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Perrine Pelosse

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THÈSE

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Perrine PELOSSE

**Rôle des compromis évolutifs dans la spécialisation et la coexistence
d'espèces compétitrices. Développements théoriques et expérimentaux chez
les insectes parasitoïdes.**

Directeurs de thèse : DESOUHANT Emmanuel
BERNSTEIN Carlos

Jury :	ALLAINE Dominique	Président
	VAN ALPHEN Jacques	Rapporteur
	CASAS Jérôme	Rapporteur
	VAN DOOREN Tom	Examineur
	OLIVIERI Isabelle	Examineur

Laboratoire de Biométrie et Biologie Evolutive – CNRS UMR 5558
Université Claude Bernard – Lyon 1
43 Bd du 11 novembre 1918
69622 Villeurbanne Cedex

Avant-propos

Après quelques hésitations, j'ai pris la décision de rédiger mon manuscrit de thèse en anglais. Mon objectif principal a été de rendre ma thèse accessible à un public non francophone pour qu'il puisse être lu par le plus grand nombre. Ayant fait le choix d'insérer des manuscrits d'articles en anglais, j'ai aussi souhaité que le document soit uniforme.

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Section 1. Introduction

Chap I. General introduction

Life-history *trade-offs* have a central position in the study of evolution since they limit the range of combinations between traits. Without considering *trade-offs*, students of life-history evolution would predict a perpetual increase of organisms' fecundity. However, because reproduction incurs costs in term of longevity, mortality or growth, observed life-histories are expected to reflect optimal compromises resulting from competitive selective forces.

Observed life-history *trade-offs* can result from the allocation of a limited set of energy resources to competitive functions such as reproduction, maintenance or growth. Energy allocation is a complex process involving several metabolic nutrients and mediated by hormones acting on several metabolic pathways. Energy allocation and individual behaviours are intimately linked and their relationship will determine organisms' reproductive success. Energy allocation constrains the energy available to fuel reproduction and survival and in turn, reproductive or feeding behaviours incur energy losses and gains. Because *trade-offs* strongly affect individual strategies, they have a fundamental role in the structuring of populations and communities.

This PhD thesis considers several of these issues, the main questions being:

- How *trade-offs* in energy allocation are shaped by habitat characteristics?
- Do organisms have the possibility to adjust their allocation strategies to the conditions they encounter in their environment?
- How *trade-offs* affect the structure of populations and communities?

These questions are addressed from the point of views of *evolutionary* and *behavioural ecology*. These scientific disciplines explore organisms' strategies by assuming that they have been shaped by *natural selection* and provide an adaptive advantage to the organism carrying them.

Natural selection can be basically defined as the process by which an organism demonstrating the most advantageous strategy in a given habitat will survive better, get more offspring than its counterparts, and therefore better spread its genes over generations. Conversely, an organism showing ‘maladaptive’ strategies in a given habitat will die or get few offspring and its genes are expected to be lost among generations. The approach which considers that *natural selection* is in most part responsible of observed characters, sometimes referred as *adaptationism*, has instigated virulent criticisms and passionate debates in the late 1970s (e.g. Gould & Lewontin 1979, Lewontin 1979). The main criticism is that *adaptationism* seeks a specific purpose or utility for every observed trait or behaviour. This is probably true that the *adaptationist* view has been exaggeratedly used to account for every observed strategy. However, as Darwin already underlined in the *Origin of Species*: ‘*I am convinced that natural selection has been the main, but not the exclusive means of modification*’ (Darwin 1872). Traits do not automatically have an ‘adaptive value’. They can be, for instance, by-products of a trait that was functional in an ancestor. *Natural selection* is only partly responsible of the diversity observed among living organisms. Genetic drift and various sources of constraints are also responsible of observed strategies.

Evolutionary and *behavioural ecology* consider *natural selection* as a major evolutionary force, and can therefore produce testable hypotheses on the strategies that should be adopted in a given set of abiotic or biotic parameters. Obviously, the ‘optimal strategy’ is not attainable in most of the cases, because of changing environments or various constraints. But the differences recorded between the expected and the observed strategies, as in every scientific field, allow assessing new factors that should be taken into account.

