

# Resource Acquisition, Allocation, and Utilization in Parasitoid Reproductive Strategies

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## Key Words

parasitoid wasps and flies, reproduction, survival, ovigeny index, oviposition, trade-offs

## Abstract

Parasitoids display remarkable inter- and intraspecific variation in their reproductive and associated traits. Adaptive explanations have been proposed for many of the between-trait relationships. We present an overview of the current knowledge of parasitoid reproductive biology, focusing on egg production strategies in females, by placing parasitoid reproduction within physiological and ecological contexts. Thus, we relate parasitoid reproduction both to inter- and intraspecific patterns of nutrient allocation, utilization, and acquisition, and to key aspects of host ecology, specifically abundance and dispersion pattern. We review the evidence that resource trade-offs underlie several key intertrait correlations and that reproductive and feeding strategies are closely integrated at both the physiological and the behavioral levels. The idea that parasitoids can be divided into capital-breeders or income-breeders is no longer tenable; such terminology is best restricted to the females' utilization of particular nutrients.

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**Egg load:** the number of mature eggs a female carries at a given moment in time

**Ovigeny index:** measure of the degree to which egg production is concentrated into early adult life

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## INTRODUCTION

It has been a longstanding aim of evolutionary ecologists to explain the broadly divergent patterns in life-history strategies that exist among and within animal species (103, 126). Research on parasitoids is contributing significantly to the achievement of this goal. Whereas insect predators often feed on many prey to attain maturity, during their development parasitoids are dependent on the nutrients contained in a single host, which usually does not grow much larger than the adult parasitoid. Consequently, host resources for parasitoid development that are utilized for multiple functions are finite and often highly limiting (124). Parasitoid life-history evolution should in theory involve optimizing and integrating three processes: (*a*) utilization of these limited resources by the parasitoid larva, (*b*) the allocation of some of these resources to the adult stage, and (*c*) the acquisition of additional nutrients during adult life. Adult parasitoids display marked variation in their reproductive and associated traits, both within and among species. Interspecific correlations have been recorded not only between pairs of traits but also among suites of several traits, and adaptive explanations, several of which are explicitly resource based, have been proposed for many of these relationships (13, 14, 73, 74, 105, 107, 108, 132, 133).

The purpose of this review is threefold: (*a*) to provide a synthesis of current knowledge of parasitoid reproductive biology relating to these findings, (*b*) to explain how diversity in the reproductive strategies of female wasps arises from various opportunities and constraints relating not only to the adult but also to the immature stages, and (*c*) to identify promising avenues for future research regarding patterns and processes of nutrient allocation, utilization, and acquisition. We focus on egg production strategies in female parasitoid wasps by placing these strategies within a physiological-ecological-evolutionary framework. However, where appropriate, parasitoid flies are discussed, and some of the likely

parallels between the sexes of parasitoids are highlighted.

## DIVERSITY IN REPRODUCTIVE STRATEGIES

### Parasitoid Reproduction and Its Measurement

In the typical insect parasitoid life cycle, the female lays her eggs on or within the bodies of other insects. As a result, parasitoid traits relating to the manufacture and deposition of eggs by females have received particular attention from researchers. Among the most important female reproductive traits are potential fecundity and realized fecundity. The former is the female's complement of immature eggs and mature eggs at the start of her life, i.e., potential lifetime fecundity. Realized fecundity is measured as either the number of eggs laid at a given age (age-specific fecundity) or the number of eggs laid until the time of death (realized lifetime fecundity). Some parasitoid species produce many hundreds or even thousands of offspring (100, 119), whereas other species produce, under optimal conditions, 50 or fewer (60, 66) (**Figure 1**). Other traits such as egg length and volume, the number of ovarioles per ovary, the size of oviducts, and the number of eggs available to lay (egg load) also differ considerably across a range of well-studied parasitoids (**Tables 1 and 2**).

Parasitoids differ with respect to the proportion of their potential lifetime complement of eggs that the females have ready to lay at adult emergence (75, 77). Jervis et al. (74) devised the ovigeny index, measured as the initial egg load (fully mature eggs) divided by the potential lifetime fecundity. An index of 1 (strict pro-ovigeny) denotes that all the oocytes are mature upon emergence, whereas an index of 0 (extreme synovigeny) denotes emergence with no oocytes ready to lay. The ovigeny index thus measures the degree of early-life concentration of lifetime

egg production. In strictly pro-ovigenic parasitoids, initial egg load and lifetime potential fecundity are the same quantity, whereas in parasitoids whose females emerge with some immature eggs (synovigenic species), initial egg load is smaller.

### Timing of Reproduction and Associated Life-History Traits

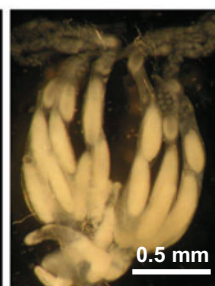
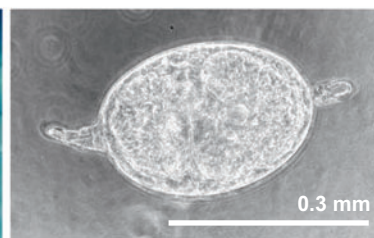
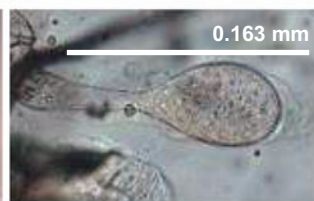
Variation in the ovigeny index is reflected in the shape of the age-specific realized fecundity curve. Interspecifically, four broadly divergent curve types are apparent from the empirical data (Table 2) (Figure 2). Type 1 species are strictly pro-ovigenic, whereas species in Types 2–4 exhibit varying degrees of synovigeny (weak to extreme). The Type 1 curve is heavily skewed and peaks early during adult life; potential fecundity varies greatly among species. In Type 2 species, initial egg loads are lower, being a large (e.g., aphidiine braconids) to small fraction of potential fecundity (74), and egg deposition increases over the first few days of adult life before declining rapidly. Lifetime potential fecundity varies markedly among species and may be high (typically >500) in some taxa (e.g., Braconidae, Ichneumonidae). Type 3 species generally have a short preoviposition period (which in some cases is due to extreme synovigeny), but thereafter the temporal pattern of egg deposition resembles that of Type 2 species except that the fecundity curve is depressed and lifetime realized fecundity is low. Type 4 species also emerge with no eggs; they may have a long preoviposition period (due to extreme synovigeny), and they lay eggs at a lower rate but for an extended period of time. Type 4 species are probably among the least fecund (<50) in the parasitic Hymenoptera.

