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## ENERGY ALLOCATION IN EPHEMERAL ADULT INSECTS<sup>1</sup>

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### ABSTRACT

Ephemeral adults must be structurally prepared to produce a certain number of progeny, because time of reproduction is not a maneuverable factor. Since structures are more visible than fecundity, reproductive strategies may be more easily studied and interpreted. A study of 10 species of parasitic wasps (Hymenoptera: Ichneumonidae), with ephemeral adults (longevity 13-31 days with only one or two generations per year), used ovariole numbers per ovary, egg volume and number, and the survivorship curve of the host, and host stage attacked, was used to interpret reproductive strategies. The balanced mortality hypothesis and Lack's hypothesis are supported. There is an evolutionary trend in the family Ichneumonidae for increased egg production paralleled by a decreased total reproductive effort.

Understanding the apportionment of energy by organisms to maximize their fitness has long been regarded as a desirable enterprise (Fisher, 1930). Under the influence of natural selection energy utilization will be geared to increase number of progeny surviving to reproductive age. The rapidly expanding literature on this subject attests to its importance as a central unifying approach in ecology. We have begun to see patterns in the diverse array of tactics in reproduction, and suddenly conceive of the whole life history and form of an organism as the manifestation of a certain reproductive strategy (Harper and Ogden, 1970). The traditional barriers between plant and animal ecology have become meaningless.

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<sup>1</sup>Manuscript received February 8, 1974 (#74-24).

and we now have a powerful tool for the analysis of population dynamics and community ecology.

Studies on vertebrates have added much to concepts on reproductive strategies. They are relatively long lived, good competitors, with low intrinsic rates of natural increase. Longevity in plants and animals adds immensely to the possible permutations of life history that lead to increased fitness. Major strategic decisions such as between semelparity and iteroparity can be made by the evolutionary process (Cole, 1954). Tinkle (1969), and Tinkle, Wilbur and Tilley (1970) have studied the closely allied strategies of breeding in only one season or in several. Small adjustments in time of first reproduction, time of peak reproduction and termination of reproduction may effect population growth rates considerably (Lewontin, 1965). Thus, a very important part of the vertebrate reproductive strategy is temporal allocation of energy.

In contrast the ephemeral nature of adult life (meaning a short adult life relative to generation time) in many invertebrates means that reproductive effort in time cannot be easily manipulated, and the factors involved in strategic evolutionary maneuvers are simplified. There is little latitude for the shifts in strategy discussed by Lewontin (1965) and no chance of postponed reproduction as seen by Tinkle (1969) in lizards, and by Murdoch (1966a, b) in beetles, or of the other major shifts analyzed by Cole (1954). We cannot conceive of ways in which rates of energy movement into reproductive material can differ substantially among ephemeral adults, because similar physiological processes are involved. Since energy usage in time is not maneuverable, we should expect ephemeral adults to be geared up structurally, rather than physiologically, for a particular reproductive strategy. In addition, parental energy to increase survival or progeny must be spent at the time of oviposition and can be easily measured. Thus, ephemeral adults offer very important advantages for studying reproductive strategies, and we can substitute measures of structural differences for more complicated measurements of fecundity.

#### STRATEGIES IN EPHEMERAL ADULTS

One type of ephemeral adult is the wasp (Hymenoptera: Ichneumonidae) which parasitizes other insects. The adult is free-living and searches for hosts, and the larva is parasitic, but eventually kills the host (typical of a parasitoid way of life). One group of 10 ichneumonids attacks the same host, the Swaine jack pine sawfly, *Neodiprion swainei* Middleton, and since they all emerge from the cocooned stage, they must all have a similar amount of food available. Only one parasitoid can mature per host, but species oviposit in the host at different times in the host's life cycle, so we can observe how energy allocation differs as a function of abundance, dispersion and protection of the host.

