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GENERAL CONCEPTS ON THE EVOLUTIONARY BIOLOGY OF PARASITES

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Parasitism is a very common way of life, and probably the prevalent means of obtaining food among organisms. Adaptive radiation among parasites has been extensive, and yet ecological and evolutionary concepts on parasitism are poorly developed. Although Elton (1927) devoted a chapter in his pioneering ecology book to parasitism his conclusion was that the resemblances between predators and parasites are more important than the differences. This attitude is now prevalent in ecology texts (e.g. Andrewartha and Birch, 1954; Odum, 1971; Krebs, 1972; Colinviaux, 1973), and although much attention is devoted to predation, parasitism is almost ignored. Therefore, by using the inductive process, this paper attempts a synthesis of ecology and parasitology, the need for which has been recognized by Kennedy (1975), and it explores the evolutionary implications of parasite ecology.

This synthesis should contribute to an understanding of parasites in three ways. First, a reevaluation of the abundance of parasitic species is made. Arndt (1940) estimated that 25% of animals in Germany are parasitic on others. Rothschild and Clay (1952) stated that parasitic animals probably exceed nonparasitic species in number of species and individuals, but provided little numerical support. A careful quantitative evaluation by Askew (1971) provided an estimate that 15% of insects, and 10% of all animal species are parasitic insects. Calculations presented in this paper indicate that well over 50% of the species of organisms extant today are parasitic. Second, general concepts on the ecology and evolution of parasites are presented, being derived from a combination of popu-

lation biology, evolutionary theory and parasite biology. Third, predictions derived from the general concepts act as a guide to critical characteristics of parasite biology which need to be examined and tested in natural populations.

Much of the logic in this paper depends upon the interpretation of the word parasite. A distillation of views would be lengthy, as no discrete limits to the parasitic habit exist which are biologically meaningful (Askew, 1971; Kennedy, 1975). Therefore, I adopt what must be a generally accepted definition of a parasite, found in Webster's International Dictionary: "An organism living in or on another living organism, obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage to its host." Thus, an individual of any parasitic species will usually gain the majority of its food from a single living organism in contrast to the more generalist browsers and predators which feed on many organisms, and saprophages which feed on dying or dead organic matter. Although a parasitic species may utilize several host species, each individual will exploit an individual host, and thus a single species. Parasites are specialists in a host environment with close coevolutionary ties.

Most parasitologists include as parasites organisms such as mosquitoes, leeches, and ticks, having a brief relationship with a host (e.g. Cheng, 1973). This convention appears to be hardly justified by the definition used above. However, parasitologists usually omit mention of parasites of plants. Nematodes, fungi, bacteria, and many in-

TABLE 1. *Feeding habits of British insect species. There is debate on the placement of several large families such as the Carabidae. These beetles are normally considered predators, but many eat vegetable matter and others are saprophagous. As in this case when accurate placement is not possible the taxon has been omitted.*

Order	Predators	Non-parasitic herbivores	Parasites		Saprophages
			on plants	on animals	
Thysanura					23
Protura					17
Collembola					261
Orthoptera		39			
Psocoptera		70			
Phthiraptera				308	
Odonata	42				
Thysanoptera			183		
Hemiptera	123		283	5	
Homoptera			976		
Megaloptera	4				
Neuroptera	54				
Mecoptera	3				
Lepidoptera			2,233		
Coleoptera	215	65	909	18	1,637
Hymenoptera	170	241	435	5,342	36
Diptera	54		922	542*	1,672
Siphonaptera				47	
TOTALS	665	415	5,941	6,262	3,646
% of insect fauna	3.9	2.4	35.1	37.0	21.5

* Many species parasitic only as adults, e.g. Culicidae (49 sp.), Ceratopogonidae (135 sp.), Simuliidae (19 sp.).

sects which feed in or on plants, fit the definition of a parasite. Day (1974) includes these organisms in his book on host-parasite interactions. The majority of insect herbivores are parasitic. The large order Homoptera, including leafhoppers, froghoppers, aphids, coccids and whiteflies, is composed almost completely of parasitic species. The larvae of the even larger order, Lepidoptera, usually feed and mature on a single individual of the host plant species, and gain a large percentage of the total nutritional requirements for the organism's life span. In addition, parasitic angiosperms are frequently ignored when parasitism is discussed (Kuijt, 1969).

Therefore the parasitic habit is of concern to a variety of disciplines each contributing its perspective and knowledge to the understanding of parasites. These disciplines include parasitology, medical ento-

mology, plant pathology, botany, agricultural and forest entomology, and biological control.

ABUNDANCE OF PARASITIC SPECIES

The proportion of organisms that are parasitic in any region is not easily estimated. Parasites are small, mostly well concealed, and thus inconspicuous elements of the flora and fauna. Few regional check lists of organisms are based on enough concerted effort that would ensure an adequate sampling of both obvious and inconspicuous species. One of the exceptions is the fauna of the British Isles which is probably the best documented fauna in the world, because relatively intensive faunistic studies have been conducted since the mid-18th century. Thus it has been possible to compile a check list of British insects (Kloet and Hincks, 1945) which represents a

reasonably complete record of the largest class of animals on the islands and in the world.

