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STRATEGIES FOR EGG PRODUCTION

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The view that egg production is adapted to counter, and thus provides a measure of, the relative hostility of the environment in which organisms must live has been expressed repeatedly (e.g., Stressemann, 1934; Rensch, 1938; Moreau, 1944; Schmalhausen, 1949; Skutch, 1949, 1967; Cole, 1954; and Smith, 1954). Cole (1954) states that the high fecundity frequently seen in parasites and marine organisms is considered commonly as an adaptation to ensure the maintenance of a population when the probability of survival of an individual is low. Dobzhansky (1950), Fretwell (1969), Pianka (1970) and Willson (1971) have added their support to this "balanced mortality" hypothesis. The rationale (following Smith, 1954) is compelling. Over long periods of time the growth rate of a population is very close to zero. Thus the difference between an average natural environment and the optimal environment can be measured by the maximal intrinsic rate of increase (r_{max}), and a comparative survey of these rates therefore permits a ranking of species in relation to the relative environmental harshness to which they are exposed (see also Hairston et al., 1970). In addition, the reciprocal of the net reproductive rate during optimal conditions, $1/R_o$, indicates the probability of survival to maturity in a natural environment, where R_o represents the average number of female progeny produced during the life of a female alive at the beginning of the generation. Thus, when comparing species with similar mean generation periods and adult mortality rates, the reciprocal of gross reproduction per female may be used as a predictor of probability

of survival (for calculation of R_o see Birch, 1948).

Lack (1947, 1949, 1954, 1966) argued against this point of view and has gained support from Cody (1966, 1971) and Johnson and Cook (1968). Lack (1947) pointed out that population balance can be achieved only by the operation of density-dependent mechanisms, and since egg production in many bird populations remains constant with changes in density it cannot contribute to population stability. Thus Lack infers that proponents of the balanced mortality hypothesis suggest an evolution of clutch size to promote population balance, which is not the case. This would clearly invoke the action of group selection. The claims of the supporters of the hypothesis that adjustment of egg production *results* in population stability is vastly different from Lack's interpretation of their argument that adjustment is in order to *achieve* population stability. Skutch (1967) and Willson (1971) have made the necessary distinction between the broad limits set by long-term adjustments to mortality and the finer tuning of egg production to current events which frequently comes under density-dependent influences. Lack seems to have considered only the finer tuning in his critique.

Lack (1954) also argues that genotypes that confer greater fecundity to an individual must become more abundant in the population and therefore the hypothesis does not permit us to conceive of ways in which reduced fecundity might be selected for. But one cannot equate fecundity with fitness. The cost of laying more eggs usually must be exacted from other energetic commitments that promote the welfare of

progeny, and it is by no means certain that more eggs will lead to the survival to reproduction of more progeny. As Skutch (1949) points out for two species of tyrannid flycatchers at the center of their distributions, the more prolific species appears to have no advantage over its congener.

Thus, the "balanced mortality" hypothesis for explaining differences in egg production appears to be viable, and should be considered concurrently with other attempts to explain the observed differences.

Lack (1954) proposed that birds produce clutch sizes corresponding to the largest number of progeny on average that can be fed by the parents, and has gained considerable support. However, Lack's theory does not account for all observed differences (see Cody, 1966 for brief summary) which prompted Cody (1966, 1971) to produce a general theory based upon the principle of allocation. Cody argues that given a quantity of energy available for reproduction, this must be optimally allocated between three energetic drains: eggs, avoidance of predation, and competitive ability. For example, as predation pressure, or competition, or both, increase, egg production must decrease in energetic equivalents, and increased egg production can be achieved only in locations of reduced predation or competition. Cody accounts for an impressive array of clutch-size differences in this way, although more extensive information is required to substantiate the predation and competition aspects of this theory (Cody, 1971).

It is, however, not clear why predation and competition should be the main drains from reproductive energy. Parasites and diseases, harsh physical conditions, absolute limitations in food supply, and food and site quality, are equally likely candidates for inclusion. Heat relations within broods must be considered also (see Royama, 1969). Cody accounts for harsh physical conditions in his theory by invoking *r* selection (Fisher, 1958; MacArthur and Wilson, 1967) which may maximize

population growth by increasing egg production. That is, he uses the "balanced mortality" hypothesis. However, to meet any environmental stress there are two evolutionary strategies available, although they are not independent of one another. Numbers of progeny may be increased or the energetic commitment to each may be increased. In the latter case *K* selection (MacArthur, 1962; MacArthur and Wilson, 1967) operates which is more likely to occur under pressure from competition and/or predation.

