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CHARACTERISTICS PERMITTING COEXISTENCE AMONG PARASITOIDS OF A SAWFLY IN QUEBEC

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Abstract.—Six parasitoid species (Hymenoptera: 5 Ichneumonidae, 1 Eulophidae) coexist on cocoon populations of the Swaine jack pine sawfly, *Neodiprion swainei* Midd. in Quebec. Their distribution between plant communities was related to host availability except for *Gelis urbanus* (Brues) which has alternative hosts. *Pleolophus basizonus* (Grav.) was dominant at high host densities, tending to displace *Pleolophus indistinctus* (Prov.) which was dominant at low host densities. *Mastrus aciculatus* (Prov.) occupied dry open sites at high host densities, where other species were less numerous. The highest species diversity of cocoon parasitoids occurred at the ecotone around jack pine stands and at moderate host densities in increasing host populations. Furthermore, parasitoids attacking larvae were well represented in moderately dense host populations. As the host density increased, *P. basizonus* became so dominant that it reduced species diversity, particularly among the parasitoids attacking the host larvae. Species diversity can be predicted from the proportion of *P. basizonus* present. This parasitoid acts as an organizer species within the parasitoid complex because of its superior competitive ability. Parasitoids of larvae have a conservative strategy for host exploitation that appears adapted for utilizing low host populations. In contrast, the parasitoids attacking cocoons gain dominance only when host-finding is easy in high host populations.

Factors which enable several species of parasitoids to coexist in the same host population are not well understood. Heatwole and Davis (1965) have found that small differences in ovipositor length enabled three species of *Megarrhyssa* (Ichneumonidae) to exploit different segments of the same host population. However, the general lack of knowledge concerning competitive interactions between parasitoids led Turnbull and Chant (1961) to caution against the multiple introduction of parasitoids for biological control. In order to gain insight on these competitive interactions, I studied the parasitoids of the Swaine jack pine sawfly, *Neodiprion swainei* Midd. in Quebec during 1967 and 1968.

Differences in habitat selection provide one obvious means for species to partition a resource held in common. In such a case, competition will occur only in those habitats that the species share. Therefore the distribution of the parasitoids on *N. swainei* was studied in the three major plant communities, across ecotones between these communities, and at different levels of the host population. The differences in distribution provided a basis for understanding the various evolutionary strategies adopted by parasitoids that exploit the same host.

My approach has been to divide the parasitoid complex on *N. swainei* into two natural categories or "guilds" (Root 1967). The guild concept focuses attention upon groups of species that are most likely to compete with one another. There-

fore all those species that attack the host in the cocoon stage, the cocoon parasitoid guild, were studied in detail. Through an understanding of the organization within this guild I have been able to assess some of its effects on the parasitoids that attack larvae, the larval parasitoid guild.

GUILD MEMBERSHIP AND LIFE HISTORIES

Two members of the cocoon parasitoid guild were introduced from Europe: *Pleolophus basizonus* (Grav.) (Ichneumonidae) during 1933–1940 and *Dahlbominus fuscipennis* (Zett.) (Eulophidae) during 1934–1948 (McGugan and Coppel 1962). These species were liberated against the spruce sawfly, *Diprion hercyniae* (Htg.), but have since become established in my study area on *N. swainei* (McLeod and Martineau 1967).

The remainder of the cocoon parasitoid guild are indigenous nearctic ichneumonids: *Pleolophus indistinctus* (Prov.), *Endasys subclavatus* (Say), *Mastrus aciculatus* (Prov.) and *Gelis urbanus* (Brues). All species oviposit within the cocoon case on the surface of the host. All species may behave as primary parasitoids and all but *E. subclavatus* are known to act as hyperparasitoids on both larval and cocoon parasitoids. The life history of *P. basizonus* in Canada was described by Griffiths (1961) and that of *D. fuscipennis* by Morris and Cameron (1935). No detailed studies have been made on the other species. In the study area all species were active from June until Oc-

tober. The ichneumonids were bi-voltine and the eulophid at least tri-voltine.

The parasitoids that attack host larvae are treated as a guild without reference to individual species in this paper. The members of the guild were the ichneumonid wasps *Exenterus amictorius* (Panz.), *E. diprionis* (Roh.), *Lamachus* sp., *Olesicampe lophyri* (Riley), and the tachinid fly, *Spathimeigenia spinigera* Tnsd. Although the species in this guild attack the host larva, the adult parasitoids emerge from the host cocoon in the following year. While in the cocoon they are available for hyperparasitism by members of the cocoon parasitoid guild. Therefore the cocoon parasitoid guild has the potential to inflict considerable mortality on the larval parasitoid population.

All larval and cocoon parasitoids mentioned in this study have been found in the same sawfly population.

Development of *N. swainei*, the most abundant host available to these parasitoids in the study area, was described by Tripp (1965). Adult sawflies emerge from overwintered cocoons in the forest litter in late June and oviposit in jack pine foliage. The eggs hatch after about 1 month and the larvae feed gregariously in the tree canopy until mid-September when they fall to the ground and spin cocoons. After adult sawfly emergence, the cocoon parasitoids encounter a severe host shortage until the larvae drop from the trees, about 10 weeks later.