Length of female adult life is short, averaging 18 or 23 days in *Pleolophus basizonus* (Gravenhorst) (Griffiths, 1969 and Price, 1970a, respectively) and 13 to 31 days in *Pleolophus indistinctus* (Provancher), depending on food availability (Price, 1970b). Thus, adults live briefly in comparison to the bivoltine or univoltine life cycles typical of this group of parasitoids. As we would expect in such an ephemeral existence, egg production rises to a peak early in adult life and then declines with age (fig. 1). As stated earlier, differences in fecundity between species must be reflected in different rates of oviposition and structural shifts to cope with different egg productions. The reproductive system of female ichneumonids is composed of an ovipositor which leads back to a median oviduct, two lateral oviducts and two ovaries composed of ovarioles, each ovariole being an assembly line for eggs, or oocytes. Accessory glands include the poison and alkaline glands, plus reservoirs. Thus the higher the fecundity of a female the larger number of ovarioles she must produce, and this feature is much easier to measure than fecundity itself (Clausen, 1940). Of course fecundity is the preferable unit

to use, but lacking this the closely correlated ovariole number will be used in its place. In a general survey of reproductive strategies in the family Ichneumonidae, Price (1973) found well defined trends in ovariole number with host stage attacked and greater development of lateral oviducts, as egg storage organs, with increasing egg production.

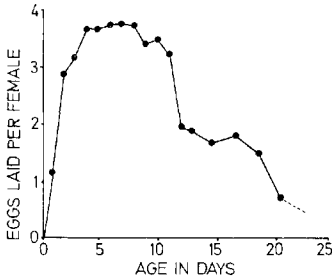


FIGURE 1. Age specific fecundity of *Pleolophus basizonus* showing rapid rise to peak production, and the short period over which eggs are laid (Griffiths, 1969).

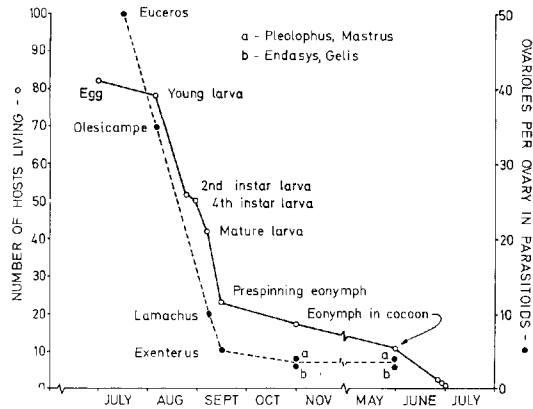


FIGURE 2. Survivorship curve of the host sawfly, *Neodiprion swainei* (open circles) (McLeod, 1972), and the number of ovarioles per ovary of parasitoids (closed circles) plotted in synchrony with the stage of the host most commonly attacked. The cohort of 82 eggs is the mean number laid by a single female. The last points on the host survivorship curve refer to adults only. (Price, 1974 with permission from Evolution).

Interpretation of differences in ovariole number between species in the parasitoid complex on *N. swainei* can be achieved by studying the survivorship data of the host (fig. 2). Host abundance declines with time, so the ovariole number in parasitoids which attack successive stages declines. As the host changes from the feeding, colonial stage in the tree, to a solitary non-feeding stage (the eonymph) which falls to the ground and spins a cocoon in the forest litter, host survivorship improves. Parasitoid larval survival also improves, and the decline in ovarioles per ovary is less rapid in subsequent parasitoid species (Price, 1972, 1973). Unfortunately fitness of parents cannot be calculated from these data, because the actual number of progeny which are deposited in hosts and survive is not known.

Since we have an estimate of the probability of survival once in the host, it is possible to test the balanced mortality hypothesis. This hypothesis infers that the number of progeny typically produced by females of a species is influenced over evolutionary time by the severity of the environment in which they must live. In harsh environments, relatively large numbers of progeny are produced to counteract high mortality rates. The hypothesis has received some criticism but much support (Price, 1974; Errington, 1946; Lord, 1960; Salisbury, 1942). If fecundity balances mortality, then the reciprocal of ovariole number should show a positive correlation with the probability of survival. In fact, this correlation explains 93% of the variance about the straight-line regression (Price, 1974),

offering support for the hypothesis. Of course, the actual number of eggs laid by each female depends not only on the number she can produce, but also on the number of hosts she can find. Thus Lack's (1954) hypothesis, which states that parents produce as many progeny as they can adequately feed, is also supported.

#### BALANCED MORTALITY OR BALANCED FECUNDITY?

Williams (1966) argues that high fecundity results in high mortality, a reverse view to the balanced mortality hypothesis. Since over long periods of time the growth rate of a population must be close to zero, an increase in fecundity must automatically doom more progeny per female. Also, with limited resources a female with many progeny can allocate little energy while a female with few progeny can allocate much energy per progeny, with consequent differential survivorship rates.

