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Author(s): Eric L. Charnov and Samuel W. Skinner

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EVOLUTION OF HOST SELECTION AND CLUTCH SIZE IN PARASITOID WASPS

ERIC L. CHARNOV AND SAMUEL W. SKINNER*

SYNOPSIS

This paper discusses the evolution of host selection, including superparasitism, and the evolution of clutch size in non-solitary parasitoids. First, we review the natural selection (as opposed to proximate mechanism) approach to understanding life-histories. We discuss this approach specifically in reference to parasitoids, reviewing previous work. Then we build a simple or first order model for a primary parasitoid's clutch size; this is tested against lab/field data for two parasitoids (*Trichogramma*, *Nasonia*). The model fails to account for the data, but the failure is in a very particular way. This leads us to revise the theory, adding factors left out of the first order approach. This new theory building is not *ad hoc* as the factors added are very natural and general considerations. We then consider the problem of superparasitism, the two key questions being, when should it be expected to happen, and what clutch size ought the superparasite have? Finally, we make some general remarks on the natural selection approach to evolutionary ecology.

INTRODUCTION

All organisms pass through a series of physiological and behavioral stages over the courses of their lifetimes. Sometimes these stages of life are reflected in profound changes in the form: for instance, a butterfly begins life as an egg, hatches into a larva, and goes through a pupal stage before emerging as an adult. Other creatures undergo less drastic physical changes.

The study of life histories takes as its subject these general patterns in the lives of individual organisms. It is a powerful tool with which to understand the compromises that organisms have evolved to deal with the many physical and biological factors that affect them during their lives.

Most of the important concepts in the study of life histories can be framed in terms of trade-offs. For example, Pacific salmon of the genus *Oncorhynchus* spend two to three years of rapid growth at sea and then travel up a river or estuary to spawn, after which they die. Trout, of the genus *Salmo*, are closely related to salmon and also come in from the sea to spawn in many of the same streams. But trout do not die after a single spawning; they return to the sea and breed again the next year. Assuming that these two patterns were produced by natural selection operating upon the reproductive advantages to an individual organism, why should any fish die after one spawning? Why not return, as trout do, to spawn many times?

*Eric L. Charnov first began working on evolutionary ecology when he was a graduate student with Gordon Orians at the University of Washington, in the early 1970's. His personal discovery of natural selection constitutes the only religious experience of his life. Currently at the University of Utah, he is a Professor in the departments of Biology, Psychology and Anthropology. His current research concerns human social development, human hunter-gatherer ecology; and sex allocation in plants and animals especially barnacles and coral reef fish.

Samuel Skinner completed a Ph.D. in Biology at the University of Utah in 1983. Presently he is an NIH Postdoctoral Fellow with James F. Crow at the University of Wisconsin. His interests include sex ratio and clutch size evolution. Current addresses: Charnov, Dept. of Biology, Univ. of Utah, Salt Lake City 84112. Skinner, Laboratory of Genetics, Univ. of Wisconsin, Madison 53706.

In this case, there is a trade-off which relates to the fact that a fish must reduce the number of eggs it produces during a single spawning if it is to have enough energy to return to the sea and survive until the next spawning season. Trout produce fewer eggs each year than they would if they invested all their energy in reproduction and died soon after spawning. With salmon, this trade-off is made differently—they put all of their energy into reproduction and in this way increase the chances that more of their offspring will survive. Just why the tradeoff is resolved differently in trout versus salmon is unclear.

The concept of fitness—an organism's genetic contribution to future generations—is central to analyses of such problems. Almost all current models use as a criterion for fitness the reproductive success of an individual, that is, the number of its offspring that survive to reproduce. But reproductive success is in turn determined by several different factors.

The general problem was first clearly posed by Darwin in 1871:

“Thus the fertility of each species will tend to increase, from the more fertile pairs producing a larger number of offspring, and these from their mere number will have the best chance of surviving, and will transmit their tendency to greater fertility. The only check to a continued augmentation of fertility in each organism seems to be either the expenditure of more power and the greater risks run by the parents that produce a more numerous progeny, or the contingency of very numerous eggs and young being produced of smaller size, or less vigorous, or subsequently not so well nurtured. To strike a balance in any case between the disadvantages which follow from the production of a numerous progeny, and the advantages (such as the escape of at least some individuals from various dangers) is quite beyond our power of judgment.”

The balance spoken of by Darwin is the basis of current life history theory. For example, there is often a trade-off between a parent's reproduction and its survival; helping offspring to survive reduces the chance that the parent will survive to reproduce again. A simplified representation of this trade-off is shown in Figure 1. The exact form of the trade-off curve depends on the species and its particular environment. To determine this form, one must know the extent to which producing more eggs or providing more care for offspring reduces the parent's chances of reproducing in the future. Given such a trade-off, the theory of natural selection allows us to calculate the point on the trade-off relation which provides greatest reproductive fitness (illustrated on the curve).

For parasitoid wasps (and many other insects), the production of offspring involves at least two general components: host selection (including the habitat searched for hosts) and determination of clutch size. For this discussion, we will generally ignore a third important component, the sex ratio (reviewed for parasitoids in Charnov (1982) and discussed in a previous symposium by Frank (1983)). The parasitoid and general insect literature shows two rather different approaches to host selection problems. The first, well illustrated by the recent reviews of Vinson (1976) and Vinson and Iwantsch (1980), is the *proximate mechanism* approach. Clearly offspring production involves the factors of (1) habitat selection (where does the female parasitoid search for hosts?), (2) the detailed search for hosts,