I have counted the number of species in each family of insects in Kloet and Hincks (1945) and classified as many families as possible into the categories: predators, nonparasitic herbivores (mostly browsers and pollinators, e.g. grasshoppers, bees), parasites on plants (e.g. thrips, bugs, caterpillars and some fly larvae), parasites on animals (e.g. lice, bed bugs, parasitic wasps and flies, and fleas), and saprophages (e.g. many beetle and fly larvae). Of the 20,244 insect species listed in Kloet and Hincks, 16,929 can be readily classified into the above categories (Table 1). The remainder cannot be classified in this manner either because of diversity of feeding habits within a family, or shortage of information on food eaten by larvae and adults.

The preponderance of insects are classified in the parasitic groups and represents 72.1% of the insect fauna (Table 1). Predators account for only 3.9% of insects in Britain by this method. Even if a conservative estimate is made by assuming all the parasites in the fauna have been identified in my classification they represent about 60% of the insects. Since about three quarters of the known animals on earth are insects, an estimate that parasitic insects represent close to half the animals on earth does not seem unrealistic. When other large groups of parasitic animals found among the nematodes, copepods, flatworms, ticks, mites and protozoa, are added to the numbers of parasitic insects it is clear that parasitism as a way of life is more common than all other feeding strategies combined.

ECOLOGICAL AND EVOLUTIONARY CONCEPTS

The following concepts are grouped as a start to the synthesis of evolutionary biology and parasitology. The concepts are necessarily basic in order to retain generality, but they may form the ground work

for development of more sophisticated concepts. The general approach will compare the ecology and evolution of parasites with that of predators.

Concept 1. Parasites are adapted to exploit small, discontinuous environments.

For a parasite each host exists in a matrix of inhospitable environment (Williams, 1975). For very small organisms a wide dispersion of resources makes colonization of new hosts hazardous. Adaptations to reduce this hazard include: i) mass production of spores or eggs (e.g. tapeworms); ii) dispersal of inseminated females which form a high proportion of the population (e.g. tetranychid mites, Mitchell, 1970); iii) dispersal by phoresy making host discovery accurate (e.g. tarsonemid mites, Lindquist, 1969). In each of these cases a single female can found a colony on a new resource remote from its origin. Multiplication in the colonizer's progeny may lead to a new and relatively isolated population. New propagules colonize other isolated resources. Thus parasites tend to exist in small homogenous populations with little gene flow between them (see also Jones, 1967).

Types of reproduction in parasites which permit a single female to found a new population include inbreeding among progeny (e.g. parasitic wasps; Askew, 1968), hermaphroditism (e.g. trematodes, cestodes), or asexual reproduction (polyembryony in digenetic trematodes and parasitic wasps, parthenogenesis in many taxa). The commonness of parthenogenesis among parasitic arthropods is not generally appreciated. Arrhenotoky (the production of males from unfertilized eggs) occurs in all Hymenoptera, probably the majority of Thysanoptera, many iceryine and aleurodid Homoptera, and in some Coleoptera (White, 1973). It is a major mode of reproduction in certain families of mites (Oliver, 1971). Thelytoky (the production of females from unfertilized eggs) occurs

TABLE 2. *Number of species in the ten largest families in the British insect fauna in each of the categories listed. Primary parasites feed on plants and secondary parasites feed on animals. Families marked with an asterisk contain some or all members reproducing through parthenogenesis. The family Cynipidae contains some secondary parasites.*

Predators		Primary Parasites		Secondary Parasites	
Dytiscidae	110	Cicadomyiidae*	629	Ichneumonidae*	1938
Sphecidae*	104	Curculionidae*	509	Braconidae*	891
Coccinellidae	45	Aphididae*	365	Pteromalidae*	493
Corixidae	32	Tenthredinidae*	358	Eulophidae*	485
Cucujidae	32	Noctuidae	298	Tachinidae	228
Hemerobiidae	29	Chrysomelidae	248	Philopteridae	176
Vespidae*	27	Cicadellidae	242	Lamprotatidae*	156
Asilidae	26	Cynipidae*	238	Platygasteridae*	147
Anthorcoridae	25	Olethreutidae	216	Encyrtidae*	144
Soldidae	20	Miridae	186	Diapriidae*	125
MEAN	45	MEAN	329	MEAN	478

sporadically in a great variety of insects (Suomalainen, 1962) and cyclical parthenogenesis (i.e., heterogonic life cycles, Williams, 1975) is prevalent in aphids (Aphididae) and gall wasps (Cynipidae), and it occurs in gallflies (Cecidomyiidae) (Suomalainen, 1962; White, 1973), and many parasites in other taxa (Williams, 1975). Thus parthenogenesis occurs in five of the ten largest families of parasitic insects on plants in Britain (Table 2): Cecidomyiidae, Curculionidae, Aphididae, Tenthredinidae and Cynipidae (see Suomalainen, 1962). In the animal parasites of the British fauna eight of the largest families have all species parthenogenetic since they are within the order Hymenoptera: Ichneumonidae, Braconidae, Pteromalidae, Eulophidae, Lamprotatidae, Platygasteridae, Encyrtidae, and Diapriidae (Table 2).