In *evolutionary ecology*, we need a common currency to compare strategies, that is, to know which strategy is the most advantageous in a given ecological context. The concept of *fitness* or *adaptive value* has been proposed to achieve this aim. In the glossary of his review on life-history tactics, Stearns (1976) defined *fitness* as ‘*Something everyone understands but no one can define precisely*’. An organism’s *fitness* can be viewed as the number of gene copies successfully transferred to the next generation, *i.e.* the number of surviving offspring. An individual’s *fitness* is necessarily relative to the *fitness* of the other individuals constituting the population. *Fitness* cannot be *a priori* defined for a genome, because the same genome may show different

effectiveness in different environments, owing to the *phenotypic plasticity*. *Fitness* is therefore more applicable for a *phenotype* in a given environment.

To seek the role of *natural selection* in shaping physiological, life-history and behavioural traits, we adopted an experimental as well as a theoretical approach. The experiments carried out in this PhD thesis are also relevant to the field of *eco-physiology* since they explore, for the most part, the relationships existing between life-history *trade-offs*, processes of nutrient allocation and behaviours. Nevertheless, the metabolic pathways of energy allocation have not been explored thoroughly. The experiments used a single species as a model system. Another approach would have consisted in comparing the ecological features of different species and exploring the evolutionary relevance of common characteristics. Even if the comparative approach has proven useful to explain broad adaptations (*e.g.* Hansen 1997), we preferred focusing on small variations occurring between individuals or population to understand how individuals finely adapt to varying circumstances (Stearns 1976). On the other hand, the theoretical modelling approach we adopted in this PhD thesis, rather than focusing on a single species, allows us exploring the factors responsible of a given strategy in a group of species sharing common features.

During this PhD thesis I adopted a phenotypic-based approach, that is, I did not consider the genetic basis of the strategies I observed. In *behavioural ecology*, we assume that the traits observed at the phenotypic level have a genetic basis and are heritable for the most part, which allows them being shaped by *natural selection*.

In this thesis, we focus on insect parasitoids. Insect parasitoids are first characterised by the fact that females lay their eggs in, or on, other insects. Since parasitoid females have to search and attack hosts in an efficient way to achieve a maximal reproductive success, they provide ideal models to test evolutionary hypotheses (Godfray & Shimada 1999). This feature provides a direct and interesting measure of *fitness*: the number of hosts successfully attacked. Parasitoids are then characterised by their original holometabolous life-history. While juvenile parasitoids are parasites, adult parasitoids are free-ranging. The different life-stages may consequently exploit highly different habitats and face different kinds of constraints. Finally, because parasitoids directly cause the death of their hosts, they provide fascinating models to test the influence of

individual behaviours on the dynamics of populations. This latter feature also makes parasitoids helpful agents for biological pest control. Insect parasitoids' reproductive success is indeed often investigated in a biological control perspective.

In the first introductory section of this manuscript, I will give an overview of the literature on *trade-offs* in energy allocation. I will particularly address the question of how *trade-offs* have been considered in studies of adaptation and depict the current state of knowledge on the mechanisms underlying them. We will see that energy allocation can be seen as a static allocation of a single energy pool to different competing functions, but that recent advances in the understanding of energy allocation suggest that energy is compartmentalised in different energy sources and that its allocation is profoundly dynamic during an organism's lifetime. I will also explore the relationships existing between energy allocation and foraging behaviours, and show how *trade-offs* are expressed at the level of behaviour. In a last part, we will see how individual *trade-offs* may affect the structure of populations and communities. Because insect parasitoids bear specific interesting features for the study of energy allocation, and that their knowledge will be useful to the understanding of this work, I will focus on these models at different points of the literature analysis. Nevertheless, for a generalisation purpose, I will also use other model systems to accurately illustrate my words.

In the second section of the manuscript, I will describe the results obtained in my PhD thesis.