STUDY AREAS

The 12 study plots were located on the Laurentian Shield, in the St. Maurice River watershed in the transition zone between the mixed hardwood-conifer and pure conifer biotic provinces (Marie-Victorin 1964) (Table 1). The local area

is dominated by three communities: pure stands of jack pine, *Pinus divaricata* (Ait.) Dumont with a floristically depauperate understory of the ericoid shrubs, *Kalmia angustifolia* L., *Ledum groenlandicum* Oeder, and *Vaccinium angustifolium* Ait.; pure stands of black spruce, *Picea mariana* (Mill.) BSP., with a similar shrub layer; and an association of hardwoods with paper birch, *Betula papyrifera* Marsh., and aspen poplar, *Populus tremuloides* Michx., with maples, *Acer rubrum* L. and *Acer spicatum* Lam., entering the community on rocky slopes and eskers. The understory of the hardwood stands has a comparatively rich floristic composition of which *Aralia nudicaulis* L., *Aster macrophyllus* L. and *Clintonia borealis* (Ait.) Raf. are typical. Linteau (1955) described these associations as the *Kalmia-Vaccinium*, *Cladonia-Vaccinium*, and *Cornus-Maianthemum* site types respectively.

Eight plots were selected in five different jack pine stands. All but plot 3 were located in closed-canopy stands of 45-yr-old trees where the moss, *Pleurozium schreberi* (Brid.) Mitt. and the lichens, *Cladonia* spp., dominated the ground cover. South slopes, such as the one where plot 8 was located, tended to be drier with a ground cover of *Cladonia* spp. and pine-needle litter. Plot 3 was located in a small stand of 20-yr-old jack pine, adjacent to an older stand (plot 2). The trees were open-grown with large unshaded areas where sweet fern, *Comptonia peregrina* (L.) Coult., and cow-wheat, *Melampyrum lineare* Desr., grew interspersed with *Cladonia* spp., dry pine-needle litter and bare sand.

Two plots, 5 and 11, were located in black spruce stands and two plots, 4 and 12, in hardwood stands. Each was typical of the communities already described, consisting of natural regeneration after logging operations about 35 yr ago.

TABLE 1. Location and main characteristics of study areas

Plot	Nearest lake	North lat		West long		Dominant tree species	No. of cages	Other features
		degrees	min	degrees	min			
1	Cousacouta	47	16	73	37	45 yr jack pine	10	Sandy plain, typical site
2	"	47	16	73	37	" " " "	25	Transect across plain
3	"	47	15	73	37	20 yr jack pine	9	Open canopy, much bare sand
4	"	47	14	73	36	Birch, poplar	5	Hardwood regeneration
5	"	47	14	73	35	Black spruce	5	Dense stand, dry site
6	McLaren	47	11	73	31	45 yr jack pine	5	Exposed hilltop
7	"	47	11	73	31	" " " "	11	Transect from sandy plain to rocky hillside
8	"	47	12	73	29	" " " "	10	Dry south slope, little ground cover
9	Chevalier	47	03	73	43	" " " "	8	Transect on undulating topography
10	Chienne	47	04	73	27	" " " "	5	Sandy plain, typical site
11	Traine	47	05	73	25	Black spruce	5	Dense stand, dry site
12	"	47	04	73	23	Birch, maple, poplar	5	Hardwood regeneration

METHODS

The distribution of parasitoids in the study areas was determined by exposing host cocoons to parasitoid attack at sample points in each of the major plant communities. Parasitoids oviposited in these cocoons and the progeny were reared individually, so that the species of the parent could be identified. This method enabled a sample to be taken without appreciably disturbing the parasitoid populations.

At each sample point, a 15 by 15 by 5 cm cage of 4 mesh (per inch) galvanized wire cloth was set into the humus to a depth of about 1.5 cm. Humus was placed in the cage, level with the humus layer outside. On this layer cocoons were placed and covered with the surface materials characteristic of that site. The cage was closed with a galvanized wire cloth lid. This cage permitted access to the parasitoids but prevented small mammals from eating the cocoons.

Five cocoons were exposed in each cage. At weekly intervals, from June through August, 1967 and 1968, fresh cocoons were exchanged with those in the cage. The previously exposed cocoons were labelled and reared in an open insectary. Each sample point therefore resulted in 12 or 13 weekly samples of parasitoid attack throughout two seasons.

A total of 119 sample points in different communities (Table 1) and across two ecotones were used in this study. The cages were located randomly within an area of 0.25 ha in plots 4-6, 8, and 10-12. Plot 7 consisted of a transect of sample points 20 m apart. These plots were used to record the presence and relative abundance of parasitoids only. In the black spruce and hardwood stands no known hosts were present. In the jack pine stands very low host populations were known to exist.

