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Incorporating physiology into parasitoid behavioral ecology: the allocation of nutritional resources

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Abstract A critical problem faced by most theoretical studies of parasitoid behavior and population dynamics has been the paucity of empirically obtained information about the pattern of resource allocation to egg production and metabolic maintenance in relation to adult diet in female parasitoids. This review calls for a shift from traditional manipulative feeding studies to studies that quantify the energetic budget of parasitoids and which take into account the dynamic nature of metabolic processes. As guidelines, we highlight the advances made along these lines with other insect groups and some of the simplest tools already available today for fulfilling this goal.

Key words Synovigenic parasitoids · Host feeding · Egg production · Metabolism · Energy budget

Introduction

Recent years have seen a definitive increase in our awareness about the need to incorporate greater physiological realism into studies of parasitoid behavior and population dynamics (Jervis and Kidd 1995). For more than a decade and in great measure thanks to the pioneering work by Iwasa et al. (1984), the number of eggs available for oviposition inside the females' ovarioles, henceforth termed egg load, has been widely accepted as a crucial determinant of many aspects of their foraging behavior (Collins and Dixon

1986; Courtney et al. 1989; Trudeau and Gordon 1989; Rosenheim and Rosen 1991; Drost and Cardé 1992; Minkenberget al. 1992; Godfray 1994; Rivero 1994; Collier 1995a; Heimpel and Rosenheim 1995; Michaud and Mackauer 1995). The proliferation of empirical studies of the behavior of parasitoids driven by egg load has been largely prompted by the development of dynamic state variable models that explicitly incorporate the changing physiological state of the female to predict her foraging decisions (Mangel 1989; Chan 1991; Chan and Godfray 1993; Houston et al. 1992; Collier et al. 1994; Heimpel et al. 1994; Collier 1995b). Interest in the physiology of egg production has been further spurred by the recent debate as to whether the reproductive success of parasitoids is mostly limited by the eggs available in the ovarioles or by the time available to lay them (Driessen and Hemerik 1992; Getz and Mills 1996; Rosenheim 1996; Heimpel and Rosenheim 1998; Heimpel et al. 1998; Mangel and Heimpel 1998; Sevenster et al. 1998; Casas et al., in manuscript; Rosenheim, in manuscript). These behavioral models, in turn, play an important role in predicting the population dynamics and stability of host–parasitoid interactions (Kidd and Jervis 1989; Briggs et al. 1995; Shea et al. 1996; Krivan 1997; Krivan and Sirot 1997) and the outcome of biological control efforts (Kidd and Jervis 1989; Murdoch 1990).

The incorporation of egg load into models of parasitoid behavior and population dynamics has raised a series of new problems concerned with understanding the pattern of resource allocation to egg production and metabolic maintenance in relation to adult diet in female parasitoids. In addition to feeding from the host's fluids or tissues (host feeding), nutritional reserves for adult parasitoids can come from reserves accumulated during larval development, or from nonhost foods, such as nectar and honeydew (van Lenteren et al. 1987; Jervis et al. 1993; Wäckers et al. 1996). Two very distinct life histories with respect to the temporal pattern of resource allocation to egg production have been identified (Flanders 1950). *Proovigenic* parasitoids emerge with a more or less fixed complement of eggs and do not host feed; all adult energetic resources are integrally allocated to maintenance. The pattern of resource allocation is,

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however, far more complicated in *synovigenic* parasitoids, in which the female matures eggs throughout her lifetime, typically after a feeding bout, and where resources can be temporarily stored in the eggs and remobilized at a later stage by a metabolic process known as egg resorption. In many *synovigenic* parasitoids, thus, the classic trade-off model in which resources are allocated to either survival or reproduction (van Noordwijk and de Jong 1986) will only partly explain the complex pattern of allocation and reallocation of resources between these two traits.

In *synovigenic* parasitoids, the relative importance of stored reserves or host and nonhost food sources on egg production and survival is largely unknown but seems to vary from species to species. Many theoretical predictions are, however, drastically different depending on the paths followed by the ingested nutrients. At the behavioral level, for example, whether nutrients obtained from host feeding are employed only for egg production, only for maintenance, or for both has consequences for the way in which parasitoids partition their time energy between reproduction and feeding activities (Chan and Godfray 1993). At the population dynamics level, the potential role of nonhost food sources in addressing metabolic and egg production costs may also have an effect on the stability of the host-parasitoid interactions (Kidd and Jervis 1989; Briggs et al. 1995).

