

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Egg load as a major source of variability in insect foraging and oviposition behavior

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Foraging and oviposition behavior of insects directly influences offspring production and fitness, and is therefore particularly amenable to analysis with optimization models. These models have identified two general constraints on female fitness: host availability and egg complement. Research on insect oviposition has thus far focused on external, environmentally-derived cues such as host density and quality. Here we review recent studies and suggest that insects adjust their foraging and oviposition behavior in response to their perceived risk of becoming egg limited. Females with higher egg loads (1) search more intensively, and therefore encounter more hosts per foraging bout, (2) accept for oviposition hosts of lower rank in a preference hierarchy, (3) spend less time handling hosts, and (4), for gregarious species, deposit larger clutches. Given the different constraints for a forager with a changing egg load, we hypothesize that an individual female may shift between maximizing the number of hosts encountered to optimizing the quality of hosts selected for oviposition. Incorporating egg load dynamics into foraging models and empirical studies will enhance our understanding of insect oviposition behavior.

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Insect oviposition behavior is central to investigations of insect population dynamics, life-history evolution, plant-insect and host-parasitoid interactions, and biological control of insect pests. Investigations of the proximal causes of variation in insect foraging and oviposition behavior have focused on responses to environmental cues (van Alphen and Visser 1990), the role of learning (Lewis and Papaj in press), and genetic variation (Futuyma and Peterson 1985). As exemplified by reviews of sources of variation in oviposition behavior, the role of internal, physiological processes has rarely been evaluated in detail (Papaj and Rausher 1983, Courtney 1984, Rausher 1985, Singer 1986, Waage 1986, Lewis et al. 1990, Roitberg 1990, Strand 1990, Vet et al. 1990, Thompson and Pellmyr 1991; but see Jaenike 1990, Vet and Dicke 1992). This is in con-

trast to studies of the foraging behavior of arthropod predators for which the role of “gut fullness”, an internal physiological factor is widely appreciated (Dixon 1959, Mols 1989, Sabelis 1990).

One physiological parameter, the number of mature oocytes available for oviposition, henceforth termed “egg load”, has been hypothesized to modify alighting behavior of butterflies (Jones 1977, Root and Kareiva 1984), response to prior fruit infestation in fruit flies (Papaj et al. 1989), clutch size in invertebrates (Godfray 1987), host acceptance in bean weevils (Wasserman and Futuyma 1981), and host acceptance and sex allocation in a parasitoid (Simbolotti et al. 1987). In addition, theoretical analyses predict that egg load influences many aspects of oviposition behavior (Iwasa et al. 1984, Parker and Courtney 1984, Mangel 1987, Charnov and

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Table 1. Influence of egg load on foraging and oviposition behavior of herbivorous and parasitoid insects.

Lepidoptera				
Species	<i>Pieris rapae</i> (Pieridae)	<i>Battus philenor</i> (Papilionidae)	<i>B. philenor</i>	<i>B. philenor</i>
Method of measurement	egg load at observed behavior = total eggs laid since observed behavior + no. chorionated eggs at dissection at end of period	no. chorionated eggs dissected plus no. of eggs oviposited	no. chorionated eggs at dissection plus no. eggs oviposited	no. chorionated eggs at dissection plus no. eggs oviposited
Level	individual (Australian market garden sample only)	individual	individual (unmanipulated females)	cohort (manipulated females)
Behavior	search intensity, i.e. host attraction index (proportion of flights into host relative to nonhost grid points)	search intensity (proportion of time spent searching)	1. search intensity (no. alightings per unit time) 2. host acceptance, i.e. selectivity index (1 – no. hosts oviposited on per total no. hosts alighted on) ^b 3. clutch size (no. eggs per plant)	1. search intensity (no. alightings per unit time) 2. host acceptance, i.e. selectivity index (1 – no. hosts oviposited on per total no. hosts alighted on) 3. clutch size (no. eggs per plant)
Association with egg load	positive relationship between egg load and host attraction index (model parameter adjusted to match observed movement) ^a	search intensity by females with higher egg loads was greater than that by females with lower egg loads (ANOVA, $P = 0.0002$)	positive correlation between selectivity index and egg load ^c ($r = 0.53$, $P = 0.02$) and between clutch size and egg load ^d ($r = 0.68-0.93$, $P < 0.008$). No association found for search intensity	search intensity by females with high egg loads was greater than in low egg load females; selectivity index was less in high egg load females ^e (ANOVA, $P < 0.05$). For clutch size, see footnote ^f
Confounding variables	experience age body size adult feeding weather	experience age body size weather	experience age ^e body size ^e weather	experience
References	Jones 1977	Odendaal 1989	Odendaal and Rausher 1990	Odendaal and Rausher 1990