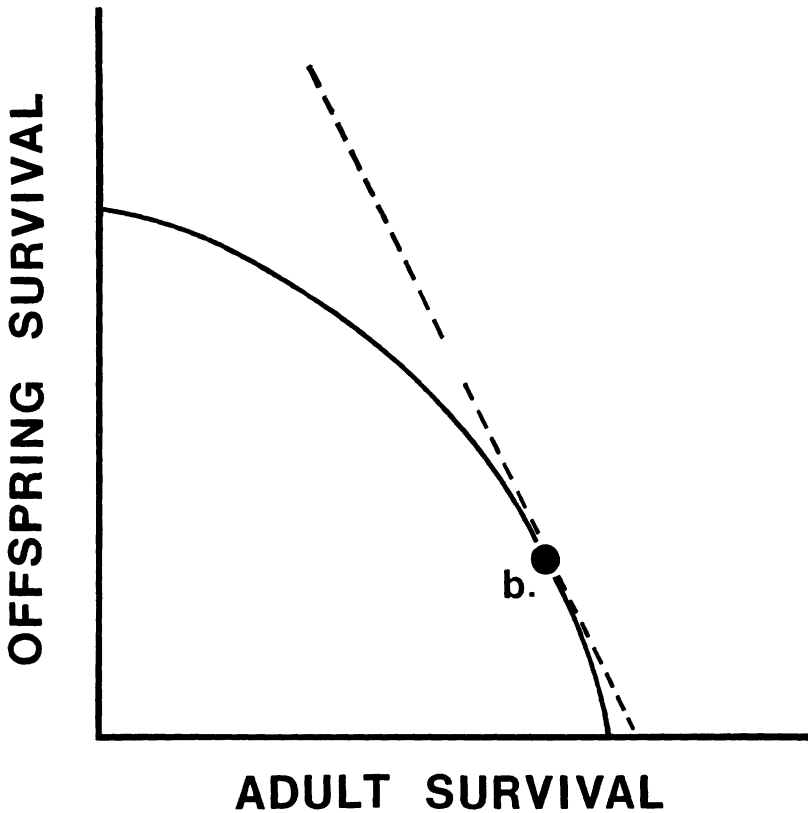


Fig. 1. An assumed tradeoff between the mother's yearly survival and the survival to adulthood of the single offspring born each year leads to an intermediate for both being favored by selection. Population genetic techniques (for example, Charnov 1982) show that the equilibrium is at point *b*, where a line of slope minus two is just tangent to the tradeoff curve.

(3) the acceptance or rejection of "hosts" found and (4) the suitability of the chosen hosts for offspring growth and survival. All of these must be mediated by various cues (chemical, tactical, etc.) and a great deal of research has been devoted to sorting them out. Thus, one attempts to understand in great detail the *immediate or proximate mechanisms* involved in the process of offspring production. This approach is rather different from the *natural selection* approach where we calculate the fitness-maximizing alternative from among those possible in a trade-off situation. This natural selection or proscriptive approach says what the beast ought to do, not how it arranges to do it. Of course, both approaches are useful and interesting; it's just that they ask different questions. That is the two approaches are not alternatives, but are complementary.

The natural selection approach is the newer of the two, although sex ratio decisions (Charnov 1982) enjoy a large literature. Let us briefly mention previous work, with parasitoids or related (life-history-wise)

insects. Two important early papers are Klomp and Teernik (1967), on optimal clutch size in *Trichogramma*, and Mitchell (1975) for the same applied to a bean weevil. More recent work on *Trichogramma* applies precise adaptational models to clutch size and sex ratio (Charnov 1982, Waage and Ming 1983, Waage and Lane 1983). Green (1982) has similarly considered the coevolution of host choice and sex ratio for solitary parasitoids. Chew and Robbins (1983) have reviewed oviposition decisions in butterflies from both the proximate and natural selection viewpoints. Weis, Price and Lynch (1983) have modeled clutch size for a gall making Dipteran. Finally, Skinner (1983a) and Parker and Courtney (1983) have discussed some general adaptational models for several aspects of insect oviposition. Our work discussed here is in the spirit of these last two papers.

LACK'S THEORY FOR BIRD CLUTCH SIZE . . . APPLIED TO WASPS

In the 1940's, the great British ecologist, David Lack, became interested in the factors affecting clutch size in birds. Why did some sea birds attempt to rear but a single offspring, while some titmice produced a dozen? And why did clutch size within a species alter from year to year or with latitude? His approach to the determinants of clutch size consisted of asking the *ultimate question* of the consequences on the parents' fitness of rearing a clutch of a particular size. The fundamental idea was quite simple. Suppose that the survivorship to adulthood of each offspring declined with increasing clutch size (perhaps due to less food available for each child), as shown in Figure 2. This figure is simply illustrative, as the survival decline may well not be linear. Disregarding clutch size influences on parental survival, this survival decline would mean that some intermediate clutch size would be the value which resulted in the largest number of surviving offspring, a fairly good measure of parental fitness. As a first order theory, we might ask if the clutch size of a primary parasitoid, *for each single host*, obeys a rule like Lack's hypothesis. Do female parasitoids lay a clutch which maximizes the number of offspring surviving to adulthood?

