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REPRODUCTIVE STRATEGIES IN PARASITOID WASPS*

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Two closely related approaches to the study of reproductive strategies have been pursued with success. Differences in timing of reproductive effort were explored in attempting to explain the adaptive nature of differences in life histories of organisms in the same taxonomic group (e.g., Cole 1954; Lewontin 1965; Murdoch 1966a, 1966b; Tinkle 1969; Emlen 1970; Gadgil and Bossert 1970). The other avenue of investigation has concentrated on numbers of progeny produced, particularly clutch size (e.g., Lack 1954; Cody 1966). The latter approach appears to be the more rewarding in relation to an insect taxon where females usually oviposit soon after emergence or as soon as hosts become available and in which are contained species showing extremes in total fecundity.

In the Ichneumonidae, a family of parasitoid wasps, the average fecundity for some species is as low as 30 eggs per female per lifetime (Price 1970) and for others well over 1,000 eggs (in the genus *Euceros* one species has 50 ovarioles per ovary and produces an estimated 1,000 eggs [Tripp 1961], while another species has 231 ovarioles per ovary on average [Iwata 1960] and presumably produces a correspondingly larger number of eggs). Here I attempt to explain such diverse approaches to leaving viable progeny, and I explore the existence of necessary correlated adaptations.

Ichneumonid wasp females actively seek insect hosts on foliage or in leaf litter. Common hosts are immature stages of moths, butterflies, sawflies, true flies, and other wasps. Some species of ichneumonid oviposit within eggs or exposed larval hosts; others oviposit on the host when it is in a cocoon, puparium, or chrysalis. The larva feeds in or on the host until pupation, followed by emergence as an adult independent of its host.

The number of ovarioles per ovary in nine species of parasitoids is well correlated with the stage in which the host is attacked, either as a young larva, mature larva, or in the cocoon (Price 1972). Those ichneumonid species attacking the most abundant and vulnerable stages of the host have large ovariole numbers, and those attacking the subsequent life-history stages have progressively smaller numbers of ovarioles per ovary. The good fit of the data when arranged in this fashion and the compelling argument that reproductive machinery in parasitoid wasps is adapted to cope with a limited host supply have prompted me to examine reproductive strategies

in the family Ichneumonidae as a whole. The family is estimated to contain 60,000 species, of which about 25% are described and placed in 25 sub-families (Townes 1969a).

Iwata (1960) wrote a remarkable paper on Japanese ichneumonids giving information on the number of ovarioles per ovary, the mature egg length and width, and the number of oocytes per ovary for 1,397 specimens in 376 species, 160 genera, and 6 subfamilies. In addition, over 140 figures illustrating ovary structure permit a comparison of modifications of the oviduct for egg storage.

The value of Iwata's data has been greatly increased by a reclassification of the eastern Palearctic Ichneumonidae by Townes, Momoi, and Townes (1965). Townes et al. divided the family into 22 subfamilies making these taxa more coherent, on the basis both of morphology and life history. Using Townes et al. (1965), I have reclassified Iwata's species to conform to modern taxonomy. Of Iwata's species, 248 are presently identifiable, representing 154 genera, 13 subfamilies, and a total of 1,209 specimens (table 1). These data represent a reasonably large sample of the Ichneumonidae on which the following analysis is based. Corroborative evidence on ovary structure and some of the trends developed here may be found in Clausen (1962) and Pampel (1914), although care must be taken with placing the species discussed by these authors in a modern taxonomic context.

Information on the typical biologies of the subfamilies was obtained from Townes (1969a, 1969b, 1969c, 1971).

AVAILABILITY AND SURVIVAL OF HOST

The evolutionary responses of parasitoids to host abundance and availability are probably influenced by two factors that are likely to reinforce

TABLE 1

NUMBERS OF GENERA, SPECIES, AND SPECIMENS USED ARRANGED BY SUBFAMILIES, AND THE MEAN NUMBER OF OVARIOLES PER OVARY FOR EACH SUBFAMILY, WITH STANDARD ERROR OF THE MEAN AND RANGE