^a Statistical criteria for when model parameter mimics observation are not available.

^b Note, an increase in the selectivity index indicates an increased selectivity.

^c Results are inconsistent with each other; interpretation in text is ambiguous.

^d Their statement [on page 184, eight lines from the bottom] should read "the value of the selectivity index will increase and clutch size will increase with increasing egg load." (F. J. Odendaal, pers. comm.).

^e Measured in Odendaal (1989).

^f Sample size is too small to evaluate effect of egg load manipulation on clutch size.

Skinner 1988, Mangel 1989). Consideration of the role of this physiological factor may be necessary for a complete understanding of variation in insect oviposition decisions (see also ovariole development and behavior in social insects, e.g. Minkenberg and Petit 1985).

Here we present recent advances in the understanding of the effect of egg load on oviposition behavior. First we present a brief overview of theoretical developments. Next, we examine four insect systems where this issue has been addressed empirically. In closing, we discuss issues of methodology and experimental design, and outline the implications of empirical studies sug-

gesting oviposition behavior has evolved under natural selection.

Theory

Employing dynamic optimization models, Iwasa et al. (1984) showed that optimal host range and clutch size can be functions of egg load and mortality risks in insect females. Mangel (1987) developed such a model for host selection and clutch size where egg load and female age are explicit temporally dynamic variables. His

Table 1. (continued).

Species	Diptera			
	<i>B. philenor</i>	<i>Dacus</i> spp. (Tephritidae)	<i>Dacus tryoni</i> , <i>D. jarvisi</i>	<i>Drosophila suboccidentalis</i> (Drosophilidae)
Method of measurement	no. chorionated eggs at dissection plus no. oviposited	no. mature eggs at dissection	no. chorionated eggs at dissection plus no. of eggs oviposited	no. mature eggs at dissection in full-sibs at beginning of trial
Level	individual	cohort	individual	sibship
Behavior	clutch size (no. eggs per batch)	host acceptance (no. eggs laid on high and low ranked host)	clutch size (no. eggs per oviposition period)	host acceptance (oviposition of at least one egg versus rejection in 24 h trial)
Association with egg load	females of the first seasonal flight with high egg loads laid larger clutches ($r = 0.66-0.87$, $P < 0.01$). No association found for females of the 2nd seasonal flight	in <i>D. tryoni</i> acceptance of low ranked host and egg load increased with deprivation (ANOVA, $P < 0.01$). In <i>D. cacuminatus</i> , <i>D. cucumis</i> and <i>D. jarvisi</i> diet breadth and egg load did not change with deprivation	clutch size in <i>D. tryoni</i> : $r = 0.79$, $P < 0.005$; in <i>D. jarvisi</i> : $r = 0.45$, $P = 0.054^b$	percentage of sibship accepting low ranked hosts related to sibship egg load ($r = 0.52$, $P < 0.01$). No association for high ranked host
Confounding variables	experience age body size weather	experience	experience body size	adult feeding ^b
References	Tatar 1991	Fitt 1986	Fitt 1990	Courtney et al. 1989

^a Statistics calculated from fig. 4.2 (Fitt 1983).

^b While the design removes effects of adult feeding on estimates of egg load it is still possible that an interaction exists among egg load, propensity to feed and the quality of the host as an adult food source.

Table 1. (continued).