The application of these ideas to parasitoids is, however, a bit more complicated than for birds, for one simple reason. Birds have determinate growth and same-sex adults of a given species are roughly all the same size. Insects have no such constraints and size variation among reproductive adults may be several-fold. Thus immatures growing up in a crowded host may simply emerge as small adults. Thus crowding may cause immature survival to decline and/or adult size to decrease. Adult body size may have large effects on adult fitness, altering both life span and egg production (cf. Charnov et al. 1981). Figure 3 shows data from the parasitoid literature which illustrate these notions. In 3a larval crowding (for a bruchid weevil attacking beans) results in a linear decline in survival. In 3b, data from Salt's (1940) work on the parasitoid *Trichogramma* shows how larval crowding lowers the resulting adult size. Figure 3c is a hypothetical relation between female adult size and lifetime egg production, a measure of lifetime fitness for an offspring. If these data were available for one parasitoid in a specified host, we could easily calculate the total fitness through offspring (here restricting our calculations to female offspring) a mother would realize through a given clutch size. This value (W_f) would be the product of:

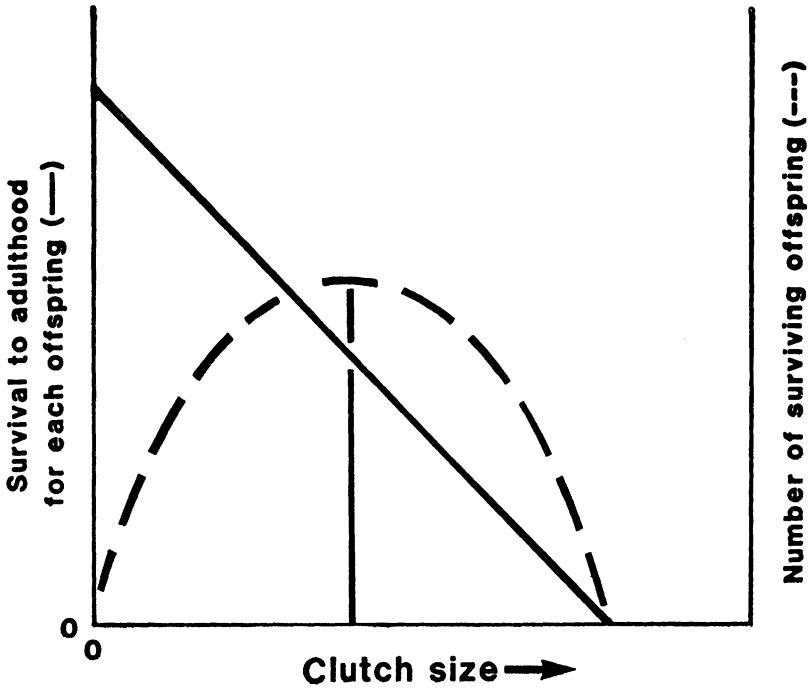


Fig. 2. Lack's hypothesis for clutch size. As clutch size increases, the survival to adulthood of each offspring declines, resulting in an intermediate clutch size which maximizes the number of surviving young. All else equal, this is the size favored by selection (Charnov and Krebs 1975).

$$W_f = (\text{clutch size}) \times (\text{proportion of offspring surviving to adulthood}) \times (\text{size of offspring}) \times (\text{lifetime egg production for offspring of this size}) \quad (1)$$

Under Lack's hypothesis applied to parasitoids, natural selection would favor the clutch size which maximizes W_f . Let us now apply this theory to two parasitoids.

A. *Trichogramma embryophagum*

Clutch size and sex ratio (from a natural selection view) have been studied in several species of egg parasitoids of the genus *Trichogramma* (Charnov 1982, Waage and Ming 1983, Waage and Lane 1983, Klomp and Teerink 1967). Here we briefly review the classic work of Klomp and Teerink (1967). For the species *T. embryophagum*, they studied clutch size in hosts of a wide size range (100-fold range, although five of the six host species were in a 10-fold size range). As expected, the wasp's clutch size increased with host size. For three of the hosts (two large, one small) they determined the effect of clutch size on offspring survival and final adult size.

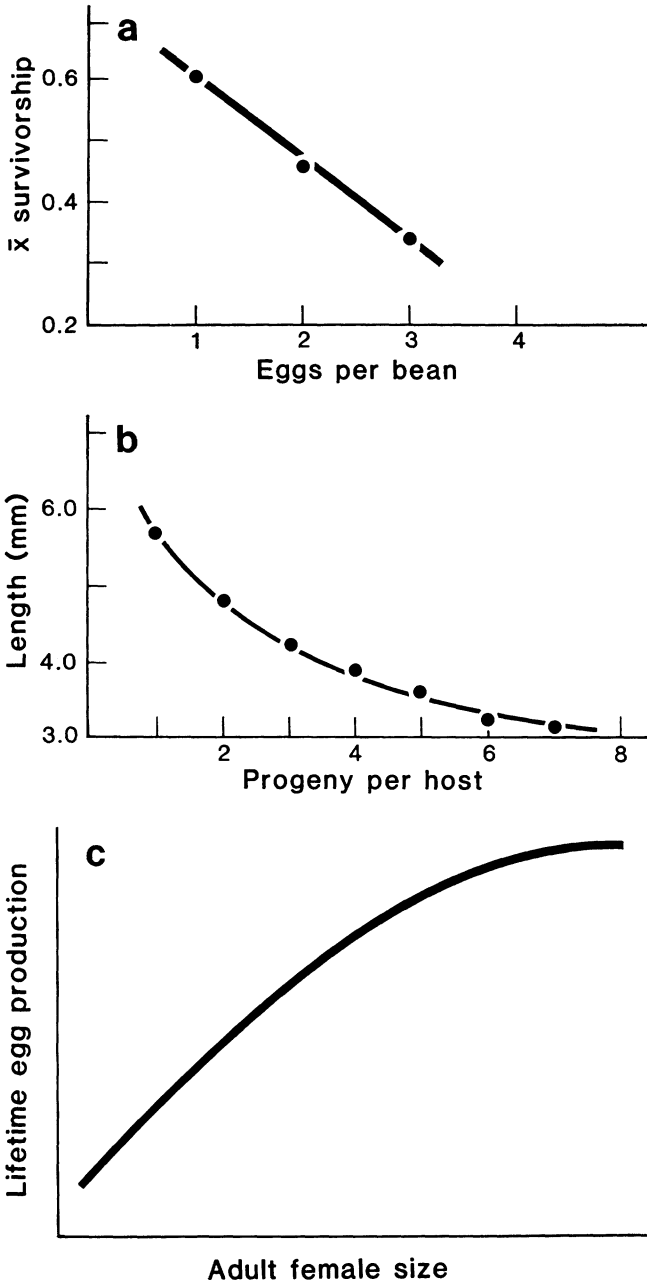


Fig. 3. Clutch size tradeoffs for parasitic insects. *a.* A bruchid weevil attacking beans; immature survival declines with clutch size (data from Mitchell 1975). *b.* The wasp *Trichogramma*; in crowded hosts, the adults emerge at a smaller size (data from Salt 1940). *c.* A hypothetical relationship between adult size at emergence and the adult's lifetime fecundity. These 3 relations allow one to calculate mom's fitness (through offspring from a single host) for a specified clutch size, and thus to derive the insect parasitoid analogue of Figure 2.