Fecundity curve shape does not evolve independently of other reproductive traits. Important trade-offs have been observed among parasitoid wasps. Blackburn's (13, 14) comparative analysis revealed a fast-slow continuum in a suite of key reproductive and related traits among 474 species. Fast parasitoid

taxa typically were more fecund, produced smaller eggs, laid these eggs more rapidly into hosts, and reproduced earlier in life (correlated with shorter preoviposition periods) than slow taxa. Overall, fecundity curves of Type 1 and 2 species exhibit fast traits, whereas those of Type 3 and 4 species exhibit 'slow' traits (Figure 2). Moreover, more fecund parasitoid species and/or those that invest more in early life reproduction have shorter life spans than parasitoids with contrasting traits. Correlations between each of these traits were independent of body size and phylogeny (14).

### Genetic Variation and Phenotypic Plasticity in Reproductive Traits

Intraspecific variation in reproductive traits is apparent, but the range is much smaller. Such phenotypic variation reflects genetic variation or environmentally induced plasticity in reproductive allocation. A quantitative genetic study of the pro-ovigenic parasitoid *Anagrus delicatus* showed that fecundity had a significant heritability of 0.47 (30). In *Heterospilus prosopidis* the rate of parasitism, measured as progeny production over 48 h, had a significant heritability of 0.57 (81). These results suggest that sufficient additive genetic variation exists in reproductive traits and allocation strategies for the traits to respond quickly to selection. Consistent with the above is the apparent genetic variation in reproductive strategies along a geographical cline in the alysiine braconid wasp *Asobara tabida*. This species shows latitudinal variation in early-life allocation to eggs (initial egg load) (83). Females from southern European populations have a larger initial egg load than females from northern populations; also, the populations do not differ in lifetime realized fecundity (38, 45). Most probably, the more-skewed fecundity schedule of southern populations has evolved in response to the higher host availability at lower latitudes. A crucial test would be to use experimental evolution and rear the southern populations under northern conditions and vice versa.



**Table 1** Variation in some key reproductive traits among and within parasitoid wasp species

Trait	Variation
Egg size (length)	Interspecifically: at least 50-fold Intraspecifically: considerably less (e.g., ~1.4-fold in <i>Aphaereta minuta</i> ) Intraspecifically: varies with body size and female age
Egg yolk-richness	Interspecifically: minimal to high yolk content, but no quantitative data available Intraspecifically: evidence that egg yolk provisioning varies with mother's age
Number of ovarioles/ovary	Interspecifically: varies between 1 and ~250 Intraspecifically: varies with factors such as body size
Egg storage capacity	Present (if significant, it takes the form of elongated/expanded lateral oviducts) or absent
Egg resorption capability	Present or absent
Ovigeny index	Interspecifically: ranges from 0 to 1, although strict pro-ovigeny (all eggs mature) is rare; forms a continuum. It is an axis of life-history diversity: Its correlates include not only reproductive traits but also life span, body size, and larval development mode. Intraspecifically: varies with body size (by as much as 0.32) and geographical location (clinal)
Initial egg load	Interspecifically: 0 to (in Eucharitidae) several thousands Intraspecifically: varies with body size and geographical location (clinal)
Lifetime potential fecundity	Interspecifically: <50 (e.g., some Ichneumonidae) to several thousands (some Eucharitidae) of eggs Intraspecifically: varies with body size
Clutch size	Interspecifically: 1 to (in Eucharitidae, Trigonalidae, <i>Euceros</i> spp.) hundreds Intraspecifically: a range of 1 to 60 recorded for one species, but usually the variation is much less. Minimum clutch size is >1 in some species.

More frequently, intraspecific variation in egg production arises from phenotypic plasticity in reproductive allocation. Empirically, the environmental factors that most commonly influence egg production are adult nutrition (11, 45, 55), host availability (23, 42, 61), and temperature (86, 111, 117). Some changes in egg production are entirely attributable to a shift in the timing of production rather than an actual increase in

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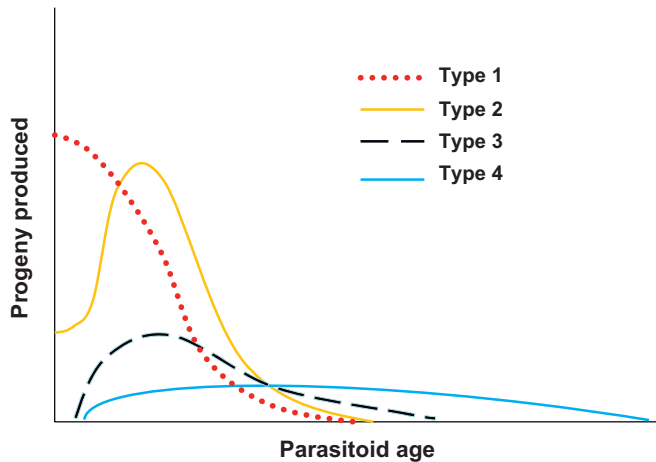
### Figure 1

Four parasitoid wasp species with highly contrasting reproductive biologies. (a) *Gelis agilis* (Ichneumonidae), a solitary idiobiont ectoparasitoid, attacks a fully cocooned pupa of its primary parasitoid host, *Cotesia glomerata* (left). *G. agilis* is an extremely synovigenic species (ovigeny index = 0), produces large, yolk-rich (anhydropic) eggs (right), and has a lifetime potential fecundity of typically <50. (b) *Copidosoma floridanum* (Pteromalidae) is a polyembryonic egg-larval koinobiont endoparasitoid that lays primary broods of 1 or 2 eggs into eggs of noctuid moths such as *Trichoplusia ni* (left). *C. floridanum* is a strictly pro-ovigenic species (ovigeny index = 1) that lays yolk-deficient (hydropic) eggs into the host (right). Owing to clonal proliferation, one egg may eventually produce >1000 offspring. Lifetime potential fecundity in *C. floridanum* may exceed 20,000. (c) *Asobara tabida* (Braconidae) is a solitary koinobiont endoparasitoid of larvae of *Drosophila* spp. *A. tabida* is moderately synovigenic, lays hydropic eggs into the host's hemocoel (right), and may produce ~600 progeny during its lifetime. (d) *Eupelmus vuilleti* (Eupelmidae) is a solitary ectoparasitoid of the larvae of bruchid beetles. *E. vuilleti* is extremely synovigenic and produces small numbers of anhydropic eggs (right). Under optimal conditions the potential fecundity in *E. vuilleti* females is between 100 and 200.