Species	<i>D. busckii</i>	<i>D. busckii</i>	<i>D. suboccidentalis</i>
Method of measurement	no. mature eggs at dissection plus no. oviposited in previous 24 h	no. mature eggs at dissection in virgin half-sibs at beginning of trial	no. eggs at dissection plus no. eggs oviposited before choosing to leave host
Level	individual	sibship	individual
Behavior	host acceptance (proportion eggs laid relative to total number available)	1. host acceptance (oviposition of at least one egg versus rejection in 24 h trial) 2. clutch size (no. eggs oviposited in 24 h trial)	clutch size (proportion eggs laid relative to total number of eggs)
Association with egg load	host acceptance increased with egg load; acceptance of lower and higher ranked hosts were equal only at the lowest and highest egg loads (<i>t</i> -test, $P < 0.05$)	genetic correlation of egg load with acceptance of low ranked host ($r = 0.79$, $P < 0.005$), and with clutch size ($r = 0.66-0.69$, $P < 0.05$) on both hosts	relative clutch size increased with egg load; the three hosts differed in the clutch sizes received
Confounding variables	body size adult feeding	adult feeding ^a	body size adult feeding
References	Courtney et al. 1989	Courtney and Hard 1990	Courtney et al. 1990

^a While the design removes effects of adult feeding on estimates of egg load it is still possible that an interaction exists among egg load, propensity to feed and the quality of the host as an adult food source.

Table 1. (continued).

Hymenoptera				
Species	<i>Trichogramma maidis</i> (Trichogrammatidae)	<i>Monoctonus pseudoplatani</i> (Aphidiidae)	<i>M. pseudoplatani</i>	<i>Venturia canescens</i> (Ichneumonidae)
Method of measurement	no. of eggs for a cohort of females dissected each day	estimate ^b of initial load of chorinated eggs = (no. of mature eggs at time $t - 7.11$)/476.15 × (tibia length) ³ - no. of hosts parasitized	estimate ^b of initial load of chorinated eggs = (no. of mature eggs at time $t - 7.11$)/476.15 × (tibia length) ³ - no. of hosts parasitized	no. eggs present in the oviducts plus no. of cocking movements
Level	cohort	cohort	individual	individual
Behavior	1. searching activity: a. percentage of time spent searching and b. walking speed (mm/s)	1. search intensity a. proportion of time spent searching b. speed of search 2. host acceptance (proportion of encountered hosts that are accepted for oviposition)	oviposition rate (no. hosts parasitized in a 15 min. foraging period)	search intensity (time spent probing)
Association with egg load	parasitoids with higher egg loads had a higher searching activity (Fig. 6, ANOVA, $P < 0.001$). No change in their walking speed was found ($\alpha = 0.05$)	search intensity (1a) and host acceptance by foraging parasitoids decreased during the day with a decreasing egg load ($r = 0.55$, $P < 0.001$ and see their Table 6 without statistics, respectively). No change in speed of search (1b) found ($r = 0.11-0.18$, $P > 0.05$)	parasitism rate positively relates to proportion ^b of initial egg load "remaining" ($r = 0.77$, $P < 0.001$)	parasitoids with a higher egg load had a higher propensity to search ^c ($r = 0.73$, $P < 0.001$)
Confounding variables	experience ^a	experience diurnal rhythm	experience	experience age body size
References	Pak et al. 1985	Collins and Dixon 1986	Collins and Dixon 1986	Trudeau and Gordon 1989

^a No statistical effect of age on searching activity was found.

^b Initial egg load was estimated as a function of the egg load determined at the end of an observation and size, i.e. tibia length, after this relationship was established for a group of parasitoids. Therefore, this study controls for wasp size. However, the number of host contacts or ovipositions is not directly measured, which implies confounding of "relative" egg load with experience.

