PARASITOIDS UTILIZING THE SAME HOST: ADAPTIVE NATURE OF DIFFERENCES IN SIZE AND FORM[1]

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Abstract. Eleven hymenopterous parasitoid species commonly exploit one sawfly host, *Neodiprion swainei.* A comparison of the area of forewing, structure of ovary, and length of ovipositor of some of these species is revealing. The three guilds of parasitoids that attack the larval, eonymphal, and cocoon stages of the host, respectively, face different problems in host exploitation. Females of the larval parasitoid guild have large egg production and large wings. They are adapted to exploit a relatively abundant, easily discovered stage of the host, but their progeny are subject to high mortality while in the host. Females of the cocoon parasitoid guild have small wings and low egg production. They seek a scarcer, well-concealed stage of the host, and their progeny suffer less mortality. Members of the eonymphal parasitoid guild show intermediate characteristics. Among the cocoon parasitoids, the species have different ovipositor lengths, presumably allowing them to utilize segments of the host population, either different size classes or hosts that are buried at different depths in the forest litter. Comparison of ovipositor lengths indicates how similar the species can be in size, and therefore larval food exploitation, before competitive displacement prevents coexistence.

Selection and adaptation will normally work toward maximization of progeny survival. Energy used for reproductive purposes must be appropriated, however, in keeping with the maintenance needs of the organism (Williams 1966). Thus demands on strength, size, and growth of individuals are balanced against longevity, ovary size, and egg production. The question that interested Fisher (1958) and others was how this balance is reached. This has lead to studies into the reproductive strategy of organisms. Williams' (1966) theoretical considerations indicated that by assessing the risks involved with reproduction, it should be possible to interpret the value of different reproductive strategies. Similar reasoning prompted Tinkle (1969) to investigate the adaptive nature of differences in life history phenomena in lizards. Mitchell (1970) related the reproductive effort of mites to the probability of survival of the progeny.

The parasitoid complex investigated utilizes as a host the Swaine jack pine sawfly, *Neodiprion swainei* Middleton. This host is univoltine. The adults oviposit in tree foliage in the early summer, larvae feed on this foliage and, when mature, they enter a nonfeeding eonymphal stage, drop to the ground, spin a cocoon in the forest litter, and overwinter. Parasitoid specimens were collected in Laviolette County, Quebec, in the years 1965–70. Principal interest was devoted to the size of the wings, the number of ovarioles per ovary, and the length of ovipositor of selected species. Taxonomic and ecological relationships of the parasitoids are summarized in Table 1.

METHODS AND RESULTS

The forewing area of specimens was measured on calibrated squared paper by projecting the image

through a drawing tube and counting the number of squares within this image. The width of the face between the eyes was measured under a binocular microscope using a calibrated ocular grid. Measurements of ovipositor length were also made on cocoon parasitoids since differences in ovipositor length are likely to reflect partitioning of host resources.

Some female specimens were dissected to observe the structure of the reproductive apparatus. General characteristics were noted as well as the number of ovarioles per ovary. Thus the capacity for egg storage, and the comparative productivity of the ovaries could be checked. For *Dahlbominus,* where many individuals emerge from a single host, only one female specimen from each host was measured.

Forewing area

Since hosts are widely dispersed in the forest, parasitoids must hunt large areas to find food for their progeny. The metabolic commitments to energy for hunting, and the development of locomotor organs, represent somatic demands on the energy available, which contribute to reproductive efficiency. It is therefore interesting to observe differences in wing size between parasitoid guilds. For males, the forewing areas differ comparatively little among the guilds, with a range less than 1 mm^2 either side of the mean (Table 2). This reflects uniformity of function in male parasitoids, i.e., they are carriers of genetic material. Wings are moderately large as males must be highly mobile in their search for females.

The forewing areas of female parasitoids differ considerably between species. Females of the two larval parasitoids *Olesicampe* and *Lamachus* have wings significantly larger than those of the males (Table 2). These females must fly in search of widely dispersed host larvae in the tree canopy. Similarly, the females of *Exenterus,* eonymphal parasitoids, must hunt for hosts in trees and on low vegetation

TABLE 1. Taxonomic and ecological relationships of the 11 parasitoid species considered

Taxonomic relationships[a]	Characteristics of the parasitoid guild

Ichneumonidae
  Scolobatinae
    Mesoleini
      Lamachus lophyri (Ashmead)
    Porozontini
      Olesicampe lophyri (Riley)
	Larval parasitoid guild.—These have short ovipositors with which they insert an egg under the host integument. The progeny develop internally. Typically, Scolobatinae have large oviducts capable of egg storage and 8–12 ovarioles per ovary (Pampel 1914, Iwata 1960).