An intuitive solution to this dilemma cannot be reached, since the proximate selective factors that act on fecundity cannot be understood except in the context of evolutionary trends within the taxon or guild under study. Following traditions in taxonomy, Townes (1969) listed the subfamilies in the Ichneumonidae from the "very primitive" Ephialtinae to the more advanced groups. Most members of the Ephialtinae attack late stages of the host, and those that do not attack well concealed hosts, or spiders. In the latter case, further development of the host is halted (Clausen, 1940), making the spider effectively a late stage of host. Members of the primitive subfamilies Gelinae and Tryphoninae (except those in the genus *Euceros*) also attack late stages of the host. Members of more recently evolved subfamilies which attacked earlier host stages would have experienced an inherently higher pre-reproductive mortality. Thus, during adaptive radiation from the primitive species strong selection for individuals with high fecundity must have existed, for only by balancing the mortality could the adaptive strategy succeed. When Townes' ranking in relative primitiveness of subfamilies is adopted and plotted against mean number of ovarioles per ovary calculated from a sample from each of 13 subfamilies (Price, 1973), we see a trend from low to high ovariole number (fig. 3). Only the Ichneumoninae show a strong reversal in the trend, no doubt in response to adoption of the tendency to

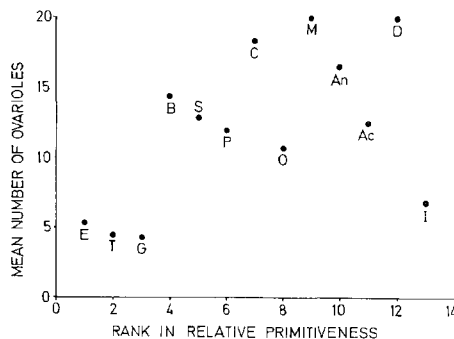


FIGURE 3. Mean number of ovarioles per ovary in a sample of females from 13 subfamilies with rank in relative primitiveness of the taxon, with E=Ephialtinae considered as very primitive. T=Tryphoninae to which the genus *Euceros* which is different from the rest of the family as it lays eggs on foliage from which planidial larvae emerge and attach onto hosts). G=Gelinae to which the genera *Pleolophus*, *Mastrus*, *Endasys* and *Gelis* belong. B=Banchinae, S=Scolobatinae to which the genera *Olesicampe* and *Lamachus* belong. P=Porizontinae, C=Cremastinae, O=Ophioninae, M=Metopiinae, An=Anomalinae, Ac=Acaenitinae, D=Diplazontinae, I=Ichneumoninae.

attack late stages of hosts, which are difficult to find but have relatively low mortality (Price, 1973).

#### REPRODUCTIVE EFFORT

An estimate of total reproductive effort should include all energetic drains incurred during reproductive activity. Usually only net effort, in terms of eggs or seeds produced, can be calculated with available data (e.g. Harper and Ogden, 1970). However, these data are inadequate for a full understanding of a reproductive strategy as shown in the following example. In data on subfamilies of Ichneumonidae (Iwata, 1960; Price, 1973) the trends were increased ovariole number with increased host accessibility, increased numbers of mature oocytes stored per ovary with increased ovariole number, and decreased egg length with increased number of ovarioles per ovary (Price, 1973).

For a comparison of reproductive efforts I have calculated mean egg volumes for samples in each subfamily from data on length and width of mature oocytes given by Iwata (1960). In doing this assumptions were made that egg shapes are approximately prolate spheroids (Iwata, 1958) and that equal volumes of egg matter cost equal amounts of energy. The inverse relationship between egg number and egg volume is clear (table 1) and expected. Less expected was the

TABLE 1

*Mean number of ovarioles per female, mean volume per egg in mm<sup>3</sup>, and mean total egg volume of mature eggs carried at any one time (total reproductive effort) in a sample from each of 13 subfamilies of Ichneumonidae. These are ranked in order of increasing egg production as estimated by the number of mature eggs contained in both ovaries. Data from Iwata (1960), and Price (1973).*