In Figure 4a, we show the survival effect for the small and one large host type. Both show declines, but as expected the smaller host goes down fastest. Figure 4b shows a similar plot for clutch size versus resulting adult size. Adult size clearly declines with clutch size. Under lab conditions they also determined the lifetime fecundity for female wasps as a function of female size. Figure 4c shows the resulting relation. While the data showed a fair bit of scatter (and the lab may not represent the field), as a first approximation we may take Figure 4c to translate female size into lifetime fecundity. Figures 4a-c provide sufficient data to calculate W_f versus clutch size for two host sizes (actually three since we omitted from Figure 4 the other large host). Figure 5 shows such a plot, with the hosts labeled. The most productive clutch sizes for the three hosts (in increasing order) are four, seven, and nine eggs respectively. From the lab data on oviposition, the parasitoid laid the following ranges of eggs in these three host species: 1-2, 5-8, 5-8. As can be seen, in general *the parasitoid laid a smaller clutch than that predicted by Lack's hypothesis.*

B. *Nasonia vitripennis*

Nasonia vitripennis is parasitic on the pupae of numerous cyclorrhaphous Diptera, particularly in the families Calliphoridae and Sarcophagidae (Whiting 1967). The ones attacked are largely carrion feeding flies, although one genus utilized by *Nasonia* (*Protocalliphora*) is parasitic on nestling birds. The wasp has been the subject of extensive laboratory research and its general biology is well known (see reviews by Whiting 1967 and Cassidy 1975). The treatment of the data presented here is from Skinner (1983b).

Nasonia attacks several fly species, which in our study sites range 12-fold in body volume. *Phormia regina* is the most abundant host. Under less than severe larval crowding, *Nasonia* shows no increased larval mortality. However, the size of emerging adults declines with crowding. Figure 6a shows data on this for 4 host sizes of *Phormia*. For each of the four there is a significant linear decline in wasp size with increasing clutch size. Figure 6b shows lab data on the number of oocytes in a female as a function of her head width. There is an almost perfect linear regression which suggests that females with heads of width .5 mm or less will have zero fecundity. Unfortunately, we have no data relating oocyte number to lifetime female fitness; thus here we will make the simple assumption that oocyte number is proportional to lifetime fitness. If we combine this with the last two figures, we can calculate W_f versus clutch size for the four host sizes. These calculations are shown in increasing order (a to d) in Figure 7. Now . . . how do the predicted "most productive clutches" (as a function of host size) compare to the clutches found in nature? Figure 8 shows field data for *Nasonia* clutch size versus host volume. The * associate the "Lack clutch size" with its appropriate host volume (for the four host volumes of Figure 6a). Again, most all the clutches found in nature are smaller than those predicted by the Lack hypothesis. Indeed, here the hypothesis predicts rather well the maximum clutch size observed.

WHY DOES THE HYPOTHESIS FAIL?