The first chapter will be devoted to the study of the relationships between energy allocation strategies, foraging behaviours and environmental characteristics at the intraspecific level. We will see how energy allocation strategies are adjusted in response to the environmental quality and which nutrients limit parasitoid reproductive success. In particular, the role of host availability, *i.e.* expected number of reproductive opportunities, and the role of food presence will be explored.

In the second chapter, I will explore the role of environmental characteristics in shaping energy allocation strategies, and see that different selective pressures most likely select for different strategies that could help two competing species to coexist. In the first part of this chapter, we will focus on the energy allocation strategies adopted

during the juvenile stage, and in the second part, I will test whether the energy allocation strategies adopted during larval stage are maintained over adult stage despite feeding activity.

In a third chapter, I will present a study examining the evolution of the *trade-off* between current and future reproduction and its role in the structuring of communities. I will focus on the *trade-off* between host and food foraging in parasitoids, since host exploitation allows gaining direct *fitness* rewards and food exploitation future *fitness* rewards. By adopting a theoretical modelling approach, I will investigate the evolution of the *trade-off* between host and food foraging and explore its potential role in the coexistence of competing parasitoids.

Lastly, in the third section of the manuscript I will discuss the implications of this work and the perspectives it opens.

Chap II. Literature analysis

1. Introduction

1.1. Life-history *trade-offs*

‘There is of course only one life history which ultimately maximises fitness, irrespective of the environment. This is the life history of an immortal organism which begins to reproduce immediately after birth and produces prodigious numbers of progeny at the shortest possible intervals thereafter.’ (Law *et al.* 1977). Obviously, this sentence does not refer to the real world but to a ‘Darwinian demon’ (*sensu* Williams 1966a). The real world is made of constraints that do not allow organisms maximising all traits associated with an increasing reproductive success.

The term *trade-off* is used in evolutionary ecology to refer to an increase in *fitness* associated with a change in one trait, which is associated with a decrease in *fitness* due to a change in another trait. *Trade-off* is generally invariably used to describe the functional relationship linking two traits and the statistical negative correlation recorded between them. Even if the latter description supposes that no interacting factor affects the observed relationship, it has been extensively used in the literature and has proven useful in demonstrating the existence of *trade-offs* (Roff & Fairbairn 2007).

Trade-offs may result from genetic, phylogenetic, biomechanical, physiological or ecological constraints. Some authors consider that the existence of *trade-offs* should necessarily be investigated at the level of genetic negative relationships between traits to determine if a response to selection will take place (*e.g.* Reznick 1985, Bell & Koufopanou 1986, Roff 1992). Negative relationships between traits can however be analysed and understood by considering other levels of analysis. Increasing brood size may for instance have the effect of increasing food provisioning to the brood, and expose the parents to predators, which would decrease the survival probability of the parents.

The term ‘life-history tactics’ has been first introduced by Stephen C. Stearns in 1976 to refer to ‘a set of coadapted traits designed, by natural selection, to solve

particular ecological problems' (Stearns 1976). The theory of life-history evolution has been developed by Stephen C. Stearns and Derek A. Roff (Stearns 1976, 1980, Roff 1992, Stearns 1992). This theory aims at exploring the diversity of life by seeking the role of *natural selection* in shaping organisms' survival- and/or reproduction-related features. The most famous life-history traits include: the age at maturity, the number and size of offspring, the reproductive effort and the interbrood interval. Life-history *trade-offs* will be used to refer to negative relationships between life-history traits. They have a fundamental position in the theory of life-history evolution because they constrain the direction and rate of evolution, and therefore bound the range of possible life-history combinations. Van Noordwijk and de Jong (1986) indeed defined life-history theory as: '[...] *an elaborate answer to the simple question of why having more offspring is not always selected for*'. Because life-history *trade-offs* in most of the cases involve costs associated with reproduction, some authors used the term *costs of reproduction* to refer to *trade-offs* involving reproduction (Williams 1966a, Law 1979, Bell 1980, Reznick 1985, Bell & Koufopanou 1986). The most studied *trade-offs* are indeed those between reproduction and survival, reproduction and growth, current and future reproduction, and between size and number of offspring (Stearns 1989).