Data were re-analyzed from their fig. 3A. Because 15 hosts were offered to each individual wasp, observations on wasps that had less than 16 eggs at the beginning of the assay were excluded from the analysis in order to prevent absolute egg-limitation from contributing to the observed result.

model predicts that acceptance of low ranking hosts increases as a function of egg load and age. Thus, clutch size should correlate positively with egg load, egg maturation rate, egg capacity, and the probability of adult mortality between ovipositions. Courtney and Chen (1988; see also Wasserman 1986) presented a verbal model for individual host selection that explicitly incorporates egg load. They postulated that hosts exist in a ranked-order of preference, with the threshold of acceptability depending on internal factors, primarily egg load. The model predicts that the host range of individuals broadens with egg load. However, their model does not consider potentially confounding factors such as female age and mortality risks.

Evidence

Recent studies reflect a growing awareness of the important role played by egg load in modifying insect oviposition behavior. We discuss below four studies of individual oviposition behavior where egg load was estimated or measured directly. We summarize other studies in Table 1; their outcome is consistent with the patterns arising from the case studies. For each study, Table 1 notes how the authors estimated egg load, the level at which they studied the association with behavior, the affected behaviors, the strength of any observed effect of egg load, and whether there were any confounding variables. Some studies were not available

Table 1. (continued).

Species	<i>Ephedrus californicus</i> (Aphidiidae)	<i>Aphytis lingnanensis</i> (Aphelinidae)	<i>Diglyphus begini</i> (Eulophidae)
Method of measurement	no. mature, chorionated eggs at dissection	no. mature eggs dissected plus eggs found on host and/or ovipositions directly observed	no. mature eggs dissected plus eggs found on hosts
Level	cohort	individual	individual
Behavior	1. search activity ^a (no. of host encounters) 2. parasitism ^a (no. of hosts parasitized) 3. host acceptance (no. hosts superparasitized)	1. searching time (time locating host) 2. clutch size (no. eggs per host) 3. handling time (time spent on host)	1. search intensity (time spent walking and flying/total foraging time) 2. parasitism rate (no. hosts parasitized/visit time) 3. parasitism (proportion of hosts parasitized)
Association with egg load	parasitoids with higher egg loads encountered and parasitized more hosts, accepted a higher proportion of the previously parasitized hosts for oviposition (see Fig. 6 for relation between egg load and age, Table 1 and Fig. 1 for behaviors 1 and 2, respectively, with no statistics applied, and Table 2 for behavior 3, $P < 0.05$, with age as the independent variable	parasitoids with a higher egg load required less time to discover a single host ($r = -0.42$, $P < 0.001$), deposited larger egg clutches ($\chi^2 = 41.1$, $P < 0.001$) and spent less time handling the host ($r = -0.46$, $P < 0.001$)	with hosts absent parasitoids with a higher egg load showed a higher propensity to initiate searching (latency time: $r = -0.47$, $P = 0.005$); on plants with hosts their search intensity was higher ($r = 0.23$, $P = 0.04$) as well as their parasitism rate ($r = 0.38$, $P = 0.002$) and the eventual proportion of hosts parasitized ($r = 0.31$, $P = 0.02$)
Confounding variables	experience age	note ^b	experience ^c body size
References	Völkl and Mackauer 1990	Rosenheim and Rosen 1991	Minkenber and Parrella, unpubl.

^a Authors interpreted these behaviors strictly as a function of age but it could well be under influence of egg load.

^b Egg load was manipulated indirectly using parasitoid size and holding temperature as experimental treatments; neither treatment had a consistent effect on parasitoid behavior.

^c No statistical effect of age was found.

at the time of the review, e.g., Minkenber et al. (in press) and van Roermund and van Lenteren (unpubl.), whereas other studies in which complete egg depletion could not be excluded e.g., Donaldson and Walter (1988), are not reviewed because females without eggs often behave differently from females that have eggs available.