**Table 2 Reproductive and other life-history traits of parasitoid wasps and flies**

Parasitoid species	Family	Koinobiont or idiobiont	Solitary or gregarious	Max. realized fecundity	Max. age-specific fecundity	Type of curve	Reference
<i>Brachymeria intermedia</i>	Chalcididae	Idiobiont	Solitary	<50	4	Type 4	35
<i>Brachymeria lasus</i>	Chalcididae	Idiobiont	Solitary	Mean 118.1	Mean 6	Type 4	88
<i>Dirhinus giffardii</i>	Chalcididae	Idiobiont	Solitary	Low	Probably <10	Type 3	138
<i>Aphelinus alhipodus</i>	Aphelinidae	Idiobiont	Solitary	294.70	~3 (at 21°C)	Type 4	8
<i>Aphelinus semiflavus</i>	Aphelinidae	Idiobiont	Solitary	308	19	Type 4	87
<i>Aphytis melinus</i>	Aphelinidae	Idiobiont	Gregarious	~100	~10	Type 4	65
<i>Trichogramma minutum</i>	Trichogrammatidae	Idiobiont	Gregarious	158	40	Type 1	5
<i>Trichogramma evanescens</i>	Trichogrammatidae	Idiobiont	Gregarious	~80	Mean 35.10	Type 1	33
<i>Dendrocerus carpenteri</i>	Megaspilidae	Idiobiont	Solitary	Mean 154, max. 175	Mean ~13	Type 3	19
<i>Asaphes suspensus</i>	Pteromalidae	Idiobiont	Solitary	Mean 834, max. 924	Mean ~23	Type 2	19
<i>Diapetimorpha introita</i>	Ichneumonidae	Idiobiont	Solitary	Max. ~60	Max. 10	Type 4	24
<i>Masturus rufibandus</i>	Ichneumonidae	Idiobiont	Gregarious	80	Mean 8	Type 3	11
<i>Gelis agilis</i>	Ichneumonidae	Idiobiont	Solitary	Mean 40, max. 72	4	Type 4	60
<i>Lysibia nana</i>	Ichneumonidae	Idiobiont	Solitary	Mean ~100, max. 138	~30	Type 3	60
<i>Eupelmus vuillei</i>	Eupelmidae	Idiobiont	Solitary	~50	Mean 4	Type 3	27
<i>Leptomastix</i> sp. nr <i>epoma</i>	Encyrtidae	Idiobiont	Solitary	~90	~5	Type 3	59
<i>Elachertus cacaoeciae</i>	Eulophidae	Idiobiont	Gregarious	Max. 187/day	Max. 140	Type 3	50
<i>Gryon gallardoi</i>	Scelionidae	Idiobiont	Solitary	Max. 8, range 8–173	Mean 67.5	Type 3	22

<i>Venturia canescens</i>	Ichneumonidae	Koinobiont	Solitary	Mean 280, max. 465	125	Type 2	61
<i>Diadegma semiclaustum</i>	Ichneumonidae	Koinobiont	Solitary	Mean 390, max. >600	21	Type 2	140
<i>Leptopilina bouvardi</i>	Eucolidae	Koinobiont	Solitary	Mean 182.10	~50	Type 1	82
<i>Gronotoma micromorpha</i>	Eucolidae	Koinobiont	Solitary	Mean 75.6	?	Type 1	1
<i>Apitidius ervi</i>	Braconidae	Koinobiont	Solitary	Mean 777, max. 1050	?	Type 2	119
<i>Lysipblebus delhiensis</i>	Braconidae	Koinobiont	Solitary	Mean 270.8, max. 304	?	Type 1	93
<i>Microplitis tristis</i>	Braconidae	Koinobiont	Gregarious	>600	Mean 16, max. 28	Type 2	46
<i>Microplitis manilae</i>	Braconidae	Koinobiont	Solitary	> 300	?	Type 2	3
<i>Cotesia marginiventris</i>	Braconidae	Koinobiont	Solitary	~100-111	85.8	Type 1	125
<i>Apanteles galleriae</i>	Braconidae	Koinobiont	Solitary	Mean 239.7	?	Type 1	134
<i>Chelonus inanitus</i>	Braconidae	Koinobiont	Solitary	Max 1647	Mean 227.7	Type 2	109
<i>Alloxysta victrix</i>	Charipidae	Koinobiont	Solitary	Mean 86, max. 108	Mean ~4	Type 3	19
<i>Thripobius semilatus</i>	Eulophidae	Koinobiont	Solitary	Mean 78.8	Mean ~23	Type 1	9
<i>Anitius benneti</i>	Platygasteridae	Koinobiont	Solitary	Max. 99	Max. 49	Type 1	36
<i>Celatoria compressa</i>	Tachinidae	Koinobiont	Solitary	Max. 33	Max. 5	Type 3	142
<i>Drino inconspicuoidea</i>	Tachinidae	Koinobiont	Solitary	Mean 163.6, range 57-271	Mean 11.6	Type 2	80



**Figure 2**  
Patterns of age-specific realized fecundity among different species of idiobiont and koinobiont parasitoids (based on data in **Table 2**).

reproductive effort, for example, those linked to host availability and temperature. Another confounding factor when considering reproductive resource allocation is female body size. Favorable larval nutritional conditions result in increased progeny size. Larger-bodied individuals have more resources to allocate, and therefore body size is positively correlated with reproductive traits such as ovariole number, egg size, initial egg load, lifetime fecundity (potential and realized), and life span (4, 39, 57, 73) (**Table 1**). It is unclear whether the proportional allocation of nutrients to reproduction changes with female size, but adaptive models predict that large females should allocate a lower relative amount of their total resources to initial egg load (41); this has recently been confirmed empirically (132).

## RESOURCE ECONOMICS UNDERLYING REPRODUCTIVE STRATEGIES

### Physiology of Reproductive Allocation

The nutrients involved in reproduction are, to a significant degree, acquired during the larval stage and are allocated either to initial

eggs or to teneral reserves that fuel somatic maintenance (thus adding to the time available for reproduction), locomotion, and (if females mature additional eggs during their lives) future egg manufacture.

Teneral reserves comprise four main nutritional components that differ in their importance regarding direct and indirect contributions to reproductive output. These components are sugars, present mainly in the blood, as well as glycogen, lipids, and proteins, present mainly in the fat body (29) (**Figure 3**). Sugars and glycogen primarily fuel somatic maintenance and locomotion, but they also contribute to ovigenesis over the reproductive life of synovigenic females (**Figure 3**). Proteins provide a source of amino acids for use in egg manufacture (29) (**Figure 3**). In sugar-starved, host-deprived females of the host-feeding species *Eupelmus vuilleti*, protein levels declined substantially, indicating the catabolism of proteins in somatic maintenance (27); whether this occurs in nonhost-feeding parasitoids is not known. Proteins may be catabolized to fuel flight. This is more likely to apply to parasitoid flies (29), but the possible use of proteinaceous materials as a flight fuel by parasitoid wasps cannot be dismissed (see Reference 129 on other Hymenoptera).