The wealth of laboratory studies comparing the impact of different adult diets (e.g., feeding on hemolymph only versus feeding exclusively on sugar) on egg production and female longevity in *synovigenic* parasitoids has been reviewed previously (Jervis and Kidd 1986; Heimpel and Collier 1996) and thus is not repeated here. These studies constitute an overwhelming body of information that remains nevertheless difficult to interpret, beyond some general well-established facts reviewed here, because of differences in the experimental protocols. The timing, availability, concentration, and composition of the diets vary. Some studies use honey as a carbohydrate source while others use glucose, fructose, sucrose, or simply "sugar" at different concentrations. Honey, however, is known to contain free amino acids and there are indications that different types of sugars have different effects on parasitoid longevity (Morales-Ramos et al. 1996). Hosts for feeding are provided to parasitoids from birth or after variable periods spent starved or sugar fed. Furthermore, host feeding is sometimes allowed in conjunction to egg laying, while occasionally physical barriers are used to prevent oviposition (Heimpel and Collier 1996). Studies in which the amounts of nutrients consumed by the females are calculated are the exception rather than the rule (e.g., Wäckers et al. 1996; Rivero and Casas, in manuscript). The quantity of diet ingested can, however, have a critical effect on both egg production and longevity (Englemann 1970). The foregoing studies have nevertheless proved valuable in indirectly highlighting the complexity of the metabolic paths followed by nutrients of different sources, supplied at different rates and different time intervals.

The aim of the present review is to stress the need for more detailed physiological studies of nutrient allocation to

egg production and maintenance in *synovigenic* parasitoids. For this purpose, we establish comparisons with what is known and the methodology employed in other insect groups, butterflies and mosquitoes in particular. We start with a reminder of some general facts about insect energetic physiology. The next two sections review the three potential sources of nutrients for egg production and maintenance in parasitoids, host- and nonhost-related nutrients (the *incoming* resources) and stored nutrients (or *capital* resources; *sensu* Sibly and Callow 1984). In these two sections we stress, respectively, the need to understand the relative contribution of host and nonhost sources to reproduction and somatic maintenance and the role of storage both as a trait to which resources are invested and as a source of energy when times are hard. The last section summarizes the methodology that could be used to answer some of the questions.

Energy metabolism in insects

Insects pay their daily energetic expenses using three different currencies: lipids, carbohydrates, and, to a lesser extent, proteins. The aim of this section is to review briefly how females acquire, spend, store, and exchange these currencies. The latter two, namely the storage of reserves and their conversion into other biologically important organic molecules, are largely carried out by the insect's own physiological bank: the fat body. The fat body is an organ equivalent in function to the human liver and thus plays a key role in the allocation of resources toward the different physiological processes.

The fat body is a loosely organized tissue with a large surface area in contact with the hemolymph. It stores carbohydrates in the form of glycogen and lipids in the form of triglycerides. Lipids, which at least in mosquitoes can be synthesized from a sugar meal (Briegleb 1990a), are a much more efficient way of storing reserves than carbohydrates for two main reasons (Clements 1992): (1) they provide more than twice the energy value per unit weight (this is calculated roughly as 16.74J per mg carbohydrate and 37.65J per mg of lipid), and (2) they can be stored in an anhydrous form and thus take up less valuable space than carbohydrates. The fat body is also the organ where nutrients are metabolized and used for building new biological molecules or exported to other parts of the body for use as energetic fuel. Aside from their crucial role as energy providers, lipids render acetyl groups that serve as the basis for the biosynthesis of nearly all other kinds of essential molecules, including amino acids (Nijhout 1994). The main circulating sugar in the hemolymph, the highly energetic disaccharide trehalose, is also synthesized in the fat body, either from newly intaken sugar meals or from stored glycogen. Perhaps the best-known role of the fat body, however, is the synthesis of the main constituent of the egg yolk, the vitellogenin. The amino acids used to build up this lipoprotein may come from exogenous sources, such as protein ingested by the adult, or from amino acids synthesized in the fat body, and in most insects

its synthesis is regulated by the juvenile hormone (Nijhout 1994).