Trade-offs are often described as the results of the allocation of limited resources to different competing traits. To maximise their number of offspring, organisms have to allocate their energy in an efficient way to several components of their reproductive success. The two major components of reproductive success, survival and reproduction, can then be separated into several elements. Reproductive costs may involve mate searching, mating, reproductive site searching, fighting, egg manufacturing, baby care, etc. Survival costs mainly involve maintenance costs, energy storage, fight against parasites, but also foraging activities. Other activities indirectly contributing to reproductive success, such as locomotion, dispersion, quiescence, are also energy-demanding.

Life-history *trade-offs*, because they have a central role in life-history evolution, have been the focuses of many empirical and theoretical investigations among ecologists. We will see here that there exist several approaches and different levels of analysis into the study of *trade-offs*.

1.2. Different levels of investigation of life-history *trade-offs*

Negative correlations between traits can be investigated at the level of an organism, the question therefore lying in the precise mechanisms that prevent maximising all *fitness*-related traits. Negative correlations can be studied at the intraspecific level as well, through the measurement of traits across different individuals. Here, negative relationships might come from the fact that some individuals invest for instance more in their reproduction at the expense of their survival, and that some others adopt the opposite strategy. *Trade-offs* are also often studied in comparative approaches at the interspecific level. In that case, mean trait values are generally compared among different species and negative relationships between traits sought among species. The latter types of *trade-offs* can be referred as ‘*inter-specific trade-offs*’ (Kneitel & Chase 2004) or ‘*demographic trade-offs*’ (Vincent *et al.* 1996). We will see in the section ‘*Role of trade-offs in population dynamics and community structuring*’ (p72) that a large literature exist on the role of such *trade-offs* in species coexistence. Because the functional causes linking traits are not generally considered here, and because genetically-fixed traits may interfere with the observed negative relationships, some researchers argue that the term *trade-off* should not be used when comparing species. In this review of the literature, I will focus on the investigation of life-history *trade-offs* at the individual level because they rely on quantifiable mechanisms such as the allocation of a limited pool of energy toward competing needs.

According to Stearns (1989), three different approaches have been used to analyse the costs of reproduction: a genetic approach seeking antagonistic pleiotropy (Williams 1957), a phenotypic approach seeking negative relationships between traits (Williams 1966a), and a physiological approach (Calow 1979).

From the early 1970’s until now, a huge number of researchers made attempts to measure *trade-offs* between life-history traits in various organisms. Advantages, drawbacks and pitfalls of the methods utilised have been extensively reviewed by Reznick (1985), Bell and Koufopanou (1986), Pease and Bull (1988), Stearns (1989), Partridge (1992) and Reznick (1992). At the phenotypic level, the most common way of investigation consists in seeking negative relationships among observations of populations’ phenotypic variability (*e.g.* Law 1979, Clutton-Brock 1982). To measure the costs of reproduction, some authors also manipulate reproductive investment and

record costs or benefits induced to other traits (*e.g.* Partridge & Farquhar 1981, Stevenson & Wilson 2001). At the genetic level, *trade-offs* are revealed through the measurement of genetic correlations among traits, either with quantitative genetics methods (*e.g.* Rose & Charlesworth 1981a), or selection experiments (*e.g.* Rose & Charlesworth 1981b, Fellowes *et al.* 1998). Nevertheless, in a relatively large number of studies, authors fail to reveal *trade-offs*. The main reasons invoked are (i) the variability in condition among individuals that has the property to mask negative relationships between traits (stressed by van Noordwijk and de Jong (1986), see below), (ii) non-limiting favourable experimental conditions which allow allocating large energy quantities to every traits (stressed by Bell and Koufopanou (1986)), and (iii) the incapacity of some organisms to re-allocate energy that prevents measuring costs in experiments manipulating reproductive investment (Reznick 1983).