Convergence of strategies may occur under conditions that are different but extreme in certain environmental characteristics. For example there is good evidence that presocial behavior in insects has evolved repeatedly in response to two environmental extremes, harsh physical conditions, and abundance of food where competition is severe (Wilson, 1971). Among plants, seeds are commonly larger in species frequently exposed to harsh drought conditions during germination (Hathaway and Baker, 1970; Baker, 1972), a strategy normally adopted by species in stable environments (Salisbury, 1942; Baker, 1972). That is, the same *K* strategy is adopted in response to very different stresses. Therefore Cody is not justified in assigning increased egg production to harsh physical environments and reduced egg production in the presence of high predation pressure. Both *r* and *K* strategies are open. This does not deny the preponderance of *r* strategists in high latitudes and the commonness of *K* strategists in the tropics, it merely cautions us to make theories more conservative.

The "counteradaptation hypothesis" proposed by Ricklefs (1970) invokes the importance of differential coevolutionary rates of predator and prey as a regulator of food intake and consequent energetic allocation to egg production. Therefore it modifies by nuance Lack's theory, but in addition incorporates some of Cody's general theory. Since evolutionary rates of predator and prey must be estimated there

are considerable difficulties in testing this hypothesis.

Ultimately we need a theory expressed in energetic units, but for the present we must work with numbers of births and deaths, and rates of population growth, r and r_{max} , and even approximations of these parameters. Although much of the theory on egg production has been developed from data on bird populations there are practical difficulties to refining concepts by their further study. To mention but three hurdles, difficulties are extreme in quantification of food availability, survivorship, and causes of mortality. Therefore a glimpse at other organisms may be worthwhile.

PARASITE POPULATIONS

"It has been said that by working with parasites one can study ecology in miniature, because the host stands in much the same relation to its parasite as the environment does to a free-living animal" (Salt, 1961).

The study of parasite populations is not plagued with the same problems as those of birds because two important factors, food availability and survivorship, are contained in the same set of data, the survivorship curve of the host. Once the time of attack of the parasite is known, we can estimate food abundance and subsequent mortality.

Five important factors in defining an egg production strategy are given below, where the equivalent factors for free-living organisms are clear.

- 1) Probability of discovery or reaching food (the host).
- 2) Availability of food in terms of its
 - i) dispersion
 - ii) abundance, and
 - iii) accessibility.
- 3) Survival of food item (host) during residence of parasite.
- 4) Effect of host resistance on survival of parasite.

- 5) Competition between members in the
 - i) dispersal phase, and
 - ii) residential phase.

The situation is greatly simplified in insects parasitic on others. For highly mobile searching forms such as parasitoid wasps, where only the larva is parasitic and the adult is free living, we may assume that the probability of host discovery is directly correlated with host availability, and this factor may be accurately estimated using some knowledge on host dispersion and accessibility. Availability of food is provided by the same data. If mortality factors act on the host independently of the presence or absence of parasites, then survival of the host and parasite are both provided by host survivorship, and a good estimate of probability of survival of the parasitoid may be obtained. This assumption will have to be modified after the data are presented. Nevertheless, some index of values for items 1-3 above may be obtained from the survivorship curve of the host, and the lower the general level of parasitism the more accurate the estimate. Ideally a host survivorship curve should be used with mortality through parasitism added.

Host resistance to parasitoids is typically circumvented by adaptations such as external oviposition and feeding, paralyzation of host by venom injected by the parent, secretion of a small trophic sac within the host, or location in tissues where resistance is apparently reduced (e.g., Hinks, 1971). Insects lack the immune response present in vertebrates, leaving phagocytosis as the remaining defense which does not appear to be a major mortality factor on the majority of parasitoid populations (see Salt, 1968).

Finally, in many species energy for competition is largely invested in allelopathic chemicals used in its avoidance. Females leave repellent chemicals on hosts and along their searching routes (e.g., Price, 1970, 1972a) and competition in the parasitic larval stage is thereby largely avoided.