In the remaining four localities, host populations were high and the sample points were used to estimate the relative abundance of the parasitoids, their distribution within stands and across ecotones between vegetation types. The large stand of

jack pine at Lake Cousacouta was sampled in two ways. Sample points about 20 m apart, near the center of the stand, provided an intensive sample (plot 1). Sample points about 200 m apart, arranged in two transects (2.5 km N-S, 2.9 km E-W) provided an extensive sample (plot 2). Plot 3 was located in a 0.25 ha stand of young jack pines near the south arm of the plot 2 transect. It contained nine sample points within 45 m of the ecotone. Together with eight sample points in the 45-yr-old jack pine stand located at intervals up to 45 m from the ecotone, they provided data on parasitoid distribution across the ecotone.

Plot 9 was used to study the relationship between the distribution of parasitoids and host density in greater detail. The 1.0 km transect traversed a jack pine stand. Eight sample points were located on the transect and another eight points were placed across the ecotone between the jack pine and aspen poplar stands. In addition to cocoon planting, the host population density was estimated. In mid-June, at each sample point three soil samples, 30 by 30 cm, dug to the pure sand were searched for cocoons to give the number of cocoons per unit area. Sawfly cocoons were also collected by hand at each sample point and reared individually. The percentage parasitism multiplied by the cocoon density gave an estimate of the parasitoid density per unit area. Thus, plot 9 provided information on both larval and cocoon parasitoids, whereas all other plot data pertained exclusively to the cocoon parasitoid guild.

To evaluate the change in species distributions and the interaction between species, the species diversity index, H' , was used where

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

and p_i is the proportion of the i^{th} species in each sample. This formula estimates changes in the relative information content of a system caused by changes in species numbers and species equitability. Since the number of species in this study is small and therefore not highly variable between samples, H' mainly reflects changes in the propor-

TABLE 2. Cocoon parasitoid distribution in plant communities

Site type	Plots	Total cocoons exposed	Total cocoon parasitoids emerged	No. parasitoids per 500 cocoons					
				P.b.*	P.i.	E.s.	M.a.	G.u.	D.f.
Black spruce	5, 11	575	3	—	—	—	—	2.6	—
Hardwood	4, 12	525	3	—	1.9	—	—	0.9	—
20 yr jack pine	3	600	8 ^c	10.8	5.8	1.7	49.2	—	4.2
45 yr jack pine	1, 2, 6, 7, 8, 9, 10	4, 360	546	28.1	28.2	1.3	1.0	2.2	1.5

*P.b.—*Pleolophus basizonus*, P.i.—*P. indistinctus*, E.s.—*Endasye subclavatus*, M.a.—*Mastus aciculatus*, G.u.—*Gelis urbanus*, D.f.—*Dahlbominus fuscipennis*

tion of each species, or their concentration of dominance (Whittaker 1965).

The influence of different litter types on parasitoid distribution was tested experimentally in 1968. Cages 92 by 92 by 50 cm were located in a mixed jack pine-black spruce stand. The floor of each cage was surfaced with jack pine litter in one half and an alternative litter (either hardwood, black spruce or moss) in the other. Fifteen cocoons were placed in each half of each cage and exposed for 6 days to three conspecific female parasitoids that could move freely throughout the cage. After 6 days the number of eggs laid in cocoons on each litter type was determined by dissection. The species *P. basizonus*, *P. indistinctus*, *M. aciculatus* and *E. subclavatus* were tested against each combination of litter types and replicates were made in subsequent weeks according to the availability of the parasitoids. Statistical differences between litter treatments indicated either parasitoid preference for one litter or easier searching conditions in that litter.

RESULTS

Distribution in plant communities and across ecotones

All species in the cocoon parasitoid guild, except *G. urbanus*, were most abundant, or occurred exclusively in the jack pine stands (Table 2), indicating that the distributions of these species were dependent on *N. swaini*. The independence of *G. urbanus* from this host can be attributed to the general behavior of *Gelis* spp. which commonly hyperparasitize braconid parasitoids of a diverse array of phytophagous insects (Townes and Townes 1951). The record of *P. indistinctus* in a hardwood stand was probably due to a migrant female traversing the area.

In the transition from the jack pine stand at plot

9 into the adjacent aspen poplar stand, parasitoid activity declined rapidly until no parasitoids were recorded 22.5 m from the ecotone. The litter preference experiment (Table 3) indicated that this fidelity to the jack pine stand was not under vegetational influence. None of the parasitoid species showed a preference for jack pine litter or the moss which occurs in jack pine stands over hardwood litter. In contrast, *P. basizonus* and *P. indistinctus* laid significantly fewer eggs in cocoons placed in black spruce litter. This reaction may reinforce other factors that influence parasitoid distribution between jack pine and black spruce stands. However, it cannot be the major contributing factor as the parasitoids laid many eggs in the black spruce litter even though they were absent from black spruce stands in the field.

At plot 3, *M. aciculatus* was the dominant species whereas in the older, less exposed jack pine stands the two species of *Pleolophus* were the most abundant. The change in dominance across the ecotone between plot 3 and the adjacent older stand was clearly defined. The numbers of parasitoids in the old jack pine stand remained fairly constant as the ecotone was approached although the species diversity index, H' , increased to a peak close to the ecotone where habitat diversity was greatest (Fig. 1). This change in species diversity resulted from the declining dominance of *P. basizonus* and a consequent increase in the equitability of the parasitoids. This high species diversity mainly resulted from the overlapping distributions of three parasitoid species. None of these species appeared to require a diverse habitat *per se*. Their concurrence merely reflects the intermixing of their specialized requirements at the ecotone.

