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LIFETIME NUTRIENT DYNAMICS REVEAL SIMULTANEOUS CAPITAL AND INCOME BREEDING IN A PARASITOID

JÉRÔME CASAS,¹ SYLVAIN PINCEBOURDE, NICOLE MANDON, FABRICE VANNIER,
 RÉMI POUJOL, AND DAVID GIRON

*Université de Tours, Institut de Recherche en Biologie de l'Insecte, Unité Mixte de Recherche 6035,
 Centre National de la Recherche Scientifique, Av. Monge, 37200 Tours, France*

Abstract. Models of host handling decisions and physiologically structured host–parasitoid population dynamics make diverging assumptions, untested as of this writing, about the allocation rules of nutrients to survival and reproduction. Our aim is to develop a data-rich multidimensional dynamical budget of nutrient acquisition and allocation in survival and reproduction in the host-feeding, synovigenic bruchid ectoparasitoid *Eupelmus vuilletti* (Hymenoptera: Eupelmidae) over the entire lifetime of the animal in order to address the above questions.

We quantified sugar, glycogen, protein, and lipid reserves of single females at birth and death and their daily maintenance needs. We recorded each host-feeding and oviposition event over entire lifetimes and quantified the amounts acquired and invested in eggs using microcolorimetric techniques. We then built two nutrient budgets, with and without hosts, encompassing 20 measured biochemical parameters and tested their predictions using time of death.

Carbohydrate reserves are burned at a high rate for maintenance and can be used to predict lifetime in absence of hosts. The model without hosts is adequate, but the one with hosts is not, as it predicts a continuous increase of proteins from the massive host-feeding intake, contrasting with the observed decline. A good prediction of time of death could be achieved in that model by assuming that the large amounts of ingested proteins and carbohydrates from host-feeding are used for maintenance, thereby enabling females to spare lipids for reproduction. We tested this assumption in a treatment with hosts and supplemental sugars, in which the maximal number of produced eggs is expected to be almost exclusively a function of lipids when other nutrients can be obtained to cover maintenance costs.

Our results enable us to discriminate between competing hypotheses about nutrient allocation in models of parasitoid behavior and host–parasitoid population dynamics. They show that *E. vuilletti* is both a capital breeder for lipids and an income breeder for sugars, implying that this dichotomy is best superseded by a multidimensional and dynamical approach to nutrient acquisition and allocation.

Key words: *host-feeding; host–parasitoid dynamics; income and capital breeding; life history strategies; lipids; nutrient acquisition; nutrient allocation; nutrient dynamics; parasitoids; population dynamics.*

INTRODUCTION

Nutrient acquisition and allocation in survival and reproduction is a central issue to all organisms with implications ranging from energy metabolism, behavioral ecology, senescence, and life history strategies to population dynamics (see the reviews of Boggs [1992], Mangel and Heimpel [1998], Zera and Harshman

[2001], Novoseltsev et al. [2002], Rausher et al. [2003]). This is particularly true for insect parasitoids that choose between laying an egg on a host or feeding on it (Godfray 1994, Rosenheim et al. 2000). In the latter case, females bypass an immediate reproductive opportunity for a potential future one. The rules determining the link between nutrient reserves and foraging behavior are therefore expected to be particularly tightly controlled in this group of organisms (Rivero and Casas 1999a). Experimental studies on nutrient allocation to reproduction and survival in individual

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¹ E-mail casas@univ-tours.fr

insects have grown in numbers recently, due to the availability of tracing techniques such as double radioactive labeling (Boggs 1997b, Rivero et al. 2001), isotope marking (O'Brien et al. 2000, 2002, 2004), precise colorimetric analysis (Giron et al. 2002, Casas et al. 2003), and enzymatic analyses (Zhao and Zera 2002, Zera and Zhao 2003). These studies, echoing pioneer studies of similar spirit on food acquisition and investment in growth by Simpson and Raubenheimer (see Simpson and Raubenheimer [1993] and Raubenheimer and Simpson [1999]), were mainly fostered by the enduring interest in parental reproductive investment (Boggs 1992, Giron and Casas 2003b). They have delivered several messages relevant to behavioral ecology, life history strategies, and population dynamics of host-parasitoid systems. First, they showed that some elements of larval origin are nonrenewable and allocated to reproduction in a finely tuned and differentiated manner. As a corollary, using a single class of "energy reserves" may be quite misleading. Second, mothers may reduce their investment in eggs over their lifetime, sometimes drastically so (Giron and Casas 2003b, O'Brien et al. 2004). Irrespective of the mechanisms leading to this pattern, this fact implies that a dynamical budget of nutrients is required over the life of an animal in order to quantify the allocation rules, the levels of nutrients, and the ensuing behavioral decisions.