Lipid reserves fuel both ovigenesis and somatic functions (**Figure 3**). Evidence for the role of lipid reserves in egg manufacture comes from *A. tabida*, in which replenishment of egg load after oviposition is accompanied by a significant reduction in fat levels (45). The age-related depletion rate of fat reserves observed in host-provided parasitoid females can only be explained if the energetic demand of egg maturation is considered along with that of somatic maintenance (38). Instead of declining over time as in starved females, lipid levels in starved males remained relatively steady in the phorid fly *Pseudacteon tricuspis* (48), presumably reflecting the much greater fuel demand of ovigenesis compared with that of spermatogenesis. A nutrient budget constructed for *E. vuilleti* over the lifetime of female wasps revealed that lipids

**Ovigenesis:** egg manufacture

**Spermatogenesis:** sperm manufacture



## Maintenance and locomotion

## Egg manufacture

Sugar feeding generally increases life expectancy, as does injection of sugars (*Eupelmus vuilleti*); some components of locomotor activity are enhanced by sugar feeding

### Blood sugar

Teneral and dietary components

*E. vuilleti* a near-complete IB; other parasitoids are likely to be the same

Fuels maintenance and, presumably, locomotion

### Glycogen

Teneral and dietary components

*E. vuilleti* occupies an intermediate position on CB-IB axis

Evidence that *E. vuilleti* catabolizes proteins in maintenance; possible role in fueling locomotion in some parasitoids

### Proteins

Teneral and dietary components

Diet of host-feeders is rich in proteinaceous materials. Diet of species that consume only nectar or honeydew is very poor in such nutrients

*E. vuilleti* occupies an intermediate position on CB-IB axis; species that feed exclusively on nectar and/or honeydew are likely to be complete CBs

Fuel maintenance and locomotion, but only as a last resort (when sugars become limiting)

### Lipids

Entirely teneral in nectar- and honeydew-feeders, partly dietary in host-feeders

Parasitoid wasps are complete or near-complete CBs; parasitoid flies appear to be the same

**Figure 3**

Key nutrients that are indirectly and directly involved in the reproduction of female parasitoids. CB, capital-breeder; IB, income-breeder. Information on *Eupelmus vuilleti* is taken from References 56 and 27.

contribute significantly to egg manufacture (27) (Figure 3).

The importance of lipid reserves to somatic functions is demonstrated by the positive correlation between the quantity of lipid reserves and life span, within species (38, 116) as well as between species (105). Furthermore, lipid levels decline in starved, host-deprived females (27, 85, 101). There is evidence that stored lipids fuel locomotion in females. Controlling for variability in longevity, the fat levels of field-released *A. tabida* declined with increasing dispersal distance (45).

The unique dependence of parasitoid larvae on a single host for nutrition and accumulation of capital reserves may have ad-

verse fitness effects if the host is too small or its nutritional quality is too low. Nevertheless, this constraint provides selection pressures to evolve some means of manipulating host metabolism and of adjusting host nutritional composition to meet the larva's dietary needs—two opportunities not available to the larvae of herbivores or predators. In several koinobiont species parasitism induces biochemical alterations in the host's hemolymph: increased concentrations of lipids, proteins, and carbohydrates (79, 95); elevated rates of gluconeogenesis (131); and decreased lipid and protein levels in the remaining host body mass (12). The active agents in manipulating host physiology include polydnviruses (104),

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**Idiobionts:**

parasitoids whose larvae utilize a nongrowing host

**Koinobionts:**

parasitoids whose larvae utilize a growing host

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venom (95), and teratocytes (94). Parasitism-induced changes in host nutritional physiology appear to be crucial to parasitoid fitness. Experimental dilution of host hemolymph concentrations led to a reduction in larval survival rate and a reduction in lipid reserves in the emerging parasitoids (79).

### **Selection and Constraints Acting upon Juvenile Larval Parasitoids**

Variation in adult reproductive traits can arise through selection and constraints acting on earlier life stages. Parasitoids can be divided into two groups according to their larval development mode: Idiobionts develop on nongrowing (including paralyzed) hosts, whereas koinobionts allow their host to continue developing. A comparative analysis showed that koinobionts have longer preadult but shorter adult life spans than idiobionts, produce smaller eggs, and have higher daily rates of oviposition and higher lifetime fecundity (89). Other reproductive traits, such as the production of yolk-rich (anhydropic) eggs and host-feeding behavior by the adult female, appear to be more prevalent in idiobionts than in koinobionts (75, 116), perhaps because many idiobionts are ectoparasitic and so must package into the egg all the resources necessary for the completion of embryogenesis. In contrast, many koinobionts are endoparasitoids whose eggs allow proteins in the host's hemolymph to be absorbed and utilized for embryogenesis (75).

Development mode appears to be linked to the ovigeny index: Koinobionts have a higher ovigeny index than idiobionts (74). Presently it is unknown why development mode might alter the proportional allocation to eggs at emergence, but the most likely causal factor is nutritional constraints imposed by the idiobiont development strategy. Because idiobionts paralyze their hosts, they are less likely to exploit the host resources by altering host metabolism. Adult acquisition of supplementary resources for egg production may alleviate this constraint, a view supported by the

subjective observation that the host-feeding habit is concentrated among idiobionts (75).

Ecological factors may determine the ability to acquire necessary nutrients in the larval stage. Many koinobiont endoparasitoids attack nutritionally suboptimal early-instar hosts that must feed and grow to provide sufficient resources for the parasitoid progeny (124). When developing in these hosts, some parasitoids must suspend their development and remain as first instars until the host reaches its maximum size (124). Delayed development may be adaptive for parasitoids in three ways: (a) Young hosts are often much more numerous than later host stages and thus easier to locate by females; (b) both physiological (immune) and behavioral defenses are usually weaker in young hosts than in older hosts; (c) if within-host competition between immature parasitoids is such that it results in larval mortality, the first parasitoid to become established in a host is often the best able to eliminate subsequent competitors (124). However, one of the costs of attacking young hosts is their higher susceptibility, compared with later stages, to mortality from other natural enemies and abiotic factors (14).

The balanced mortality hypothesis was first proposed by Price (107) and has been used to explain the correlation between larval mortality risks and female reproductive traits among parasitoids (57, 107, 108). Parasitoids attacking early-instar hosts need to have higher fecundity to offset the mortality suffered by the parasitoid progeny. On the other hand, many idiobionts attack only later, more demographically stable, larger host stages such as final larval instars or pupae. In this case, the lower mortality of parasitoid progeny reduces the need to invest in a higher fecundity (this in turn allows resource investment per egg to be increased). This hypothesis thus can explain why koinobionts have been selected for fast reproductive traits (e.g., a high ovigeny index, shorter life span, smaller egg size, earlier reproduction, and higher fecundity) and idiobionts have been selected for

“slow” traits. A comparative test of the hypothesis has yet to be undertaken.

