aust. J. Zool.* **10**, 537 (1962).
56. R. R. White, *Oecologia (Berlin)* **14**, 307 (1974).
57. T. C. Emmel and J. F. Emmel, *Ecology* **50**, 158 (1969).
58. Examples are given in C. G. Johnson, *Migration and Dispersal of Insects by Flight* (Methuen, London, 1969).
59. J. O. Tahvanainen and R. B. Root, *Oecologia (Berlin)* **10**, 321 (1972).
60. C. P. Ralph, *Ecology* **58**, 799 (1977); W. J. Cromartie, Jr., *J. Appl. Ecol.* **12**, 517 (1975); R. B. Root, in *Ecosystem Analysis and Prediction*, S. A. Levin, Ed. (SIAM Institute for Mathematics and Society, Philadelphia, 1975), p. 83.
61. P. P. Feeny, *Recent Adv. Phytochem.* **10**, 1 (1976).
62. A. M. Shapiro, *Am. Midl. Nat.* **93**, 424 (1975); J. Thompson, *Ecology* **59**, 443 (1978); R. E. Jones, *J. Anim. Ecol.* **46**, 195 (1977).

63. J. D. Hodges and P. L. Lorio, *For. Sci.* **21**, 283 (1975).
64. T. C. R. White, *Ecology* **50**, 905 (1969); *Oecologia (Berlin)* **16**, 279 (1974); *ibid.* **22**, 119 (1976); J. P. Kimmins, *Can. J. Zool.* **49**, 1005 (1971).
65. G. F. Edmunds, Jr., and D. N. Alstad, *Science* **199**, 941 (1978).
66. B. L. Bentley, *Ecology* **57**, 815 (1976); *Annu. Rev. Ecol. Syst.* **8**, 407 (1977).
67. M. J. Way, *Annu. Rev. Entomol.* **8**, 307 (1963).
68. C. Wicklund, *Entomol. Scand.* **5**, 151 (1974); A. Joern, *Oecologia (Berlin)* **38**, 325 (1979); J. Jaenike, *Evolution* **32**, 676 (1978).
69. T. W. Schoener, *Brookhaven Symp. Biol.* **22**, 103 (1969); *Annu. Rev. Ecol. Syst.* **2**, 369 (1971); *Science* **185**, 27 (1974).
70. P. M. Klopfer and R. H. MacArthur, *Am. Nat.* **94**, 293 (1960); R. Levins and R. H. MacArthur, *Ecology* **50**, 910 (1969); V. G. Dethier, in *Chemical Ecology*, E. Sondheimer and T. B. Simeone, Eds. (Academic Press, New York, 1970), p. 83; G. H. Pyke, H. R. Pullium, E. L. Charnov, *Q. Rev. Biol.* **52**, 137 (1977).
71. H. F. Rowell, *Entomol. Exp. Appl.* **24**, 651 (1978).
72. Monophagous herbivores are especially common among sucking insects and among gall formers and leaf miners that live within their hosts as well as relying on them for food [A. F. G. Dixon, *Annu. Rev. Ecol. Syst.* **8**, 329 (1979); V. F. Eastop, in *Insect/Plant Relationships*, H. F. van Emden, Ed. (Blackwell, Oxford, 1973), p. 157; J. H. Lawton and P. W. Price, *J. Anim. Ecol.* **48**, 619 (1979); J. H. Lawton and S. McNeill, *Symp. Br. Ecol. Soc.* **20**, 223 (1979); (*73, 74*)]. The tendency of certain insect taxa to specialize is also related to mating and dispersal behavior; herbivores actually mating on or very near their host plants [for example, *Rhagoletis*, many butterflies (*20, 48*)] may show rapid host shifts, formation of sibling species, or reduced taxonomic affinities of food plants used by related herbivores, that is, patterns different to those described in (*5*).
73. R. D. Goerden and D. W. Ricker, *Environ. Entomol.* **2**, 827 (1974); *ibid.*, p. 837; *ibid.* **4**, 301 (1975); *ibid.* **5**, 45 (1976); *ibid.*, p. 1171.
74. J. H. Lawton and D. Schroder, *Nature (London)* **265**, 137 (1977); J. H. Lawton, *Bot. J. Linn. Soc.* **73**, 187 (1976); D. R. Strong, Jr., and D. A. Levin, *Am. Nat.* **114**, 1 (1979).
75. Proportions of true specialists and local specialists cannot be estimated from the published papers because the necessary data are often not presented or even collected. Data will always be biased toward an appearance of true specialization because the number of sampling periods and habitats sampled are restricted; conspecifics on rare hosts may often be missed. However, the extensive Forest Insect Survey of Canada found that only 18.5 percent of 552 species of Macrolepidoptera were strictly monophagous, while 22 percent fed on more than ten plant species [K. E. F. Watt, *Can. Entomol.* **97**, 887 (1965)]. Of 31 species of woodland leafhoppers in three samples from Wales, 16 species were on only one of the 12 host plant species sampled [M. F. Claridge and M. R. Wilson, *Ecol. Entomol.* **1**, 231 (1976)]; but most of the 42 leafhopper species from an acidic grassland in southern England used more than one host species [N. Waloff and M. G. Solomon, *J. Appl. Ecol.* **10**, 189 (1973)]. A recent survey of lepidopterans from 18 species of trees in New York State showed that 23 percent of 57 herbivores were monophagous, while another 23 percent fed on more than half of the available species; the range of plants used by these very polyphagous species could not be related to taxonomic or chemical attributes of the plants (*76*).