The choice between feeding on a host or laying an egg on it is a function of the host's intrinsic qualities as well as the state of reserves in the parasitoid female's body (Jervis and Kidd 1986, Collier et al. 1994, McGregor 1997). The gain in fitness of the different strategies has been used as a benchmark for developing dynamic state variable models in ecology from the early days on (Mangel 1989). Since then, a whole array of different models has been put forward (Houston et al. 1992, Chan and Godfray 1993, Heimpel et al. 1994, Collier 1995b). Assumptions regarding nutrient allocation vary from model to model. In some models, food is exclusively allocated to reproduction, in others exclusively to maintenance, and in others to both. These models are best applied to so-called synovigenic species in which adults emerge without their full complement of eggs. Feeding or simply time allow the maturation of potentially numerous supplementary eggs. Synovigeny among parasitoids is the rule rather than the exception (Jervis et al. 2001). All these models use the egg load, the complement of eggs available at a given time, as a proxy for reserves for two reasons. First, quantification of reserves in small insects requires tedious biochemical analyses while egg load is comparatively easy to measure. Second, resorption of eggs is a common occurrence in these animals. It is usually assumed that the nutrients saved through egg resorption are for maintenance (Bell and Bohm 1975, Papaj 2000), and a few studies have indeed shown a correlation between the number of eggs resorbed and

an extension of life (Collier 1995a, Heimpel et al. 1997). Thus, egg load can be a priori considered as a nutrient store. While this assumption has been well supported by several observations, the unexplained residuals are often very large (Heimpel et al. 1998). The models of host use became thus very detailed and physiologically realistic, but outgrew the physiological knowledge on which they were based. Proper testing requires indeed tracking of the fate of different classes of nutrients from ingestion to allocation. Such studies were not conducted, leaving an array of models without further assessment. As summarized in a recent overview, there is incomplete resolution of the different model predictions because one of the state variable is considered unobservable, the determination of reserves being "still essentially impossible" (Clark and Mangel 2000).

A parallel increased physiological realism pervaded host-parasitoid population dynamics models, in which both the egg load and the reserves are key variables (Yamamura and Yano 1988, Kidd and Jervis 1991a, b, Briggs et al. 1995, Kirvan 1997, Shea et al. 1997, Murdoch et al. 2003). Host feeding per se has no effect on the stability of the interaction, but simply lowers the conversion efficiency from a host meal into parasitoid offspring. Host-feeding merely increases the stability level of the host population, but does not otherwise alter the system in a profound way. The predictions about the stability of these interactions depend on the details of nutrient acquisition and allocation. An interaction is destabilized if one assumes that nutrients gained through host-feeding are allocated both to maintenance and reproduction (Kidd and Jervis 1991a, b, Briggs et al. 1995, Kirvan 1997). It is also destabilized if eggs are resorbed for maintenance purposes (Briggs et al. 1995). However, if the death rate is function of reserves, failure to meet maintenance becomes stabilizing. A system can therefore shift from stability to instability depending on the exact formulation of the path followed by nutrients gained from host-feeding and as function of the relation between death rate and reserves (see Briggs et al. [1995], Kirvan [1997]). The net effect of these processes can be either stabilizing or destabilizing, depending on their respective values. As these authors rightly point out, it is therefore important to determine which nutrients are gained and how they are allocated. Furthermore, their own results suggest that quantification is needed in order to make predictions, simpler tracking of nutrient pathways being not sufficient (Rivero et al. 2001). Here again, competing hypotheses leading to opposite dynamics were left without experimental data of matching precision.

Our aim is to develop a dynamical model of nutrient acquisition and allocation in survival and reproduction in the host-feeding, synovigenic ectoparasitoid *Eupelmus vuilletti* (Hymenoptera: Eupelmidae) over the entire lifetime of the animal in order to reduce the large number of possible scenarios of resource acquisition

and allocation and the ensuing consequences at the population dynamics and life history strategies levels described above. This parasitoid species is the only one for which we have quantitative data on food composition, food consumption, and nutrient allocation to eggs. We have quantified the nutritional value of single host-feeding events in terms of both survival and fecundity gains (Giron et al. 2002, 2005, Giron and Casas 2003a, b). In order to achieve our aim, we recorded the complete sequence of host-feeding and oviposition events over the lifetime of a large series of females in a highly controlled situation. We then quantified sugar, glycogen, protein, and lipid reserves of single females at birth, death, and over their entire lifetimes using microcolorimetric techniques. We combined our results with the ones previously obtained (Giron et al. 2002, 2005, Giron and Casas 2003a, b) in two simple balance models, one in a situation without hosts, the other with access to hosts. We tested our understanding of the flow of nutrients and allocation rules obtained from these models and experiments by running another set of experiments with hosts and with supplemental food.