Pexton & Mayhew (105) challenged the balanced mortality hypothesis on the basis that it conflicts with a body of life-history theory known as optimal investment theory. The latter predicts that a relatively high level of juvenile mortality will shift investment away from reproduction toward adult survival. Furthermore, Pexton & Mayhew suggest that the low availability of later life stages (not reduced juvenile mortality) could be the key selective force that increases investment in parasitoid adult survival at the cost of fecundity. The latter hypothesis is not entirely at odds with Price’s thinking, since he acknowledged (108) the importance of the relative abundance of successive life stages as a codeterminant of fecundity.

While Pexton & Mayhew found empirical support for optimal investment theory by comparing two congeneric parasitoid species sharing the same host, the theory is, in our view, not broadly applicable. For example, pupal parasitoids tend to have lower fecundities but longer life spans (60).

An increased risk of predation or parasitism might also select for reduced pupal development time. Under these conditions, the developing parasitoid will not have sufficient time to allocate sufficient resources toward egg production, leading to adult wasps emerging with smaller egg loads and a lower ovigeny index (52).

Another aspect of larval life that has important implications for egg production is host food plant quality, in particular the array of toxic secondary compounds (allelochemicals) that may accumulate in the tissues of herbivores (99). Parasitoids obtain their nutrition indirectly from the plant through the herbivore, and so parasitoids developing on hosts feeding on more toxic species or genotypes are often smaller as adults, which negatively affects reproductive and related traits (99). The precise physiological effects of phytotoxins on parasitoid physiology are, however, poorly understood. Some specialized parasitoids that

are well-adapted to the host and its food plant may actively incorporate allelochemicals into their own tissues as a means of defense against their own predators and hyperparasitoids, although this is little studied. Alternatively, phytotoxins may hinder the ability of less well-adapted parasitoids to utilize host tissues and to metabolize host lipids, proteins, and other host resources for reproduction.

### **Selection and Constraints Acting upon Adult Parasitoids**

Variation in adult reproductive traits arises through the interaction of opportunities and constraints. From the time that the parasitoid completes its larval development to its emergence as an adult, it does not feed and so resource allocation is constrained by the amount of available resource capital. Therefore, two main trade-offs occur regarding the proportionate allocation of resources of larval origin.

**Allocation of larval resources to soma and nonsoma.** The first trade-off occurs in the proportionate allocation to soma versus nonsoma. Soma mainly comprises the adult’s exoskeleton and musculature, and nonsoma mainly comprises the reproductive tissues and gametes, together with initial nutrient reserves (thus nonsoma is not synonymous with germ line). The trade-off is likely to vary interspecifically in females of holometabolous insects (15). First, species whose females are longer-lived should invest relatively more resources during metamorphosis into building a sturdy body (soma), compared with shorter-lived species. Second, in many holometabolous insects investment in the thoracic musculature and wings (and thus aerial dispersal capability) is expected to occur at the cost of investment in reproductive tissues and eggs, and vice versa, in accordance with the oogenesis-flight syndrome theory (32). Although there is support for this prediction in Lepidoptera (72), our subjective assessment is that aptery in parasitoid wasps involves somatic resources allocated away from

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**Soma:** the adult’s exoskeleton and musculature

**Nonsoma:** the reproductive tissues and gametes, together with initial nutrient reserves

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**Egg limitation:**

when the number of current oviposition opportunities exceeds the number of mature eggs available for laying

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the flight apparatus toward the construction of a robust thorax (in particular the prothorax, propodeum, and legs)—not toward nonsoma. This may partly explain why apterous Ichneumonidae and Dryinidae are typically strongly synovigenic, rather than pro-ovigenic (74).

At the intraspecific level, natural conditions of larval nutritional stress due to factors such as reduced host quality (71, 91) and disturbances (127, 128), and a phase of diapause, can be expected to not only reduce the total amount of carried-over resources but also alter the shape of the trade-off between soma and nonsoma (96, 128). However, such effects may depend on the developmental stage. For example, a reduction in the amount of capital resources due to the metabolic costs of pupal diapause causes an increase in body size of the emerging females (43). This unexpected result may be attributable to larvae needing sufficient resources to survive diapause. If adult and larval body mass are linked genetically, selection for heavier larvae would result in larger adults, with likely consequences for allocation to nonsoma (43).

**Adapting reproductive allocation to reproductive opportunity.** The second hypothesized major trade-off in resource capital occurs within nonsoma with regard to the relative allocation to initial eggs versus initial reserves. A trade-off between initial egg load and teneral lipid levels has been recorded between populations of the parasitoid *Asobara tabida* (44). This trade-off has also been demonstrated interspecifically and is linked to body size: In the genus *Aphaereta* the smaller-bodied species (*pallipes*) has the higher initial egg load and the lower teneral fat level compared with the larger-bodied species (*genevensis*) (105).

During adult life, initial reserves can be used as a source of nutrients both for manufacturing additional eggs (synovigenic species) and for fueling somatic functions. This leads to the so-called cost of reproduction, which is a key tenet of life-history theory and is widely supported empirically (7, 110). Although for

a long time this cost was assumed for parasitoids to be negligible because of the small size of their eggs, several studies have shown that there is a detectable energetic cost of reproduction that is mediated by the amount of lipid reserves (44, 82, 121; but see 5). Experimental manipulation of egg production has shown a negative linear relationship between egg load and longevity, with a set reduction in life span for each egg produced (40).

Ellers et al. (42) modeled the evolution of optimal egg load as a function of the mean and variance in host availability. Host availability is likely to vary considerably depending upon spatial and structural aspects of the host's environment, and these aspects affect the foraging ability of the parasitoid female (20, 58). In more complex or heterogeneous environments, parasitoid foraging efficiency, and hence reproductive success, is likely to be less than in more simple, homogeneous environments (20). Allocation to eggs is likely to be particularly marked in habitats where host density is high or where there is a large degree of variation among female parasitoids in the number of hosts encountered. Especially when hosts are aggregated among patches, the optimal egg load exceeds the expected number of hosts found. The outcome of the model is robust for a wide range of parameter conditions, including pro-ovigenic and synovigenic reproductive modes. Because hosts are typically patchily distributed, in many species the majority of females have eggs remaining in their ovaries at the end of their lives, i.e., the females will be time limited. Only in rich habitats, or habitats with a uniform distribution of hosts, will a significant percentage of females end their lives egg limited (42).

The predictions of the aforementioned modeling seem to be supported by most field studies (26, 34, 44, 63). However, in no way do these models exclude the possibility that some parasitoids can change their oviposition behavior when they run the risk of experiencing egg limitation (62, 68, 92, 102). In many synovigenic parasitoids maximum egg load is markedly constrained by egg storage capacity

(the maximum egg load that can be borne at any given time). Their females can therefore experience transient egg limitation. However, by manufacturing additional eggs, females can still experience time limitation at the end of their lives. Even so, simulations for synovigenic parasitoids show that owing to their ability to replenish their egg supply throughout their lives, the incidence of egg limitation is even lower than in pro-ovigenic parasitoids (42). However, mismatches in functional responses of parasitoids with host abundance have been described (60), suggesting that the ability of parasitoids to match egg production with host abundance may be correlated with the degree of host specialization exhibited by the parasitoid (67).

