NICHE BREADTH AND DOMINANCE OF PARASITIC INSECTS SHARING THE SAME HOST SPECIES[1]

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Abstract. A guild of six parasitic insects (Hymenoptera) which attack cocoons of the same sawfly populations was composed of four indigenous and two introduced species. The indigenous parasitoids included the ichneumonids, *Pleolophus indistinctus* (Prov.), *Mastrus aciculatus* (Prov.), *Gelis urbanus* (Brues), and *Endasys subclavatus* (Say), and the introduced species were the ichneumonid, *Pleolophus basizonus* (Grav.), and the eulophid, *Dahlbominus fuscipennis* (Zett.). Their distributions were sampled on five variable requirements, or resource sets. Litter moisture content and seasonal activity varied within plots, and host density, host species, and plant community varied between plots. Although the distributions of the indigenous species overlapped, in relative terms each species occupied one position in the niche space that was poorly exploited by all other guild members. Such an "enclave" permitted each of the first three species to develop a zone of dominance over the other parasitoids. The introduced species had no recognizable enclave. The most abundant guild member, *P. basizonus*, was dominant in the sites most favorable to litter-searching parasitoids. It had the broadest niche over the range of litter moisture content and length of seasonal activity, and it interacted more with all other species than any other guild member. It was a better competitor than the next most broadly adapted species, *P. indistinctus*. Competitive superiority is proposed as the driving force behind abundance, leading to dominance in favorable sites. The density-dependent interaction between individuals, which results in dispersal, appears to be responsible for the occupation of a broader niche.

Interest in natural insect populations has focused on mortality factors that are likely to contribute to population fluctuations. In some studies, mortality caused by parasitoids was the most potent single factor in the prediction of the subsequent host population (Morris 1959, Nielson and Morris 1964, Auer 1968). In these investigations and others, parasitoid numbers showed a positive response to an increasing host population (Klomp 1968, Varley and Gradwell 1968). In every study cited, this response reached a peak before the host population was completely exploited. The correlative method used in these large projects precludes an insight into the reasons for this truncated response. Because it is a prominent feature of natural host-parasitoid relationships, it is of interest to examine the interaction carefully. As one approach to the problem, I have studied the organization within the parasitoid complex as it is influenced by the host population and other environmental factors.

Field studies were made on six species of hymenopterous parasitoid which attack the same host, *Neodiprion swainei* Midd., in the cocoon stage. They constitute a guild of species, exploiting the same resource in a similar manner (Root 1967). Two species, *Pleolophus basizonus* (Grav.) (Ichneumonidae) and *Dahlbominus fuscipennis* (Zett.) (Eulophidae),

are introduced from Europe. The remainder are indigenous species of ichneumonids: *Pleolophus indistinctus* (Prov.), *Mastrus aciculatus* (Prov.) *Endasys subclavatus* (Say) and *Gelis urbanus* (Brues).

The parasitoids are active in June when the host cocoons are abundant (Fig. 1). The host emerges from the cocoon in late June, and only already parasitized cocoons remain as food supply for the active parasitoid population. In July, the most abundant parasitoids that attack larvae emerge, leaving only cocoons containing parasitoids that attack cocoons in the forest litter. Intense competition for oviposition sites results, and hyperparasitism becomes common until the supply of cocoons is replenished in September (Price and Tripp, *unpublished data*). At this time mature larvae, with and without larval parasitoids, fall to the ground and spin cocoons. In some years, a small proportion of hosts in the study area remain in prolonged diapause during the summer. Those that are not too deeply buried become parasitized early in the season.

Previous results (Price 1970a) indicated that *P. basizonus* was dominant at high host densities and acted as an organizer species in the parasitoid fauna. Two other species, *M. aciculatus* and *P. indistinctus*, became dominant in less favorable, peripheral zones. This paper examines more closely the qualities of *P. basizonus* that may contribute to its dominance in favorable sites. The causes and consequences of these qualities are suggested. The analyses also suggest how
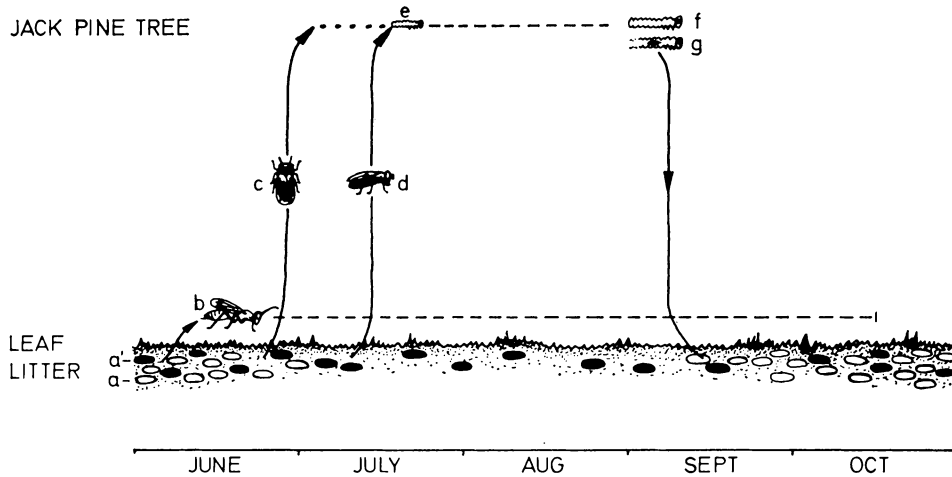
Fig. 1. Phenology of events affecting competition for hosts by cocoon parasitoids. The overwintered host-cocoon population is composed of unparasitized cocoons (a), and parasitized cocoons (a'). From a', cocoon parasitoids (b) and larval parasitoids (d) emerge. From a, the host sawfly (c) emerges to oviposit in the jack pine tree. Eggs hatch, the larvae (e) feed in the tree until maturity (f) and then drop to the ground to spin cocoons. Some host larvae contain larval parasitoids (g).

the indigenous species are able to coexist with this introduced competitor.