In the young jack pine stand the numbers of parasitoids increased because of an abundance of

TABLE 3. Influence of litter type on parasitoid oviposition

Species	No. of replicates	Alternative litter type	Mean no. eggs laid		
			Jack pine litter	Alternative litter	Probability of difference ^a
<i>P. basizonus</i>	6	Hardwood	11.2	12.7	0.22
	6	Black spruce	12.8	10.5	0.03
	6	Moss	19.5	16.3	0.25
<i>P. indistinctus</i>	4	Hardwood	18.5	18.8	0.31
	4	Black spruce	17.5	13.3	0.00
	4	Moss	18.8	16.3	0.06
<i>M. aciculatus</i>	4	Hardwood	15.8	8.8	0.06
	3	Black spruce	9.0	6.0	0.25
	3	Moss	15.0	9.7	0.13
<i>E. subclavatus</i>	2	Hardwood	15.5	10.0	No test
	2	Black spruce	14.0	16.5	No test
	2	Moss	11.0	7.5	No test

^aCalculated by use of Wilcoxon's paired comparison test (Hodges and Lehmann 1964).

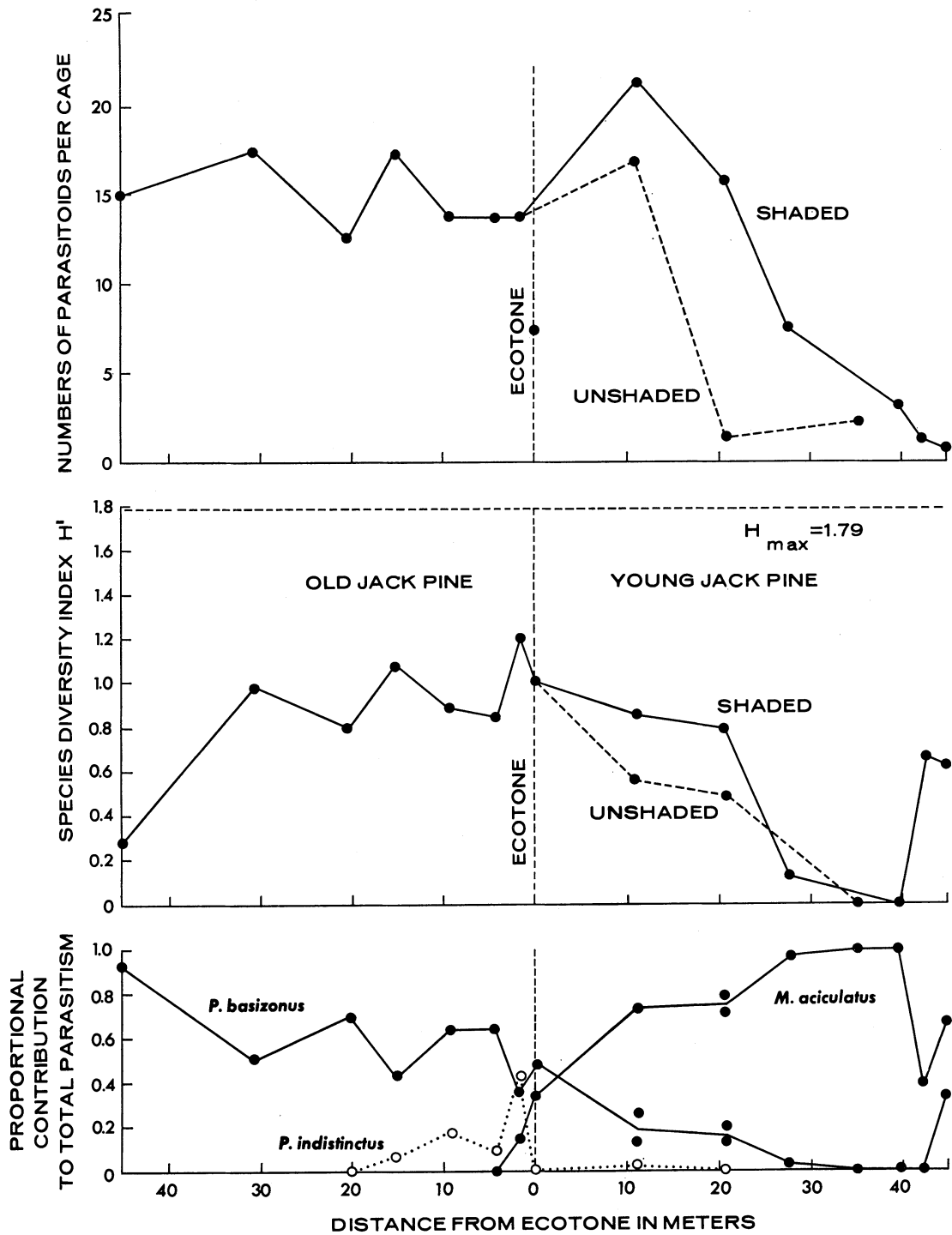


Fig. 1. Transect at plot 3 across an old jack pine-young jack pine ecotone. Each point represents one sample point. Top, numbers of parasitoids per cage; middle, species diversity index (H') per cage; bottom, proportional contribution of *P. basizonus*, *P. indistinctus* and *M. aciculatus* to total parasitism.