Throughout this literature analysis, I wished to give a synthetic overview of all the domains and questions I handled during my PhD thesis. I will especially focus on the physiological basis of life-history *trade-offs*. My aim here is to explain the main physiological mechanisms underlying *trade-offs*, show how *trade-offs* in energy allocation have been introduced in the study of animal adaptation and show to what extent they impact organisms' strategies, population dynamics and community structuring. I will describe first the mechanisms responsible of observed *trade-offs*, and explain how *trade-offs* in the allocation of limited resources have been taken into account into theoretical and empirical studies of animal adaptation. Here, rather than giving an exhaustive picture of studies on life-history *trade-offs*, I chose to depict a gradual consideration of complexity into the processes of energy allocation. Then, attention will be given to the close relationships taking place between the processes of energy allocation and foraging activities. In a last section, I will show that *trade-offs* have fundamental roles in the structuring of populations and communities.

2. Energy allocation toward contradictory needs: Proximal causes and mechanisms of observed *trade-offs*

In this section, we will see first that a large literature developed in the 60's, which aimed at explaining organisms' life-histories, considered the existence of *trade-offs* to predict the optimal investment toward the different components of reproductive success. These works particularly considered that *trade-offs* could be linked to underlying physiological mechanisms such as the allocation of limited resources toward maintenance and reproduction. In these studies, the process of resource allocation toward competing needs has often been described as a common pool of energy that has to be divided between competing traits. We will then see that gradual advances in physiological knowledge put forward that resources are actually compartmentalised in distinct energetic pools that differentially contribute to the different components of *fitness*, and that the processes of energy allocation are dynamic throughout an organism's life.

2.1. Mechanical constraints underlying reproductive effort

The first works on *natural selection* carried out by Fisher, Haldane and Wright in the 30's already appealed for the consideration of underlying mechanisms such as the genetic architecture or the allocation of limited resources to understand the role of *natural selection* in shaping organisms' biological features. Fisher (1930) claimed that: *'It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction'*. The first consideration of the allocation of a limited set of resources came with Lack's works on optimal clutch size in birds (Lack 1954). Lack argued for instance that females have a limited food supply that has to be allocated to the provision of energy to both the quality and the quantity of offspring. Williams (1966b) later refined Lack's argument by explicitly dividing an organism's reproductive value into its reproductive effort, *i.e.* the resources allocated to the current reproductive event, and a residual reproductive value, *i.e.* the resources saved for future reproductive events.

The consideration of constraints in term of life-history *trade-offs* definitely arose with the theoretical models of Cody (1966), Williams (1966a), Gadgil and Bossert (1970), Charnov and Krebs (1973) and Schaffer (1974b). Charnov and Krebs (1973) for instance proposed a graphical analysis to predict the optimal clutch size in birds, in which offspring survival is a decreasing function and parental mortality an increasing function of clutch size. By introducing these two constraints, they predicted an inferior clutch size than studies that did not take them into account (*e.g.* Lack 1954), which was more in accordance to those recorded in the field.

In this section, I chose to focus mainly on theoretical models considering life-history *trade-offs*, because there already exist a large number of works reviewing empirical investigations of *trade-offs* (*e.g.* Bell & Koufopanou 1986, Stearns 1989, Roff 1992, Stearns 1992, Rivero & Casas 1999a, Zera & Harshman 2001, Roff & Fairbairn 2007), and to my knowledge no review on theoretical approaches to the study of life-history *trade-offs* (but see the introduction of Perrin and Sibly (1993)). I will mainly adopt a historical approach and try to give a picture of the large number of theoretical optimisation models developed in the 60-70's that considered the allocation of limited resources to competing traits.

2.1.1. Levins' fitness set and Cody's '*Principle of Allocation*'

To my sense, the most critical works that have initiated a large field of theoretical investigations of life-history strategies are those of Levins, who introduced a popular graphical analysis for finding the optimal life-history strategy based on the shape of the negative relationships linking traits (Levins 1962). The less known work of Cody also provided a clear setting linking optimisation theory with the principle of allocation of limited resources toward competing life-history traits (Cody 1966).