The study area was located on the west side of the St. Maurice River watershed in Quebec, Canada. The vegetation of this area has been described (Price 1970a). Field data were collected in 1967 and 1968 and laboratory observations were made in 1969.

METHODS

The description of the niche as an n-dimensional hypervolume, given by Hutchinson (1957), provides a conceptual basis for a method of estimating the niche size occupied by organisms. By studying the distribution of parasitoids on five variable requirements or resource sets, I have attempted to identify differences in niche occupation between parasitoid species. The resource sets were composed of units, in which sample points were located. When these units could be ranked, the set formed a gradient. Three resource sets represented gradients: litter moisture content (7 units), seasonal activity (12 units), and host density (3 units). Two sets could not be ranked: host species (2 units) and plant community (3 units). The first two resource sets varied within sample plots. They represented microenvironmental differences, and the remaining sets varied between plots, since the units in them were large in comparison to the sample plots. The space that each unit occupied in the study area and the distance between units on a gradient were not measured. They were treated as if equal.

The within-plot factors are important in determining which species can coexist in the same small locality. Between-plot factors refer to major environ-

mental requisites that species may utilize as enclaves from competition. Because these effects represent different scales of influence on parasitoid distributions, they are treated separately in this study.

The distributions of parasitoids in the microenvironments were evaluated by locating sample points in different types of soil cover. These units represented a spectrum of moisture contents and, when arranged in order, gave an estimate of the activity pattern of parasitoids on a moisture gradient. The gradient was composed of seven soil-cover types, listed from dry to wet: sand, pine litter, a mixture of pine litter and lichens (*Cladonia* spp.), lichens alone, a mixture of lichens and moss [*Pleurozium schreberi* (Brid.) Mitt.], moss alone, and the hardwood litter of small shrubs and trees in forest stands of jack pine, *Pinus banksiana* Lamb. Sampling was continued from June through August so that the seasonal activity pattern of each species could be studied within a jack pine stand.

Sample points were also located in different jack pine stands and other plant communities, to detect the macroenvironmental influences on parasitoid distribution. Three levels of host (*N. swainei*) density were sampled: high (about 3–5 cocoons per 30 by 30 cm sample), moderate (about 0.5–1 host cocoons per sample), and low (about 0.01 host cocoons per sample). High populations of two host species, *N. swainei* and *Neodiprion pratti banksianae* Roh., that occur in jack pine stands were also sampled. The latter species was sampled only in 1968. These data were used as an estimate of the host species set in calculations for niche overlap in 1967. Three plant communities were sampled: jack pine; black spruce,

Picea mariana (Mill.) BSP.; and hardwood. The hardwood stands included paper birch, *Betula papyrifera* Marsh.; trembling aspen, *Populus tremuloides* Michx.; and maples, *Acer rubrum* L. and *A. spicatum* Lam.

Each sample point consisted of a 15 by 15 by 5 cm cage of galvanized wire cloth, with wires 6.5 mm apart, containing humus, level with that outside the cage. Five cocoons were placed on the humus and covered with the same type of soil cover as was around the cage. The cage was closed and left for a week, after which time the cocoons were removed and immediately replaced by another five cocoons. Female parasitoids searching in the litter could enter the cage, oviposit, and leave unimpeded. Therefore, the sampling procedure did not appreciably influence the parasitoid population outside the cage. The removed cocoons were reared to maturity. From the rearings, the species of female that laid the eggs could be determined. The cages were necessary to protect the cocoons from small mammal predation. As the sample points were minute compared to the area outside, they sampled without interference the natural parasitoid population outside the cages which was influenced by small mammal predation of cocoons.

Sampling lasted 12 weeks each season. A total of 146 and 140 cages, and 8,760 and 8,400 cocoons, were used in 1967 and 1968, respectively. They yielded 688 and 1697 parasitoid individuals on which the analyses are based. The percentage parasitism of the planted cocoons was therefore 8% and 20% in the 2 years.

The extent to which each species of parasitoid exploited the different portions of the resource sets available to it was calculated by Levins' (1968) niche breadth formula,

$$B = 1/\sum_{i=1}^{n} pi^2$$

where p_i is the proportion of a species found in the *i*th unit of the resource set and n is the number of units in the set. For the range of values obtained in this study, B was closely correlated with the niche width measure, W, proposed by McNaughton and Wolf (1970) (e.g., on the moisture gradient the correlation coefficient, $r = .99$, df $= 11$, $P < .01$; on the time gradient, $r = .97$, $df = 11$, $P < .01$).

Interaction between species was estimated by Levins' (1968) formula for niche overlap,

$$\alpha_{ij} = \sum_{h} p_{ih} p_{jh} (B_i)$$

where α_{ij} is the niche overlap of species *i* over species *j*, p_{ih} and p_{jh} are the proportions of each species in the *h*th unit of the resource set, and B_i is the niche breadth of species *i*.