Rather than predicting the average clutch size, the Lack hypothesis ap-

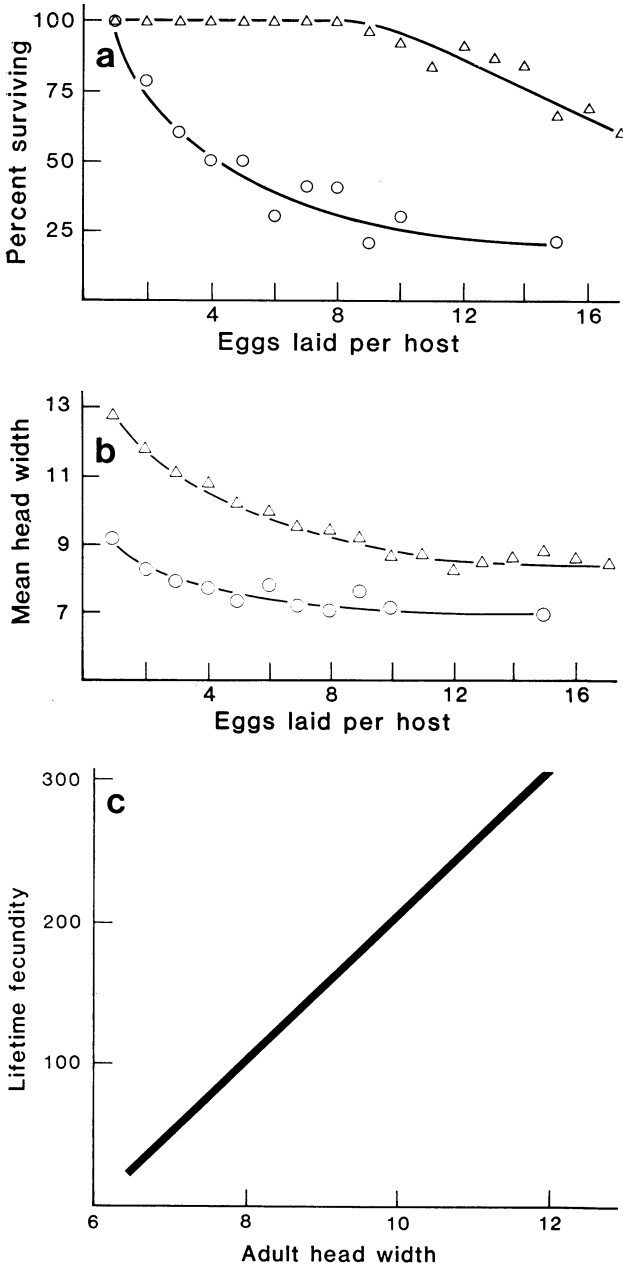


Fig. 4. Progeny fitness for the wasp *Trichogramma*. *a.* Immature survival as a function of clutch size for a large (Δ) and small (\circ) host species. See Figure 5 for host key. *b.* Emerging adult (♀) size versus clutch size for the same two hosts. *c.* Lifetime female fecundity (total number of eggs produced) versus female size in laboratory experiments. (Data from Klomp and Teerink 1967)

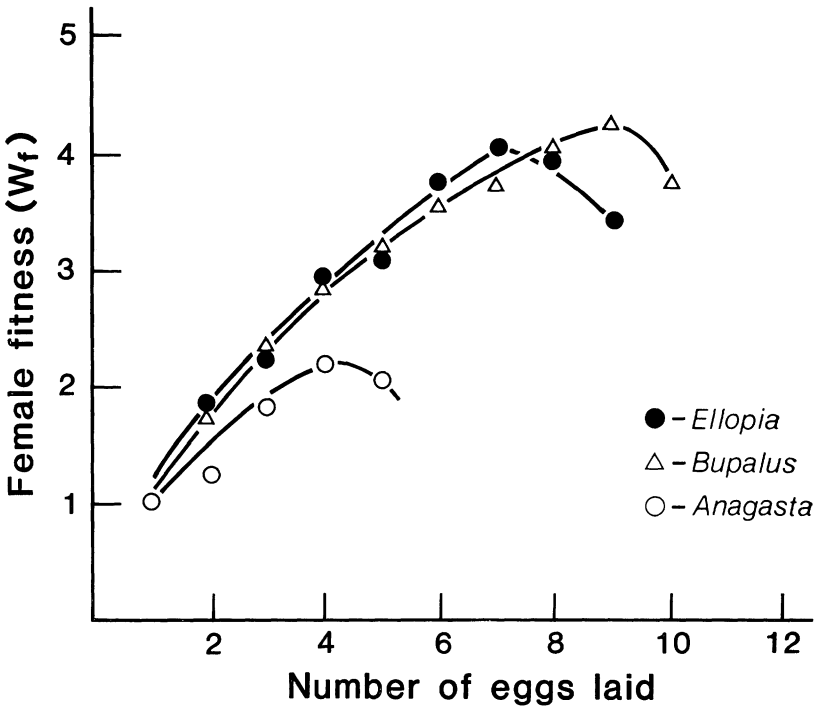


Fig. 5. Data from Figure 4 allow us to plot the mother's fitness (through offspring on a host) versus clutch size. Shown here are plots for 3 host species (2 of them from Fig. 4). See text for further discussion.

pears, in the case of both species, to be predicting clutch sizes just a bit larger than typically observed. The hypothesis fails. But why? We could at this point simply give up the natural selection approach to clutch size but such a decision seems very premature. There are at least three very natural life history factors which we ignored in equation 1, either in the original hypothesis or in its application to the wasps. Actually, we (i.e., we two authors) did not ignore these factors in our theory making (we built a large range of selection models at the beginning of the research), but for this exposition chose to present the simplest model and use its confrontation with data to suggest what to do next. The three factors we have so far ignored are:

- (1) A possible negative correlation between increasing clutch size and the mother's adult survival (or a negative relation between the rate of egg production and mother's survival).
- (2) The possibility that our measure of offspring fitness (i.e., their lifetime egg production) is incomplete.
- (3) The possibility that offspring production per host (that is, the mother's fitness through the offspring she produces in each host) is an incomplete measure of maternal fitness.

Factor 1: It is interesting to note that several years of applying Lack's hypothesis to birds showed a pattern similar to the wasps; the clutch sizes

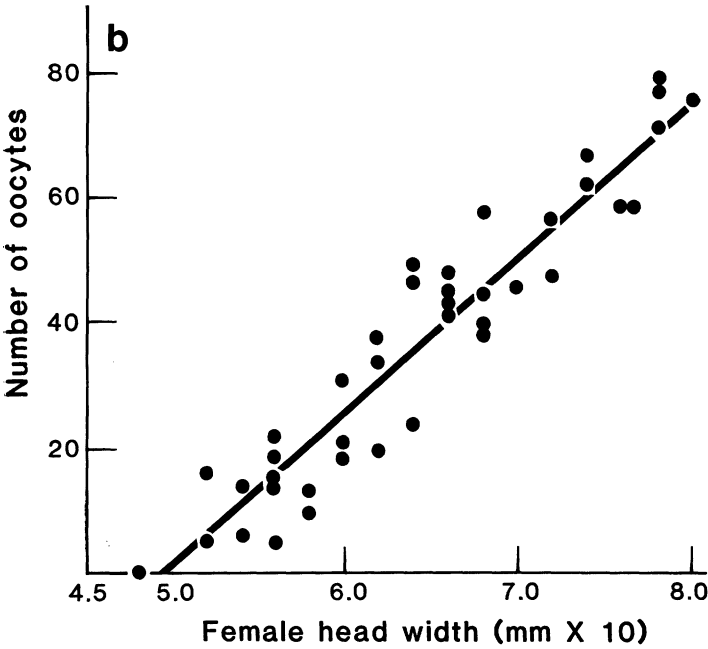
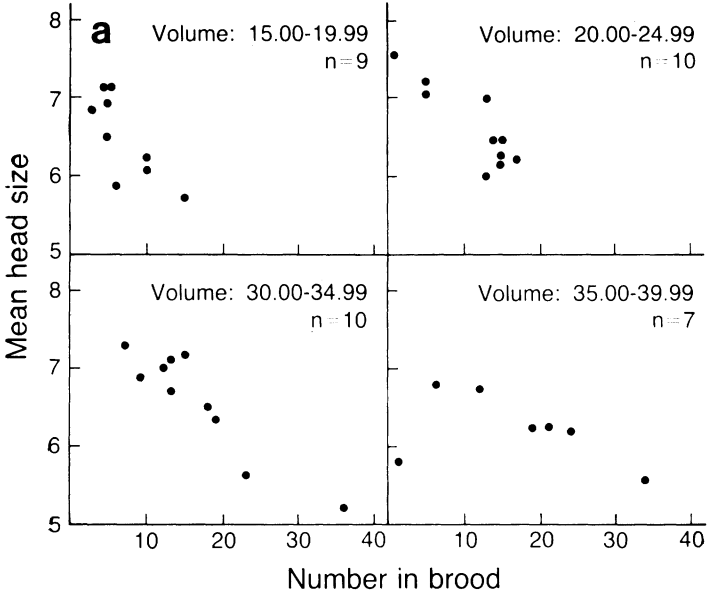