What are the relative roles of lipids and carbohydrates and proteins in the energetic budget of the insect body? Fed insects seem to use carbohydrates as their main ready-to-use source of metabolic energy while lipids tend to be utilized by individuals passing through prolonged periods without feeding, once the sugar reserves have decreased below a certain threshold. In some species of Lepidoptera and Orthoptera lipids have been conclusively shown to be the main source of energy for sustained flight. In *Locusta migratoria*, for example, the adipokinetic hormone in charge of releasing stored lipids into the hemolymph acts such that lipids are liberated only when the trehalose concentration of the hemolymph has declined below a certain value (van der Horst et al. 1979). In mosquitoes, on the other hand, flight seems to be fueled exclusively by carbohydrates, circulating sugars if fed and glycogen reserves if starved (Nayar and van Handel 1971), while lipids are the main source of energy when at rest (Clements 1992).

The physiological role of stored lipids in hymenopteran parasitoids is, by contrast, only beginning to be understood. By using a relatively simple technique consisting of extracting the fat with ether and calculating the change in dry weight of the parasitoid before and after the procedure, Ellers (1996) was able to quantify the amount of fat in *Asobara tabida* females at different time intervals. This and subsequent studies have provided three very valuable pieces of information about the potential role of fat reserves in parasitoids. First, fat reserves decrease linearly with age, proving the role of lipids in metabolic maintenance. Second, *A. tabida* females that had laid eggs a few days previously had similar egg loads but significantly lower fat reserves than nonovipositing females (Ellers and van Alphen 1997), indicating that fat reserves are also used to build eggs. Concomitantly, these two results provide the first proven physiological mechanism for the trade-off between reproduction and survival in parasitoids. Finally, a release-recapture experiment showed that there was a significant negative correlation between fat content and the distance from the release point at which the females were recaptured, indicating that in this species fat is used for sustaining locomotion (Ellers et al. 1998).

While the experiments of Ellers et al. provide an encouraging start to the inclusion of physiological realism into parasitoid ecology, there is still much work to be done. To date, no quantification of sugars or glycogen has been made in parasitoids. Relatively simple and precise colorimetric techniques that permit the simultaneous quantification of lipids, sugars, and glycogen from the same individual are widely used to calculate the overall energetic budget under different nutritional conditions in other insect groups (see following). Evidence of the relative role played by lipids and carbohydrates in the metabolic budget of the female parasitoid is qualitative and based on comparisons of longevity and egg production in females under different food regimes. This question is discussed in the next section.

Incoming resources: the role of host and nonhost foods in egg production and maintenance

Adult feeding in synovigenic parasitoids can come from two different sources: from the hosts themselves or from nonhost sources such as nectar or honeydew. A complete review of the diversity of host-feeding strategies and their occurrence among parasitoids has been carried out by Jervis and Kidd (1986) and Heimpel and Collier (1996). The prevalence of nonhost feeding in the field is, by contrast, considerably less well documented, although Jervis et al. (1993) recorded more than 200 species of hymenopteran parasitoids feeding on flowers in the field.

The way in which the parasitoids forage for feeding sites has motivated a considerable number of empirical and theoretical studies that have provided us with a good understanding of the behavioral trade-offs faced by the foraging females (Godfray 1994). On finding a host, for example, many parasitoids are faced with a decision: whether or not to renounce the opportunity for current reproduction (oviposition) in favor of anticipated chances for future reproduction (host feeding). Similarly, parasitoids relying on sugar sources for survival, and those where hosts and food are found in different parts of the environment, have to decide when to search for nectar instead of hosts. These decisions are inevitably triggered, at least in part, by physiological thresholds. Indeed, all the dynamic models developed so far have placed the female's energetic reserves high on the list of state variables determining host-feeding (Houston et al. 1992; Chan and Godfray 1993; Collier et al. 1994; Heimpel et al. 1994; Collier 1995a) and sugar-feeding (Sirost and Bernstein 1996) decisions. In most of these models the body of the females is approximated to an energetic pool that is replenished every time the parasitoid feeds. If the reserves in the pool fall below a certain threshold the female will preferentially allocate her time and energy to feeding instead of reproductive activities. The main differences between these models result from the assumptions they make with respect to two physiological aspects: (i) the way the nutrients are allocated within the body of the adult parasitoid and (ii) whether the speed of conversion of nutrients into eggs is taken into account.