The similarity in distribution of species was calculated using the estimate of proportional similarity,

$$PS = \sum_{i=1}^{n} p_i$$

where p_i is the proportion of the less-abundant species of a pair in the *i*th unit of a resource set with *n* units. This formula (using percentages) has been employed frequently in comparative studies of communities and species (e.g., Whittaker 1952, Whittaker and Fairbanks 1958, Southwood 1966).

As the parasitoids operate in a highly competitive situation (Price and Tripp, *unpublished data*), factors which may influence their direct interaction were examined. These observations were restricted to the two most closely related species, *P. basizonus* and *P. indistinctus*. The length and width of the eggs of each species were measured to give an estimate of the relatives sizes of the first instar larvae. When the larvae hatch they attack and kill any other eggs or larvae present in the host cocoon (Price 1970b) so that the larger larvae should be the stronger competitors in direct aggressive encounters. To test this directly, one egg of each species was introduced into a host cocoon following the method developed by Green (1938). As only one larva can survive on a host, rearings to maturity indicated which species had the superior competitive ability.

The longevity and fecundity of *P. basizonus* and *P. indistinctus* were measured using the techniques already described (Price 1970b, c).

RESULTS

Distribution within plots

The three most abundant species of parasitoid, *P. basizonus, P. indistinctus,* and *M. aciculatus,* exhibited different patterns of distribution on the moisture gradient (Fig. 2). The pattern of each species was similar in 1967 and 1968, although *P. basizonus* was much more abundant in 1968. The broad and flat distribution of *P. basizonus* contrasted with the peaked distributions of *P. indistinctus* and *M. aciculatus*. The abundance of *P. indistinctus* reached a peak in the moist units of the gradient, while *M. aciculatus* was concentrated in the drier units of the gradient. The minor species, *E. subclavatus, G. urbanus,* and *D. fuscipennis,* showed narrow occupation of the moisture gradient in 1967 and broad occupation in 1968. The small sample sizes for these latter species were probably responsible for this large variation.

May temperatures were higher in 1968 than in 1967, so sampling was started earlier in the warmer spring (Fig. 3). *Pleolophus basizonus* was active for longer than any other species in 1967, although its abundance was less evenly distributed throughout the season than that of *P. indistinctus*. In 1968 the activity period of *P. basizonus* must have been longer
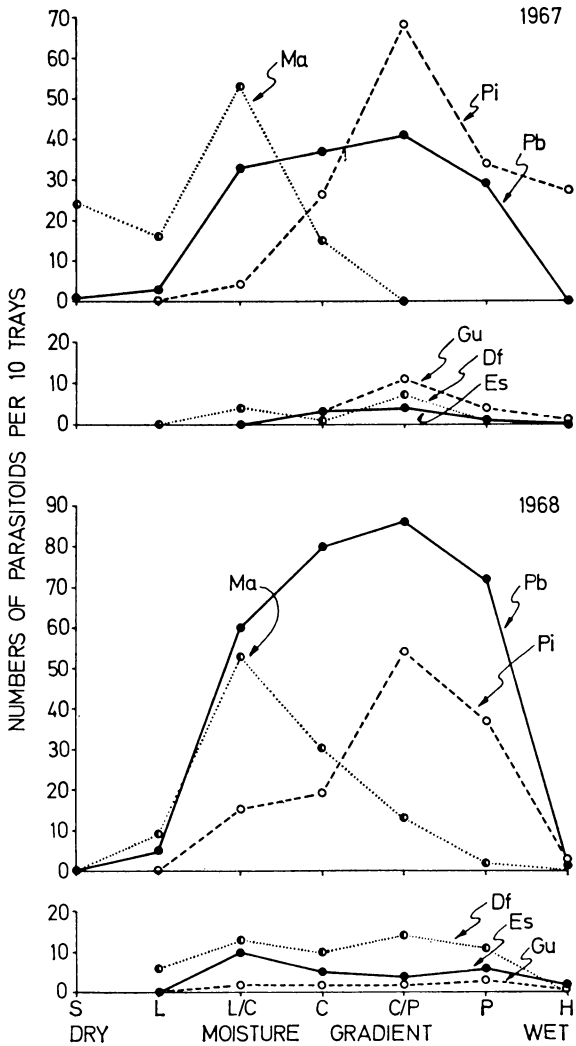
FIG 2. Distribution of parasitoids on a moisture gradient. The six species are divided into the three major and the three minor guild members for each year. S, sand; L, pine litter; L/C, litter plus lichen; C, lichen; C/P, lichen plus moss; P, moss; H, hardwood litter. Pb, *P. basizonus;* Pi, *P. indistinctus;* Ma, *M. aciculatus;* Es, *E. subclavatus;* Gu, *G. urbanus;* Df, *D. fuscipennis.*

than any other species, judging by the level of activity at the start of sampling. Also, its proportional distribution of activity was more even throughout the season than other species, indicating that *P. basizonus* tended to exploit the time available in a season more fully than other species.

Distribution between plots

In the set of host densities sampled, *P. indistinctus* was the most evenly distributed species (Fig. 4). In contrast, the numbers of *P. basizonus, M. aciculatus,* and *D. fuscipennis* were concentrated in the moderate and high host-density units.