Fig. 6. a. In the wasp *Nasonia*, increased larval crowding typically results in smaller emerging adults, illustrated here for four host sizes of the fly *Phormia*. Immature survival did not decline with increasing clutch size. b. Larger females have more oocytes and presumably greater lifetime fitness (data from O'Neill and Skinner).

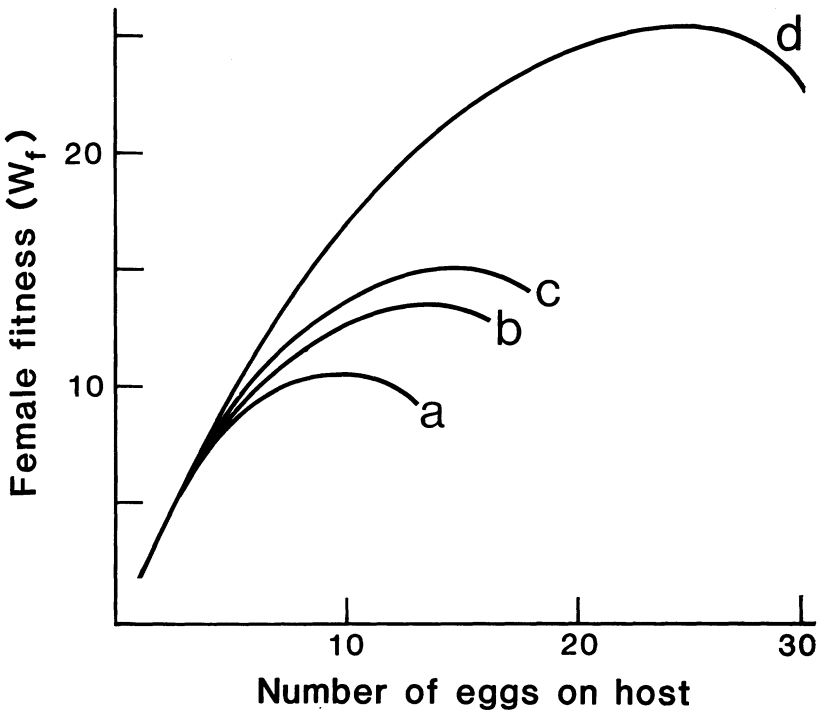


Fig. 7. Relative *Nasonia* adult fitness (through offspring production) as a function of clutch size for the four host sizes of Figure 6 (under the assumption that oocyte production is proportional to lifetime egg production).

observed in nature were generally smaller than the theory predicted. A decade ago Charnov and Krebs (1974) suggested that this might still follow from the natural selection model if adult yearly survival decreased with increasing clutch size. While supporting data are scant, the theoretical effect is real. There are several ways in which “egg production rate” might be negatively related to the parents’ survival rate. Since natural selection is concerned with “lifetime adult fitness”, such a correlation would mean that “fitness” would often be maximized at a smaller than Lackian clutch size (the math details will be published elsewhere).

Consider (2): in the *Nasonia* calculations we assumed that lifetime offspring (daughter) fitness was *proportional* to oocyte production. This is the same as assuming that each female lays the same proportion of her potential brood. Clearly, this need not be the case; a likely possibility is that larger wasps have relatively longer lifespans and thus lay relatively more eggs. If so, then small wasps are penalized more than the proportional assumption allows; then the “true” Lack clutch size is smaller than our calculated one. The same might apply to the *Trichogramma* data if the field is harsher on small females than the lab tests suggest (see also Waage and Ming 1983).