According to definitions accepted since the work of Stearns (1992) and Jönsson (1997), income breeders use energy acquired during the reproductive period rather than stored energy for reproduction. We tested the validity of this dichotomy using the simultaneous recording of several categories of nutrients. While our work has been carried out with one particular species, several results apply to a large portion of the myriad of synovigenic insects and other animals. We spell out the implications of our results for physiologically based behavioral and population dynamics models of increasing realism as well as for the life history theory of breeding strategies.

MATERIAL AND METHODS

Parasitoid biology and sample preparation

Eupelmus vuilletti (CRW) (Hymenoptera, Eupelmidae) is a tropical solitary host-feeding ectoparasitoid of third- to fourth-instar larvae of *Callosobruchus maculatus* (F) (Coleoptera, Bruchidae) infecting *Vigna unguiculata* (Fabaceae) pods and seeds. Females are synovigenic, i.e., they are born with some immature eggs and need to feed from the host in order to sustain egg production and maturation. Females, however, rarely use the same host for egg laying and for feeding (D. Giron, *personal observation*). Culturing and all experimental procedures were carried out at the Université de Tours, Institut de Recherche en Biologie de l'Insecte, in a controlled room with a 13:11 light:dark photoperiod, a temperature cycle of 33°C (light):23°C (dark), and a constant 75% relative humidity.

In the following experiments, hosts provided to females had been previously extracted from the *V. unguiculata* seeds and placed inside a gelatin capsule following Gauthier and Monge (1999). This system does

not alter the natural behavior of females nor their life expectancy (Giron et al. 2002) and allows us to control for the number and the developmental stage of the hosts. It also facilitates the recording of the number of eggs laid and the number of host-feeding events. Host-feeding consists of puncturing the host, constructing a tube made either of substances from the host or from the female, and licking the exudates.

Quantification of lipids, carbohydrates (glycogen and sugars), and proteins was carried out using the colorimetric techniques developed for mosquito analysis as modified by Giron et al. (2002) for this parasitoid species. Carbohydrates comprise sugars and glycogen. The proteins, lipids, and sugars reserves at birth and death were analyzed for individuals as in Giron et al. (2002), and the glycogen reserves were analyzed as in Giron and Casas (2003a).

Nutrient budgets

The daily nutrient balance is valid for an average individual. It starts with the mean amounts at birth and sums the mean daily gains from host-feeding and the mean daily losses from maintenance and ovipositions. Model accounting is done before feeding and oviposition occur. Hence, the amount of a nutrient class j in a female's body in the presence of hosts on day i , $N_j(i)$, is

$$N_j(i) = N_j(i-1) - M_j(i-1) + [\alpha_j \beta f(i-1)] - [\delta_j \gamma E(i-1)]$$

where M_j is the maintenance loss for nutrient j , α_j is the gain through a single host-feeding event for nutrient j , β is the nutrient conversion factor, $\gamma = (1/\beta)$ is its inverse, f is the number of host feeding events, δ_j is the amount of nutrients in an egg, and E is the number of eggs laid.

The first model without hosts does not contain the last two terms, oviposition and host-feeding. The second model with hosts is the most complete one. In that model, only the values at birth time and the maintenance costs used in the treatment without females were kept. We assumed a constant gain of 0.25 mg host haemolymph per host-feeding event (Giron et al. 2002) and a nutrient conversion factor of 0.7 for all nutrients (McNeill 1999, McDonald et al. 2002). This factor takes into consideration the fact that both feeding and digestion are processes with energy costs that must be paid out using the energy gained immediately. The same consideration applies to building eggs, whose energy content is only a portion of the energy used to build them. All parameters are given in Table 1. They were either estimated from the experiments described below or taken from works previously published.

We used the predicted time of death to test our models against reality. Time of death is predicted to occur within two boundaries. It may occur earliest when one of the nutrients attains the level observed at time of death and latest when energy attains its respective death

TABLE 1. Parameter values used in both models, without and with hosts.

Nutrient	Without hosts	With hosts	Source
At birth			
Lipids	84.5	84.5	this study
Proteins	27.54	27.54	this study
Glycogen	53.58	53.58	Giron and Casas (2003a)
Sugars	10.69	10.69	Giron and Casas (2003a)
At death			
Lipids	18.67		this study
Proteins	4.44		this study
Glycogen	8.25		this study
Sugars	3.88		this study
Lipids		24.67	this study
Proteins		6.21	this study
Glycogen		11.66	this study
Sugars		4.21	this study
For maintenance			
Lipids	7.72	7.72	this study
Proteins	2.57	2.57	this study
Glycogen	9.6	9.6	Giron and Casas (2003a)
Sugars	11.5	11.5	Giron et al. (2002)
Gain in one host-feeding			
Lipids		0.57	Giron et al. (2002)
Proteins		5.27	Giron et al. (2002)
Glycogen		2.06	Giron et al. (2002)
Sugars		4.45	Giron et al. (2002)
In a single egg			
Lipids		0.29	Giron and Casas (2003a)
Proteins		0.29	Giron and Casas (2003a)
Glycogen		0.46	this study
Sugars		0.33	Giron and Casas (2003a)

Notes: The values are mean values expressed in micrograms per individual. Maintenance costs are expressed per day.

level. The width of this predicted interval is a function of the interchangeability of nutrients.