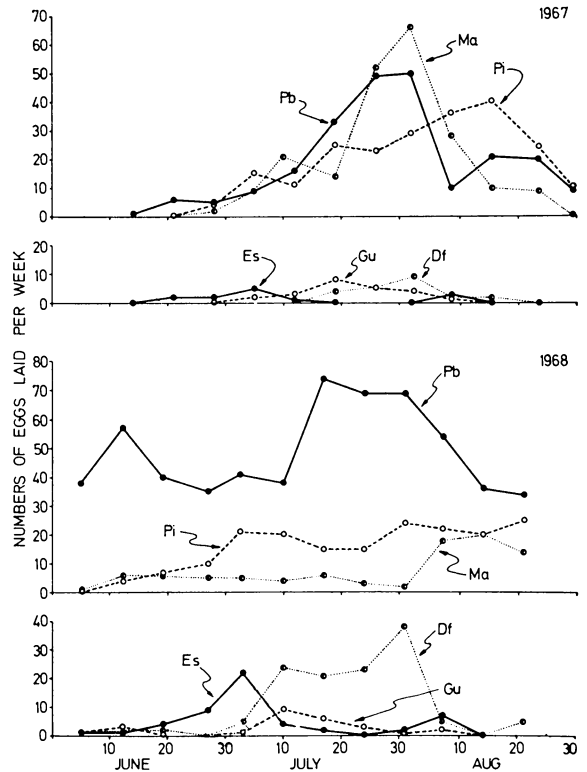Only *E. subclavatus* was evenly distributed be-

FIG 3. Seasonal activity of parasitoids, estimated by the number of eggs laid in all cocoons exposed in that week. Division of species and symbols as in Fig. 2.

tween the two host species *N. swainei* and *N. pratti banksianae* (Fig. 4). *Pleolophus basizonus* was dominant in jack pine stands where *N. swainei* was abundant and *P. indistinctus* was even more dominant in *N. pratti banksianae* populations.

Of the three plant communities studied, jack pine stands supported the only appreciable parasitoid population (Fig. 4). The host species required by the parasitoids were clearly concentrated in jack pine stands. Only *G. urbanus* was evenly distributed between plant communities, indicating a different spectrum of host utilization.

The difference in distribution of species on the moisture gradient within a plot, and host densities between plots were combined to show how the species divide up the area available to them (Fig. 5). There was a strong interaction between these two influences on parasitoid distribution. *Mastrus aciculatus* was dominant in dry sites having a high host density. Conversely, in a high host density on moist sites, *P. basizonus* was dominant, while in a low host density on moist sites, *P. indistinctus* was dominant. No species exploited low host populations in dry sites. In each case, dominance was associated with reduced species diversity (H'), leaving the moderate host densities, in mesic sites, with the highest species diversity of parasitoids. The most abundant species,
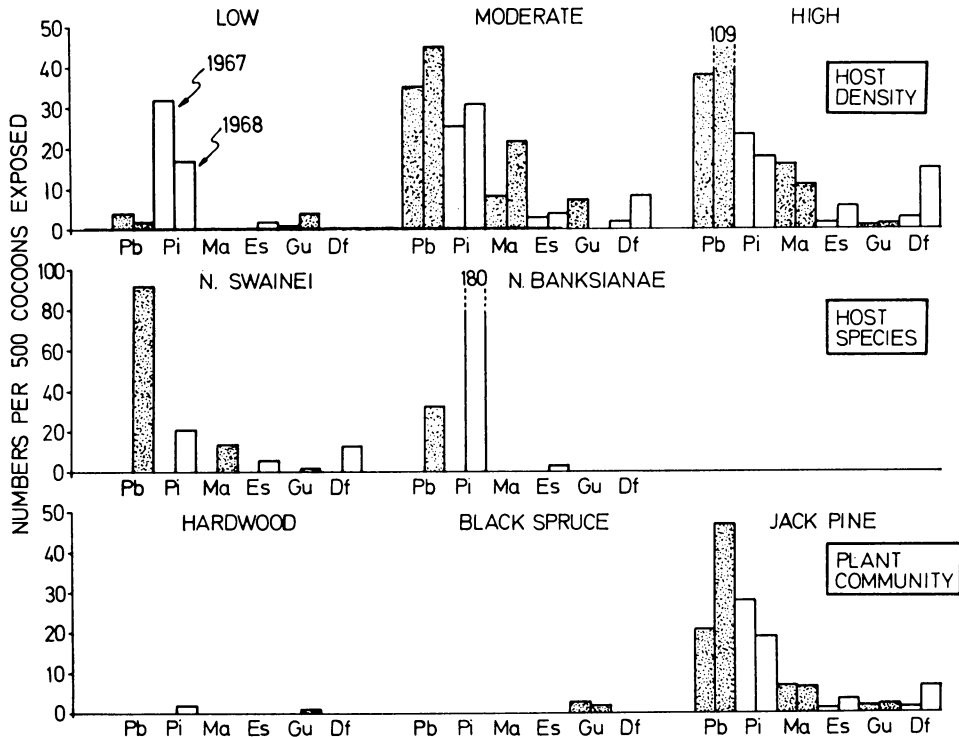
FIG 4. Distribution of parasitoids in three resource sets: top, host density; middle, host species; bottom, plant community. Symbols as in Fig. 2. In each unit of the resource set each species is represented by two bars, one for each year, except in the host species set which was sampled only in 1968. Alternate species are stippled for clarity.
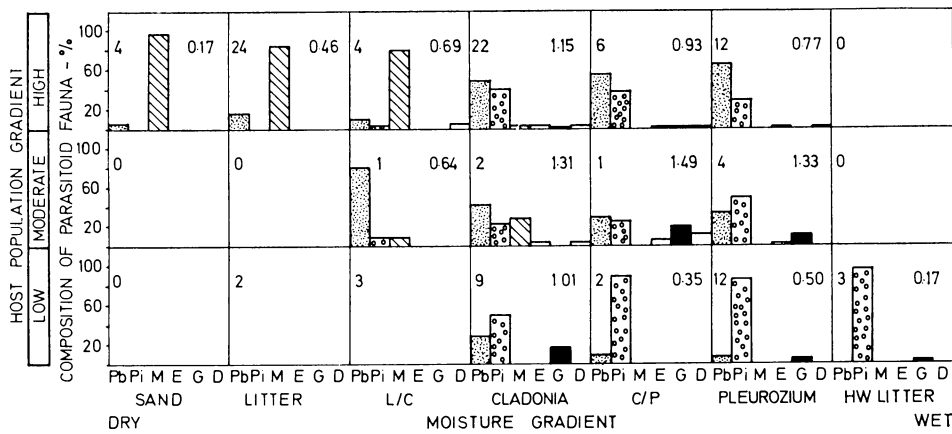