M. aciculatus about 10 m from the ecotone and then declined steadily. The species diversity also declined as *M. aciculatus* developed its dominance. The changes in species diversity beyond 40 m were spurious results caused by the small numbers of parasitoids at these sample points.

The lower numbers of parasitoids and the reduced species diversity in unshaded sites suggest that heat extremes and sparse ground cover were important factors influencing parasitoid distribution in plot 3. Low-humidity stress may be a critical determinant of ichneumonid distribution (Townes 1958). It appears that the more highly sclerotized, darker *M. aciculatus* is better adapted for exploiting hosts in this dry site than the other parasitoid species.

Distribution in relation to host density

Data in the previous section indicated that five of the six cocoon parasitoid species occurred almost exclusively in jack pine stands and that there was only a narrow margin around these stands in which they were active. It is clear that the proximal influence on parasitoid fidelity to jack pine stands was host availability. The parasitoids actually showed a positive numerical response to increases in host density (Fig. 2). This within-plot response was also observed between plots having different host densities (Table 4). Coupled with the numerical response there was a reversal in species dominance from *P. indistinctus* at low host densities to *P. basizonus* at high host densities. Again *G. urbanus* showed a distribution more or less independent of *N. swainei* numbers whereas the three remaining species were limited to the higher host densities.

Interaction within the cocoon parasitoid guild

There were three parasitoid species present at low host densities (Table 4). In plot 9, all six species were present. In plots 1 and 2, where the

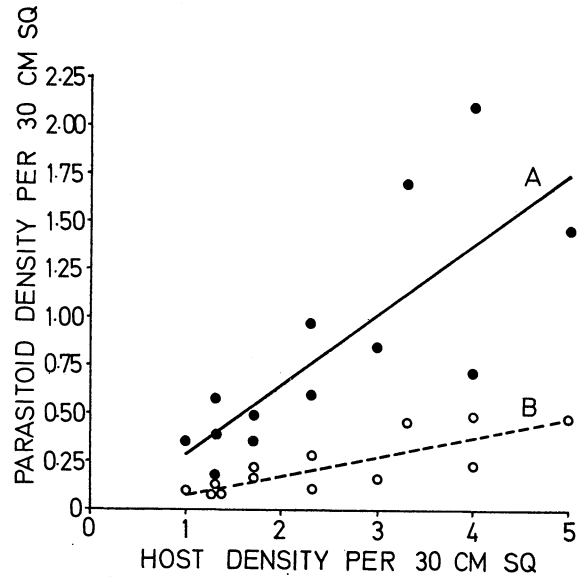


FIG. 2. Absolute numbers of parasitoids in relation to host densities at plot 9. Data are from the hand collection of cocoons and soil sample. A—regression line of cocoon parasitoids per 900 cm² on host density where $Y = 0.3595X - 0.0650$, $r = 0.7831$, $df = 11$, significant at 1% level. B—regression line of larval parasitoids per 900 cm² on host cocoon density where $Y = 0.0968X - 0.0106$, $r = 0.8160$, $df = 11$, significant at 1% level.

host density had been higher, the number of species was reduced to four and five respectively. This pattern was repeated within plot 9. Cocoon parasitoid species diversity increased with host density, reaching a peak at about 2 cocoons per 900 cm² and then declining (Fig. 3). The response of four species of parasitoid (Fig. 4) produced the high diversity at intermediate host densities. As the host density increased beyond 2 cocoons per 900 cm², *P. basizonus* developed a dominance at the expense of all other species. Clearly, *P. basizonus* was the most capable of responding positively to host density. The fact

TABLE 4. Relative abundance of cocoon parasitoids in jack pine stands with different densities of sawfly cocoons

Sawfly cocoon density per 900 cm ²	Plot	Total cocoons exposed	Total cocoon parasitoids emerged	No. parasitoids per 500 cocoons						
				P.b. ^b	P.i.	E.s.	M.s.	G.u.	D.f.	
Low	0.01	6	600	7	1.2	0.8	—	—	3.3	—
	0.01 ^a	7	660	47	1.5	31.8	—	—	2.3	—
	0.01	10	275	24	5.5	38.2	—	—	—	—
	0.01	6	300	39	6.8	58.4	—	—	—	—
High	1.55 ^a	9	550	89	35.5	25.5	2.7	8.2	7.3	1.8
	0.79	2	1,375	219	46.9	26.2	2.9	—	0.7	2.9
	0.79 ^a	1	600	121	57.5	39.2	—	—	1.7	2.5

^aDensities calculated from 125, 900=cm² random soil samples. Other densities were estimated on the basis of the site's proximity and similarity of these areas. At plots 1 and 2, the cocoon density was 3.9 per 900 cm² in 1965 before an aerial insecticide application reduced the density. Since then parasitoid numbers have remained high and reflect a response to the earlier density rather than the one shown. Plot 9 was not treated with insecticide.