We did not carry out further biochemical analyses of female reserves in the treatment with hosts and without sugars. Instead, we chose to test the internal logic of our understanding of nutrient allocation by designing a treatment with hosts and supplemental sugar, the nutrient running out earliest. With supplemental sugar, we expected an increase in survival or fecundity or both. Carbohydrates available *ad libitum* were expected to cover a larger proportion of maintenance costs and to enable an increase in survival and/or in egg production thanks to the spared lipid and protein nutrients.

Experiments without hosts and without sugar

In the treatment without hosts, 55 females were kept individually without water in Petri dishes of 8.5 cm diameter in the same conditions as described above for estimating their lifetime. Quantification of daily maintenance requirements in lipids and proteins was carried out using a second set of females. They were isolated singly in tubes at their emergence and a group of usually 10 individuals were killed every second day up to day 8, which corresponded to the longest lifetime. The daily maintenance was obtained through linear regression of body contents over days.

Experiments with hosts and without sugar

In the treatment with hosts and without sugar, a group of 39 females was isolated at emergence and kept in individual Petri dishes in the same conditions as described above for estimating the lifetime, fecundity, and number of host-feeding events. Single hosts were offered daily to each female over their entire lifetime. The foraging window was set from 08:30 to 14:30 hours, corresponding to the peak foraging activity (D. Giron, *personal observation*). Hosts were renewed every hour for six hours. All oviposition and host-feeding events were recorded. Host-feeding trials separated by <10 min were pooled, as a completed construction of a feeding tube lasts for at least 10 min. Every host was examined later under the stereomicroscope to collect the eggs laid. Twelve females were analyzed for amount of nutrients at the time of death.

Experiments with hosts and sugar

The set-up was the same as in the treatment with hosts and supplemental sugar; a cotton plug with a sucrose solution was offered and changed daily. Wasps were not observed and the number of host-feeding events was estimated using the number of host-feeding tubes. The number of eggs laid was also recorded. No biochemical analyses were carried out in this treatment.

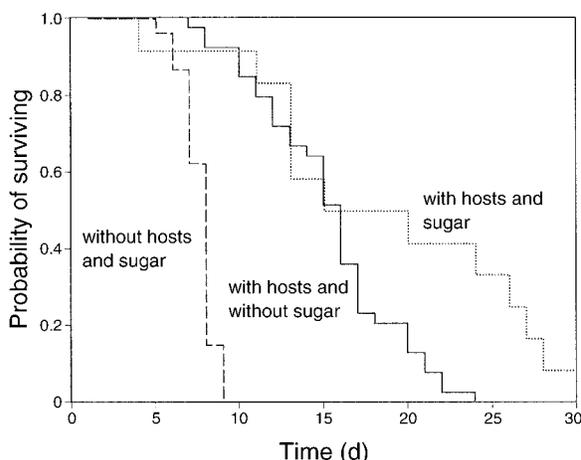


FIG. 1. Probability of survival of the solitary host-feeding ectoparasitoid *Eupelmus vuilletti* with and without *Callosobruchus maculatus* hosts and supplemental sugar over time.

Amounts of glycogen in eggs

Quantification of glycogen in eggs was carried out by choosing at random a group of 50 females of unknown age in the rearing cages, isolated and given hosts as above. Fifteen batches of 10 eggs each, one egg per female, were analyzed for glycogen following the procedure for nutrient extraction from eggs detailed in Giron and Casas (2003b).

RESULTS

Experiments without hosts

Females survived on average 6.6 ± 1.06 d (means ± 1 SD, $n = 55$) without hosts (Fig. 1). Females emerged with 84.5 ± 8.55 μg lipids ($n = 12$) and 27.53 ± 3.18 μg proteins ($n = 15$).

Without hosts, their reserves at death amounted to 18.67 ± 11.57 μg lipids ($n = 40$), 3.88 ± 1.31 μg sugars ($n = 18$), 8.25 ± 2.67 μg glycogen ($n = 10$), and 5.44 ± 3.07 μg proteins ($n = 15$). This represents a decrease of nearly 80% in lipids and proteins. For carbohydrates, comparisons with previously obtained data at emergence led to a similar decrease (12.13 μg at death, 64.27 μg at birth, see Table 1).