FIG. 5. Percentage of the parasitoid fauna represented by each species in each unit of area on two gradients, moisture and host density, 1967. In each unit, the species are arranged in order as in Fig. 4, and the units are as in Fig. 2. The number of sampling trays per unit is shown on the left of each unit and the species diversity index, H', on the right.

P. basizonus, was dominant in the most favorable site, where hosts were abundant and where the moist litter conditions resulted in little physiological stress.

Niche breadth

The proportion of the available resource that was utilized by each species on the five resource sets was compared by calculating their niche breadths, B (Fig.

6). In both within-plot variables, moisture and time, *P. basizonus* had the largest average niche breadth. Of the three major species, *P. indistinctus* had the next broadest niche and *M. aciculatus* the narrowest niche. The values obtained for the minor species in different years on the moisture gradient were highly variable.

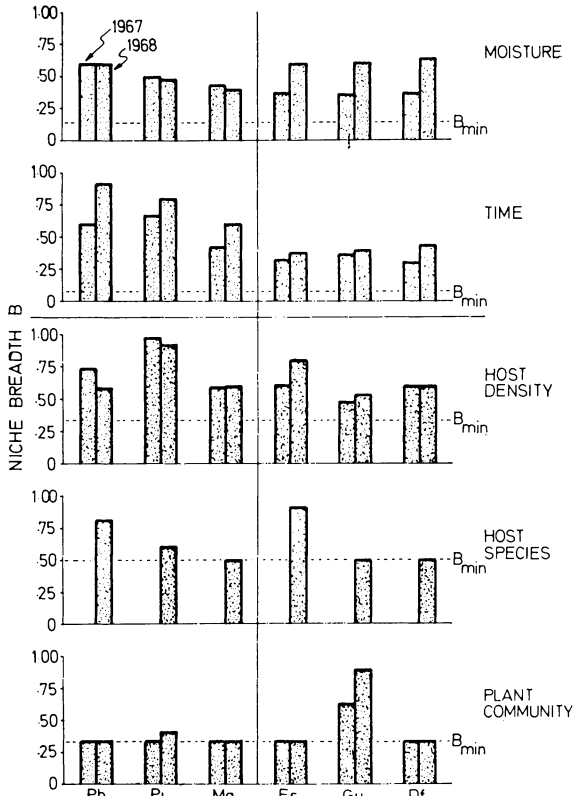*Pleolophus basizonus* did not have the broadest

FIG. 6. Niche breadths, B, of parasitoid species within plots, above transverse line, and between plots, below. Major species are on left of vertical line, minor species on the right. Symbols as in Fig. 2. B_{min} is the reciprocal of the number of units in the habitat set.

niche on resource sets that varied between plots. However, it was broadly distributed on two sets, host density and host species. *Pleolophus indistinctus* had a broader niche in the range of host densities, *E. subclavatus* in the two host species, and *G. urbanus* in the plant communities.

Niche overlap

The niche overlap, α, of one species over another was calculated for every combination of species in each resource set. This value gave an estimate of the impact one species was likely to have on another. As Levins (1968) pointed out, the overlap of activity, or impact, will be lessened by the influence of more than one resource set operating together, provided that each set influences each species in a different way. Therefore the overlaps occurring on the resource sets, when multiplied together, gave a relative value to the amount each species overlapped another when factors were considered together. These values were calculated for each pair of species and the products obtained for within-plot effects were kept separate from those for between-plot effects. The reasons for this have been given in the methods.

For each species five values were obtained, there being five other guild members any one species could interact with. The mean of these five values gave an estimate of the relative interaction each species experienced with the remainder of the parasitoid complex. To obtain absolute estimates of mean overlap each unit of a resource set should be calibrated equal to other units, and the same scale should be utilized for each resource set. These conditions are not met in the present study, and the values calculated are therefore used only as relative estimates of overlap.