Ichneumonidae
  Tryphoninae
    Cteniscini
      Exenterus amictorius (Panzer)
      Exenterus diprionis Rohwer
	Eonymphal parasitoid guild.—These have short ovipositors that puncture the integument of the host and insert a modified stalk of the egg, which remains firmly affixed to the host surface. Cteniscini generally have small egg storage capacity and about 5 ovarioles per ovary (Pampel 1914, Iwata 1960).

Ichneumonidae
  Gelinae
    Gelini
      Gelis urbanus (Brues)
      Mastrus aciculatus (Provancher)
      Endasys subclavatus (Say)
    Echthrini
      Pleolophus basizonus (Gravenhorst)
      Pleolophus indistinctus (Provancher)
  Chalcidoidea: Eulophidae
    Eulophinae
      Dahlbominus fuscipennis (Zetterstedt)
	Cocoon parasitoid guild.—These pierce the host cocoons and lay eggs on the host surface. The ovipositor of each species is long because it must pierce the host cocoon, and perhaps some litter in which the cocoon is embedded. Gelinae generally have no egg storage capacity, other than the ovarioles themselves, and only 3 or 4 ovarioles per ovary (Pampel 1914, Iwata 1960). As in the other guilds, Gelinae oviposit one egg per host. However, the chalcidoid *Dahlbominus fuscipennis* lays up to 40 eggs per host, after which the parasitoid larvae develop gregariously.

Ichneumonidae
  Tryphoninae
    Eucerotini
      Euceros frigidus Cresson
	Obligatory hyperparasitoid.—Females lay their stalked eggs on foliage, the planidial first instar larvae attach to the sawfly larvae and do not develop until a primary parasitoid develops in or on the host (Tripp 1961). Therefore, members of this genus may interact with any or all members of other guilds. *Euceros* species have short ovipositors and are capable of massive egg production, having from 50 (Tripp 1961) to about 230 ovarioles per ovary (Iwata 1960).

[a]Classification of Ichneumonidae follows Townes (1969*a*, *b*, *c*), that of *Dahlbominus* follows Peck (1963).

TABLE 2. Size of forewing of parasitoids that utilize the available host material completely

Species[a]	Wing area (mm² ±SE) ♂	♀	Probability[b] that ♂ = ♀	Sample sizes ♂	♀
Larval parasitoids					
Olesicampe lophyri	5.68±0.21	6.61±0.23	<.025	16	30
Lamachus lophyri	7.18±0.25	9.32±0.45	<.001	30	16
Eonymphal parasitoids					
Exenterus amictorius	7.55±0.32	9.15±0.27	<.001	22	30
Exenterus diprionis	6.88±0.63	6.52±0.39	>.500	10	6
Cocoon parasitoids					
Pleolophus basizonus	6.19±0.21	4.28±0.14	<.001	30	30
Endasys subclavatus	6.73±0.16	4.82±0.12	<.001	30	30
Pleolophus indistinctus	5.69±0.18	0.32±0.01	<<.001	30	30
Mean	6.56	5.86			

[a]Only those species that completely utilize the available host material were compared. Those that do not are naturally smaller, and their wing sizes cannot be directly compared for the purpose of interpreting adaptations. However, data from these species (*Mastrus* and *Gelis*) do support the trends indicated in the table. *Euceros* was omitted because of shortage of data, and *Dahlbominus* because of its distant taxonomic relationship to the ichneumonids.
[b]Student's *t* test.

after the eonymphs descend. In *E. diprionis,* females and males have wings about the same size, and in *E. amictorius,* female wings are significantly larger.

The situation is reversed in the cocoon parasitoid guild: females of the genera *Pleolophus* and *Endasys* have wings significantly smaller than those of the males. These females search in the forest litter for host cocoons. The alate females of *Pleolophus basi-* zonus and *Endasys subclavatus* fly infrequently and are not strong fliers (Price 1970*a*). They have small wings that in resting position fit closely over the abdomen, not protruding beyond its margins. Clearly, locomotion by walking is the more important means of travel, and an economy has been made on wing development. The logical extreme in this has been attained by the brachypterous *Pleolophus indistinctus,*

which has nonfunctional wings and a correspondingly large saving in wing musculature and thoracic housing for the muscles (see Price 1970b).