^bP.b.—*Pleolophus basizonus*, P.i.—*P. indistinctus*, E.s.—*Endasys subclavatus*, M.s.—*Mastrus aciculatus*, G.u.—*Gelis urbanus*, D.f.—*Dahlbominus fuscipennis*

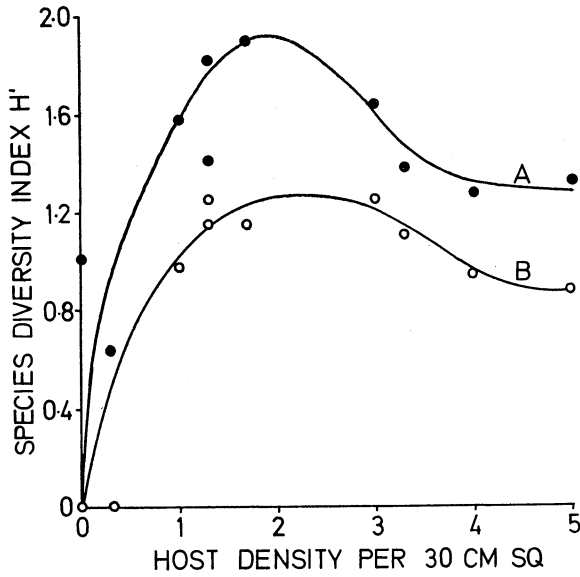


FIG. 3. Change of species diversity index (H') in increasing host cocoon populations at plot 9. A—all parasitoids, B—cocoon parasitoids only. The contribution to species diversity made by the larval parasitoid guild is the difference between A and B. Data are from the hand collection of cocoons and soil sample.

that *E. subclavatus* showed such a rapid increase at the lower host densities and then a decline suggests that it was checked by competition with the more successful *P. basizonus*. This competitive ability of *P. basizonus* was maintained in decreasing host populations where the proportion of *E. subclavatus* continued to decline.

There was also a competitive interaction between *P. basizonus* and *P. indistinctus* seen at other plots. Except in the dry plot 8, *P. indistinctus* tended to be more abundant at low host densities than at high, the reverse of what would be expected unless interaction with *P. basizonus* is invoked as a cause (Table 4). The distribution of parasitoids in plot 2 lends support to this interpretation of the data (Fig. 5). At the edge of the stand, *P. indistinctus* was the most abundant species. As *P. basizonus* became more abundant towards the center of the stand, probably in response to an increasing host density, the numbers of *P. indistinctus* declined to the point where the species appear to be on the verge of local extinction.

In fact, *P. basizonus* dominates the cocoon parasitoid guild and acts as a key factor (Morris 1959) in the prediction of species diversity (Fig. 6). Of course, as the proportion of any species increases beyond that for maximum diversity of a complex, so the species diversity declines, and therefore these attributes are not independent of