Allocation paths of nutrients

In some of the behavioral models nutrients are allocated exclusively to egg production (Chan and Godfray 1993; Collier et al. 1994; Heimpel et al. 1994), exclusively to maintenance (Houston et al. 1992; Chan and Godfray 1993), or to both (Chan and Godfray 1993; Collier 1995b; Heimpel et al. 1998). The energetic threshold and critical egg load below which the parasitoid will host feed instead of laying an egg in a host may indeed depend on such allocation rules (Chan and Godfray 1993). At a population dynamics level, the stability of host-parasitoid interactions may also depend on whether there is a metabolic demand on nutrients obtained from host feeding (Briggs et al. 1995). Further-

more, nonhost food sources may act in a way analogous to refuges, stabilizing the host–parasitoid interactions, if nutrients obtained from them can be used for both egg production and maintenance (Kidd and Jervis 1989; Briggs et al. 1995).

How do host and nonhost foods contribute to the parasitoid's different metabolic demands? Experiments in which the effect of different adult diets on fecundity and longevity are compared (reviewed by Jervis and Kidd 1986; Heimpel and Collier 1996) suggest that, in general terms, host feeding allows the female to obtain proteins to meet the high amino acid demands associated with egg production, while feeding from nonhost sources provides the female with sugars to meet the body's energetic demands. Exceptions to this general principle, however, abound. In some species, for example, host feeding will increase both egg production and longevity, while in others the female will die if kept exclusively on a host diet. Some parasitoids, on the other hand, are able to produce some eggs while feeding exclusively on a sugar source, suggesting that in some species sugars may also be a specific requirement for reproduction. These inconsistencies may be partly explained by the complex nature of the nutrients ingested. Nectars and honeydew, for example, are known to contain amino acids (Baker and Baker 1973; van Lenteren et al. 1987), which could be directly invested in egg production, as has been found to be the case in *Heliconius* butterflies (Gilbert 1972). Host feeding probably involves the consumption of a variety of substances, extending from hemolymph to other body components such as loose fat body cells, hemocytes, or gut contents. The insect hemolymph itself contains many substances, such as water (constituting as much as 75%), free amino acids, proteins, peptides, trehalose and other carbohydrates, lipophorin and other lipids, vitamins, and inorganic ions, among others (Florkin and Jeuniaux 1964; Mullins 1985). In addition, the host's hormones may be used to the parasitoid's advantage, as has been shown to be the case in some blood-feeding insects (Englemann 1970). Furthermore, the composition and densities of the different constituents of the hemolymph change over time, sometimes rapidly, as a function of the activity and hunger level of the host as well as that of different environmental factors (Mullins 1985).

Whether host feeding provides nutrients for maintenance as well as for egg production is a question that seems to have different answers depending on the parasitoid species, although the reasons for this are not yet clear. The extent to which feeding from nectar or honeydew can address the egg production needs of parasitoids is also unclear, although the effect of sugar on egg production is almost certainly not a direct one. Sugar, however, may be an indirect but necessary requirement for reproduction in some insects, either by meeting the energetic demands of reproduction (Clements 1992) or by mobilizing reserves stored in the fat body for egg production (Englemann 1970). There is thus an impending need to study the physiological budget of parasitoids and the metabolic path followed by nutrients to answer these questions unequivocally.