Parthenogenesis is so common in parasites and yet its adaptive nature for parasites is not well understood. Some adaptive features follow: 1. A single female can establish a new colony (White, 1973; Williams, 1975), and multiplication can occur when the probability of contact between more than one individual of the same species is very low (Tomlinson, 1966). 2. Parthenogenetic parasites may seem to be maladapted to a patchy, complex and changing environment since prog-

eny of a single female are likely to be more uniform than progeny from females producing fertilized eggs (Mayr, 1963; White, 1970; Williams, 1975). However, this disadvantage can be reduced by utilization of highly stable and predictable microenvironments provided by the homeostasis of living organisms. A positive feedback may reinforce the evolution of parthenogenesis in parasitic organisms (Fig. 1). 3. The gross reproductive rate of thelytokous females is doubled (White, 1973; Williams, 1975), so the probability of finding a new host is similarly increased. 4. Particularly adaptive combinations of genes are fixed in perpetuity in thelytokous multiplication: automictic thelytoky tends to produce homozygous individuals while apomictic thelytoky involves mitotic divisions only (White, 1973). This locking of gene combinations may be especially important in parasitic organisms where large banks of genes are likely to be involved with close coevolutionary tracking of the host system (see Fig. 1). Disruption of such a block would generate gross maladaptions with almost certain lethal results.

Parthenogenesis is relatively rare in predatory taxa such as Odonata, Heteroptera and spiders (White, 1973). Of the 10 largest families of predators in the British insect fauna only the two hymenopterous

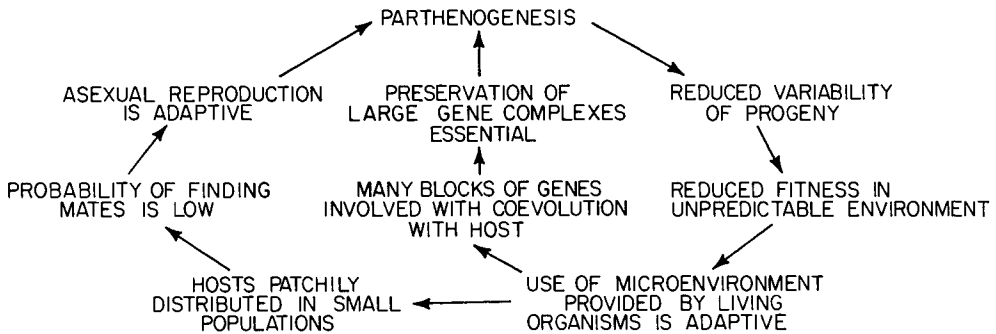


FIG. 1. The positive feedback loop which may promote the evolution of parthenogenesis among parasitic organisms or at least permit it to exist. It is assumed that parthenogenetic species may revert back to sexual reproduction under favorable selection pressure.

families, Sphecidae and Vespidae, show any form of parthenogenesis (cf. Suomalainen, 1962; White, 1973).

Concept 2. Parasites represent the extreme in the exploitation of coarse-grained environments.

The small size of parasites, the specific cues used in discovery of relatively large food items (e.g. Vinson, 1975), and the poor mobility of many stages in the life cycle means that they must exploit a coarse-grained environment in the sense of MacArthur and Levins (1964) and MacArthur and Wilson (1967). Such small organisms, which face relatively large habitat differences compared to the tolerance of individuals may respond in two ways to environmental variability (Levins, 1962). If the environment is stable in time and variable in space, Levins predicts that the population should be monomorphic and specialized with a geographic pattern of discrete races. If the environment is uniform in space and variable in time the population should be polymorphic, with specialized types, and have a geographic pattern of clines in frequencies of these specialized types. Since hosts probably represent a variable resource both in time and space the development of both geographic races and polymorphism in parasites may be common, although races will

be more frequent than polymorphism with the population structure as envisioned here. Specialization permits a relatively large number of species to pack into a given set of resources so many species may coexist under equilibrium conditions.

In contrast to parasites, predators are relatively large and mobile and exploit a relatively fine-grained environment. Habitat differences are small compared to the tolerance of the animals. Levins (1962) predicted that such populations will be monomorphic and unspecialized, with geographic patterns showing continuous clines. Few of these generalists can coexist under equilibrium conditions.

Concept 3. Evolutionary rates and speciation rates are high.

The environmental constraints on the parasitic habit described in *Concepts 1* and *2* promote the fractionation of gene pools and produce an advantage to inbreeding or asexual reproduction. They foster rapid divergence of populations, race formation, and eventual speciation. Short life cycles, short generation times and high fecundity result in high reproductive rates which permit dramatic changes in population size and rapid differentiation of populations under dissimilar selective regimes. Predominantly homozygous populations (or haploid males in parasitic Hymenoptera) have

all genes exposed to selection in each generation. Both the founder effect and genetic drift are probably significant in speciation of parasites. Both Wright (1940, 1943, 1949) and Carson (1968, 1975) have explored the evolutionary potential of populations with this structure and they concluded that the probability of evolution and speciation was much higher than in a randomly breeding population of the same size.