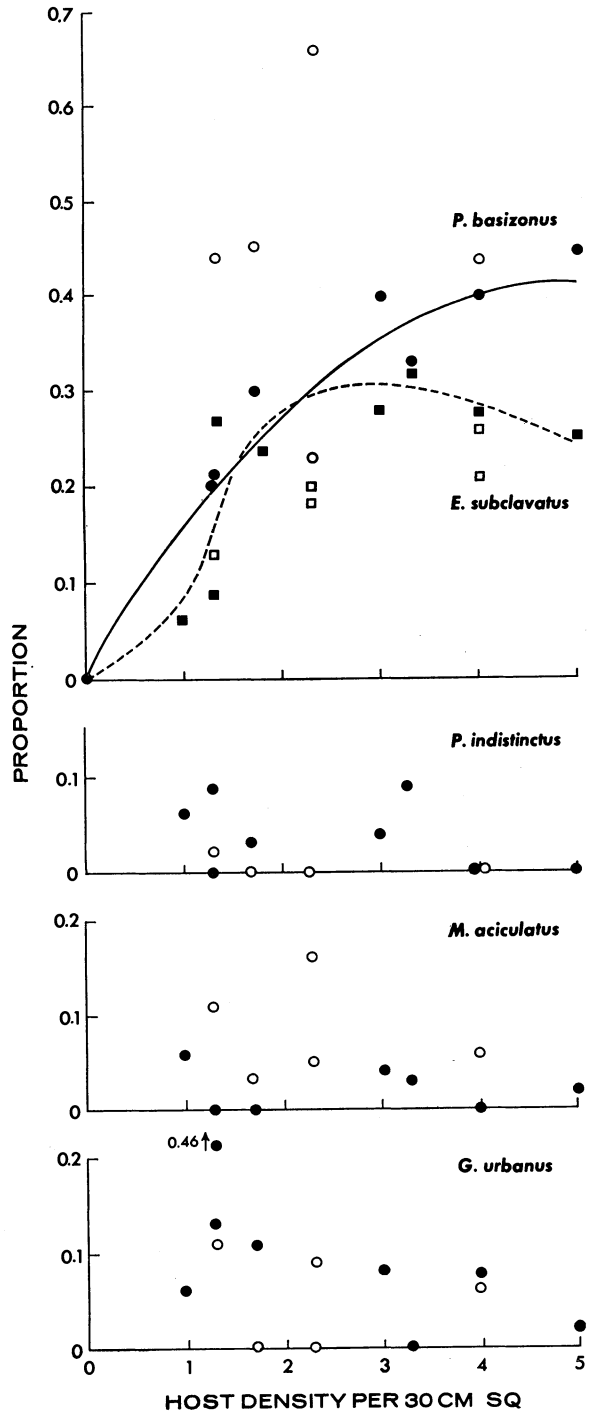


FIG. 4. The proportions of *P. basizonus* and *E. subclavatus* in the total parasitoid complex and of *P. indistinctus*, *M. aciculatus* and *G. urbanus* in the cocoon parasitoid complex in plot 9. Data are from the hand collection and soil sample. Closed circles and squares—proportions in increasing host populations, open circles and squares—proportions in decreasing host populations. The regression line for *P. basizonus* proportions in increasing host populations is $Y = 0.1720X - 0.0178X^2$, $R = 0.9748$, $df = 5$, significant at 1% level.

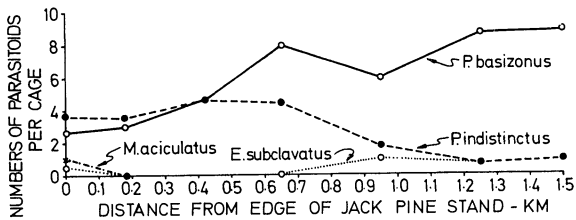


FIG. 5. Cocoon parasitoid distribution in relation to the distance of sample points from the edge of the jack pine stand at plot 2. Each point represents the mean of sample points located on the four arms of the transect which radiates from the center of the stand.

each other. However, *P. basizonus* is the only species that has its proportional representation in the parasitoid complex so regularly related to species diversity.

Interaction between cocoon and larval parasitoid guilds

The larval parasitoid guild showed a weak response to increases in host density (Fig. 2). It contributed greatly to species diversity at low to moderate host densities, but beyond 2 cocoons per 900 cm² its contribution was rapidly reduced (Fig. 3). Several species of larval parasitoid were not found at the highest host densities. Since their numbers were so low in relation to host numbers, competition within the larval parasitoid guild could not have accounted for the reduced species diversity in high host populations. This was probably due to a competitive interaction with the cocoon parasitoid guild whose members readily hyperparasitize larval parasitoids (Tripp 1960, Pschorn-Walcher 1967). Within the cocoon parasitoid guild *P. basizonus* was the most potent species in reducing species diversity of the whole parasitoid complex (Fig. 6).

DISCUSSION

Probably changes in host population quality, and especially rates of change of the host population, have a profound influence on the parasitoid complex. A growing host population, which provides an increasing resource, should lessen competition and enable less aggressive species to coexist with those of superior competitive ability. Conversely, a decreasing host population should tend to increase competition and cause the rapid decline, or local extinction, of some species. A gradual rise in a host population allows time for organization to develop in a community, with a predictable outcome. When large host populations become available, as a result of mass immigrations, the assortment of parasitoids should be less predictable. In this case, lack of organization would result from the rapid increase in those parasitoid

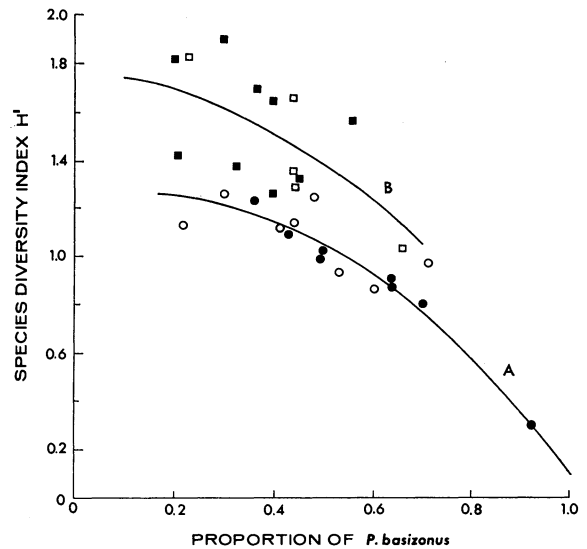


FIG. 6. Regression of species diversity index (H') on proportion of *P. basizonus*; A—in the cocoon parasitoid guild; B—in the total parasitoid complex. Closed circles—data from cocoon planting in the old jack pine stand adjacent to plot 3 given in Fig. 1. The regression line is $Y = 1.2121 + 0.4525X - 1.5685X^2$, $R = -0.9892$, $df = 5$, significant at 1% level. Open circles—data from increasing host population at plot 9, hand collection. Squares signify the same as in Fig. 4. The regression line in $Y = 1.7820 - 0.1474X - 1.2459X^2$, $R = -0.6155$, $df = 11$, significant at 10% level.

species that chanced to discover the host concentration.