The mean niche overlap within plots was greatest for *P. basizonus* (Fig. 7). Its closest relative, *P. in-*
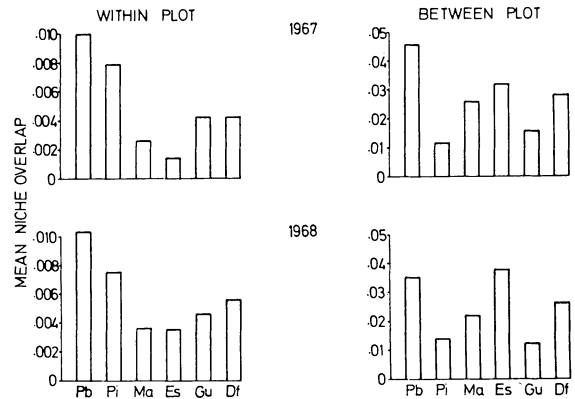

FIG 7. Mean niche overlap for each parasitoid species, derived from the products of niche overlap values in within-plot and between-plot habitat sets. Symbols as in Fig. 2.

distinctus, had the next broadest mean niche overlap. *Dahlbominus fuscipennis,* one of the introduced species, showed moderate overlap over all other species. The mean niche overlap between plots was again greatest for *P. basizonus* in 1967. The lower value obtained for this species in 1968 was due to its great increase in numbers in the most favorable sites, which resulted in less-even distribution on the host-density gradient. The outcome was reduced niche breadth, in contrast to the increased niche breadth of the minor species, *E. subclavatus.* The latter species had the broadest mean niche overlap in 1968 although, as a minor species, it could never greatly influence the parasitoid fauna. Between plots, *P. basizonus* therefore had the greatest influence on the parasitoid complex.

Of the four indigenous parasitoid species, two, *M. aciculatus* and *E. subclavatus,* had effective means of partitioning the resources so that they interacted little with the other species. This was reflected in the low values for mean niche overlap within plots. Conversely, the remaining species, *P. indistinctus* and *G. urbanus,* had low values for mean niche overlap in between-plot resource sets. By considering the hab-

itat sets together, an enclave for each of the indigenous species has been identified where they can exist without severe interference from the other species. This amelioration of interaction over parts of their distributions has not been observed for the two introduced species.

Once the relative value for overlap had been calculated, the species that were the most similar in their distributions were determined. This indicated the species that experienced the greatest interference from the most abundant species, *P. basizonus*. The proportional similarities, *PS*, were calculated using the same approach as for niche overlap, only the means were not used, leaving five values of similarity for each species. Within plots, when litter moisture and seasonal activity were considered together, *P. basizonus* and *P. indistinctus,* the two most closely related species, showed the greatest similarity (Fig. 8). With such broadly overlapping distributions as
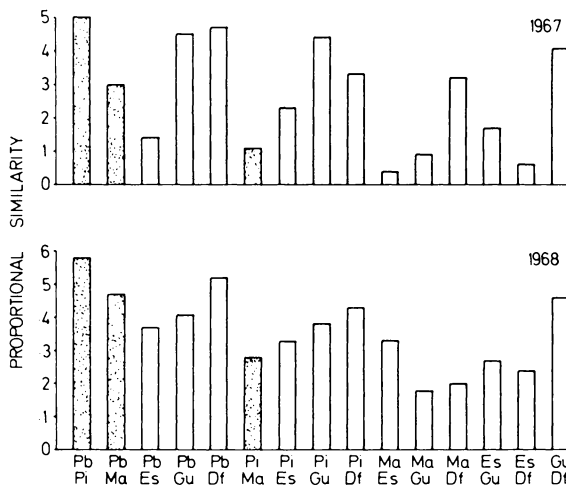

FIG. 8. Within-plot proportional similarity of parasitoid distribution. Columns for similarities between major species are stippled. Symbols as in Fig. 2.

50% in 1967 and 58% in 1968, competitive interaction was likely to be severe. Many of the other high values of similarity involved one or both of the introduced species.

Between-plot similarities showed that the introduced species had high values when compared to the indigenous species (Fig. 9). In five of the six high values of similarity, the introduced species were involved. The indigenous species generally showed low values of similarity, indicating an effective partitioning of the area between species with respect to the three habitat sets.

The value of between-plot similarity for *P. basizonus* and *P. indistinctus* was low each year. Therefore, the existence of the latter species was not threatened since it had an effective refuge from severe interaction with *P. basizonus*.
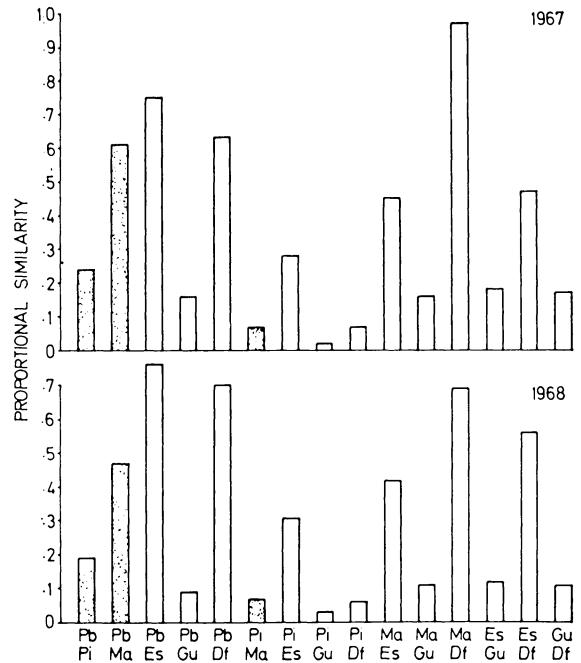

FIG. 9. Between-plot proportional similarity of parasitoid distribution. Columns for similarities between major species are stippled. Symbols as in Fig. 2.