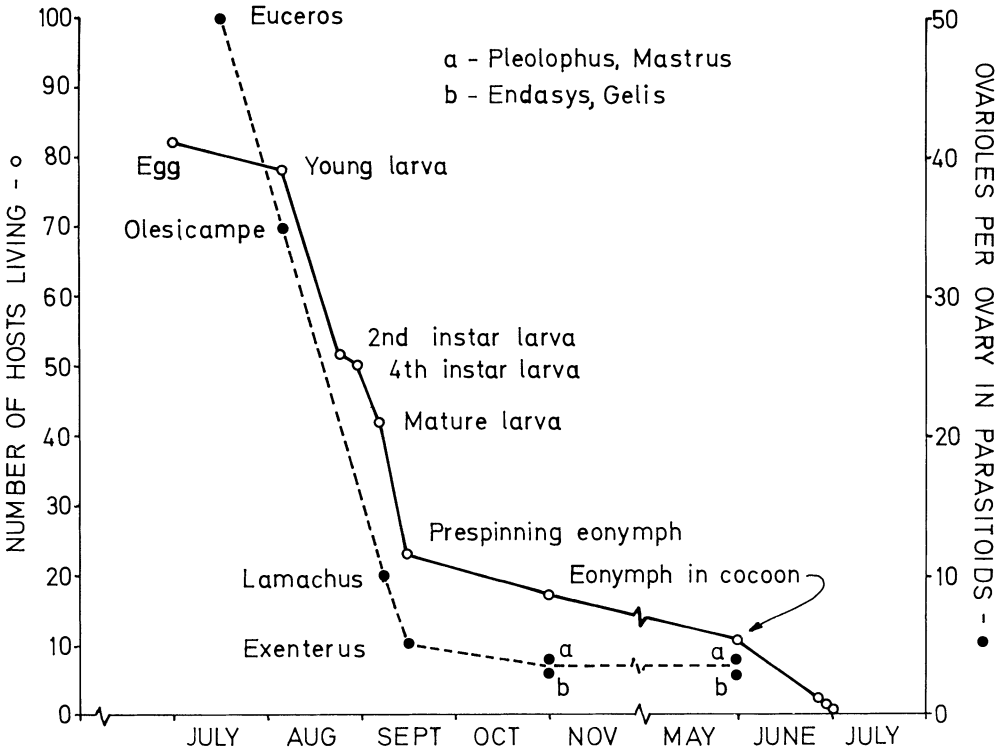


FIG. 1. The survivorship curve of the host, the Swaine jack pine sawfly, in a typical generation, ○ (from McLeod, 1972), and the number of ovarioles per ovary in parasitoids, ●, plotted in synchrony with the time at which each species most commonly attacks the host. The data for *Exenterus* and *Pleolophus* represent the two species per genus in the parasitoid complex.

This phenomenon has usually gone under the title of discrimination (e.g., Salt, 1961), although for many species it is more parsimonious to explain its evolution by natural selection for protection of progeny by the deposition of a repellent chemical (see Price, 1972a). Although the energetic commitment to allelochemicals may be high, no estimates have yet been made.

Therefore, for parasitoid wasps it appears that the best available estimate of egg production strategies can be obtained by knowing the host survivorship curve, time of attack and emergence, and some estimate of population growth characteristics, for a complex of parasitoids that utilize this host. An example follows. Here I concentrate on egg production, one aspect of parasitoid reproductive strategies

which are treated more fully in Price (1973).

A PARASITOID COMPLEX

Ten species of parasitoid in the family Ichneumonidae (Hymenoptera) attack the Swaine jack pine sawfly, *Neodiprion swainei* Middleton. This host overwinters in cocoons in the forest litter, adults emerge to oviposit on jack pine foliage on which the larvae feed colonially until the final, eonymphal, instar which leaves the colony, falls to the ground, spins a cocoon and overwinters. The parasitoid complex, listed in the order in which they attack a generation of hosts with stage attacked in parentheses, includes *Euceros frigidus* Cresson (oviposits on foliage close to a host egg cluster), *Olesicampe lophyri* (Riley)

(young larvae), *Lamachus lophyri* (Ashmead) (older larvae), *Exenterus amictorius* (Panzer) and *E. diprionis* Rohwer (solitary eonymphs before cocoon spinning), *Pleolophus basizonus* (Gravenhorst), *P. indistinctus* (Provancher), *Endasys subclavatus* (Say), *Mastrus aciculatus* (Provancher), and *Gelis urbanus* (Brues) (eonymphs and pupae within cocoons) (see Price, 1972*b*; and Price and Tripp, 1972 for more detailed accounts). All parasitoid species overwinter in the host cocoon and emerge in the spring. Thus the early attackers must remain in or on the host for periods much longer than those which attack later host stages.