Clutch size in the butterfly *Battus philenor*

Oviposition of the pipevine swallowtail *Battus philenor* on Dutchman's pipevine, *Aristolochia* spp., has been extensively studied. Variation among females in search image, inter- and intra-specific host selectivity, oviposition rate and clutch size is related to differences in female age and experience, season, host and non-host density, and host quality (Rausher 1983, Papaj 1986a, b, Papaj and Rausher 1987a, b). While arguing that variation in clutch size within a seasonal brood is a response to variation in host quality, Pilson and Rausher (1988) demonstrated experimentally with

holding host plants from butterflies, that the time since the last oviposition was a concurrent factor of behavioral plasticity. Egg load, potentially increasing during the deprivation period, was the suggested causal factor.

Investigations of unmanipulated females in the field support the hypothesis that egg load is a primary factor generating variation in clutch size within a seasonal brood. The rank correlation coefficient between clutch size and egg load in Texas (early-spring brood) is between 0.6 and 0.9 (Odendaal and Rausher 1990). In California (early-spring brood), variation in egg load explains 30–75% of the variation in clutch size whereas host characteristics and host quality, as reflected by larval success, play secondary roles, explaining 4–19% of the variation (Tatar 1991). To assess the possibility that an important role of host quality is masked by absolute constraints on clutch size set by the total number of eggs available for laying, Tatar (1991) repeated his analysis using only those females that laid less than

65% of their mature eggs; egg load was retained as the most important influence on clutch size.

For *Battus philenor* in California, the observed influence of egg load on oviposition changes seasonally (Tatar 1991). In the late-spring brood, variation in clutch size is about half that of early-spring. Clutch size was not correlated with egg load, host characteristics, or larval success. Mean clutch size in the late-spring is also about half that of the early-spring. This seasonal difference in mean clutch size is not explained by changes in mean egg load; egg load at the time of oviposition in the two seasonal flights is similar. Instead the difference may be due to a behavioral response to the decrease in overall host quality and/or may be related to the increase in egg mortality that occurred in late spring.

Host location and diet breadth in *Drosophila* flies

Courtney et al. (Courtney and Chen 1988, Courtney et al. 1989) used both direct behavioral assays and quantitative genetics to investigate relationships between egg load and acceptance of low ranking hosts in *Drosophila busckii* and *D. suboccidentalis*. For individual females of *D. busckii*, behavioral assays showed that the acceptance of low ranking hosts over a 24 h oviposition period is associated with large egg loads. Mushrooms, high-ranked, become most acceptable when egg load exceeds 20 mature eggs, while cucumber, low-ranked, attains this level of acceptance only when egg load exceeds 50 mature eggs (Courtney et al. 1989).

To avoid the complication of egg maturation during an oviposition trial, *D. suboccidentalis* that shared parental and larval environments were exposed to mushroom (high-rank), cucumber (low-rank), or were dissected at the beginning of the trial to provide an estimate of initial egg load for the sibship. Again, acceptance of the low-ranked host was related to high egg load (now of the sibship), while the high-ranked host was acceptable regardless of egg load (Courtney et al. 1989). Half-sib breeding designs of both *D. suboccidentalis* and *D. busckii* demonstrated that egg load and acceptance of low ranking hosts are heritable and positively genetically correlated (Courtney and Chen 1988, Courtney et al. 1989, Courtney and Hard 1990).

Drosophila oviposition studies differ from the other studies reviewed here in several ways. First, they provide evidence of genetic correlations between egg load and oviposition behavior. Second, clutches are produced by oviposition of single eggs over many hours rather than in a single oviposition bout; preference, therefore, is typically assayed by the relative number of eggs that are deposited in 24 h periods on different hosts (Jaenike 1987, 1990, Courtney et al. 1989). Lastly, adults use the host source for feeding as well as oviposition (Sang and King 1961, Markov et al. 1990). With some experimental designs it is therefore possible that adult nutritional state and egg load covary across experimental treatments e.g., exposure to different host

types, potentially confounding the influence of egg load.