Evidence for high evolutionary rates may be seen in the many sibling species, subspecies, host races, and different types observed in parasitic organisms (e.g., Thorpe, 1930; Mayr et al., 1953; Brown, 1959). Mayr (1963) states that sibling species are especially common among insects and singles out the Lepidoptera, Diptera, Coleoptera and Orthoptera as providing abundant examples. In the Coleoptera he notes that sibling species are particularly common in the Curculionidae, Chrysomelidae, and Cerambycidae, three of the largest families in the order with the majority of species parasitic on plants. Zimmerman (1960) suggests that five or more new species of *Hedylepta* (Lepidoptera) must have evolved within 1000 years in Hawaii since they are endemic and specific to banana which was only introduced that long ago. Roelofs et al. (1972) and Klun et al. (1973) describe the sibling species of the corn borer which respond to different isomers of the otherwise identical pheromones. Bush (1975a) states that a new race of the western cherry fruit fly (*Rhagoletis indifferens*) was extant on domestic cherry within 89 years of the plants' introduction to Northwest North America. Jones (1967) discusses the several types of leishmaniasis caused by biologically distinct forms within each of the species *Leishmania donovani* and *L. tropica*. He also suggests on theoretical grounds that speciation can occur in one generation, a view held by Bush (1974, 1975a, b) based on studies of herbivorous parasites.

The large size of many families of parasitic insects (Table 2) also supports the

concept of high evolutionary and speciation rates. Even though some parasitic taxa evolved much later than some predatory taxa, families of parasites on plants are on average almost eight times larger than those of predators, and families of parasites on animals are over ten times larger. In both groups of parasites the tenth family is larger than the first ranked family of predators.

Concept 4. Adaptive radiation is extensive and its degree of development in each taxon of parasites depends upon

a) *the diversity of hosts* in the taxon or taxa being exploited (i.e., numbers of species and the degrees of difference between species)

b) *the size of the host target* available to potential colonizers (body size, population size, geographical distribution)

c) *the evolutionary time available* for colonization of hosts

d) *the selective pressure for coevolutionary modification* (i.e., for specialization)

e) *the mobility of hosts.*

To understand the evolution of the large numbers of parasite species part of the answer can be found in an understanding of why there are so many resources available and what influences the presence or absence of parasites on these resources. Some of the factors are treated in this section.

Diversity of hosts.—Adaptive radiation can be most extensive when many related species of host are available for colonization, particularly if the hosts within a taxon differ in an important way relative to the requirements of the parasites. Many examples could be given of a fairly weak relationship between size of family of hosts and numbers of parasites that exploit members of that family. For example, there are more of the leaf mining flies in the family Agromyzidae on large families of plants than small families (Fig. 2). However, the regression accounts for only 61% of the variation and much of the remaining scat-

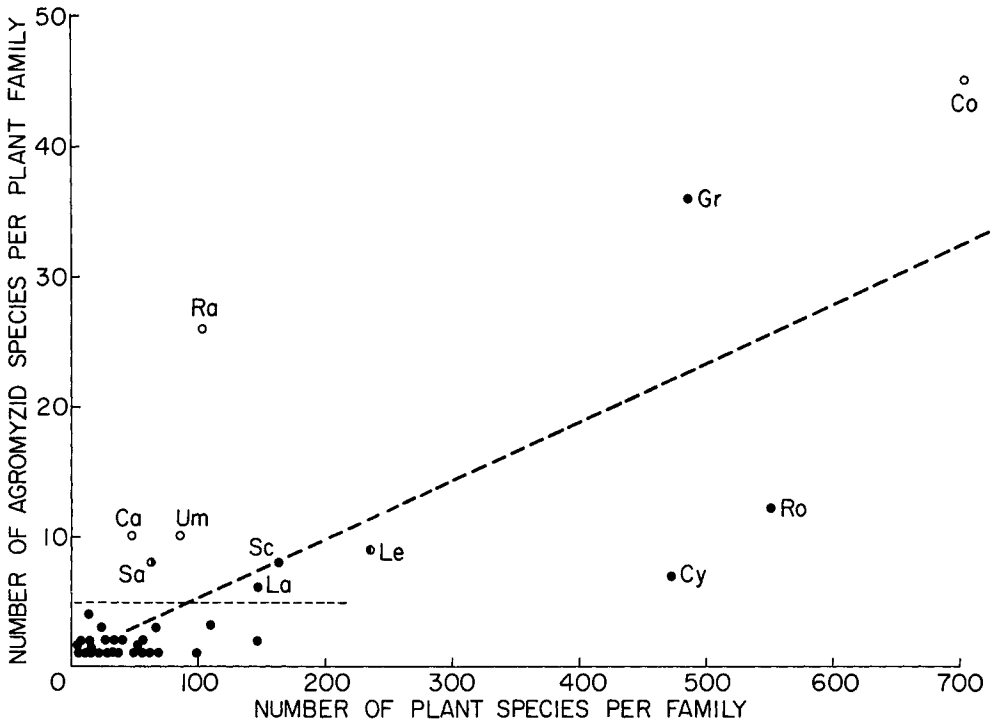


FIG. 2. Relationship between number of species in each plant family (from Fernald, 1950) and the number of agromyzid flies attacking each family in Canada and Alaska (from Spencer, 1969). For those plant families attacked by more than five agromyzid species (above small dashed line) the following symbols are used: (open circle) agromyzids monophagous, (closed circle) agromyzids oligophagous, (closed/open) some monophagous and other oligophagous, (open/closed) only two genera in family. Sa—Salicaceae, Ca—Caprifoliaceae, Um—Umbelliferae, Ra—Ranunculaceae, Sc—Scrophulariaceae, La—Labiatae, Le—Leguminosae, Gr—Graminae, Cy—Cyperaceae, Ro—Rosaceae, Co—Compositae. The regression line is described by the formula $Y = 0.7648 + 0.0455X$ ($r^2 = 0.61$, $P < .01$).