Subfamily	Number of Genera	Number of Species	Number of Specimens	Mean Number Ovarioles per Ovary ± S.E.	Range
Metopiinae	3	9	37	19.9 ± 5.4	8.0–59.3
Diplazontinae ...	3	4	13	19.8 ± 2.5	16.0–27.0
Cremastinae	2	2	7	18.3 ± 1.5	16.8–19.8
Anomalinae	9	15	69	16.4 ± 2.4	7.5–36.0
Banchinae	9	16	62	14.3 ± 4.0	6.0–28.1
Scolobatinae	6	9	25	12.8 ± 2.1	5.0–25.2
Acaenitinae	6	8	37	12.3 ± 3.2	3.0–27.5
Porizontinae	6	7	21	11.9 ± 1.4	8.0–19.0
Ophioninae	3	7	17	10.6 ± 1.0	6.0–13.8
Ichneumoninae ..	37	77	325	6.7 ± 0.3	2.8–15.0
Ephialtinae	23	38	280	5.3 ± 0.5	3.0–13.5
Tryphoninae	9	14	48	4.4 ± 0.5*	3.0–6.3*
Gelinae	38	42	268	4.2 ± 0.2	2.0–8.5
Total	154	248	1,209	...	...

* Excluding *Euceros*.

each other. First, as Gadgil and Bossert (1970) predicted for a resource-limited organism, greater availability of a resource will lead to a greater reproductive effort. Second, the intrinsic rate of natural increase (r_{max}) reflects the environmental resistance to which a species is habitually exposed (Pianka 1970, following Smith 1954).

Host availability incorporates two interacting components, abundance and accessibility (host size may act as another component, although since only one parasitoid matures per host in most Ichneumonidae, it is less critical than in gregariously developing species). For parasitoids, a host that is readily available—that is, an abundant, exposed organism such as many caterpillars—is also a vulnerable host, as many mortality factors, other than parasitoids, are likely to reduce its population size. A parasitoid attacking in this situation can evolve a high fecundity because its food resource is abundant. Reinforcement comes from high mortality of parasitoids in the host, selecting for fecund individuals whose fitness is thereby directly increased. The probability of survival of the parasitoid on or in the host is inversely proportional to host availability.

The other extreme occurs if the host is scarce or deeply concealed, such as wood-boring hosts, and thus difficult to discover. The resource is in short supply or well protected. Fecundity of the parasitoids should be low because of the same two mutually reinforcing factors mentioned above.

Several factors influence host availability to parasitoids. As mentioned, microhabitat is important. Hosts in leafrolls and webs, or otherwise concealed, are relatively inaccessible. Hosts with effective defensive mechanisms have the same effect (Prop 1960). Availability also changes through the season as the egg stage is always more abundant than the pupal stage in any one generation. In parasitoids specific to a host stage, corresponding adaptations in fecundity are to be expected. Finally the general, year-to-year commonness or rarity of a host species will influence all members of the parasitoid complex on that species. Biological information on ichneumonids is insufficient to examine all these possibilities, although some trends in seasonal and microhabitat influences on availability are evident.

Members of some subfamilies and tribes of Ichneumonidae typically attack a rather narrowly defined stage of the host. For example, members of the Diplazontinae attack eggs and very young larvae of syrphid flies, Gelinae attack cocoons of sawflies and puparia of true flies, and Tryphoninae attack last instar larvae of sawflies. When parasitoids are ranked according to the stage of the host attacked and then plotted against the potential fecundities (mean number of ovarioles per ovary) of the parasitoids, a well-defined trend is evident (fig. 1). The higher the seasonal abundance of the host, the higher is the potential fecundity of the subfamily or tribe. Lacking extensive data on actual fecundity of ichneumonids, ovariole number is the next best indicator of egg production. Ovariole number per ovary evidently gives a good estimate of both rate of egg production and total egg production (Price 1972).

The accessibility of the host can be inferred from examination of ovipositor
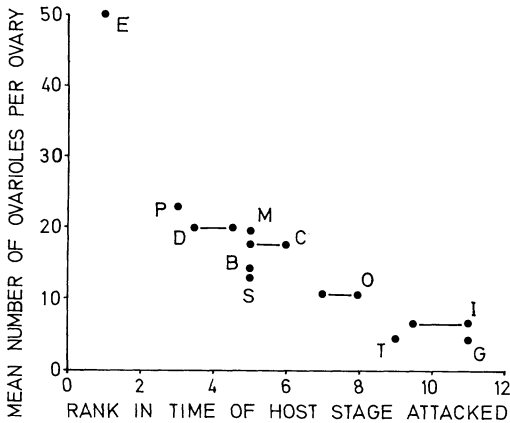
FIG. 1.—Relationship between the stage of development of the host (ranked) and the number of ovarioles per ovary expressed as a mean of the specimens in the taxon indicated. Ranking indicates the following categories: 0–2 oviposition is on foliage close to the host eggs but not into the host; 2–4, egg stage attacked; 4–6 young larva; 6–8 middle larva; 8–10 old larva; 10–12 pupal, puparium, or cocoon stage attacked. Two rank points were assigned to each developmental stage of the host to permit an indication of an early or late attack within that stage. Lines between points indicate variation within a subfamily, for example members of the Diplazontinae (D) are known to attack both eggs and early larvae of hosts. E = Eucerotini, a tribe in the Tryphoninae. This datum is based on figures provided by Tripp (1961) for *Euceros frigidus*. The species studied by Iwata (1960) had an average of 231 ovarioles per ovary. P = Pionini, a tribe in the Scolobatinae, D = Diplazontinae, M = Metopiinae, C = Cremastinae, B = Banchinae, S = Scolobatinae, O = Ophioninae, T = Tryphoninae, I = Ichneumoninae, G = Gelinae.