The relative egg production strategies of these parasitoids, both in terms of rate of production and total production, are best estimated by the number of ovarioles in each ovary (Price, 1972*b*, 1973). As later stages of the host are attacked ovariole number declines (Fig. 1). The strategies appear to be geared to the relative abundance of the host. This abundance can be estimated by the survivorship curve of a cohort of hosts, provided by McLeod (1972) (Fig. 1). The cohort of 82 represented the mean number of host eggs in a cluster in a year with highest mean fecundity of females, and the mean total fecundity of a female. The correlation between host abundance in a generation and the ovariole number of a parasitoid attacking a particular stage is evident. We can see which are the most hazardous stages of the host to attack, as a resident parasitoid will suffer the same levels of mortality as the host, and the corresponding evolutionary strategies in egg production. Of course changes in dispersion and accessibility of the host heighten the differences in host abundance for a parasitoid. All stages up to and including the mature larva are colonial and are thus easily discovered. Particularly striking is the simultaneous change in slope of the host survivorship curve and trend in parasitoid ovariole number at the prespinning eonymph stage when the host suddenly be-

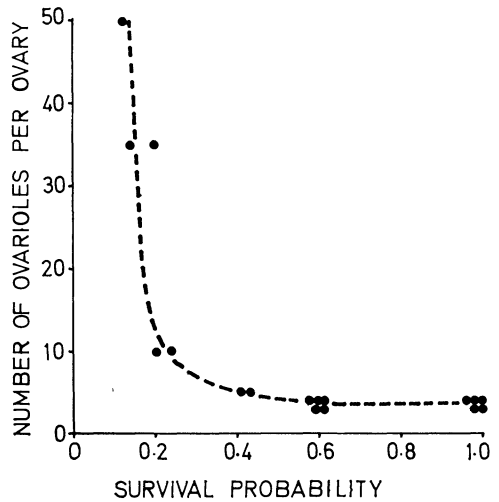


FIG. 2. The number of ovarioles per ovary in parasitoids in relation to the probability of survival to maturity of the progeny, P_p . Two values of P_p are given for *Olesicampe*, *Lamachus*, and the five species of cocoon parasitoids since they commonly attack two stages of the host.

comes solitary and harder to find. Survival rate of the host at this stage improves and decline in ovariole numbers becomes less precipitous.

If the probability of survival of the host, calculated from McLeod's (1972) data is used to express the probability of survival of the parasitoids (P_p) during their residence in or on the host, we see a clearly defined trend of decreased egg production with increased P_p (Fig. 2). Since all parasitoids emerge from cocoons in the spring I assume that the number of eonymphs in cocoons at this time is equivalent to the number of parasitoid survivors, and P_p is thus calculated as the number of hosts in the spring divided by the number of hosts at time of attack. Since the species in the genera *Olesicampe*, *Lamachus*, *Pleolophus*, *Endasys*, *Mastrus* and *Gelis*, attack two or more host stages two values for P_p are given for each species, representing the stages at which the majority of attacks occur (see Price and Tripp, 1972 for details). I emphasize, however, that an egg production strategy

not adapted to cope with the most stringent conditions is doomed. Therefore, particularly for the cocoon-attacking parasitoids, we must assume that the strategy is related to the P_p from October ($P_p = 0.6$) and not from the following May and June ($P_p = 1.0$). Clearly if the strategy does not ensure survival of sufficient progeny through the winter there will be none to attack in the spring. Egg production strategies must be conservative and geared to the most limiting conditions in each year.

The relationship of number of ovarioles per ovary and P_p is not linear for several reasons. Parasitized larvae show a delayed development to the eonymphal stage and are therefore subjected to increased chances of mortality (e.g., Tripp, 1960). Parasitized larvae are also more likely to die from predation (Tostowaryk, 1971). Early parasitoids are internal and must combat host resistance. Inevitably some die in the host whereas later parasitoids are external and the host may be permanently paralyzed by venom from the parent. Finally, parasitoids that attack larvae remain longer in cocoons in the spring than cocoon-attacking parasitoids as they emerge in synchrony with the host stage attacked. Thus P_p is overestimated for these species. Conversely, in the case of cocoon-attacking species P_p is underestimated because they emerge early and attack unemerged hosts and larval parasitoids. Therefore, mortality is relatively higher for parasitoids of larvae and lower for parasitoids of solitary stages than is predicted by calculation of P_p . This accounts in part for the sudden rapid increase in egg production in parasitoids that attack larvae as the estimated P_p declines.

Thus we have an observed P_p derived from the host survivorship curve with which to compare the predicted P_p based on the reasoning behind the balanced mortality hypothesis given in the first paragraph of this paper. Ovariole number is probably the best available criterion for comparing gross reproduction per female,