Now consider (3): Begin with a simple question—which of these two situations produces greater maternal fitness? (Assume offspring survival and size are the same for both.):

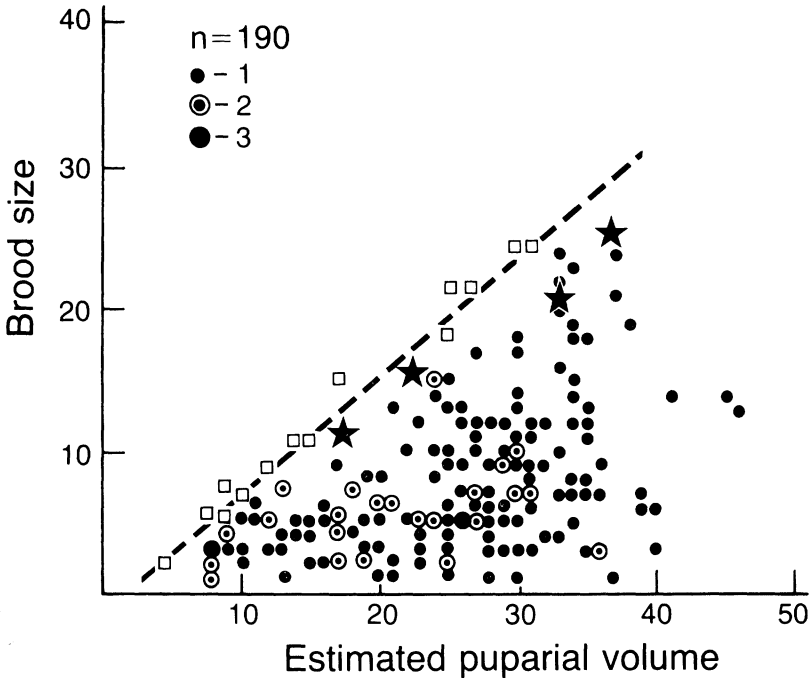


Fig. 8. Field clutch size data for *Nasonia* (*Phormia* hosts). The dotted line, through the \square points, shows the *maximum observed clutch sizes*, as a function of host volume. The four stars (*) are the calculated "Lack clutch size" from the two previous figures. Note that the Lack hypothesis predicts fairly well the largest clutches, but certainly not the average clutch sizes (see Skinner (1983b) for more details).

- a) 20 eggs per host, 40 minutes to find and handle each host
- b) 30 eggs per host, 65 minutes to find and handle each host

Clearly, *b* provides greater maternal fitness under the Lack hypothesis (that is, greater fitness through the offspring produced in *each host*), but (a) provides greater maternal fitness *per unit time* since each host requires relatively less time to find and attack. The latter can be written as:

$$\frac{\text{Total fitness through offspring/host}}{\text{Total time per host}} \quad (2)$$

We have studied several population genetic models on these clutch size problems and this latter *rate measure of fitness* is usually a better indication of the direction of natural selection. (See also Parker and Courtney (1983) and Skinner (1983a).) And this *rate measure* applies even if the other two considerations do not (indeed its use often depends on the assumption that clutch size and mother's survival are uncorrelated). We now consider the implications of this alteration of the Lack hypothesis.

ON USE OF THE RATE DEFINITION OF FITNESS

To use the rate definition of fitness, we must first translate clutch size into

time. Upon encountering a host at least two sorts of time might be involved in producing a particular clutch size: time to mature the eggs and time to lay them. The first of these may be related to the general nutritional condition of the mother, or perhaps the time since the last oviposition. Considering both times (called here oviposition time) should allow us to associate with a given clutch size a particular time to get it into a host just discovered. If this is known, then the clutch size or X-axis of Figures 2, 5 or 7 can simply be rescaled into oviposition time. We have done this, for a hypothetical example, in Figure 9a. Such a plot gives us the mother's fitness through the offspring produced on a host as a function of time at the host. But the total time per host includes the search time between hosts, and this is also indicated on the graph. For simplicity, we limit this discussion to a single kind of host. Note that the "Lack clutch size" is the time which gives the greatest maternal fitness per host; i.e., the peak of the curve. However, the *rate* hypothesis says that selection favors the clutch size which maximizes the fitness gained per unit time (Equation 2). To find this, note the following on Figure 9a. We graph the time between hosts (the search time) *increasing to the left* of the oviposition curve. Now, if we draw a line from the search time (t_s), the line has a slope which is in units of $W_f/(t_s + t)$, which is equivalent to Equation 2. Thus, we can find the optimal clutch size (here, optimal oviposition time) by finding the line through the specified search time which intercepts the W_f curve at the highest point possible. This is illustrated in 9a. In 9b we illustrate the effect of increasing search time, while holding the W_f curve (the oviposition relation) constant. Here the predicted clutch increases in size (from t_2 to t_1). We note here that only if search time is large is the predicted clutch size as big as Lack's hypothesis would predict. Otherwise, the clutch size favored by natural selection is smaller than the Lack size. This is exactly what the parasitoid data show—the Lack size is an outer bound and most clutches are smaller. This rate hypothesis makes two other sorts of predictions. First is that shown in 9b. Increasing search time should increase the clutch size. The second is that the oviposition relation may be sensitive to the rate at which eggs can be matured. It includes at the minimum the time to lay the eggs; if this is all it includes, then the faster they are laid the steeper the W_f curve rises, and the closer the optimum clutch is to Lack's. By manipulating maternal nutrition, one ought to be able to alter the oviposition relation, and see if the clutch laid alters accordingly. Unfortunately, we know of no data which bear on these issues. (Nor do we know of any data which bear on whether maternal survival is itself negatively related to the egg production rate (Factor 1). Such a correlation would similarly favor a smaller clutch size, as previously discussed.)

We now turn to a second general question for parasitoids, that of which hosts to attack in the first place.