Interactions between P. basizonus and P. indistinctus

Since *P. basizonus* and *P. indistinctus* showed the greatest similarity in their distributions on the two within-plot sets, these species were likely to show the strongest competitive interaction. The fecundity and longevity of each species were not significantly different (mean fecundity: *P. basizonus* 1.68 eggs per day, *P. indistinctus* 2.18 eggs per day, $P_{Pb=Pi} > .40$, $n = 6$ and 4, respectively; mean longevity: *P. basizonus* 23.1 days, *P. indistinctus* 28.7 days, $P_{Pb=Pi} > .10$, $n = 24$ and 17, respectively). *Pleolophus basizonus* was active earlier in the spring than *P. indistinctus* (Fig. 3) at a time when host cocoons were most abundant and competition for them was least severe. *Pleolophus basizonus* therefore had an early advantage.

Pleolophus basizonus had a larger second generation than *P. indistinctus.* Of the eggs laid in 1967, 51% of *P. basizonus* females emerged the same year and 49% emerged in 1968. Similarly, of the eggs laid in 1968, 58% emerged in that year, and 42% emerged in 1969. There were two well-defined, more or less equally abundant generations each year. In *P. indistinctus* populations, the second generation in a year was very poorly developed. Eggs laid in 1967 produced 2% of the females in the same year and 98% in 1968. Eggs laid in 1968 produced 12% of the females in the same year and 88% in 1969. The response of this native species to high host numbers must be slower than that of its European relative.

Pleolophus basizonus eggs were 7.5% longer and 10.0% wider than those of *P. indistinctus* (*P. basizonus* mean egg size, 1.14 by 0.33 mm, *P. indistinctus* mean egg size, 1.06 by 0.30 mm. $P_{Pb=Pi} < .005$ and .001, $n = 20$). Therefore, *P. basizonus* larvae have an advantage when confronted with *P. indistinctus* larvae within the cocoon. This advantage is reflected in the results of the experiment when an egg of each species was introduced within the cocoon. Of the 100 replicates, *P. basizonus* emerged from 68% and *P. indistinctus* from 32%.

DISCUSSION

Usually, in competition for a nonrenewable resource, time of utilization does not provide an effective means of avoiding competition. However, although host cocoons were not renewed naturally during the 12-week period of study each year, the course of time presented the parasitoids with a complex set of conflicting selective pressures. Although hyperparasitism was frequent during the summer, at each successive attack there was progressively less food in a cocoon. Thus there was a partial advantage to early oviposition in a cocoon that had the maximum food supply available. Also, the act of searching and ovipositing helped to reduce immediate competition among the progeny, since other females would avoid the trail left by the previous female (Price 1970d). The earliest egg laid in a cocoon had the greatest chance of hatching first and consuming other eggs laid subsequently. However, when the parasitoid larva was larger, it became subject to parasitism itself, and the parasitoid acting later in the season had a partial advantage. Differences in seasonal activity also resulted in the different exploitation of the two hosts, *N. swainei* and *N. pratti banksianae* (Fig. 4). *Pleolophus basizonus*, with its early first generation, exploited *N. swainei* while this host was abundant in the spring. The life cycle of *N. pratti banksianae* was quite different: the eggs overwintered and cocoons were spun in late July. Therefore, the cocoons became available just as *P. indistinctus* was reaching its peak abundance for that season. These factors, acting on the temporal differences in parasitoid activity, probably exerted a strong selective pressure on each guild member for an efficient strategy to survive the difficult period through the summer. It appears that the combination of early seasonal activity, two equal generations per season, and superior competitive ability within the cocoon has enabled *P. basizonus* to exploit most successfully the most abundant host, *N. swainei*.

I found that *P. indistinctus* was dominant in plots with a low host density, but this species was competitively displaced from high host populations by *P. basizonus* (Price 1970a). Also, *M. aciculatus* prevailed in dry plots, and *G. urbanus* had an enclave in black spruce and hardwood stands. Similar zones of dominance for these species were evident in the present study. However, the distributions of *M. aciculatus* and *E. subclavatus* included enclaves of reduced interaction with the other species when litter moisture and time dimensions were considered as microenvironmental variables. The remaining indigenous species, *P. indistinctus* and *G. urbanus*, experienced little interaction with other guild members in between-plot influences, just as they were identified in the previous study.

It is significant that no clearly defined enclaves from interference were observed for the two introduced species, *P. basizonus* and *D. fuscipennis*. These parasitoids were selected for introduction as biological control agents because of their abundance and wide distribution in Europe (Morris and Cameron 1935; Morris, Cameron, and Jepson 1937). On introduction to Canada they might therefore be expected to show broad niche exploitation and competitive superiority. There is evidence that *D. fuscipennis* becomes more abundant in the decline phase of a host population (Bobb 1965, Nielson and Morris 1964). Its narrow niche observed on some dimensions in this study may result from incomplete exploitation of the available resources since the host population was still increasing.

Another possible manifestation of the dominance of *P. basizonus* is its broad natural distribution, not only in Europe but throughout the Palearctic region (Townes, Momoi, and Townes 1965). Its range includes the center of distribution for the tribe Echthrini, to which the genus *Pleolophus* belongs (Townes 1969). Therefore, this species may have the potency expected of species existing in the center of distribution for the taxon (Darlington 1959). In this species, potency is manifested as competitive ability which acts as a general adaptation (Brown 1958) not influenced greatly by local conditions.