ter is probably accounted for by the chemical diversity of plants in each family. Where species in a family are chemically distinct, for example in secondary metabolic products, or as Hering (1951) noted, in plant proteins, parasites are predominantly monophagous (i.e., feed on host species within a single genus). Parasites utilizing hosts in families of low chemical diversity tend to be oligophagous (i.e., feed on species in several genera). Monophagous species have a narrow feeding niche, therefore many species can pack onto a given number of host species relative to oligophagous parasites. Only the family Graminae is an exception to this pattern,

perhaps because of the exceptional commonness of species and individuals making colonization more probable. The example of the Agromyzidae supports Eichler's (1948) rule, well known to parasitologists, which states (from Noble and Noble, 1971): "When a large taxonomic group (e.g., family) of hosts consisting of wide varieties of species is compared with an equivalent taxonomic group consisting of few representatives, the larger group has the greater diversity of parasitic fauna."

At each successive trophic level the diversity of potential hosts increases and the opportunities for adaptive radiation expand, within the limits discussed below.

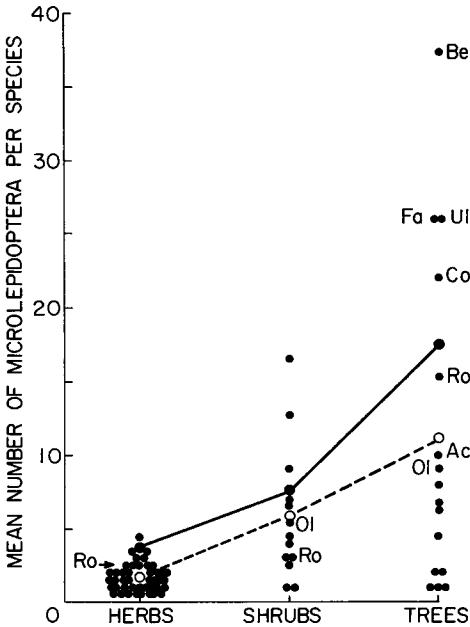


FIG. 3. Relationship between plant form of a family and the average number of microlepidoptera per plant species attacked in each family. Host species from Ford (1949). Ol-Oleaceae, Ro-Rosaceae, Be-Betulaceae, Fa-Fagaceae, Ul-Ulmaceae, Co-Corylaceae, Ac-Aceraceae. Open circles = the mean number for each plant form. Dashed line = the trend of increased parasites per plant species as plant size increases. Mean number of leafmining Lepidoptera per plant genus for each plant form = large closed circles. Solid line = trend per plant genus. Host species from Hering (1957). Families with representatives in more than one plant form were subdivided, as shown for the Oleaceae and Rosaceae. The large range in numbers of species on trees is discussed in Concept 4c.

Thus, primary parasites (parasitic herbivores) may be abundant, with many large families included, but radiation has been even more extensive in the largest families of secondary parasites (parasitic carnivores) (Table 2). The family Ichneumonidae is over three times larger than the largest family of primary parasites in the British fauna, and Townes (1969) estimates a total of about 60,000 species must exist in the world. Only at the fourth

trophic level in a parasite food chain (e.g., the obligate hyperparasites of parasitoids) resources may be so dispersed and hard to find that a trend towards generalization, and reduced numbers of species, might be expected (Darwin, 1872; Janzen, 1975).

The resulting diversity of parasitic organisms supported after the evolution of a new genus or species may be impressive. An extreme case is seen in the genus *Quercus* where even in the small fauna of Britain the oak supports at least 390 species of parasitic herbivores (Barnes, 1951, 1955; Southwood, 1961; Darlington, 1974; Askew, 1975; and Morris, 1974 provide numbers of species in various taxa). The number of secondary parasites supported by these herbivores must be even higher. The winter moth, *Operophtera brumata*, is known to support 63 species of parasite (Embree, 1971) and microlepidoptera in the genus *Phyllonorycter* may support about 50 species of parasitic insects (Askew, 1975).

Size of host target.—The large number of parasites which coexist on oaks is possible partly because of the tree's large size. The many resources available for colonization and the species that exploit them have been described by Morris (1974). The average numbers of microlepidoptera per species in a family of plants are much less limited in trees than in shrubs and much less in shrubs than in herbs (Fig. 3). Leaf mining Lepidoptera, Coleoptera and Hymenoptera illustrate similar trends when Hering's (1957) keys are analyzed. A similar response may be observed among ectoparasites (e.g., biting lice, Mallophaga, and feather ticks, Sarcoptiformes) of birds, with large birds having more regions of the body which are sufficiently distinct so that different parasites can colonize and maintain a competitive edge in each region (Dogiel, 1964). For example, in an extensive survey Foster (1969) discovered three species of mallophagan which occupied two regions of the body on the orange-crowned warbler, *Vermivora celata*, whereas Dubinin (in Dogiel, 1964) found seven species

on the larger *Ibis falcinellus* located in four distinct body regions.