During their adult lives, female parasitoids possess a degree of flexibility in adjusting the resource trade-offs described above. Plasticity in utilization of carried-over resources is seen in the form of resorption of eggs (non-soma) or musculature (soma) in individuals deprived of food and/or hosts from eclosion (102). Egg resorption capability is concentrated mainly among synovigenic species (74). Resorption takes several hours to several days and, if concurrent in all ovarioles, precludes oviposition. It would thus be least costly, in terms of the female's time budget (i.e., opportunity costs via egg limitation), in longer-lived species (72, 75). Females of *Pimpla turionellae* practice a rarer type of plasticity in utilization of capital resources when host deprived: muscle resorption; this enables egg production to continue until egg resorption commences (118). It is not known whether muscle resorption fuels maintenance only or also fuels ovigenesis.

## INTEGRATION OF REPRODUCTIVE STRATEGY WITH FEEDING STRATEGY

### Integration at the Physiological Level

Generally, parasitoids feed as adults (52, 70), that is, they also obtain income. The adult

uses this to supplement and/or replenish some (though not all) of its existing array of nutrient reserves. In pro-ovigenic parasitoids, dietary inputs are needed to fuel somatic functions only: maintenance (and thus life expectancy) together with locomotion (i.e., dispersal and host-finding behavior), as the female's entire lifetime potential egg complement is, by definition, mature. Because the females have converted all their egg production resources into eggs by the time they emerge as adults, they are true capital-breeders. Among synovigenic parasitoids a dual function of feeding (maintenance, ovigenesis) is possible, although it may not be practiced in many cases (10, 62, 75).

A priori, feeding should be more common in females, given both the greater amount of resource investment that is required to produce eggs (assuming females are synovigenic) compared with spermatozooids and the generally greater life span and thus greater lifetime somatic maintenance requirement of females compared with males. This hypothesis is supported by results of a field survey of parasitoid wasps visiting flowers (77). Only female parasitoids consume host blood or tissues as adults (62, 75).

To understand the indirect and direct effects of feeding on reproduction, it is necessary both to examine the nutritional composition of food and to appreciate how the nutrient components of foods and of carried-over resources interact dynamically (27, 98). Studies of nutrient dynamics, coupled with the measurements of longevity and fecundity, reveal which nutrients (**Figure 3**) are limiting for parasitoids with respect to a given physiological function. They also provide measurements of the fitness gain obtained from feeding in relation to a particular nutrient. In parasitoids, carbohydrate and lipid dynamics are better understood than protein dynamics.

The foods of parasitoids can be categorized as nonhost and host (10, 75, 77, 123, 137, 140). The main nonfoods of parasitoids comprise nectar (both floral and extrafloral) and the honeydew that is excreted by phloem-feeding

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**Time limitation:** when the number of mature eggs available for laying exceeds the number of current oviposition opportunities

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Hemiptera. Deliberate and major (as opposed to inadvertent and trivial) consumption of pollen is practiced by only a few parasitoids (mutillids, scoliids, and some bombyliids). Feeding on other materials, such as fungi, is likewise generally rare. Nectar and honeydew are rich in carbohydrates, and both the sugar and the glycogen reserves of parasitoids can be replenished through feeding on them, allowing females to maintain high levels of sugars and glycogen over their lifetimes (27, 47, 84, 101). Nectar and honeydew are also generally poor in nitrogen. Nectar contains only minute quantities of amino acids, and the total nitrogen content of honeydew is similarly low. Nectar, honeydew and sugar-rich substitutes for such foods (i.e., honey and sucrose solutions, widely employed in the laboratory and under mass-rearing conditions) are also poor in lipids.

For some species, an additional source of exogenous nutrients is host materials, which comprise blood and/or tissues such as the host's fat body. A diverse array of species practice host feeding (62, 75). Host blood is rich in both nitrogen and carbohydrates, with a lesser but nontrivial lipid component (55). The nitrogen in host blood comprises amino acids and proteins, and the carbohydrate mainly comprises the sugar trehalose (56).

Generally, the life expectancy of starved insects is much lower than that of insects provided with food. Female *Cotesia rubecula* must feed at least once a day in order to avoid death from starvation (120). Inputs of dietary sugars can also positively influence components of locomotory activity in parasitoids: flight initiation and capacity (51, 139) and walking activity (106) (**Figure 3**). A higher rate of ovigenesis in fed females than in starved females has been observed in some parasitoids (10, 62, 65), but caution should always be exercised in interpreting such a result as meaning the food is used in fueling egg manufacture: The effect could be attributable to the nutrients in the food lessening the catabolic drain that somatic maintenance exerts upon carried-over resources that fuel ovigenesis (10). Nutrient-

tracking techniques are required to establish unequivocally whether exogenous nutrients are directly involved in ovigenesis; this applies both to nonhost-feeders and to host-feeders (16, 97, 113, 114). It is likely, however, that parasitoid wasps whose diet is confined to both nitrogen- and lipid-poor nonhost foods such as nectar and honeydew can gain little in terms of egg manufacture by feeding (10) (they appear incapable of manufacturing lipids from dietary carbohydrates, see below). In the nonhost-feeder *Macrocentrus grandii*, egg maturation rate is highest when females are starved than when sucrose-fed, a surprising effect that may be an adaptive response to a lowered life expectancy (101).

Host feeding, on the other hand, can increase egg production as well as life expectancy. Whether both or one of these fitness components is enhanced depends on the parasitoid species. In some species, such as *Encarsia formosa*, longevity is enhanced by the consumption of blood, but ovigenesis is unaffected (21). Conversely, in species such as *Nasonia vitripennis* and *Pimpla nipponica*, host feeding increases egg production but has no effect on the longevity of females (116, 135). In some other species, host feeding increases both egg production and longevity (55). In the host-feeder *E. vuilleti*, the increase in fecundity is determined mainly by the quantity of lipids obtained, whereas the life span extension is determined mainly by carbohydrates (55). Although amino acids derived from host blood are incorporated into eggs (112, 114), the acquisition of proteins is not the sole or even primary purpose of host feeding. *E. vuilleti* invests only one-tenth of the protein gained from host feeding over its lifetime in eggs (54). In *Trichogramma turkestanica*, host feeding decreases longevity, which is probably due to the allocation of carbohydrates to egg production at the expense of somatic maintenance (49).