lengths. Short ovipositors function in attacking exposed hosts; long ovipositors are needed to attack a deeply concealed host. Because of the great size variation of parasitoids in any population and the lack of extensive data on ovipositor lengths, ratios of ovipositor length to body length were obtained from published habitus drawings of ichneumonids (Townes 1969a, 1969b, 1969c, 1971). Also, an indication of depth of host concealment relative to the size of the parasitoid is of more comparative value than the absolute depth of host. Without enough information on Japanese ichneumonids, ratios were calculated from other species in the same genera represented in Iwata's lists. Because ovipositor length varies considerably within genera, the relationship between this and potential fecundity cannot be expected to be exact. Nevertheless, an obvious trend is evident (fig. 2). Even if better information were available, the correlation would probably be reduced by data on parasitoids attacking concealed but very abundant hosts.

OVARY ADAPTATIONS

Several modifications of the ovary structure and egg production parallel the increase in ovariole number per ovary, with increasing host abundance.
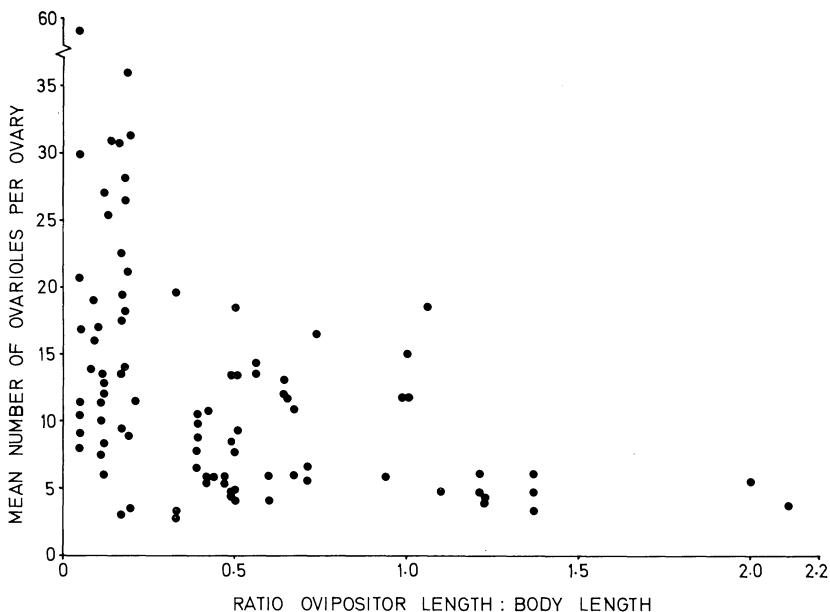
FIG. 2.—Decline in number of ovarioles per ovary as the relative accessibility of the host is reduced (inferred from an increasing ovipositor length–body length ratio). Data points are for the 90 genera in the subfamilies Metopiinae, Diplazontinae, Cremastinae, Anomalinae, Banchinae, Ophioninae, and Ephialtinae, for which both pieces of information are available.

First, the number of mature oocytes that can be carried in each ovary increases (fig. 3). This represents the female's store of mature eggs that can be laid in quick succession should an abundant supply of hosts be discovered. Those species with few ovarioles per ovary can carry only one mature oocyte per ovariole. Thus, a female may carry a total of only eight or 10 eggs that are ready for oviposition. The increase in oocytes stored with ovarioles per ovary is exponential. Therefore, the most fecund species store about three oocytes per ovariole (e.g., Cremastinae and Anomalinae), with each female carrying a complement of about 120 mature eggs in the Cremastinae. More data are needed to ascertain why the Metopiinae and Diplazontinae do not better fit the well-defined trend.