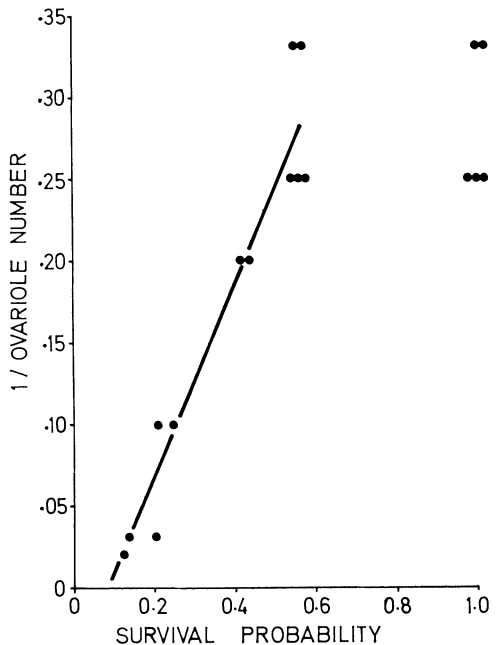


FIG. 3. The reciprocal of ovariole number, which predicts the probability of survival to maturity of progeny, P_p , in relation to the "actual" P_p estimated from the host survivorship curve. The regression line $Y = 0.59X - 0.05$ accounts for 93% of the variance (correlation coefficient = 0.96, significant at 1% level).

as there is no doubt that ovariole number is positively correlated with fecundity (Price, 1973). Data on real fecundities, generation times and survivorship curves for parasitoids in this complex are not available. The reciprocal of ovariole number, predicted P_p , is closely correlated with the observed P_p , where the regression accounts for 93% of the variance between the two sets of data (Fig. 3). The data at $P_p = 1.0$ were omitted from the regression because, as explained earlier, the egg production strategy must be geared to the harshest conditions, so only P_p of parasitoids that must overwinter has been considered.

DISCUSSION

Of course a strategy for high egg production can only succeed when food is abundant. Therefore, it must be inferred

from the data that a combination of levels of availability of food and mortality of progeny largely account for the differences in egg production by parasitoid wasps of *N. swainei*. Thus both Lack's theory and the "balanced mortality" hypothesis are supported. Fretwell (1969) reached a similar conclusion from a consideration of egg production strategies in bird populations organized by dominance hierarchies or territoriality. Although Cody's general theory may be useful when more comparative data on parasitoids become available, it does not appear to aid explanation of egg production differences at present. Certainly it is more parsimonious to consider mortality as a whole than to single out factors that contribute to mortality, or increase energetic commitments to prevent it, as Cody did.

Note that use of the structural feature of ovariole number, that is genetically determined, neglects phenotypic variation considered in the bird clutch size debate. Ovariole number remains virtually unchanged in contemporary time, and with changing size of organism, and population density. It must represent a major structural commitment to a certain reproductive strategy, moulded by a long evolutionary history with a powerful inbuilt averaging effect in response to environmental factors. Thus there exists an essential difference between conclusions reached in this paper which consider this gross adaptation and Cody's theory that attempts to account for phenotypic variation also.

The example provided cannot be discounted as a special case as the same trends are evident in the whole family Ichneumonidae for which there are data, a family that contains about 60,000 species. This statement is based on a study of 248 representative species in 13 sub-families (Price, 1973), and there is much anecdotal evidence that parasitoids in general may show the same strategies. Also, apart from the differences between poikilotherm and homiotherm energetics, the situation is not vastly different from that

seen in vertebrate populations, only food and mortality levels can be estimated more easily.

Since the reciprocal of gross reproduction (or $1/R_{o\max}$ for species with different mean generation periods and adult mortality rates) appears to be a good predictor of the probability of survival to maturity of the progeny, P_p , we must consider if this will be equally useful for both r and K selected species. During r selection numbers of progeny are increased in proportion to the hostility of the environment and the correlation of predicted P_p with actual P_p must be close. During K selection more energy is put into ensuring survival of progeny so the predicted P_p may well underestimate the actual probability, and the slope of the relationship will be reduced. But egg production will still be geared to compensate for differences in mortality factors that parents cannot possibly ensure against, so the relationship must still hold.

The principle of allocation cited by Cody (1966) brings to mind the broken stick model of MacArthur (1957, 1960) and other methods of visualizing the importance value structure of a community (see Whittaker, 1965, 1970). If each component of fitness were ranked according to its importance value in producing mature progeny and its energy input, the different strategies might be more easily visualized, particularly the differences between r and K strategists.

SUMMARY

The "balanced mortality" hypothesis, that egg production is adapted to counter relative environmental harshness is supported, and other theories on the evolution of egg production strategies are discussed. The refining of concepts relating to these strategies may be enhanced by studying parasite populations since two parameters, food availability and survivorship of the parasite, are both contained in the host survivorship curve and are thus relatively

easy to assess. An example of strategies in ten insect parasitoid species is provided which indicates that a combination of levels of availability of food (Lack's theory) and mortality of progeny (balanced mortality hypothesis) largely account for the observed differences in egg production.

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