The daily maintenance was linear for lipids, with a mean rate of 7.7 ± 0.6 $\mu\text{g}/\text{d}$ over the entire lifetime ($n = 47$, $t = 12.9$, $P < 0.001$, $R^2 = 0.789$, Fig. 2). No obvious pattern was detected in a residuals analysis. The daily maintenance in proteins was also linear, with a mean rate of 2.57 ± 0.18 $\mu\text{g}/\text{d}$ over the entire lifetime ($n = 37$, $t = 14.4$, $P < 0.001$, $R^2 = 0.856$, Fig. 2). Again, no obvious pattern was detected in a residuals analysis.

Experiments with hosts and without sugar

Females survived on average 14.25 ± 4.18 d with hosts ($n = 39$, Fig. 1), oviposited 39 ± 17.6 times ($n = 39$), and host-fed 21.7 ± 10.86 times ($n = 38$).

Ovipositions peaked 6 d after emergence and declined sharply thereafter (Fig. 3).

Reserves at death amounted to 24.67 ± 3.91 μg lipids ($n = 10$), 4.21 ± 2.87 μg sugars ($n = 10$), 11.66 ± 1.74 μg glycogen ($n = 10$), and 6.21 ± 3.03 μg proteins ($n = 10$). While reserves at death were slightly higher than without hosts, the two groups were statistically identical for proteins ($U = 92$, $P = 0.34$) and sugars ($U = 79.5$, $P = 0.61$). The amounts with hosts were, however, significantly higher for lipids ($U = 333$, $P = 0.001$) and glycogen ($U = 83$, $P = 0.013$).

Glycogen in eggs

The mean quantity of glycogen per egg was 0.46 ± 0.245 μg (mean over 15 batches of 10 eggs each).

Modeled nutrient budgets

Without hosts, all three nutrient classes as well as energy in the female's body are predicted to decline monotonically, carbohydrates levels dropping to lethal levels (i.e., levels observed at time of death) earliest (Fig. 4). The observed mean time of death occurred earlier (day 6) than the predicted exhaustion time of energy reserves (day 8), but it corresponds quite well to the predicted exhaustion of carbohydrates (day 6).

With hosts, predicted carbohydrate levels dropped again to observed exhaustion levels earliest (day 7), followed by lipids (day 8, Fig. 5). These two predicted times of exhaustion are much earlier than the observed time of death (day 14). Proteins are predicted to increase continuously, mainly due to the high intake through host-feeding, which is higher than the con-

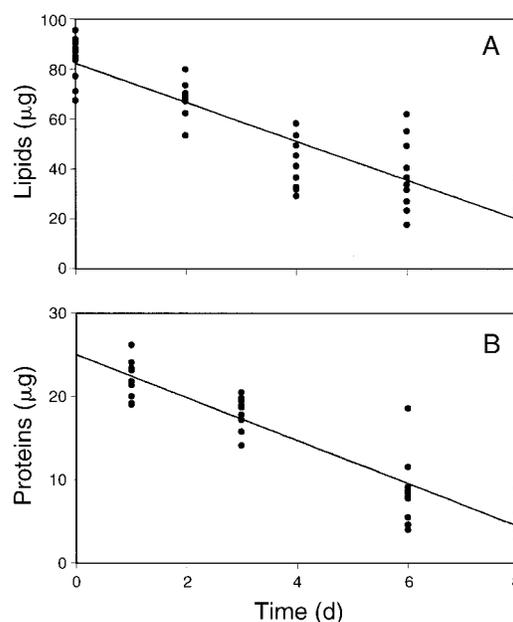


FIG. 2. Body reserves (in micrograms per female) of (A) lipids and (B) carbohydrates for female *Eupelmus vuilletti* without hosts and supplemental sugar over time.

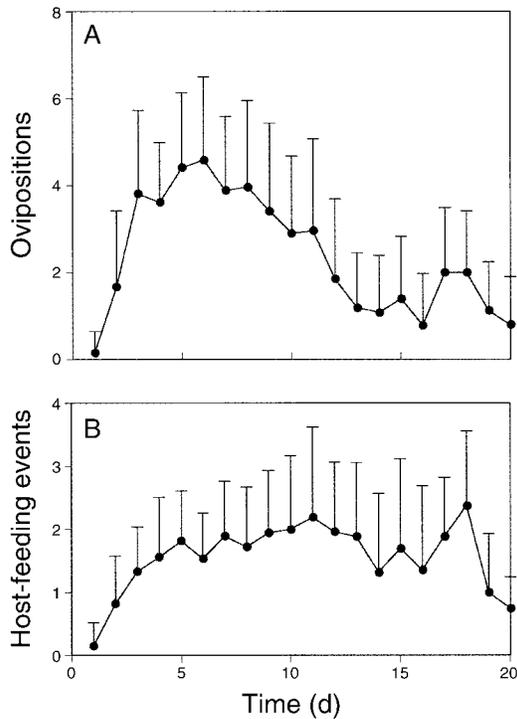


FIG. 3. Number of (A) daily ovipositions and (B) host-feeding events of *Eupelmus vuilletti* females on *Callosobruchus maculatus* hosts without supplemental sugar (means \pm SD).

sumption for maintenance. Thus the model is wrong in several ways. A sensitivity analysis of the nutrient conversion coefficient, spanning the range of values observed in the literature (McDonald et al. 2002), shows that changes of $\pm 30\%$ have large effects on the body's carbohydrate reserves, but still insufficient to explain the discrepancy (Fig. 6).