Richard Levins' pioneering mathematical study of adaptation provided graphical and analytical tools to explore the evolution of life-history traits (Levins 1962, 1968). Levins' study aimed at investigating the optimal production, by an organism or a population¹, of two different phenotypes in a variable environment, the phenotypes differing in the environmental conditions in which they successfully reproduce. Instead of drawing two *fitness curves* or *adaptive landscapes* (Wright 1931) for the two

¹ The theory of group selection was still widespread at that time.

phenotypes, *i.e.* the expected value of a *fitness* component along an environmental variable for each phenotype (Figure 1 A and B), Levins' proposed to represent simultaneously the two *adaptive landscapes* in a *fitness set*. The *fitness set* whose axes are directly composed of the two *fitness* components in the environmental conditions 1 and 2, W1 and W2, depicts the concomitant increases or decreases of the values of the two *fitness* components along the environmental variable (Figure 1 C and D).

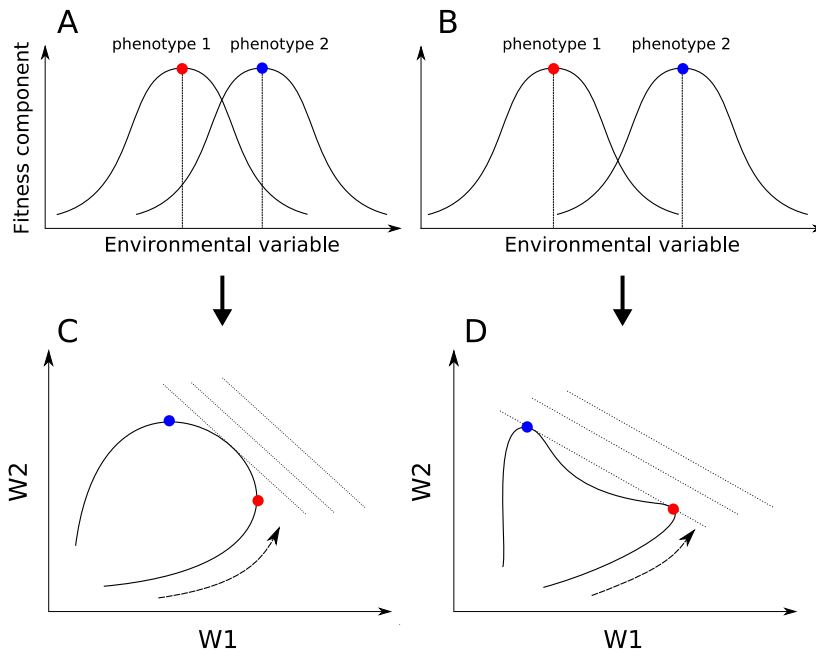


Figure 1. Levins's graphical approach of adaptation. A and B: *Adaptive landscapes* for an organism showing two phenotypes. The value of the *fitness* component (*e.g.* fecundity) is represented as a function of an environmental variable (*e.g.* temperature). The phenotype 1 will have a maximum fecundity (red dot) for low and the phenotype 2 (blue dot) for high temperatures. C and D: *Fitness sets* and *adaptive functions*. The curves, the *fitness sets*, represent the combined increase or decrease of the *fitness* components W1 and W2 of the two phenotypes, when we follow the environmental variable (represented by the arrow). The straight dotted lines, the *adaptive functions*, represent all points in the trait space that yield equal *fitness*. The dots give the *fitness* rewards of the production of a single phenotype. The optimal strategies lie at the tangential points of the *adaptive functions* and the *fitness set*. If the two phenotypes have relatively close adaptive peaks (A), the resulting *fitness set* is *convex* and the optimal strategy is to produce a mixture of phenotypes 1 and 2 (C). If the two phenotypes' adaptive peaks are apart one from another (B), the resulting *fitness set* is *concave* and the optimal strategy is to produce only one of the two phenotypes (D) (reproduced from Levins (1968)).