Host population size as well as the geographic distribution of a species are equally important in determining the probability of a parasite reaching a new host, colonizing it and maintaining a lasting relationship with the host. Large populations and extensive range of a potential host must increase the chances of colonization by parasites (Strong 1974a, b; Strong and Levin, 1975). Perhaps Kellogg (1913) was the first to regard hosts as islands. Janzen (1968, 1973) also points out that hosts can be regarded as islands available for colonization by parasites and they are therefore subject to the insights of the theory of island biogeography (MacArthur and Wilson, 1967), as Dritschilo et al. (1975) have demonstrated for mite species on cricetid rodents in North America. Probability of colonization is influenced by island size which can be regarded as host size, host population size or range size.

Evolutionary time available.—In the previous section trees were shown to support on average more parasitic herbivores than herbs (Fig. 3). However, the range in average numbers of parasites per species of tree is extreme and is not accounted for by the size of the host individuals. Most of this range can be explained by the relative evolutionary opportunity provided by each species of tree. Common trees which have existed in a region over considerable spans of time have high numbers of parasites whereas recently available hosts with a restricted range have small numbers (Southwood, 1961; Opler, 1974).

Once parasites have colonized a host, divergence of host stock and eventual speciation leads to divergence of the parasites and, depending on the time involved, results in host-race formation or new parasite species. Thus parasites can be extremely useful in elucidating the phylogenetic relationships of their hosts (Jordan, 1942, on Siphonaptera; Harrison, 1914; Metcalf, 1929; Hopkins, 1942, 1949; Clay, 1950, on

Phthiraptera; Lindquist, 1969, on Acarina; see also Mayr et al., 1953; Mayr, 1963, for use of parasites to distinguish sibling species in the host group). Such diverse groups as beetles on pines, termitophiles in termite colonies, and ciliates on turbellarians have provided clues to inconspicuous differences between hosts. This concept has been formalized into a rule by Fahrenholz: common ancestors of present-day parasites were themselves parasites of the common ancestors of present-day hosts. Degrees of relationship between modern parasites thus provide clues as to the parentage of modern hosts (Noble and Noble, 1971). The more specific Fuhrman's rule (Dogiel, 1964), that each order of birds has its particular cestode fauna, implies a similar relationship between the evolution of host and parasite.

Selective pressure for coevolutionary modification.—The importance of interaction between host and parasite in the evolution of both has been stressed by numerous authors (e.g., Brues, 1924; Hegner, 1927; Dogiel, 1964; Ehrlich and Raven, 1964). The stepwise coevolutionary process results in extreme specialization and complex defense mechanisms (e.g. Whittaker and Feeny, 1971). As described in *Concepts 2 and 3* specialization is likely to increase the rate of speciation which may occur in both host and parasite. Indeed, as Atsatt (1973) points out, parasites may have increased the adaptive potential of their angiosperm hosts enabling the evolution of heterotrophic species, including the parasitic flowering plants.

The importance of coevolutionary pressure was illustrated in the relationship between agromyzid leaf miners and plants (Fig. 2). Families containing species which are biochemically distinct had relatively high numbers of agromyzids which were also specialists. This is seen particularly clearly when host ranges are compared for agromyzid leaf miners on Graminae and Umbelliferae. The latter family is composed of aromatic plants which produce a

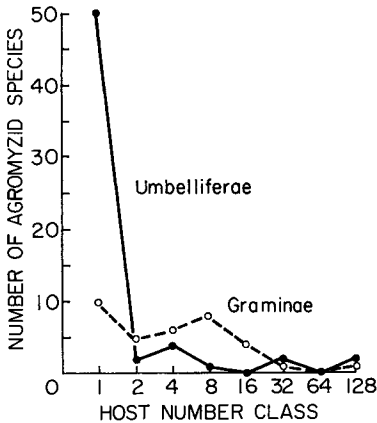


FIG. 4. Frequency distribution of the number of genera attacked by agromyzid parasites in the host plant families Graminae and Umbelliferae. Host number classes on a logarithmic scale with the first number in the class given. Thus class 8-15 = 8. Data are from an analysis of keys on leafminers in Europe by Hering (1957).

diverse array of essential oils and related resins (Hegnauer, 1971) with a large number of pharmaceutically interesting species (Heywood, 1971). Although the Umbelliferae is a much smaller family than the Graminae many more agromyzid species attack members of the family in Europe (61 species on Umbelliferae, 35 species on Graminae; from analysis of keys by Hering, 1957). This is apparently because the chemical diversity of potential hosts within the Umbelliferae has forced specialization of the parasites and 82% of the species of agromyzid attack only one genus each; they are monophagous (Fig. 4). In contrast only 29% of agromyzids are monophagous on grasses. In addition, there are fewer agromyzids on each genus of Umbelliferae than of Graminae (Fig. 5). No more than seven species occur on any one genus in the former family and 15 genera have only one parasite species. When there are few parasite species per host, coevolution can proceed rapidly since adaptive reactions need not be compromised by conflicting adaptations in response to other parasites exerting different selective pres-

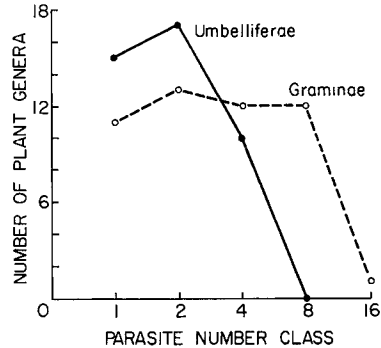


FIG. 5. Frequency distribution of the number of parasitic agromyzids per genus of plants in the families Graminae and Umbelliferae. Parasite number classes arranged on a logarithmic scale as in Figure 4. Data are from an analysis of keys on leafminers in Europe by Hering (1957).

ures. Thus adaptations for specialization are reinforced, isolation of populations becomes more likely, and speciation is more rapid. As Mayr (1963) expresses it, "Host specificity is thus an ideal prerequisite for rapid speciation" (see also Ross, 1962). The end result is a comparatively large number of specialists attacking the Umbelliferae whereas many more generalists attack the Graminae.