Experiments with hosts and with sugar

The purpose of this experiment was to test through manipulation the internal logic of our understanding of nutrient allocation. Females survived on average 18 ± 8.67 d with hosts and supplemental sugars ($n = 12$) (Fig. 1), oviposited 101 ± 54.65 times ($n = 12$), and host-fed 11.66 ± 6.9 times ($n = 12$) (Fig. 7).

DISCUSSION

Assumptions and validity of our models and approach

Even though our most complete model contains 20 measured parameters, it still contains several important assumptions. First, maintenance costs were not directly measured, but were only approximated using the disappearance of materials in the bodies of nonfeeding, nonovipositing females and are thus at the lower end of possible values. Females are obviously more active searching for hosts, ovipositing, feeding on them, and digesting. For instance, digestion is known in insects

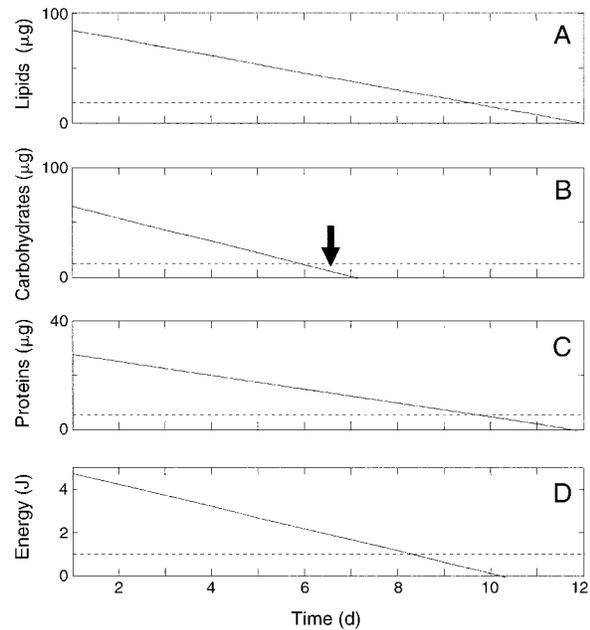


FIG. 4. Predicted mean levels of (A) lipids, (B) carbohydrates, (C) proteins, and (D) energy reserves in the body of parasitoid female *Eupelmus vuilletti* held without hosts. The observed mean amounts at death are indicated by a dashed horizontal line. The observed mean survival time is indicated by the arrow.

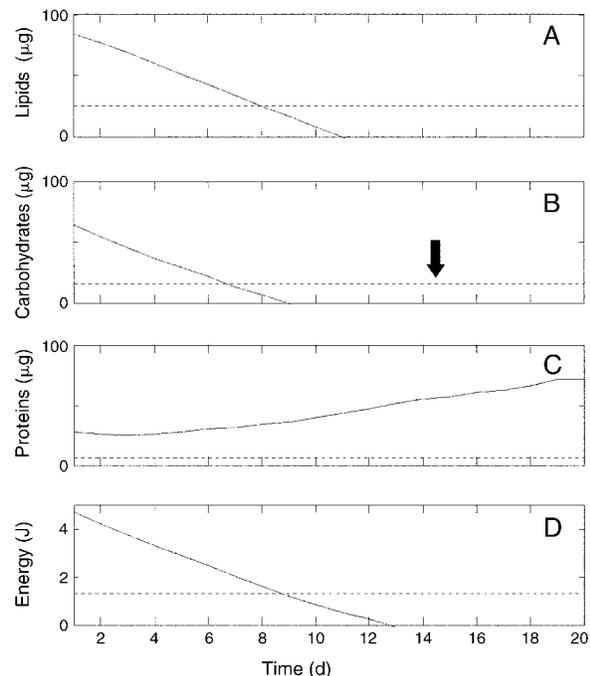


FIG. 5. Predicted mean levels of (A) lipids, (B) carbohydrates, (C) proteins, and (D) energy reserves in the body of parasitoid female *Eupelmus vuilletti* held with hosts. The observed mean amounts at death are indicated by a dashed horizontal line. The observed mean survival time is indicated by the arrow. The scale for proteins has been doubled, compared with the situation without hosts.