Presumably, parasitoid wasps generally can synthesize storage proteins de novo from dietary amino acids. However, only host-feeders have a diet rich enough to supplement or

replenish their protein reserves from dietary income to a significant degree. In *E. vuilleti* females that were deprived of hosts and sugar, protein levels dropped by 80% over the insects' lifetimes (as did lipid levels). The protein levels of females provided with only hosts likewise declined markedly, but survival time was doubled, an effect attributable to the high input, and involvement in maintenance, of proteins and carbohydrates (27).

Generally, parasitoids cannot replenish their lipid reserves by feeding. There are no known reports of parasitoid wasps that can raise their lipid level above the teneral level. It is therefore inferred that they are incapable of lipogenesis (38, 53, 101, 114). Although the principal nonhost foods are rich in sugars [which in other insects are used to synthesize lipids (143)], and host blood contains nontrivial amounts of carbohydrates, biochemical analysis and radiotracer studies have produced no evidence of *de novo* lipid synthesis in adult parasitoid wasps (45, 53). Sugar feeding usually results in a slower decline of lipid reserves (25, 38, 85) or (in a parasitoid fly) even stable lipid levels over time (48). Females must be prudent in utilizing this key egg production resource [in *Venturia canescens* lipid composes 94% of teneral resources (25)], by using it to fuel somatic functions as a last resort only (10, 25). The absence of lipogenesis in parasitoids is unique and deviates from the practically universal metabolic model.

The study by Casas et al. (27) was a major advance in our understanding of the relationship between capital, income, and reproduction in parasitoids. While the host-feeder *E. vuilleti* is an almost complete capital-breeder for lipids, it is an almost complete income-breeder for sugars, and is an intermediate breeder for proteins and glycogen (**Figure 3**). A significant glycogen requirement for egg manufacture is expected in this species, given that its yolk-rich eggs contain an amount of carbohydrate equivalent to that of either protein or lipid (55).

## Integration at the Behavioral Level

Females that have low nutrient levels are expected to practice behavior associated with food searching opposed to host searching. Support for this prediction comes from studies on Braconidae and Ichneumonidae (31, 120). Further evidence that the nutritional state influences foraging decisions comes from both host-feeding and nonhost-feeding species. In the host-feeder *Aphytis melinus* the decision to take a blood meal varies with the food type given beforehand: The tendency to host feed is lower when females have previously fed on a diet containing yeast than when they have fed on a pure sucrose solution (attributable to the yeast diet containing proteinaceous materials that fuel ovigenesis) (64). *Leptopilina heterotoma*, a nonhost-feeder, feeds only when its fat reserves are low (37).

Evidence that egg load influences food versus host patch choice in parasitoids is scarce. Approximately one-third of female *Mesochorus* sp. (a synovigenic parasitoid), collected from the center of a wheat field, lacked mature eggs, in contrast to over 90% of females caught in a flowering verge adjacent to the field (136).

At the within-patch level, females with a lower egg load are expected to opt for feeding rather than oviposition when they have immature eggs in reserve and are thus faced with choice between the two behaviors (18, 28, 62, 76, 78, 90). This has been confirmed empirically for host-feeding parasitoids, both in the laboratory (64) and in the field (63). This expectation assumes that females with a low egg load are egg limited and that the decision to feed favors egg production rather than oviposition. If, however, a parasitoid female is not egg limited, she could prefer to host search (10). Also, in many synovigenic parasitoids the female's food is deficient in egg production nutrients; therefore if egg load is low, and egg production reserves are at a low level, there is little to be gained, fitness-wise, from feeding (10).

Most nonhost-feeding (and some host-feeding) parasitoids exploit sugar-rich

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**Capital-breeder:**  
gamete production is fueled entirely by nutrients acquired during larval life

**Income-breeder:**  
gamete production is fueled entirely by nutrients acquired during adult life

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materials that are usually located some distance from host patches (10, 77; but see 37 and 123). A parasitoid female therefore must decide whether to seek a host patch or a food patch. By opting for the former, she obtains an immediate fitness gain through oviposition. By opting for the latter, she (if she has eggs to lay) incurs an oviposition opportunity cost; furthermore, she is subject to the time and energy costs (and the mortality risks) associated with searching for food. By opting to food search, the female may obtain a net fitness gain through an increase in her life expectancy and (if she is synovigenic) an increase in future egg production (10, 122, 130). The most recent dynamic programming modeling that takes account of the effects of variation in egg load and nutrient (energy) levels on food patch versus host patch choice behavior has generated conflicting predictions regarding optimal behavior (10). A sensitivity analysis has yet to be conducted to resolve this problem. Furthermore, the effects of both time limitation and egg limitation on decisions have yet to be explored. Nevertheless, the model parasitoid's optimal behavior varies according to whether she is pro-ovigenic or synovigenic (10).

## CONCLUSIONS AND FUTURE DIRECTIONS

We have presented a body of evidence that resource-based trade-offs underlie key inter-trait correlations, and that the ovigeny index is an organizing trait and thus a useful tool for exploring the functional significance of variation in other reproductive and related traits (e.g., egg load, life span) in parasitoids. Empirical evidence and theoretical modeling have revealed how reproductive and feeding strategies are closely integrated at both the physiological and the behavioral levels.

Future research should include investigations into the role of parasitoid venom on the nutritional quality of hosts and how this affects the allocation of acquired host resources

to female reproduction, maintenance, and locomotion. To gain a deeper understanding of the evolution of resource allocation, it is necessary to explore the molecular basis of differential resource allocation and the absence of lipogenesis. A genomics approach would identify the genes involved in resource utilization as well as shed light on constraining factors. Several genes play a key role in lipogenesis in *Drosophila* [FlyBase (143)], and a number of these are upregulated under an adult diet rich in carbohydrates (143) or prevent lipogenesis in knock-out experiments (2). Using the swiftly accumulating functional genomic information on several insect taxa (e.g., *Apis mellifera*, *Drosophila melanogaster*, *Anopheles gambiae*), it is possible to draw a more complete picture of the unique adaptations that allow adult parasitoids to forego lipid manufacture.

Comparative studies are needed to assess variation in the ovigeny index and correlated traits (particularly life span and feeding habit) in relation to the pattern of physiological resource allocation. A possible link between clutch size variation and the ovigeny index (72) also needs to be examined. The revealed trade-offs will need to be confirmed through physiological investigation, not only by nutrient tracking but also by hormonal manipulation (141). If possible, germ-line ablation [previously applied to *Drosophila* (6)] might be used, because it provides a means of critically testing whether resource limitation actually underlies the reproduction-survival trade-off. The genetic control of resource allocation should be investigated by selection and breeding experiments and through the study of clinal variation in traits in species such as *A. tabida*.

The further application of a stochastic dynamic programming modeling (10, 122, 130) approach is needed to integrate intraspecific variability in resource carryover with (a) the state dependence in individual adult host- and food-foraging behavior, and (b) the stochasticity the insects experience in terms of both oviposition site and food site availability. This



would enable the comparison of the relative fitness advantages of different egg maturation and feeding strategies. Also, studies exploring the role of spatial heterogeneity in the structure of plant communities on reproductive strategies in parasitoids would show how reproduction is tailored to, or constrained by, the spatial distribution pattern of the host's food plants.