Although available data were few, there is a strong indication that the relative abundance of the parasitoid species changes as host populations decline. *Pleolophus basizonus*, which is dominant at peak densities of the host, continues to increase its dominance in a decreasing host population (Fig. 4). As a result, other species in both guilds contribute less to total parasitism.

When guild members overlap broadly in exploiting a limiting resource, only one can be competitively supreme and the remainder must occupy refuges from its competition. Furthermore, the specializations of the most aggressive species limit it from exploiting all of the available resource. The cocoon parasitoid guild shows this type of organization. This is particularly interesting because the guild composition has been modified by recent introduction and cannot be considered the product of a long coevolution. At least part of the ecological refuge from competition for each of three species of cocoon parasitoids is now known. *Gelis urbanus* is not dependent upon *N. swainei* as a host and therefore it can maintain a population on hosts not available to the other species in the face of severe competition. *Mastrus aciculatus*

appears best adapted for exploiting high host populations in dry areas of open-grown, young jack pine trees, and *P. indistinctus* has the ability to exploit low host populations where other species fail. A fourth species, *P. basizonus*, has no known ecological refuge, but its competitive ability enables it to become dominant in high host populations. Apparently it is less efficient in its search for hosts than *P. indistinctus* at low host densities.

Thus *P. basizonus* acts as the organizer species for both the cocoon and larval parasitoid guilds at high host densities. When host populations are low, the larval parasitoids contribute more to the total parasitoid diversity (Fig. 3). Their search for the well exposed larvae is easier than the search for cocoons by the cocoon parasitoids. Hassel (1968) found an increased larval parasitoid efficiency with a resultant greater host mortality, at low winter moth densities. Thus, in recently established host populations, larval parasitoids are likely to colonize this new resource first. Cocoon parasitoids follow as the host population increases and cause a rapid rise in species diversity. Diversity peaks and then falls off as competition for host cocoons increases. During the host increase, *P. basizonus* develops its influence. This leads to a predictable organization within the parasitoid complex. At this stage, it is apparently impossible for new species to colonize the host population and some parasitoid species are pushed to local extinction.

The interaction of parasitoid species has long been discussed in relation to the biological control of insect pests (Smith 1929, Flanders 1965, 1966). The value of multiple and sequential parasitism has been considered in terms of the mortality caused in the host population rather than the adaptive strategies demonstrated by the parasitoids. In the parasitoid complex studied here, two main strategies for host exploitation are evident. The larval parasitoid guild exploits the host early in the season, when larvae are easily accessible on foliage, are contagiously distributed, and when the host population is near its maximum for that year. To succeed, the females must be highly mobile to colonize the widely dispersed, small populations of sawfly, where they can establish resident populations before the cocoon parasitoids have migrated into the area. Their fecundity must be high, as the long period spent in the cocoon makes them vulnerable to hyperparasitism by members of the cocoon parasitoid guild, when they are present in the community. Typical features of the parasitoids in this guild are large wings, long abdomens, and a potential for massive production of eggs (about 600 per female in *O. lophyri*).

In contrast, the cocoon parasitoid guild, which

attacks the host late in its life history, has a less dense, more evenly dispersed, better concealed and better protected host population to exploit. Females have a robust morphology, with a powerful ovipositor in a relatively squat abdomen. They are small winged (brachypterous or apterous) and even those females that have functional wings rarely fly (Price in press). Presumably these are adaptations for searching in the moist forest litter. Their fecundity is relatively low (about 50 eggs per female in *P. indistinctus*). Here a premium is placed on efficient searching in a difficult habitat and the laying of at least a few eggs that develop rapidly and thereby avoid subsequent mortality. The result is the very close relationship observed between host and parasitoid distributions with only a very small proportion of the parasitoid population migrating beyond the limits of the host distribution. Two or more generations per year lead to a rapid increase of the population permitting a more prompt numerical response to host numbers than is possible for larval parasitoids.

As host populations rise and the cocoon parasitoid guild increases its dominance, some locations probably remain as refuges for larval parasitoid populations. For example, at the ecotone around jack pine stands where species diversity is high, no clear dominance is developed, so that the occurrence of larval parasitoids is unchallenged. Also in dry sites, such as plot 8, where few species and low numbers of cocoon parasitoids are active, the larval parasitoids may become dominant because they are not so dependent upon moist litter conditions for their survival.

Thus the coexistence of the two guilds depends upon inherently different strategies rather than divergence from a common exploitation pattern. Even within the cocoon parasitoid guild, there is no evidence that original patterns of exploitation have been modified through competitive pressure as in other organisms (e.g., Lack 1947, Hairston 1951, Brown and Wilson 1956). However, now that the introduced *P. basizonus* is the dominant member of the parasitoid complex, there is probably selective pressure on *P. indistinctus* to diverge in its exploitation pattern from its European vicariate.

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