The *fitness set* can be seen as the boundary of all feasible combinations of the two phenotypes' production, which resulted from the negative functional relationship linking them (W1 can only be increased at the expense of W2). To find the optimal strategy, Levins proposed to represent on the *fitness set* graph the *adaptive functions*,

i.e. the curves combining all points providing equal *fitness* according to W1 and W2. *Fitness* generally increases as both W1 and W2 increase, but the strategies lying outside the *fitness set* cannot be realised. The optimal strategies therefore lie at the tangential points of the *adaptive function* and the *fitness set*. Depending on if the peaks of the *adaptive landscapes* for the two phenotypes are either relatively close or distant one from another, the resulting *fitness sets* will be *convex* or *concave*, respectively. For a *convex fitness set*, when W1 (*e.g.* the fecundity of phenotype 1) starts declining a little bit, W2 already increases a lot and has almost reached its maximum. On the other hand, for a *concave fitness set*, W1 is already rapidly declining before W2 starts slightly increasing. The curvature of the upper-right-hand boundary of the *fitness set* is of utmost importance for the evolutionary outcome of the production of the two phenotypes. Whereas for a *convex fitness set*, the maximum *fitness* will be gained for an intermediary production of the two phenotypes, *i.e.* for a *mixed phenotypic strategy* in Levins' work, for a *concave fitness set*, the optimal strategy will be to produce only one of the two phenotypes (Levins 1962, 1968). Levins' approach is not restricted to variable environments. W1 and W2 may for instance represent two substitutable food resources for which individuals will specialise or generalise according to the shape of the *fitness set* linking them.

As demonstrated by Levins (1962), the shape of the functional relationship linking traits involved in a *trade-off* crucially impacts the evolutionary outcomes. This approach has been applied or extended to the theoretical study of various life-history strategies (*e.g.* Cody 1966, Gadgil & Bossert 1970, Schaffer 1974b, a, Bell 1980). We will see in the section '*Role of trade-offs in population dynamics and community structuring*' (p72) that this approach has also proven useful in the study of the coexistence of competing species.

In Cody's approach (see below), W1 and W2 refer to two competing life-history traits of an organism. Interestingly, even if Cody did not cite Levins, his work introduced underlying mechanisms into Levins' graphical approach (Cody 1966).

The first consideration of the allocation of limited resources to competing ecological functions came with the work of Cody (1966), who introduced the concept of a '*Principle of Allocation*'. In his paper, Cody criticised the works of Lack that predicted the variations occurring in bird clutch size with the limited property of food supply only

(Lack 1954). He proposed a more integrative approach to understand clutch size variation: his graphical analysis, an extension of Levins' *fitness set*, shows a 3-dimensional space whose axes represent the advantage obtained from energy invested in competing traits such as clutch size (X1), predator avoidance (X2) and competition (X3) (Figure 2). A surface containing points equidistant to the origin represents the limit of all possible phenotypes combining X1, X2 and X3. The strategy which will maximise the number of offspring for given conditions will be the one where the grey surface will touch tangentially the *adaptive function*, *i.e.* the function linking all points of equal *fitness* (Levins 1962).

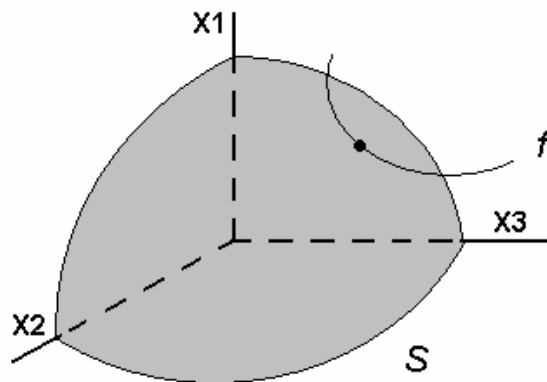


Figure 2. Cody's 'Principle of Allocation'. X1, X2 and X3 represent three components of reproductive success: clutch size, predator avoidance and competition for resources. The grey surface *S* where every point is equidistant to the origin and the volume under the surface represent all possible phenotypes. The curve *f* is the *adaptive function*, *i.e.* the function providing equal *fitness* for a given set of environmental conditions. The optimal strategy lies at the tangential point between *S* and *f*, and will be given by the relative positions of *S* and *f*. The intercepts of the optimal strategy on the axes represent the advantage gained by the individual (reproduced from Cody (1966)).