Second, accompanying the increase in ovarioles per ovary and storage capacity of oocytes in the ovarioles is an increasing potential for storage of eggs in the oviduct (fig. 3). The Gelinae, Ephialtinae, and Ichneumoninae have no storage capacity in the very short oviduct. More fecund species, the Porozontinae for example, have longer oviducts where some eggs may be stored. Members of subfamilies (e.g., Scolobatinae, Metopiinae, and Cremastinae) with greater egg production have an even greater storage capacity, in the form of an enlarged oviduct capable of storing over 100 mature eggs in some cases. Females of a species in these latter subfamilies may thus have over 200 eggs ready for oviposition as opposed to the eight or 10 carried by
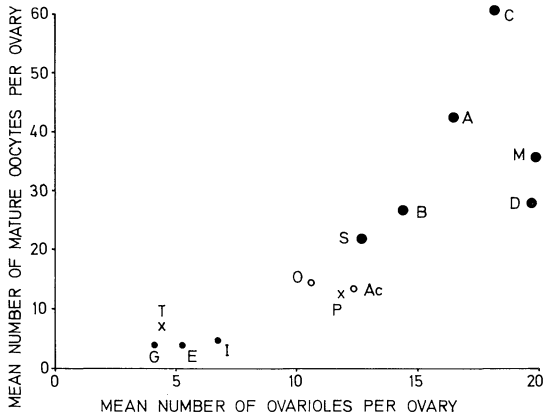
FIG. 3.—Increase of mature oocytes stored per ovary and the capacity to store eggs in the oviduct in relation to the mean number of ovarioles per ovary in each subfamily of Ichneumonidae. ●, Enlarged oviduct present for egg storage; x, egg storage in oviduct evident but oviduct not obviously enlarged; •, no egg storage in oviduct; o, information not available. G = Gelinae, T = Tryphoninae, E = Ephialtinae, I = Ichneumoninae, O = Ophioninae, P = Porizontinae, Ac = Acaenitinae, S = Scolobatinae, B = Banchinae, A = Anomalinae, C = Cremastinae, D = Diplazontinae, M = Metopiinae.

a geline female. The Tryphoninae, with a low number of ovarioles per ovary, are also able to store a small number of eggs in the oviduct. Members of this subfamily face a unique problem, as they have become specialized to exploit last instar larvae. This stage is often nonfeeding, and an individual soon begins to spin a cocoon in which to pupate, when it is again unavailable to the parasitoid. Therefore, each host may be available to parasitoids for only 24–48 hours. If development of the host is well synchronized, a host population may provide individuals suitable for parasitism for only a little longer period of time. Therefore, rapid oviposition is essential for these species, with selection tending to increase egg storage. This selection pressure, although achieving the same design, contrasts with that for other subfamilies with oviduct storage, and the result does not fit the general trend (cf. fig. 3 and discussion).

Finally, as egg production increases, the size of the eggs decrease (fig. 4). The relationship between egg length and ovariole number per ovary is exponential. Thus, the greater reproductive effort expended in the production of many ovarioles and eggs is balanced by an economy on egg size. Parasitoids with low fecundity, that experience low mortality in the larval stage produce large eggs which enable a briefer immature existence.

DISCUSSION

Considered together, the adaptive factors discussed above may form the basis for an understanding of reproductive strategies in the Ichneumonidae
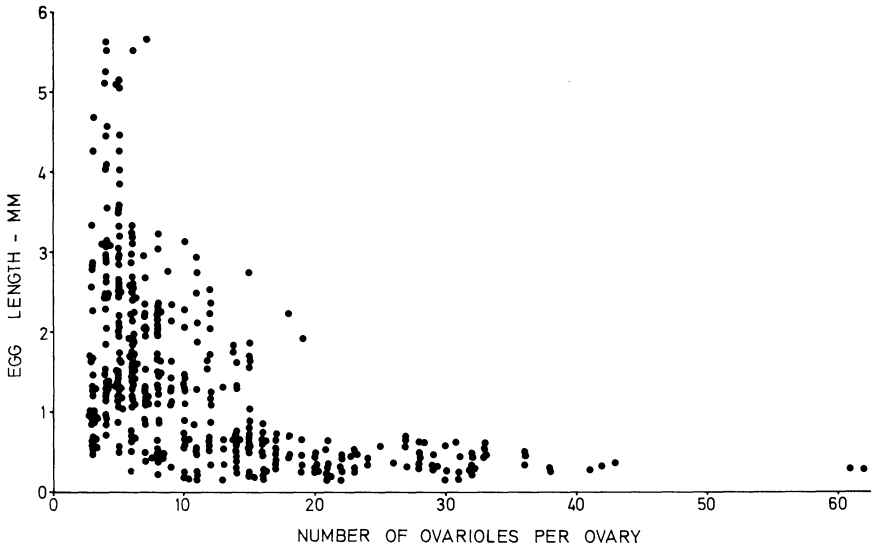
FIG. 4.—Relationship between length of mature egg and the number of ovarioles per ovary for individual specimens in the subfamilies Metopiinae, Cremastinae, Anomalinae, Banchinae, Ophioninae, and Ephialtinae.