The degree to which specialization is demanded is a potent force in adaptive radiation. Szidat's Rule (Eichler, 1948) states that the more specialized the host group, the more specialized are its parasites; and, conversely, the more primitive or more generalized the host, the less specialized are its parasites. Hence, the degree of specialization may serve as a clue to the relative phylogenetic ages of the hosts (as stated by Noble and Noble, 1971). Predators must remain generalized and radiation has been unimpressive (Table 2). Plant parasites show varying degrees of radiation depending on the intimacy of their association with the host. Plant bugs (Miridae) are mobile, relatively large ectoparasites, although immature stages spend much time on a single host. In the British fauna 186 species have been identified.

The much smaller plant lice (Aphididae) are more sessile, more intimately associated with the host and have undergone more extensive radiation (365 species in British fauna). Some are gall-makers (Eastop, 1973). The largest families of plant parasites are predominantly endoparasitic. The weevils (Curculionidae) as larvae mine in leaves, under bark, in shoots or roots, or feed in rolled leaves, fruits and seeds. They number 509 species. The most highly coevolved parasitism occurs in the gall-forming endoparasitic flies, Cecidomyiidae, which are also the most numerous (629 species) primary parasites in the British fauna (Table 2). Eastop (1973) referring to aphids noted that the production of a distinctive gall is always associated with host-plant specificity. Members of the Cynipidae (238 species) also form galls but radiation has not been so extensive; evidently the opportunities for radiation have not been as fully exploited as by the gall flies.

Specialization in parasites on animals should be more highly developed than in parasites on plants. Although animals as a group are chemically more similar than plants, herbivores have a greater diversity of places to live than plants, and strong and diverse behavioral, phagocytic and immune defenses against parasites. Thus, finding and living with hosts seems to demand a greater number of adaptations per species for parasites of animals than for parasites of plants, and therefore a narrower host range. Members of the largest families in the British fauna are parasites of insects: the Ichneumonidae (1938 species) and Braconidae (891 species) (Table 2).

Probably the degree to which species of host and parasite are coevolved and the proportion of the genome devoted to coadaptation could not have been appreciated without extensive breeding of plants for parasite resistance. Flor (1971) and Day (1974) provided strong evidence from plant breeding experiments that there is a gene-for-gene relationship between the

plant host's resistance and the associated parasite's virulence. After prolonged coevolution, where the stepwise process has escalated defenses many times, many such complementary gene-for-gene pairs must exist between parasite and host. This complex of genes coadapted to counterparts in the host, like the closed variability system described by Carson (1975), must be maintained or fitness is reduced drastically. These blocks of genes may be maintained by inversions, development of supergenes, or by cloning, the last so often seen in parasitic organisms (see *Concept 1*).

Mobility of hosts.—The mobility of hosts may either dampen or promote the evolutionary process towards speciation of parasites. High mobility of host stages which are infected with parasites reduces isolation of parasite populations important in speciation of parasites, discussed under *Concepts 1* and *3*. Static hosts such as plants, or hosts of low mobility reinforce isolation of parasite populations. Plants disperse as seeds, a stage usually not infected by parasites (important exceptions are fungi, seed wasps and seed weevils). Similarly, insects tend to disperse as very early larval stages before parasites attack (e.g. *Choristoneura fumiferana*, Morris, 1963; *Porthetria dispar*, Leonard, 1970) or more commonly in the adult stage which is relatively free from parasitic insects. The contrary situation exists among some mammals, birds and fish, which are relatively large, highly mobile animals. Parasitized animals disperse, gene flow between parasite populations is high and rates of divergence and speciation are reduced. It is among the students of parasites on these groups that the concept of slow evolution of parasites, relative to that of their hosts, seems to have originated. Jordan (1942) supported this view based on studies of fleas (Siphonaptera) which are restricted to birds and mammals, as are the lice (Phthiraptera) studied by other supporters such as Metcalf (1929) and Hopkins (1949).

Concept 5. Types of speciation other than through geographic isolation are at least as important as allopatric speciation.

There are probably several routes by which species can be formed (Kinsey, 1937; White, 1968, 1973; Scudder, 1974; Bush, 1975*b*) and sympatric speciation is one likely route (Stebbins, 1964; Grant, 1966; Maynard Smith, 1966; Spieth, 1968; Dobzhansky, 1970; Thoday, 1972; Bush, 1975*b*). Ross (1962) emphasized the importance of host shifts that isolate sympatric populations and Mayr (1963) stated that host races of phytophagous animals provide the only case where incipient sympatric speciation seemed to be possible. If host race formation can lead to speciation of plant parasites it can also be important among animal parasites. Rapid evolutionary rates and such extensive adaptive radiation as seen among parasites is not easily explained by allopatric speciation over extended time periods. The large numbers of sibling species are equally hard to explain by this model. Bush (1975*b*) concluded that host races of plant parasites evolved sympatrically and that these were undoubtedly the progenitors of the many sibling species so often found to be sympatric on different hosts.