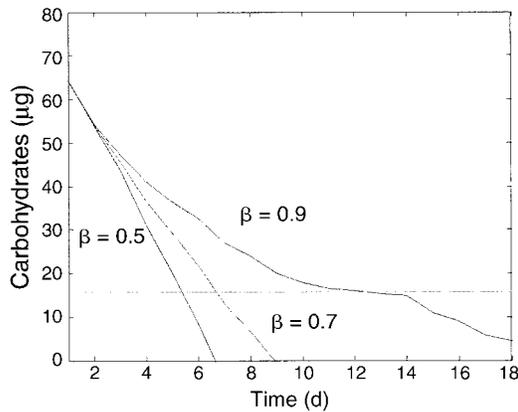


FIG. 6. Sensitivity analysis of the conversion factor on the carbohydrate budget for the full model.

to increase respiration rate markedly, up to 60% (Wightman 1981, Chaabane et al. 1996).

Second, we did not take into account the decline in the amount of nutrients invested in each egg (Giron and Casas 2003b), nor the delay between food intake and incorporation in eggs (Rivero and Casas 1999b). The first aspect is negligible in a quantitative budget running over the entire lifetime, and the second is of prime importance when studying individual time series. Furthermore, we assumed that the amount of food taken in each host-feeding event was constant, contrary to the observed increasing trend over the lifetime (Giron et al. 2005).

Multidimensional dynamics of nutrient reserves

Nutrient classes have varying functions and cannot automatically be considered solely as energetic building blocks. In the case that they may function in an interchangeable way, as for carbohydrates and proteins, our results show that they do so over the entire lifetime with varying degree. A differential use of nutrients over a lifetime of an insect is a fascinating area of research explored only recently. While insects of different orders switch from carbohydrate to lipids or proline during longer flights (see for example Scaraffia and Wells [2003]), it is only very recently that moths and flies have been shown to use both carbohydrates and lipids at the same time (O'Brien 1999, Marron et al. 2003). For moths, the relative proportion of the two fuels used is a function of the amount of nutrients available in reserves.

Among all nutrients, the allocation of lipids in parasitoids is of special interest. A female invests daily more in its eggs than what she obtains from food and must therefore tap continuously into its reserves. However, these are fixed at birth and will never increase due to the high demands from maintenance on the one hand and the inability to enter lipogenesis on the other (Giron and Casas 2003a). When lipids and perhaps sugars levels are getting low, proteins could cover

maintenance costs at the end of the life. This hypothesis can be supported by two observations. First, several insects living on protein-rich diets are able to convert proteins into lipids or carbohydrates and to use them as fuel (von Dungen and Briegel 2001). Locusts deaminate excess ingested proteins and the nitrogen is excreted via the feces, while excess carbohydrates are metabolized through increased metabolic rate and the carbon component eliminated as carbon dioxide (Zanotto et al. 1994, 1997). Only simultaneous measurements of CO_2 production and O_2 consumption could allow us to infer the type of fuels (Hoferer et al. 2000). Second, a massive rupture of excess proteins for energetic needs and for incorporation into other energetic metabolites, in particular sugars, has been reported during metamorphosis of a fruitfly (Nestel et al. 2003). An alternative use of proteins could be the construction of feeding tubes, most likely made of proteinaceous substances. However, it is unclear whether feeding tubes are produced by the parasitoid or from the host exudates and how much this could weigh in a quantitative budget (Quicke 1997).

Lifetime nutrient dynamics and life history traits

Without hosts to feed and oviposit on, carbohydrate reserves appear to determine survival. Survival time is doubled with hosts, mainly due to the large amounts of proteins and carbohydrates obtained through host-feeding. A heavy use of these proteins and carbohydrates for maintenance, concomitant with a decreased use of lipids, would enable females to invest more lipids in reproduction. Further availability of nonhost carbohydrate sources reinforces these mechanisms, leading to a further increase in survival time and strong increase in fecundity, as nutrient investment in single eggs are a small fraction of investment in survival. An exclusive use of lipids for reproduction would then lead

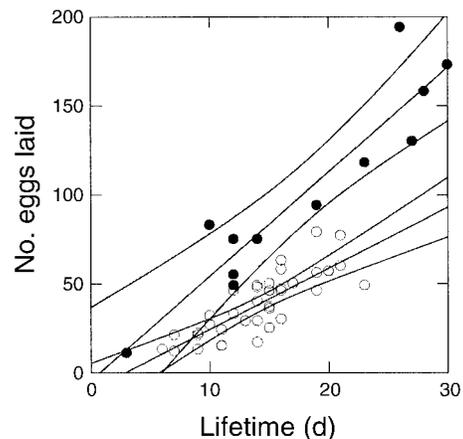


FIG. 7. Effect of supplemental sugar on survival and fecundity of female *Eupelmus vuilletti* (filled circles, with hosts and supplemental sugars; open circles, with hosts but without supplemental sugar). Linear regression line and 95% confidence intervals are shown.