The speed of nutrient incorporation into egg production

The time required for the nutrients ingested through feeding to be converted into eggs (egg maturation delay) and the number of eggs produced as a result (feeding gain) are two related physiological variables that have been the focus of much recent attention. Dynamic state variable models making the simplifying assumption that eggs are produced immediately after a feeding bout predicted that females should only host feed when their egg load has dropped to zero (Chan and Godfray 1993; Collier et al. 1994). The recent incorporation of realistically long egg maturation delays into the models has drastically changed these predictions: host feeding should occur at nonzero egg loads to avoid becoming egg limited (Collier et al. 1994; Collier 1995b; Heimpel et al. 1998). Furthermore, the host feeding gain is also expected to determine the critical egg load at which host feeding should occur (Collier 1995b). Both these variables are likely to vary depending on the metabolic paths followed by nutrients once ingested, which in turn may depend on the composition of the diet as well as on the amount of eggs and energetic reserves stored in the ovarioles and in the fat body, respectively.

Only a limited number of studies exist in which the host feeding gain and egg maturation delay have been empirically quantified. Through comparisons between host-fed and control females, it has been estimated that *Aphytis melinus* females mature approximately two eggs during a 2-day period (Heimpel et al. 1994; Collier 1995a). When the host feeding gain was integrated over the whole life of the parasitoid, however, the host-feeding gain was found to be four eggs (Heimpel et al. 1997). More such studies are needed to determine the range of host-feeding gains and egg maturation delays in other synovigenic parasitoids. By providing radioactively labeled nutrients to *Dinarmus basalis*, Rivero and Casas (in manuscript) were able to detect the presence of marked nutrients in eggs laid as soon as 2 h after a short feeding bout. Nutrients were still being incorporated into the egg 15 days after the feeding event, showing that, as Heimpel et al. (1997) suggested, the host-feeding gain is spread over the lifetime of the parasitoid. More information is needed as to how the preexisting nutritional and egg load state of the female may change the values of these parameters. Anopheline mosquitoes, for example, show a very low efficiency of protein utilization for oogenesis, as most of the nutrients are diverted to the buildup of fat body reserves, which has been interpreted as an adaptive response to the low level of stored reserves (Briegel 1990a). Among the methodology available, the possibility of radioactively marking parasitoid eggs through feeding is particularly promising. This technique was first employed in *Bracon* by Grosch and Sullivan (1953) but has not, to our knowledge, been employed since although it is commonly used in other insect groups (King and Wilson 1955; Gilbert 1972; Kloft 1992; Boggs 1997a). Radioactive labeling offers numerous possibilities and may prove to be a key nutrient tracking tool in years to come.

Capital resources: the role of storage

Nutrients ingested by the adult parasitoid pass on to the crop and from there to the hemolymph, from which they will be assigned to either energy production, egg production, or storage. Storage should thus be considered a trait in which resources are invested, equivalent to maintenance or reproduction (Boggs 1992). Nutrients in storage can at a later stage be remobilized, thus providing the female with a safety energy margin when environmental resources are limiting. Mobilization of lipids and glycogen stored in the fat body is, however, bound to incur significant metabolic costs, although to date these costs have never been quantified in insects. Although there is a growing awareness of the importance of adult feeding among behavioral ecologists and theoretical population biologists (Jervis and Kidd 1995), the pattern of utilization of stored versus incoming sources has been largely overlooked in parasitoids.

Models aiming to predict the foraging decisions of parasitoids on the basis of their physiological state assume the body of the female to work as a pool of resources, consisting of an initial energy stock that gets replenished every time the parasitoid feeds (see foregoing discussion). Nutrients for egg production or maintenance are extracted from this noncompartmentalized common pool following different allocation rules but with no loss of energy or materials involved. The only models in which the female is allowed to revert to nutrients stored at some other point in her life when faced with adverse conditions are those that take into account egg resorption (Jervis and Kidd 1986; Collier 1995b). Egg resorption involves the enzymatic digestion of the oocytes and the subsequent reallocation of the resulting resources for adult maintenance and for sustaining future oogenesis (Flanders 1942; King and Richards 1968; Cassidy and King 1972; Bell and Bohm 1975). The remobilization of nutrients stored in the eggs has been rightly assumed to take place at an energetic loss. Jervis and Kidd's simulations assumed the recovery rate of nutrients stored in the egg to be 80%. Collier (1995b), on the other hand, included a cost of resorption by assuming that resorbed eggs are less effective at fulfilling the female's metabolic requirements than the nutrients coming straight from the gut. As a result of this cost, Collier predicted that the energetic requirement should be first taken from the gut and only when no more nutrients are left should the parasitoid resort to resorbing their eggs. Most empirical egg resorption studies indeed suggest that egg resorption takes place only when the female is deprived of food. In some parasitoids, however, eggs are resorbed even when incoming food sources are available (e.g., Rivero-Lynch and Godfray 1997). Despite the potential importance of eggs as storage units in parasitoids in which egg resorption exists (Antolin and Williams 1989), the main storage of energy in insects takes place elsewhere, in the fat body.