Subfamily	Mean number of ovarioles	Mean number mature eggs per female A	Egg volume mm <sup>3</sup> B	Total reproductive effort A x B
Ephialtinae	10.6	8.0	0.1104	0.88
Gelinae	8.4	8.0	0.0940	0.75
Ichneumoninae	13.4	9.2	0.1065	0.98
Tryphoninae	8.8	14.8	0.0772	1.14
Porizontinae	23.8	24.1	0.0140	0.34
Acaenitinae	24.6	26.2	0.0269	0.70
Ophioninae	21.2	29.3	0.0239	0.70
Scolobatinae	25.6	43.9	0.0161	0.71
Banchinae	28.6	53.1	0.0035	0.19
Diplazontinae	39.6	55.3	0.0090	0.49
Metopiinae	39.8	70.4	0.0092	0.65
Anomalinae	32.8	84.1	0.0019	0.16
Cremastinae	36.8	120.5	0.0002	0.02

decline in total reproductive effort with increasing egg number (table 1). I used the total number of mature oocytes carried by a female in ovarioles at any one time, because data on total fecundity are not available. Even if total fecundities were used, the trend would probably hold since geline females may lay only 30 eggs in a lifetime (Price, 1970b) and cremastine females may lay 500 eggs (Clausen, 1940). Total egg volumes would then be calculated as 2.82 mm<sup>3</sup> for a geline female and 0.10 mm<sup>3</sup> for a cremastine female.

The reasons for this reduced reproductive effort in highly fecund species can only be guessed. Perhaps adult food in the form of nectar and honeydew is less available to species which typically hunt in the tree canopy for early host stages or energy expended on very large flight muscles and their thoracic housing drains energy from reproductive output (Price, 1970b, 1972). It is also possible that temperatures are cooler in the tree canopy during foraging (which may be noc-

turnal or crepuscular in many cases), therefore energetically more expensive to maintain operational body temperatures. Alternatively, energetic cost of eggs may be relatively inexpensive compared, for example, to energy for host searching, and I may have ignored a most important energetic drain on the parasitoids. Clearly, energy budgets of ichneumonids must be further studied.

*Further Study.* As everyone who has worked on reproductive strategies has found, efforts are frustrated by a lack of pertinent data in the literature (c.f. Tinkle, 1969; Tinkle, Wilbur and Tilley, 1970). Ecological life history studies will be most productive when concentrated on answering specific questions. Tinkle, Wilbur and Tilley, 1970 press for more studies on tropical species, intra-specific population variation, exact ages at first breeding, number of eggs produced, absolute size of eggs, egg size relative to weight of female, the reproductive life expectancy of adults, their age-specific fecundities and mortalities, and the survivorship of progeny to sexual maturity.

If we are to understand reproductive strategies fully we must also study energy budgets and nutrient budgets (Harper and Ogden, 1970) since the principle of allocation (Cody, 1966) is involved. For example, tests of Cody's general theory of clutch size (the number of progeny produced per female, and their size, are determined by the energetic drains of competition for food and predator defense, and the force of density-independent mortality) require data on the energetic drain on reproductive effort caused by competition and anti-predation activities. Therefore energy budgets (Batzli, 1974) must be extremely detailed (fig. 4). Clearly allo-

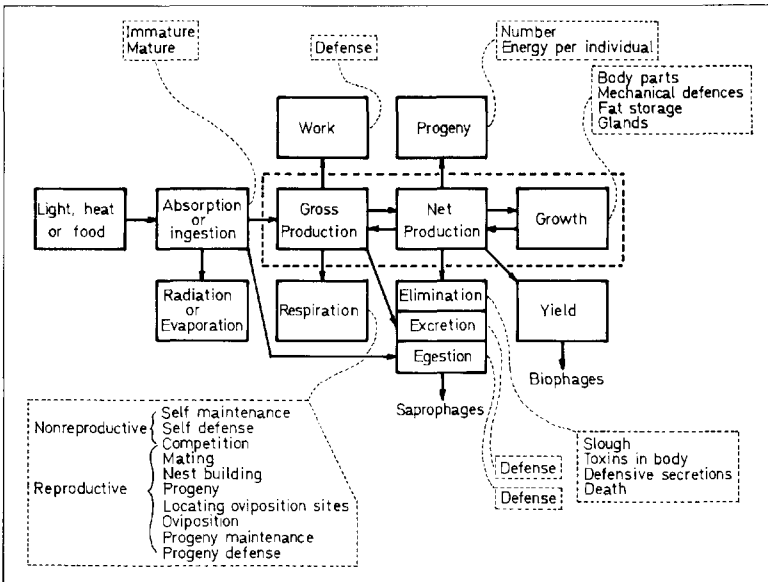


FIGURE 4. Energy flow through individual organisms (heavy lines, slightly modified from Batzli, 1974) with the detailed information required for resolving debates on reproductive strategies (light dashed lines). The heavy dashed box represents the boundary of the organism.