Search intensity in the solitary leafminer parasitoid *Diglyphus begini*

Host acceptance and sex allocation behavior of *Diglyphus* wasps has been examined in response to host size (Heinz and Parrella 1990). Minkenberg and Parrella (unpubl.) investigated the role of host density and egg load in the foraging behavior of *Diglyphus begini* in laboratory assays that enabled parasitoids to move between a number of plants. Search intensity, the time spent walking or flying divided by total time, was positively related to egg load (Table 1). Increased search intensity led to a greater number of hosts parasitized per unit time in the foraging arena. Since each encountered host was typically accepted for oviposition, the increase in oviposition rate appears to reflect the more rapid location of hosts by individuals with high egg loads. Finally, the proportion of all hosts parasitized before dispersal from the test arena was higher for wasps with large egg complements, but only at high densities of hosts.

Latency time, the interval between a parasitoid's introduction to the test arena and the initiation of foraging, is also a function of egg load, but host odor may interact with egg load (Minkenberg and Parrella, unpubl.). When hosts are absent from the arena, latency time was inversely related to egg load. When hosts were present, latency time was a function of density of hosts per plant and not of egg load. Such interactions confound latency time studies if host absence is used as a control treatment.

Clutch size in the solitary armored scale parasitoid *Aphytis lingnanensis*

Variation in host acceptance and clutch size decisions in *Aphytis* spp. parasitoids has been extensively studied as a response to variation in host quality, as measured by host age, size, species, and whether the host was already parasitized by con- or heterospecific parasitoids (van Lenteren and DeBach 1981, Luck et al. 1982, Reeve 1987, Walde et al. 1989). Learning and experience with host contact were also demonstrated to be potentially important (Baker 1976).

Rosenheim and Rosen (1991) reported a manipulative laboratory experiment whose aim was to distinguish the effects of host quality, parasitoid experience, and egg load on foraging and clutch size in *A. lingnanensis*. Egg load was manipulated without concurrent effects on experience by (1) exploiting size-related variation in female fecundity and (2) by holding parasitoids at different temperatures to modulate the rate of egg maturation. Females with fewer eggs took longer to locate hosts within a small foraging arena. Clutch size allocation was fundamentally dynamic; parasitoids with

smaller egg loads and parasitoids with prior experience with host contact deposited smaller clutches. Host size also significantly affected clutch size allocation and the decision to oviposit versus host feed (Rosenheim and Rosen, unpubl.). Egg load also influenced total host handling time; parasitoids with larger egg loads showed an accelerated completion of all components of host handling, including examination of the host, oviposition, and post-oviposition grooming and resting.

Methodology

How should egg load be measured for analysis of insect behavior? In principle, egg load at the time of oviposition can be determined by dissecting the subject following the behavioral assay and then summing the number of mature eggs with the number of eggs deposited during the assay. Mature eggs are usually distinguishable by their size, color, chorion (no uptake of aceto-carmin, toughness) or location in the reproductive tract (Bell and Bohm 1975). Eggs still in the process of yolk deposition absorb the dye trypan blue and turn blue, whereas those that have ceased vitellogenesis remain clear, suggesting ripeness (Telfer and Anderson 1968, Barbosa and Frongillo 1979).

Some ovarian eggs may be counted as mature, however, but not be available for oviposition because of oosorption. Oosorption, the degradation of eggs to recycle their contents, may occur when an insect does not have access to food and hosts, and may increase adult survival (Hinton 1981). During oosorption the terminal eggs in the ovarioles or, as described for some species, even mature, chorionated eggs in the oviduct disintegrate and are resorbed. Eggs in the first phase of this irreversible process may not be recognizable and estimates of mature egg load may then be inflated. Errors in quantifying egg load associated with oosorption may be especially common when host deprivation is used as an experimental treatment.

Egg load variation and confounding variables

Egg load is the result of a dynamic process with input from egg maturation and output from oviposition, and potentially, oosorption. Pro-ovigenic insects eclose with a full complement of mature eggs, and supposedly only their output need be considered. For synovigenic insects, egg maturation proceeds through adult life and may depend on weather, time of day, female age, egg parity, mating experience, male contribution, egg storage capacity and adult feeding (Dunlap-Pianka 1979, Leather 1984, Boggs 1986). Oviposition rate may vary with many external factors such as host quality, density and distribution, temperature and predation risk. Oosorption also reduces mature egg load, either with or

without antagonizing egg maturation, and occurs under cases of oviposition or food deprivation in several taxa (Bell and Bohm 1975, Hinton 1981). In addition, a trade-off may exist between the number of eggs and the size of each egg (Leather and Burnand 1987). The whole of these processes determines the egg load at the time of oviposition.