Number of ovarioles

Since, in general, only one egg per ovariole matures at a time, the number of ovarioles per ovary reflects the rate of egg production for a given species, and since egg production is usually maintained at a high rate for only 2–3 weeks per individual, it also reflects total fecundity of the species. Therefore, ovariole number per ovary gives a good estimate of both rate of egg production and total egg production. In those species with egg storage capacity in the oviducts, egg production can continue independently of egg deposition. In the other species a new egg is usually not matured in an ovariole until one is oviposited. Thus the use of ovariole number can only underestimate egg production.

The numbers of ovarioles per ovary in specimens collected for this study were mostly in keeping with those generally found in their respective taxonomic groupings. Only *Olesicampe*, with an average of 35 ovarioles per ovary, showed a considerable difference from the norm for its subfamily. When the parasitoid species are arranged in the sequence in which they attack the host, and related to ovariole number, it becomes clear that there is a pattern in ovarian productivity (Fig. 1). Parasitoids that attack the host early in its development have high ovariole numbers
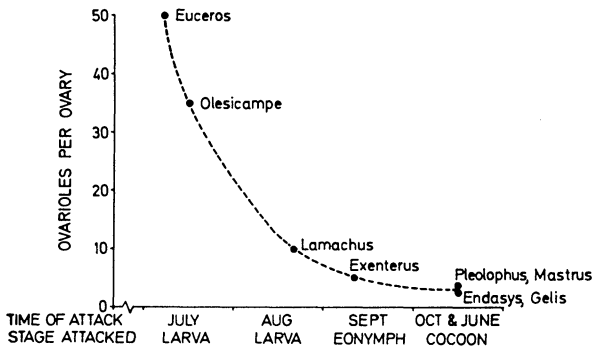

FIG. 1. Chronology of parasitoid attack on sawfly hosts in relation to the number of ovarioles per ovary of each parasitoid species. Datum on ovarioles in *Euceros* is from Tripp (1961). Data on other species are mean numbers of ovarioles per ovary for 10 specimens of each species. The chronology of attack is based on studies by Tripp (1961) and Price and Tripp (1972). Although the hyperparasitoid *Euceros* begins to emerge a little after *Olesicampe*, emergence of these two is completed at about the same time. Since *Euceros* lays eggs in clusters of about 100, about 10 cm from a host larval colony (Tripp 1961), total egg deposition can take place rapidly and is probably completed long before that by *Olesicampe*. The latter species must stalk its host, deal with the host defensive behavior, and oviposit in hosts individually (see Prop 1960). Therefore *Euceros* is placed slightly before *Olesicampe* in the chronology.

while those that attack later stages have successively smaller numbers of ovarioles.

As the host develops it is subjected to many mortality factors with the result that hosts are most plentiful in the egg stage and least abundant in the cocoon stage. While it might seem to be a good strategy to search for hosts in the plentiful phases, this adaptive advantage is balanced by the large mortalities inflicted subsequently, both directly on the host and indirectly on the contained parasitoids. The important mortality factors, other than primary parasitism, are predation and secondary parasitism.

The host larvae feed colonially and therefore are relatively easy to find for members of the larval parasitoid guild. Eonymphs disperse individually from the colony and drop to the ground, and are less easily discovered by *Exenterus*. Finally, the cocoons are spun in the forest litter and become dispersed and well concealed from members of the cocoon parasitoid guild. Because cocoons are difficult to discover, only a few eggs can be deposited per unit time and therefore low egg production is adequate for cocoon parasitoid guild members.

Ovipositor length

Only members of the cocoon parasitoid guild have relatively long ovipositors. Different size classes of host, or hosts that are more or less deeply concealed in the forest litter may be exploited by species with differing ovipositor lengths (e.g., Heatwole and Davis 1965). Female cocoon parasitoids are able to burrow into the loosely compacted forest litter in which cocoons are embedded. Parasitized cocoons are found 2–3 cm below the litter surface. In many cases the
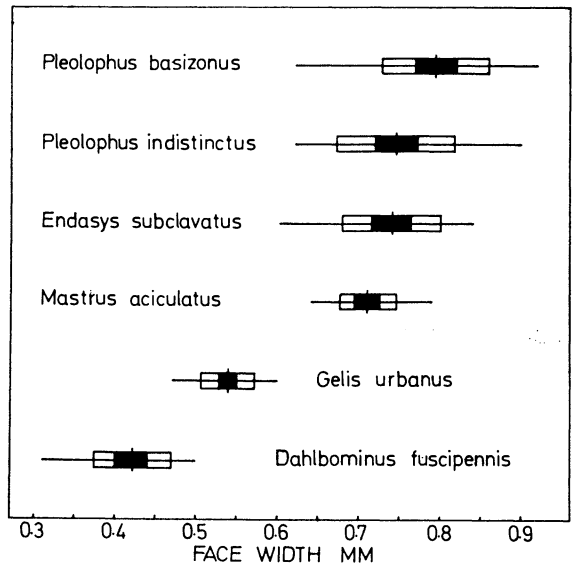

FIG. 2. Face widths of members of the cocoon parasitoid guild. Data calculated from measurements on 30 specimens of each species. See Fig. 3 for interpretation of symbols.

female may detect a cocoon in a crevice by antennal contact although unable to mount the cocoon for oviposition in the usual way. Therefore the lengthy ovipositor permits exploitation of an additional part of the host population.