and perhaps for parasitoid wasps in general. All factors can be related to the probability of survival of the parasitoid on or in the host (which is inversely proportional to the availability of the host). As the probability of survival decreases, for various reasons, some or all of the following adaptations are likely to be evident in the parasitoid fauna: (1) fecundity will increase; (2) number of ovarioles per ovary will increase; (3) capacity for storage of mature eggs in ovarioles will increase; (4) capacity for storage of mature eggs in oviducts will increase; (5) size of eggs will decrease; and (6) length of ovipositor will decrease. Data provided by Iwata illustrate these trends remarkably well when it is realized that significant variables have been ignored. These would include size variation between individuals and between species, differences in life histories of the host species, and average host abundance—all factors that would tend to increase variability of data in the trends examined.

Several other factors should be examined before a complete explanation can be formulated. For example, parasitoids that lay their eggs on the host have very low fecundities (see Gelinae and Tryphoninae in fig. 3), whereas those that oviposit within host tissues have higher fecundities (Ephialtinae to Metopiinae in fig. 3). Exoparasites, which produce the larger eggs, may gain advantage from larger, more developed larvae which thus are better able to pierce the host integument and move over a host that has been paralyzed during parasitoid oviposition. Endoparasites, with smaller eggs, may benefit from ease of rapid oviposition and a low-level rejection reaction

in a host that continues an active existence. No doubt there are subfamily differences in wing size and flying ability associated with the different modes of host searching, as I have shown for the parasitoid complex on a sawfly host (Price 1972). Large differences in egg production must surely be reflected in sperm production by males and perhaps the necessity for multiple matings. Also, longevity of females may be negatively correlated with their fecundity per unit of time, as in lizards (Tinkle 1969) and beetles (Murdoch 1966a). Females of some species of Ichneumoninae and Gelinae are the most frequently found overwintering (cf. Seyrig 1924; Townes 1938), and therefore live at least 6 months in temperate regions, whereas the more fecund summer species probably live less than 2 months (cf. Clausen 1962). Finally, the use of trail pheromones, or host odor, in searching behavior is likely to vary from one subfamily to another as the types of searching demanded of the parasitoids change.

Ultimately the explanation of reproduction strategies must be framed in energetic terms because the energy allocated to egg production clearly depends on the energetic content of the host and how this is partitioned among maintenance, body building, and egg production. In the absence of data on energy budgets, this is not yet possible for Ichneumonidae. Mitchell (1970) came closer to this objective by using data on biomass to explain the adaptive allocation of resources in dispersing mite populations. However, every adult parasitoid emerges with a certain amount of energy to be devoted either to activity or eggs. Feeding by adults will modify such partitioning of energy, although the surest strategy is to allocate enough energy from host tissues to egg production to permit considerable oviposition before feeding in case of adult food shortage. In species with abundant hosts, activity can be low, and therefore egg production can be high. Conversely, parasitoids attacking low-abundance hosts must devote more energy to searching and economize on egg production. In the latter category, many females are largely pedestrian, a means of travel more energetically expensive per unit distance than flight (Tucker 1969; Schmidt-Nielsen 1972). We should expect a rapid decline in egg production as the means of locomotion changes from flight to walking.

SUMMARY

In an effort to explain different reproductive strategies among parasitoid wasps, differences in potential fecundity of members of the family Ichneumonidae were compared in relation to the availability of the host and the probability of survival of the parasitoid once it was associated with the host. As host abundance declines during a generation, the ovarioles per ovary are less numerous in parasitoid species attacking successively less abundant stages of the host. Those parasitoids that attack well-concealed hosts relative to their body size (inferred from a high ovipositor length–body length ratio in the parasitoid) have fewer ovarioles than those attacking

exposed hosts. A decline in storage capacity for mature oocytes both in the ovarioles and in the oviduct, and an increase in the size of eggs produced, is associated with a decline in ovariole number.

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