The characteristics of the most abundant species, *P. basizonus*, in the parasitoid guild were dominance in the most favorable sites (Fig. 5), broadest niche on microenvironmental dimensions (Fig. 6), greatest mean niche overlap (Fig. 7), competitive superiority and lack of an enclave from interference (Fig. 7). *Pleolophus basizonus* was the only species to respond constantly and positively to increasing host density in the field, and may displace *P. indistinctus* into peripheral zones of the host population (Price 1970a).

There are probably several factors that permit high relative abundance. The first species to reach a new resource can increase rapidly, free from competition, and become abundant. In the presence of others, one species can specialize so that it becomes competitively superior over a portion of a resource set. If the conditions in this portion are widely distributed, then the

species can become abundant (McNaughton and Wolf 1970). A third situation can result when a generally adapted species, which exploits a broad spectrum of resources, becomes abundant in the presence of other species. This broad distribution of activity must depend on competitive ability of a very general nature, different from the ability derived from specialization (Brown 1958). Specialization, with the consequent narrowing of the exploitation curve, tends to reduce competition. Broad exploitation increases competition. Thus what may be termed "competitive dominance" involves a broadly adapted organism that becomes the most abundant species through competitive ability. It results in the dominant occupying potential niche space of other species. This prevents the subordinates from attaining an abundance that could be realized in the absence of the dominant. Since food is frequently in limited supply, the influence of the dominant species will usually involve coexisting members of the same guild and trophic level. Therefore the characteristics of *P. basizonus* listed above are probably typical of many competitive dominants.

One difficulty with this concept is that dominance cannot easily be demonstrated, since abundance and distribution data usually measure only realized niche occupation, or the outcome of competition. Ideally, the *process* of competition should be analyzed to determine potential niche occupation by the subordinate species. Dominance is more readily observed experimentally (e.g., Connell 1961) or when a species is introduced into an area, as in the present study.

In this concept competitive superiority is seen as the driving force behind dominance. Four of the characters of the dominant species in this study that may contribute to its competitive prowess are: (i) it is the earliest to emerge in the spring, (ii) there are two equally abundant generations per year, (iii) it is the largest parasitoid in the guild (Price, *unpublished data*), and (iv) it lays the largest eggs (*unpublished data*). These characters are specific adaptations of *P. basizonus* which may be important only within the context of the guild and resources under study. The adaptations that confer competitive ability will differ between systems and can be understood only within the context of a particular system. Thus, an insight into community organization may depend upon an understanding of the detailed strategy of the dominants.

Competitive ability enables *P. basizonus* to become abundant in the face of competition, and ultimately dominant in the guild. Abundance permits high genetic diversity within a population, and this, in turn, may result in broad exploitation of a resource (McNaughton and Wolf 1970). The colonization of new niche space through genetic diversity is probably a

slow process, taking several generations, with a relatively permanent result.

In contrast to the genetic diversity effect, I suggest that density-dependent dispersal can result in the rapid occupation of uncolonized niche space. This dispersal, from centers of abundance in favorable sites, would be driven by increasing interaction between individuals. Female parasitoids recognize and avoid the trails of others, both intra- and interspecifically, and tend to walk faster and to fly, with increased exposure to these trails (Price 1970c, d). This behavior provides the density-sensitive mechanism for dispersal.

The suggested forces leading to the exploitation of a broad niche are summarized on the diagram. The inputs to competitive superiority will be specific to each dominant species.
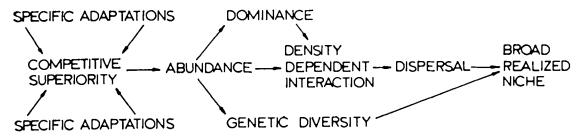
The historical details of parasitoid distribution in the study area lend support to the idea that niche breadth is a density-dependent phenomenon for these parasitoids. In 1965 host populations were high throughout the study area. In August of that year some areas were sprayed with insecticide, which resulted in the areas of low host density sampled in 1967 and 1968. The moderate and high host populations remained in areas left as controls. Thus in early 1965, parasitoid populations were similar in all locations (Price 1971). If genetic diversity had generated broad niche occupation by *P. basizonus,* assuming that insecticidal action was equal on each phenotype, then niche occupation should not have changed appreciably within 2 years. In fact the niche breadth of *P. basizonus* on the moisture gradient was 0.59 in 1967 in high host densities and only 0.30 in low host densities (cf. Fig. 5). The same trend was evident in 1968 (0.56 and 0.41, respectively) indicating a strong density-dependent response in niche occupation.

The ability of a female to leave viable progeny depends on the compromise between remaining in a host population where exploitation by parasitoids is reaching completion, and emigration into areas of unknown host resources. This emigration stage should be reached before the host resource is fully utilized because hyperparasitism becomes less rewarding, hosts become harder to find, and the chances of progeny being hyperparasitized are greater. Thus the density-dependent emigration caused by mutual interaction can be adaptive. Insect herbivores can reach high population densities (e.g., 10 cocoons per 900 cm^2 of litter by *N. swainei*) and interaction between

parasitoid females is likely to become severe at 1 per 900 cm². Therefore the capacity of the habitat to support a parasitoid population is more likely to be dictated by the level of interaction between individuals than by the supply of host cocoons. This would result in the inability of parasitoid populations to fully exploit hosts at high population levels.

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