cation of net production is divided between growth, progeny, elimination in the form of caste skins and secretions, and loss of food to other organisms (yield). Some net production may be used subsequently as maintenance energy; such as that stored in a fat body. The energy available for net production is limited by the energetic drains on gross production, respiration, work, and excretion. In

turn gross production is limited by foraging efficiency and assimilation efficiency (plus factors that select for reproductive effort below the physiological maximum).

Ideally, we need to know more than that shown in Batzli's (1974) model. To understand adult size differences within populations and their impact on reproduction we must know the proportions of gross production attributable to the immature and mature stages which will be defined by the proportion of energy ingested by each stage. Energy drains on gross production must be further compartmentalized. For example how much work is involved in defense against predators? A great deal of work is involved for a tortoise or a chrysomelid beetle larva which carries a fecal shield (Eisner, van Tassel and Carrel, 1967). In the latter example egested and excreted materials (inevitable energetic losses) are used as a defense, as in many other insects, reducing the total energy cost of defense against predators. Respiration however, is the most important drain on gross production, and the measurement of allocation of energy for respiration offers great difficulty. We need to know how much energy is spent on non-reproductive and reproductive functions. In the former category self maintenance, defense and competition must be segregated if we are going to test the hypotheses on progeny size and number. Reproductive functions must be compartmentalized between competition, purely reproductive activities such as mating, nest building, locating oviposition sites, oviposition, the energetic cost of manufacturing the progeny themselves, and progeny maintenance and defense. We should also compartmentalize growth to study energy allocation to different body parts, mechanical defenses, fat storage and glands involved in defensive and competitive activity. Finally, elimination may play a major role in predator defense in the form of defensive secretions, the sloughing of body parts such as tails of lizards and legs of arthropods, and even moulting by arthropods may have an adaptive advantage by removing ectoparasites. Defensive chemicals in the body are not strictly part of the eliminated energy, although in many cases, such as in the secondary metabolic products of plants, internal chemicals have such similar functions as secreted chemicals that they may be better considered together.

Few studies have come close to gaining all the information needed for a full description of reproductive strategies. The task ahead is an awesome one, but the potential rewards are immense. We should focus on the essential motivation of life, and gain an evolutionary perspective on the data collected on biological energetics. We should see as one enterprise studies on life history, foraging, predation, energetics, competition, physiology, behavior and community ecology. In fact, the power of this conceptual tool that focuses our attention on reproductive strategies, and unites many aspects of ecology, promises a view of many of the presently invisible patterns in nature.

*Acknowledgements.* I thank George O. Batzli, Donald W. Tinkle and Richard R. Vance and anonymous reviewers for constructive criticism of an earlier draft of this paper. I am grateful for financial support during this study through U.S. Public Health training grant PH GM 1076.

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**The Vascular Flora of Glen Helen, Clifton Gorge, and John Bryan State Park.** *Sture F. Anliot.* Ohio Biological Survey, Biological Notes No. 5: vi+162 p. 1973. Available from the Ohio State University, University Publications Sales, Room 20 Lord Hall, 124 W. 17th Ave., Columbus, Ohio 43210. \$3.00 (spiral bound).

This flora will be great value to the many people who use the Glen Helen and John Bryan area in Greene County for recreation or educational purposes. The introduction discusses the physical and biological features which make the area floristically unusual for this part of Ohio. Each plant community is characterized emphasizing the unique and rare components. Both past and present vegetation are discussed along with patterns of secondary succession. The list of 872 species is usually well annotated with information on abundance, phenology, habit, origin, and local and geographic distribution. Although the statements on Ohio distribution of taxa often seem speculative, the inclusion of information on local abundance and frequency should be of value to both botanists and the park managers.

The ten black and white photographs and cover illustrations are of high quality and well chosen. The printing is clear but the format of the list hides categories by a lack of contrast. The flora is complemented by a list of excluded species and concluded with an index of both common and scientific names. The nomenclature is slightly dated but the book is otherwise accurate and thorough. This area is worthy of a flora, and this contribution is a useful addition to floristic studies of southwestern Ohio.

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