The mouthparts of all species are used primarily for biting an emergence hole through their own cocoon and that of the host from which they emerge, and for lapping at various sources of nutrient solutions later in life (e.g., nectar and honeydew). Therefore, differences in size of mouth parts reflect only differences in general size. The width of the face between the bases of the eyes, a part of the head that forms the housing for the base of the mandibles, was therefore used to gain an estimate of the size of the species within the cocoon parasitoid guild (Fig. 2). In Hymenoptera, head width is a convenient measurement and one conventionally used for size comparisons. The four largest species differ little in size, while *Gelis* and *Dahlbominus* are considerably smaller. It is significant that the two species that do not completely utilize the host, *Mastrus* and *Gelis,* show less size variation than the other species (cf. 95% confidence limits and standard deviations in Fig. 2). *Dahlbominus,* as a gregarious feeder, does utilize the host completely and therefore shows a larger deviation because of variation in host size.

When the lengths of ovipositors are compared, the ordination of the species changes and the magnitude of the differences between species increases (Fig. 3). *Mastrus* has a longer ovipositor than any other species, and there is much less overlap of dimensions than with face widths. It is interesting that most overlap occurs between *Mastrus* and *Pleolophus basizonus* and between the two species of *Pleolophus.*

The larger species of *Pleolophus* was introduced into Canada from Europe between 1930 and 1940 and therefore is a novel member of the guild. The similarity in lengths of ovipositors between the introduced and indigenous species suggests similarities in host exploitation. It appears that the species are too closely packed to allow coexistence, if indeed differences in ovipositor length do allow different segments of the host population to be exploited. This assumption is generally held to be valid for culmen lengths of birds (e.g., Hutchinson 1959, Schoener 1965, Van Valen 1965). However, Root (1967) has argued that beak width is also an important parameter in ecological segregation of a resource by some birds, and that length alone may be inadequate to define this segregation. Therefore, ovipositor length may provide a purer measure for comparing parasitoid species than culmen length does for comparisons among birds, other than for those bird species seeking food in crevices, such as nuthatches (Vaurie 1951).

Since five parasitoid species have converged in their exploitation patterns to exploit one host and one stage of the host (with a sixth guild member added by introduction), how similar can the species become and yet remain sympatric? Hutchinson (1959) found that, in various parameters related to trophic apparatus, sympatric species at the same trophic level ranged in ratio of the larger to the smaller from 1.1 to 1.4. Schoener (1965) chose a "somewhat arbitrary" ratio of 1.15 as an indication of a significant separation of ecological niches by food size and so on. Using the mean ovipositor lengths of the six members of the cocoon parasitoid guild (Fig.
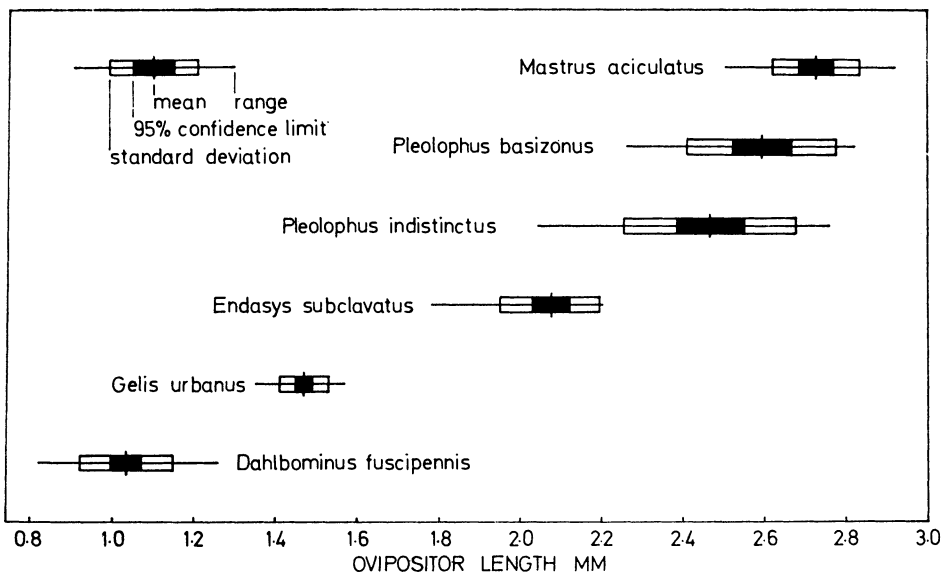

FIG. 3. Ovipositor lengths of members of the cocoon parasitoid guild. Sample size for each species was 30.