HOST SELECTION

A vast literature documents that parasitoids of a given species "prefer" some host types to others. It seems reasonable to conceptualize this choice in the same fitness terms as the clutch size problem. This is not a new suggestion; models of optimal foraging (patch choice, food item choice, etc.) have long been used to view insect (including parasitoids) diet choice

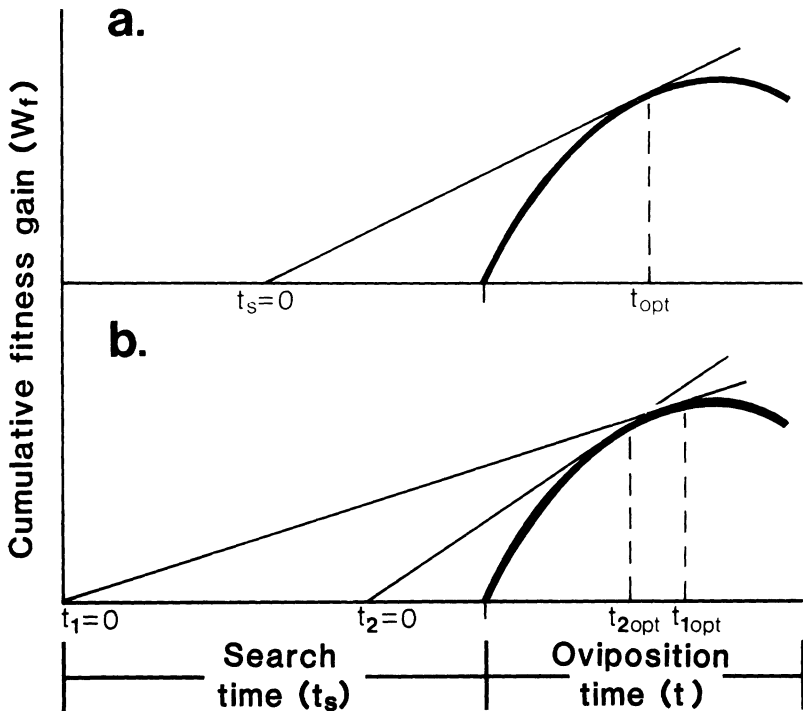


Fig. 9. Natural selection should favor the maximum rate of fitness production through offspring (all else equal), rather than the maximum per host (Lack's hypothesis). *a.* This figure shows how to calculate that clutch size, as a function of the search time between hosts (t_s), the oviposition time once a host is encountered (t) and the parent's fitness through offspring (W_f); related to clutch size, thus to the time (t) to deposit a clutch of a given size). The clutch size (= oviposition time) favored under Lack's hypothesis is at the peak of the curve. *b.* If the search time between hosts increases ($t_2 \rightarrow t_1$), the most fit clutch size increases. The limiting or largest clutch is Lack's.

(e.g., Waage 1979, Green 1982, Charnov 1976a,b, Charnov and Orians 1973). We will not review this literature here but instead will view one new problem: superparasitism. Superparasitism, where a host already attacked by a member of species Z is then further attacked by a second individual of Z, is widely described in the parasitoid literature as a "screw up", a mistake on the part of the second individual (van Lenteren 1981). Recently, Alphen and Nell (1982) suggested that superparasitism may sometimes be an advantageous (adaptive) response for the second individual. Independently, we reached the same conclusion through treating the host population as two separate kinds of prey (unattacked and attacked) and simply asking when the mother *should* include the poorer, already attacked hosts in those she attacks. In general, the answer to this optimal foraging question turns on factors such as how abundant the good hosts are, how easy eggs are to produce, how poor the already attacked hosts are for offspring pro-

duction, and so forth. In Figure 10, we show graphically how to answer the question of whether superparasitism ought to occur or not, using our previously defined oviposition relation. If superparasitism happens, there is the further question of the respective clutch sizes for the 1st and 2nd parasite. Such clutch size questions are beyond the technical scope of this paper and the reader is referred to the work of Parker and Courtney (1983).

IN CONCLUSION

We close this paper with the simple observation that our natural selection perspective has focused attention upon specific variables (e.g., search time, maternal survival, offspring survival and size related to brood host) seemingly important in understanding host utilization in parasitoids; variables which become part of a comprehensive and integrated approach to the problem. Of importance to us is not the present lack of answers, but the host of new questions, ones which readily suggest tests in lab and field. The natural selection approach also raises questions about the nature of the proximate mechanisms involved with the adaptations.

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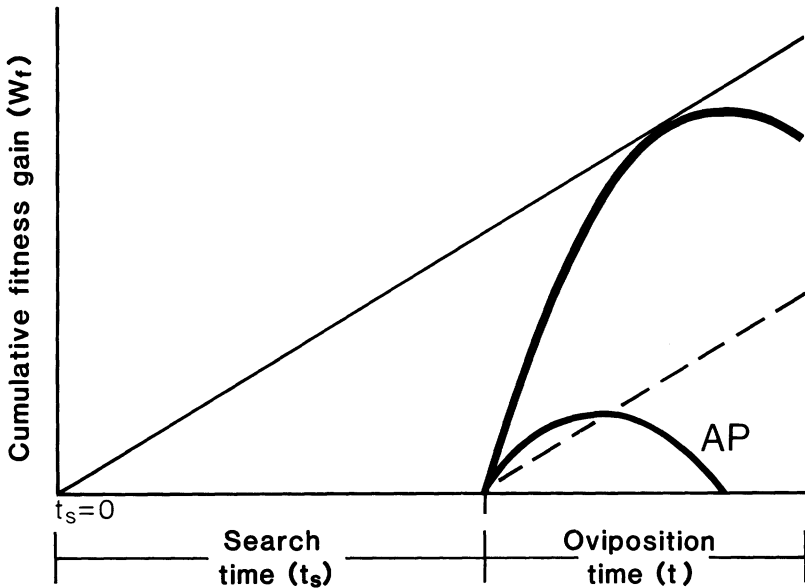


Fig. 10. When is it advantageous to superparasitize? The upper curve is a non-parasitized host, and the tangent argument from Fig. 9 shows the optimal oviposition time (in the absence of superparasitism). The AP curve shows the mothers fitness gain for attacking an "already parasitized" host. The dotted line is parallel to the upper tangent line. If it passes through the AP curve, as it does here, superparasitism is favored. (Argument from Charnov 1976a,b.). Optimal clutch sizes under superparasitism are treated in Parker and Courtney (1983).

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