Bush (1974, 1975*a*) suggested that the establishment of new host races may require only minor alterations in the genome. His basic model accounts for speciation involving only two alleles at each of two loci; one locus controlling host selection and the other controlling survival in the host. One allele at each locus carries these traits adapted to host species A and the other alleles enable the parasite to discover and exploit host species B. If host species A and B have different phenologies, and the parasites adapt to these differences, reproductive isolation is reinforced. Bush (1975*a*) provided several examples of this allochronic isolation involving host shifts which can occur only through "a narrow window in space and time." For example,

on Mount Shasta in California a host shift of the fruit fly, *Rhagoletis indifferens*, from bitter cherry, *Prunus emarginata*, to introduced domestic cherry, *P. avium*, could occur only at about 5,000 feet during the last two weeks of July, whereas the fly occurred from sea level to 9,000 feet and from May to October.

Hosts with different phenologies or breeding cycles may effectively isolate their parasites allochronically and may play an important part in sympatric speciation. Triggering of reproductive activity may be initiated by the host as in the rabbit and hare fleas (Rothschild, 1965; Rothschild and Ford, 1964, 1973), insects parasitic on others (Salt, 1941; Lees, 1955), and possibly among blood-feeding Mallophaga on birds (Foster, 1969).

From the gene-for-gene hypothesis Day (1974) predicted the number of host races that a set of resistant varieties will select for. With 19 genes for resistance in apple, for example, each of which may have two phenotypes, resistant or susceptible, there would be 2^{19} or 524,288 races of a parasite adapted to exploit fully the range of apple varieties. This may seem an extreme number, but we have every reason to infer that a parasite must be closely attuned morphologically, physiologically and biochemically to the host, and, therefore, such extensive race formation may be necessary and realistic. Once the races have differentiated in this way subtle, ecological or temporal isolation could easily promote the independent differentiation of populations.

Since most parasites are small, usually with narrow tolerances to environmental factors, they are susceptible to minor spatial or temporal change. When tolerances are narrow slight differences between habitats may cause isolation where habitats may be only 100 meters apart. If reproductive or dispersing individuals live only a few days, a week's difference in phenology may prevent gene flow between populations. Many more ecotones exist for parasitic species and it is in these intermediate

and changeable zones that Stebbins (1974) sees the cradle for rapid evolution. For such small, short-lived, precisely adapted organisms as parasites, evolution will operate in miniature: short times, small spaces, but impressive results.

FURTHER STUDY

The general patterns envisaged for parasitic species include small, relatively homozygous populations with little gene flow between populations, which results in many specialized races, rapid evolution and speciation without geographic isolation, and an abundance of sibling species. Short generation times, with large fluctuations in population sizes, and narrow environmental tolerances contribute importantly to the evolutionary potential of parasitic species. Thus many of the factors involved in defining the "kind of species" (Mayr, 1963, Table 14-1) a parasite is, or the sort of genetic system likely to be found in parasites can be inferred. These generalizations, reached by using the inductive process, need critical evaluation based on more information on natural populations in order to test the generality of the concepts proposed here. Parasitic species are not peculiar in having their genetic systems inadequately understood (cf. Mayr, 1963; Wilson et al., 1975), and all aspects of the biology of these organisms need further investigation. Here aspects central to the understanding of parasite evolutionary biology are considered.

In sexually reproducing parasites population structure requires much attention. What is the effective population size, the distance moved by the dispersal phase of parasites, the frequency of gene flow from one population to another, the behavior of individuals which influence mating patterns within and between populations? The genetics of parasite species and races should receive much more attention. A comparative approach using both sexually and asexually reproducing parasites should be em-

ployed to examine the variation inherent in siblings and populations, and its effect on survivorship; the physiological tolerances of individuals and its variation, both within and between population centers. Finally, the influence of host shifts should be investigated by direct observation of natural examples, especially before speciation, and by experimental manipulation. An experimental approach to the evolutionary biology of parasites, inadequately used to date, holds great promise for the further development of concepts on the ecology and evolution of parasites.

SUMMARY

There are probably more species of parasite than all non-parasite species combined. In the British insect fauna only 3.9% are estimated to be predators, whereas 35.1% are parasitic on plants, and 37.0% are parasitic on animals. In a parasite food chain based on plants, trends are probably in the direction of i) smaller size, ii) shorter life cycles, iii) more specialized species (i.e., lower ranges of tolerance), iv) less predictable resources, v) greater population fluctuations, vi) more patchily distributed hosts, vii) greater isolation between populations, viii) higher evolutionary rates. Five concepts are generated to account for the extensive adaptive radiations seen among parasitic taxa: 1) Parasites are adapted to exploit small, discontinuous environments. 2) Parasites represent the extreme in the exploitation of coarse-grained environments. 3) Evolutionary rates and speciation rates are high. 4) Adaptive radiation is extensive and depends upon, a) the diversity of hosts being exploited, b) the size of the host target, c) the evolutionary time available, d) the selective pressure for coevolutionary modification and e) the mobility of hosts. 5) Types of speciation other than through geographic isolation are at least as important as allopatric speciation. Areas of emphasis for further study are discussed.

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