Resources stored in the fat body may come from reserves accumulated during the larval period (teneral reserves) or from surplus nutrients acquired as an adult. In *Asobara tabida* a decrease in fat reserves with age occurred

more slowly in fed females (Ellers 1996), which suggests that incoming nutrients may be used concomitantly with fat reserves. Fat may still be burned even in the presence of a relatively rich diet if the incoming nutrients are simply not sufficient to cover the energetic requirements of the females. Alternatively, the fat body may constitute the source of specific nutrients, e.g., certain vitamins or minerals, that are essential but scarcely found in the adult diet or not found at all. Using double-marking with ^3H - and ^{14}C -labeled nutrients, Boggs (1997a) determined that in *Heliconius* butterflies the pattern of utilization of larval reserves for egg production depends on the abundance of nutrients in the environment. For compounds abundantly available in the adult diet, such as sugar, incoming nutrients are used in preference to stored nutrients. For amino acids, however, which are present in low amounts in the adult diet, juvenile reserves were used through adult life, although incoming nutrients were used if available. Such specific patterns of resource allocation have a direct influence on the fitness of the individuals subjected to different types of nutrient stress but also on the resiliency of the populations to environmental variation (Boggs 1997a,b).

Conclusions: looking to the future

Given the importance of parasitoids as models to study the adaptive nature of behavioral decisions and the effect of behavior on population dynamics, it is surprising that knowledge of parasitoid physiology in relation to nutrient allocation is still so poorly characterized, in particular considering that such studies have been long been available in other insect groups. In contrast, during the past three decades development of new or modified chemical methodology has made it possible to follow the appearance and disappearance of reserves in mosquitoes, a group of insects with similar nutritional requirements (blood versus nectar), and arguably similar foraging decisions (search for sugar versus protein sources) as parasitoids. Determining the quantity of lipids (through a vanillin reaction), total sugars (hot anthrone reaction), and glycogen (chemical precipitation followed by hot anthrone reaction) are possible within a single individual (van Handel 1985a,b; van Handel and Day 1988). Quantifying the importance of nectar feeding from field-caught individuals is also possible because fructose (one of the main sugars present in nectar) reacts with cold anthrone (van Handel 1972). Proteins can be determined using a standard Bradford technique (Bradford 1976) or, alternatively, total nitrogen can be quantified using a Kjeldahl digestion and subsequent Nesslerization (Minari and Zilversmit 1963). Such quantifications have hence served to comprehend how mosquitoes budget their energetic resources under different nutritional situations (van Handel 1984; Briegel 1990b; Briegel and Hörler 1993; Yuval et al. 1994; Foster 1995) and to develop realistic models that explain several aspects of the foraging behavior of these insects in the field (Roitberg and Friend 1992).

Comparative feeding experiments already indicate the great variety of allocation strategies employed by different species of parasitoids fed from different sources. Physiological studies that actually quantify the incorporation of nutrients from different sources into reproduction and body maintenance should be the next step. These studies should combine quantification of lipids, glycogen, sugars, and proteins in parasitoids fed on different diets in the laboratory, or collected in the field, with determinations of the rate incorporation of specific nutrients into the fat body and the eggs using radiolabeled nutrients. Among the important questions that bear consequences on the way parasitoids forage in their environment and which would benefit from such studies are the following. (1) What is the role of nonhost feeding in egg production? (2) Why do some species of parasitoid resorb eggs even when they have a ready source of food and why are others not able to resorb eggs at all? (3) What is the rate of recovery of nutrients coming from egg resorption and how does it compare to the costs associated with mobilizing fat? (4) Do parasitoids budget their resources according to the predictability of the environment? The answers to these and other related questions would be a major step toward the development of more realistic models of parasitoid behavior and population dynamics.

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