Variation in egg load may be either naturally occurring, as in the studies of *Battus*, *Drosophila* and *Diglyphus*, or be manipulated, as in the study of *Aphytis*. In both cases, confounding variables can be introduced into experimental analyses of the role of egg load whenever factors that affect egg load dynamics exert additional independent influences on oviposition behavior. As summarized in Table 1, the interpretation of many studies on the influence of egg load on oviposition behavior is complicated by the presence of such confounding variables. The most widespread problem e.g., in experiments using host deprivation treatments, is the confounding of egg load with oviposition history or "experience". Experience with hosts can influence behavior both through positive and negative effects on egg load i.e., egg accumulation and oosorption, through direct modification of perceived resource availability, and through effects on the nervous system. Likewise, female size may be correlated with egg load and have additional independent effects on search rate, host choice, and perhaps other aspects of behavior. Host feeding, the use of hosts as a source of adult nutrition, occurring in drosophilids and in many parasitoids may influence egg load (Jervis and Kidd 1986). The influence of host feeding on oviposition behavior may be complex; e.g., through effects on egg maturation or through processes independent of egg load, such as adult somatic nutritional status or habitat selection. In theory, female age, independent of host experiences, may influence both egg load and behaviors such as clutch size and host acceptance. Finally, temperature may increase egg load through acceleration of egg maturation and have direct effects on oviposition by accelerating search rates. More complete understanding of the influence of egg load on behavior will require, if possible, the use of manipulative experiments that isolate the effect of egg load from the effects of other important factors.

Implications

The reproductive success of a female insect is a function of the number of eggs laid and the survivorship and fecundity of each resulting offspring. Egg load, and more specifically egg load dynamics, plays a central role in regulating the rate of reproduction. Hence, the evolution of oviposition behavior is expected to reflect constraints imposed by egg load on the forager. The studies reviewed here demonstrate that a relationship between egg load and oviposition behavior does indeed exist in

both herbivorous and parasitoid insects, as predicted previously by theory. The evidence further supports the view that insect oviposition behavior is conditioned on egg load: when egg load is high, and thus the risk of becoming egg limited as perceived by the forager is low, behavior may maximize the rate of host encounter and exploitation; but when egg load is low, and thus the perceived risk of egg limitation is high, behavior may instead maximize the quality of hosts accepted for oviposition.

The observed influence of egg load on oviposition behavior suggests that models of oviposition will benefit from inclusion of egg load either as a decision variable in a rule-of-thumb (Skinner 1985, Tatar 1991) or as a state variable in dynamic optimization analyses (Iwasa et al. 1984, Mangel 1987).

Our review suggests several unsolved issues. First, how can problems associated with confounding variables be avoided in experimental investigations of the effect of egg load? If egg load is perceived by proprioceptive stretch receptors, then direct rather than indirect manipulations of perceived egg load may be possible e.g., through inflating the ovaries or the abdomen or through surgical manipulations of the oviduct content. Second, for most insects, to what extent is oviposition behavior influenced by current egg load relative to anticipated future egg production? Finally, a recurrent observation as shown in Table 1 is that search intensity is positively related to egg load. If reproductive success is greatest when search intensity is maximized, why would a female with low egg load forage less intensively than a female with a high egg load? We suggest that there exist unrecognized costs to high search intensity, perhaps related to energetics or mortality risk.

Behavioral studies of insect oviposition have begun to demonstrate the importance of egg load as a proximate source of variation in search intensity, oviposition rate, host acceptance, handling time, and clutch size. Consideration of the role of egg load, egg load dynamics, and the function of egg load responses will lead to a more complete understanding of variation in oviposition behavior.

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