to a maximal egg production, as lipids are set at birth and available in food only in very small quantities. The availability of hosts leads in fact to a shorter time of exhaustion of lipids, as parasitoids gain less per day through host-feeding than they lose through oviposition. If one therefore assumes that the available lipids are used exclusively for egg production, a female can produce at most 200 eggs. This is in good agreement with some of the maximal values observed. This maximal production was observed within some 30 d, leading to an estimated daily production of six eggs. This estimate matches nicely with the number of ovarioles in this species, an important parameter setting the maximal egg production in other parasitoids and insects (Carlson et al. 1998, Casas et al. 2000).

*Physiologically based behavioral ecology
and population dynamics of parasitoids*

A direct transfer of the insights gained from this study into the existing population dynamics models is not straightforward, because we developed a budget for a particular species and because other species, in particular the well-studied *Aphytis*, have poorly known nutritional requirements and sources. However, our work enables us to point to several promising avenues of general applicability. First, food obtained from host-feeding increases survival and fecundity. Thus, a good approximation for population modeling incorporates gains on both counts. In population modeling terms, it is likely irrelevant at this stage to distinguish between cases in which investment in reproduction comes from reserves or directly from ingested food. Second, the death rate ought to be modeled as dependent on reserves, an aspect shown in the introduction to determine whether the system is stable or unstable. Third, egg resorption for maintenance needs can be neglected for modeling purposes, and only detailed biochemical studies will provide firm evidence about the traffic of nutrients out of the eggs, a call also issued by Papaj (2000). Our study is indeed the first to put egg resorption in a quantitative context of nutrient fluxes. The generally accepted view of resorption of eggs is the reuse of the nutrients for maintenance at times of food unavailability (Bell and Bohm 1975, Papaj 2000). Egg load has been therefore invariably measured and used as a surrogate for reserves, but our analysis shows that eggs can hardly function that way, except in the case of extreme starvation, as a single egg contains less than 10% of the daily maintenance of each nutrient class. The construction of physiologically structured population models of increasing realism can now proceed through a further phase for host–parasitoid interactions.

Income and capital breeders: a static dichotomy

The results obtained in this study have important and general implications for life history theory. The dichotomy between capital and income breeders is a scheme that is increasingly used to understand the life

history strategies of birds (Meijer and Drent 1999, Klassen et al. 2001, Gauthier et al. 2003), reptiles (Bonnet et al. 1998), and butterflies (Boggs 1997a, b, Bergström and Wilkund 2002). Besides being used as a convenient way to differentiate between nutrient allocation and life history strategies, it has also been implemented in predator–prey game theory (Alonzo 2002).

The simultaneous quantitative recording of the flow of several nutrients over the entire lifetime of the animal enables us to assess the validity of this dichotomy. The capital reserves can be estimated as the difference between reserves at birth and death. A comparison of capital reserves and lifetime intake (summing up over host-feeding events) shows that capital reserves represent some 82% of the total amounts available for lipids, 48% for glycogen, 15% for proteins, and 6% for sugars. The amounts invested in eggs represent a small fraction of the total amounts available: 15% for lipids, 20% for glycogen, 8% for proteins, and 12% for sugars. If females were exclusive capital breeders, they would use for reproduction a proportion from the capital reserves ranging from 18% for lipids to 200% for sugars (53% and 42% for proteins and glycogen, respectively). The comparison of investment in reproduction for sugars and lipids shows therefore strikingly dissimilar strategies, from almost complete capital breeder for lipids to almost complete income breeder for sugars. This species is therefore bound to be simultaneously a capital breeder and income breeder, with intermediate strategies for proteins and glycogen. Thus, the usual dichotomy is only appropriate as long as one considers a single nutrient class or a generic “energy” measure, which we showed to be inadequate to predict time to death. Furthermore, previous studies using double radioactive tracers in eggs of a parasitoid species showed a gradual replacement of nutrients of larval origin by nutrients obtained during the adult phase (Rivero et al. 2001). This observation has been confirmed in several species of butterflies using stable isotopes (O’Brien et al. 2002, 2004). Thus, income breeders mix nutrients of differing dietary origins over time.

A multidimensional and dynamical approach to optimal nutrient allocation, forcefully advocated by McGinley and Charnov (1988) two decades ago, has been developed for nutrient acquisition largely by Simpson and Raubenheimer (Simpson and Raubenheimer 1993, Raubenheimer and Simpson 1999). Such an approach is long overdue for nutrient allocation and is by large preferable to the ongoing ranking of strategies along a one-dimensional continuum.

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