3), the following ratios between pairs of species were obtained.

$$\left.\begin{array}{c} \textit{Mastrus aciculatus} \\ 1.05 \\ \textit{Pleolophus basizonus} \\ 1.05 \\ \textit{Pleolophus indistinctus} \\ 1.19 \\ \textit{Endasys subclavatus} \\ 1.41 \\ \textit{Gelis urbanus} \\ 1.41 \\ \textit{Dahlbominus fuscipennis} \end{array}\right\} \quad 1.11$$

It is evident that until *P. basizonus* was introduced, all species had ovipositors that differed in length by more than 10% from the species next in size. Now that *P. basizonus* is present in the guild with only 5% differences between the closest species, these three are too crowded to allow coexistence according to Hutchinson's predictions. Indeed, in studies on the ecological partitioning of resources by members of this guild based on spatial factors, differences between the three species with the largest ovipositors were the easiest to define (Price 1970c). There is also evidence that competitive displacement occurs between the two species of *Pleolophus* (Price 1971). At low host density *P. indistinctus* was the most abundant cocoon parasitoid in moist sites. As host density increased, *P. basizonus* became dominant in these sites and displaced its congenor to the margin of the host population where conditions for survival were less favorable.

For members of this guild, Hutchinson's lowest estimate of 10% difference between sympatric species seems to be realistic and is supported by statistical evidence. All pairs of species show very high probabilities of significant differences when tested with Student's *t* test, except those with ratio differences of 1.05. When compared, these species showed *t* values not significant at the 0.01 level for the two *Pleolophus* species and not significant at the 0.001 level for a comparison between *P. basizonus* and *M. aciculatus*. All other species comparisons show a statistical significance much higher than the 0.001 level. Thus ecological segregation of a resource permitting coexistence may result when parameters based on morphological characters related to feeding behavior show a highly significant difference (in the statistical sense, assuming that 30 or more specimens are available for study).

THE STRATEGY OF HOST UTILIZATION

The utilization of food by parasitoids for the construction of wings and ovaries can be regarded in the same way as Mitchell (1970) considered the adaptive nature of mite reproduction. He related the number of founders reaching a new habitat (F) to the original number of progeny produced by a female (N), and the probability that the progeny discover a new resource (P) in the following way:

$$F = NP.$$

In the case of ichneumonids, if F represents the founders that survive to exploit the next host population, and P the probability of survival of the larval stage of the parasitoid, the same relationship holds. If P is low N must be maximized by leaving many progeny, as in the case of *Euceros* and *Olesicampe*. In order to leave many progeny (high N), dispersal must be rapid for efficient hunting, and ovaries must be relatively large for high egg production, and therefore females must have large wings to gain lift and speed. This strategy may be likened to the concept of maximum power output (Odum and Pinkerton 1955) where rate of production (or oviposition) is selected for more than for optimum efficiency. These species are inefficient, particularly in low host populations, as females must carry a large ovarian load. If P is high, N can be low to achieve the same number of founders. An economy on wing and ovary formation enables utilization of food resources toward robust construction of legs and body for searching in the forest litter, in the case of cocoon parasitoids. Thus a more conservative strategy is evident, one that is perhaps more efficient since there is a smaller material commitment to ovary development and therefore less redundancy when parasitoids search in low host populations.

However, when several species evolve with the same general strategy for host exploitation, as in the cocoon parasitoid guild, where progeny production and survival for all species are comparable, other methods of partitioning host resources are necessary. Specialization for exploiting one segment of the host cocoon population by modification of the apparatus for acquiring food, in this case the ovipositor, provides one solution that permits coexistence. The five original members of the cocoon parasitoid guild have apparently achieved this end. When this method of niche segregation fails, competitive displacement will result in species occupying adjacent microhabitats, with little overlap between species distributions. Now that *P. basizonus* is a member of the guild, this compromise in niche occupation has resulted (Price 1971).

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