Comparative studies of the spermatogeny index (a measure of male reproduction, analogous to the ovigeny index) (17) would also provide significant insights into resource allocation. Because constraints imposed by several life-history traits (particularly body size and life span) are likely to be common to both sexes, the two indices should be correlated among species. The spermatogeny index may be correlated with the type of mating system, given that species differ as to whether

males remain at the emergence site or disperse to mate elsewhere. In the former case, there should be less of a proportionate allocation to soma (males do not need to be long-lived to find females, and winglessness is a common feature). In the latter case, there should be more of an investment in soma, as males will need to be longer-lived, and males of some species practice lekking behavior (69), which is likely to be highly energy demanding. Mating system and proportional investment in soma are also likely to be correlated with the likelihood of consumption of sugar-rich food by males. Another promising area for future research is the role of plant allelochemicals in metabolic allocation to reproduction in parasitoids, given how the growth and development of immatures may be negatively affected on more toxic plant species or cultivars.

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#### Spermatogeny

**index:** measure of the degree to which sperm production is concentrated into early adult life

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### SUMMARY POINTS

1. Parasitoids display remarkable variation in their reproductive traits.
2. Interspecifically, both positive and negative correlations have been recorded not only between pairs of traits but also among suites of several traits.
3. The ovigeny index is an axis of life-history diversity, enabling generalizations and predictions to be made regarding correlations, including trade-offs, occurring among reproductive and other traits. The spermatogeny index may be used in a similar capacity.
4. Parasitoids are not necessarily constrained in their patterns of resource allocation, utilization, and acquisition. They show adaptive plasticity in relation to host-quality constraints upon body size, to constraints upon nutrient intake, and to variation in host availability.
5. Females of synovigenic species draw upon a diverse set of biochemical resources in fueling egg manufacture and somatic functions—not a common resource pool as has often been assumed by theoreticians.
6. The fitness gain from feeding may be restricted to either an increase in life expectancy or an increase in fecundity.
7. Potentially fruitful areas of future research include modeling of the integration of resource allocation, acquisition, and utilization with food- and host-foraging behavior.

### DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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17. Devised a comparative index of early-life concentration of sperm production in insects.

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27. A multi-nutrient budget, constructed for a parasitoid, challenges the widely assumed capital-breeders versus income-breeders dichotomy.

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62. Review of parasitoid feeding biology, from the perspective of behavioral ecologists.

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63. A major contribution to the debate over the importance of time limitation and egg limitation in constraining parasitoid fitness.

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68. The first study to show that a female parasitoid's foraging decisions are likely to be state dependent.

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74. Devised a comparative index of early-life concentration of egg production in insects.

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75. The first modeling conducted to relate nutritional state to foraging decisions by parasitoids.

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77. Large-scale survey of flower-visiting and feeding by parasitoid wasps, showing that most species consume only nectar.

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# Contents

Frontispiece	
<i>Geoffrey G.E. Scudder</i> .....	xiv
Threads and Serendipity in the Life and Research of an Entomologist	
<i>Geoffrey G.E. Scudder</i> .....	1
When Workers Disunite: Intraspecific Parasitism by Eusocial Bees	
<i>Madeleine Beekman and Benjamin P. Oldroyd</i> .....	19
Natural History of the Scuttle Fly, <i>Megaselia scalaris</i>	
<i>R.H.L. Disney</i> .....	39
A Global Perspective on the Epidemiology of West Nile Virus	
<i>Laura D. Kramer, Linda M. Styer, and Gregory D. Ebel</i> .....	61
Sexual Conflict over Nuptial Gifts in Insects	
<i>Darryl T. Gwynne</i> .....	83
Application of DNA-Based Methods in Forensic Entomology	
<i>Jeffrey D. Wells and Jamie R. Stevens</i> .....	103
Microbial Control of Insect Pests in Temperate Orchard Systems: Potential for Incorporation into IPM	
<i>Lawrence A. Lacey and David I. Shapiro-Ilan</i> .....	121
Evolutionary Biology of Insect Learning	
<i>Reuven Dukas</i> .....	145
Roles and Effects of Environmental Carbon Dioxide in Insect Life	
<i>Pablo G. Guerenstein and John G. Hildebrand</i> .....	161
Serotonin Modulation of Moth Central Olfactory Neurons	
<i>Peter Kloppenburg and Alison R. Mercer</i> .....	179
Decline and Conservation of Bumble Bees	
<i>D. Goulson, G.C. Lye, and B. Darvill</i> .....	191
Sex Determination in the Hymenoptera	
<i>George E. Heimpel and Jetske G. de Boer</i> .....	209

The Argentine Ant: Challenges in Managing an Invasive Unicolonial Pest <i>Jules Silverman and Robert John Brightwell</i> .....	231
Diversity and Evolution of the Insect Ventral Nerve Cord <i>Jeremy E. Niven, Christopher M. Graham, and Malcolm Burrows</i> .....	253
Dengue Virus–Mosquito Interactions <i>Scott B. Halstead</i> .....	273
Flash Signal Evolution, Mate Choice, and Predation in Fireflies <i>Sara M. Lewis and Christopher K. Cratsley</i> .....	293
Prevention of Tick-Borne Diseases <i>Joseph Piesman and Lars Eisen</i> .....	323
Entomological Reactions to Darwin’s Theory in the Nineteenth Century <i>Gene Kritsky</i> .....	345
Resource Acquisition, Allocation, and Utilization in Parasitoid Reproductive Strategies <i>Mark A. Jervis, Jacintha Ellers, and Jeffrey A. Harvey</i> .....	361
Population Ecology of Insect Invasions and Their Management <i>Andrew M. Liebhold and Patrick C. Tobin</i> .....	387
Medical Aspects of Spider Bites <i>Richard S. Vetter and Geoffrey K. Isbister</i> .....	409
Plant-Mediated Interactions Between Whiteflies, Herbivores, and Natural Enemies <i>Moshe Inbar and Dan Gerling</i> .....	431
Ancient Rapid Radiations of Insects: Challenges for Phylogenetic Analysis <i>James B. Whitfield and Karl M. Kjer</i> .....	449
Fruit Fly (Diptera: Tephritidae) Host Status Determination: Critical Conceptual, Methodological, and Regulatory Considerations <i>Martín Aluja and Robert L. Mangan</i> .....	473
Codling Moth Management and Chemical Ecology <i>Peter Witzgall, Lukasz Stelinski, Larry Gut, and Don Thomson</i> .....	503
Primer Pheromones in Social Hymenoptera <i>Yves Le Conte and Abraham Hefetz</i> .....	523