76. D. J. Futuyma and F. Gould, *Ecol. Monogr.* **49**, 33 (1979).
77. J. D. Holloway and P. D. N. Hebert, *Biol. J. Linn. Soc.* **11**, 229 (1979).
78. P. A. Morrow, in preparation. Some general consequences of local specialization for diversity in terrestrial communities are briefly mentioned by Janzen (*6*). J. Lubchenco [*Am. Nat.* **112**, 23 (1978)] demonstrated effects of grazers in intertidal communities and discussed more general effects of grazing preferences.
79. C. B. Huffaker and J. K. Holloway, *Ecology* **30**, 167 (1949); C. B. Huffaker and C. E. Kennett, *J. Range Manage.* **12**, 69 (1959); C. B. Huffaker and P. S. Messenger, *Theory and Practice of Biological Control* (Academic Press, New York, 1976).
80. H. N. Comins and M. P. Hassell, *J. Theor. Biol.* **62**, 93 (1976); M. P. Hassell, *The Dynamics of Arthropod Predator-Prey Systems* (Princeton Univ. Press, Princeton, N.J., 1978); C. S. Holling, *Can. Entomol.* **91**, 293 (1959); W. W. Murdoch, *Ecol. Monogr.* **39**, 335 (1969); *Theor. Popul. Biol.* **11**, 252 (1977); ——— and A. Oaten, *Adv. Ecol. Res.* **9**, 2 (1975); R. T. Paine, *Am. Nat.* **100**, 65 (1966); J. Roughgarden and M. Feldman, *Ecology* **56**, 489 (1975).
81. H. T. Gordon, *Annu. Rev. Entomol.* **6**, 27 (1961); G. P. Waldbauer, *Recent Adv. Insect Physiol.* **5**, 229 (1968).
82. R. I. Krieger *et al.*, *Science* **172**, 579 (1971).
83. R. H. Whittaker and P. P. Feeny, *ibid.* **171**, 757 (1971).
84. J. Smiley, *ibid.* **201**, 745 (1978); L. R. Fox, in preparation.
85. J. M. Scriber and P. Feeny, *Ecology* **60**, 829 (1979).
86. L. B. Brattsten, C. F. Wilkinson, T. Eisner, *Science* **196**, 1211 (1977).
87. M. Auerbach and D. R. Strong, Jr., *Ecol. Monogr.*, in press.
88. Even closely related herbivores may show marked differences in allocation of larval tissues to reproduction, presumably affecting feeding efficiencies of immatures. Thus comparisons among species need to be made with care [H. Dunlap-Pianka, C. L. Boggs, L. E. Gilbert, *Science* **197**, 487 (1977)].
89. L. R. Fox and B. J. Macauley, *Oecologia (Berlin)* **29**, 145 (1977); J. M. Scriber, *ibid.* **28**, 269 (1977); *Entomol. Exp. Appl.* **24**, 494 (1978); L. A. Schroeder, *Oikos* **27**, 259 (1976); C. F. Soo Hoo and G. Fraenkel, *J. Insect Physiol.* **12**, 693 (1966); *ibid.*, p. 711; F. Slansky, Jr., and P. Feeny, *Ecol. Monogr.* **47**, 209 (1977); C. P. Onuf, J. M. Teal, I. Valiela, *Ecology* **58**, 514 (1977).
90. See H. F. Van Emden, in *Biochemical Aspects of Plant and Animal Coevolution*, J. B. Harborne, Ed. (Academic Press, New York, 1978) in addition to many of the examples discussed in this article.
91. Many assumptions about resource partitioning derive from studies on birds (*2, 7*) although the ideas have been applied to many other organisms (*69*). However, May has proposed that insect and plant communities might be much more complex (complex multidimensional niche structures), in part because of chemical interactions, and that they would not be expected to show clear patterns of resource partitioning [R. M. May, *Stability and Complexity in Model Systems* (Princeton Univ. Press, Princeton, N.J., 1973), p. 166].
92. P. A. Opler, *Am. Sci.* **62**, 67 (1974).
93. We hesitate to generalize our arguments to other groups because we are less familiar with these. However, several terrestrial vertebrate grazers (including deer, moose, sheep, cows, ptarmigan) have geographically variable diets reflecting local community situations and could be considered local specialists; several papers in A. Watson, Ed., *Animal Populations in Relation to Their Food Resources* (Blackwell, Oxford, 1970) describe regional feeding patterns of terrestrial herbivores, particularly those of J. Eadie, p. 7; D. R. Klein, p. 25; A. Gardarsson and R. Moss, p. 47. Additional examples are in S. J. McNaughton, *Science* **199**, 806 (1978); D. Miguelle, thesis, University of Minnesota (1979); J. L. Harper, *Population Biology of Plants* (Academic Press, New York, 1977); and (*19*). Marine herbivores such as some sea urchins, snails, and possibly limpets show local variation in diet [J. Lawrence, *Oceanogr. Mar. Biol. Annu. Rev.* **13**, 213 (1975); R. L. Vadas, *Ecol. Monogr.* **47**, 337 (1977); V. Fretter and R. Manly, *J. Mar. Biol. Assoc. U.K.* **57**, 999 (1977); D. A. S. Smith, *ibid.* **53**, 493 (1973); D. R. Lindberg, personal communication]. Patterns that can be interpreted as "local specialization" are also found among insect pollinators [A. R. Moldenke, *Oecologia (Berlin)* **21**, 219 (1975)].

94. We began to discuss these ideas while members of the Research School of Biological Sciences at the Australian National University. We thank the following for reading and discussing earlier drafts: J. H. Connell, D. Dykhuizen, J. Estes, J. Langenheim, S. M. Louda, W. W. Murdoch, C. P. Onuf, D. C. Potts, P. Regal, M. Silver, M. C. Singer, S. M. Stanley, M. Stanton, P. Steinberg, D. R. Strong, and D. Tilman.