Levins and Cody's works initiated a large body of theoretical works considering either costs of reproduction or the allocation of limited resources.

2.1.2. Models considering costs of reproduction

One of the first influential theoretical study of life-history adaptation has been the one of Cole (1954), who explored the *fitness* consequences of changing from a semelparous life-history (*i.e.* breeding only once) to an iteroparous one (*i.e.* breeding repeatedly). His conclusion was that the *fitness* advantage of breeding several times rather than once is gaining one individual offspring, and therefore questioned the evolution of iteroparity

(Cole 1954). Cole's eccentric result motivated a large number of theoretical works that criticised the fact that his model did not incorporate any cost of reproduction in term of survival (Gadgil & Bossert 1970, Charnov & Schaffer 1973, Schaffer 1974b, Bell 1976, 1980).

To improve Cole's model and explain how iteroparity evolved, Charnov and Schaffer (1973), followed by Bell (1976, 1980), introduced costs of reproduction in term of adult and/or offspring juvenile survival. They put forward that iteroparity has a higher probability to be selected for, for instance if the offspring juvenile survival is relatively low compared to adult survival.

As pointed out by Schaffer (1974b) and Bell (1980), these previous models neglected age structure: all the life-history variables (*e.g.* age-specific rates of survival, fecundity) are independent one from another and constant through time. In others words, these models assumed that reproduction at time t has no effect on survival or fecundity at time $t+1$. Age-structured models have indeed been developed to explore the evolution of iteroparity as well as the optimal distribution of reproductive effort along lifetime (Gadgil & Bossert 1970, Schaffer 1974b, Hirshfield & Tinkle 1975, Charlesworth & Leon 1976, Schaffer & Rosenzweig 1977, Caswell 1982). Williams' idea that reproductive effort should increase with age has also partly motivated these investigations (Williams 1966a). Gadgil and Bossert (1970) were the first to design an age-structured model in which reproducing at time t affects survival at time $t+1$, to model the optimal distribution of the reproductive effort along lifetime in an iteroparous organism. Gadgil and Bossert (1970) particularly applied Cody's idea of optimal resource allocation (Cody 1966), by considering that energy can be differentially allocated to maintenance, growth and reproduction. These authors were the firsts to link reproductive effort to the resource allocation principle: '[The reproductive effort] *may be visualized as the fraction of the total amount of resources of time and energy available to the individual at that age that is devoted to reproduction*'. They translated this idea by introducing *trade-offs* between reproductive effort and survival or growth rate in their model. The probability of survival from birth to age x , l_x , is for instance given by:

$$l_x = \prod_0^{x-1} \alpha_i \cdot f_1(\theta_i) \cdot g_1(\psi_i) \cdot \eta_i, \quad (\text{Eq. 1})$$

where α_i is the survival probability from age i to $i+1$, θ_i the reproductive effort of an individual at age i , ψ_i the fraction of energy available to an individual, and η_i the probability of escaping from predation. The function f_i , which relates the survival rate to the reproductive effort θ_i , is assumed to be a monotonically decreasing function of θ_i , therefore reflecting the following *trade-off*: the more energy is invested in reproduction, the less energy is remaining for survival. On the other hand, g_i relates the survival rate to the energy available ψ_i and is assumed to be a monotonically increasing function of ψ_i . A decreasing function is also assumed in the model, between growth rate and reproductive effort, and increasing functions between the amount of energy available, the growth rate and the number of offspring produced (Gadgil & Bossert 1970). This pioneering study led to the unexpected result that the reproductive effort should continuously increase with age, which has already been suggested by Williams (1966a). A similar model has been subsequently developed for the same purpose by Schaffer (1974b), who criticised their study for the reason that it relied on numerical simulations only, and therefore developed an analytical and graphical analysis of a relatively similar model. Schaffer also discussed Gadgil & Bossert's unrealistic assumption that both fecundity and survival probability are constant whatever the age class, and hypothesised that the reproductive effort should decrease with age in some species (Schaffer 1974b).

Bell (1980) criticised the use of the reproductive effort to seek the optimal life-history for the reason that it is defined in units such as seconds or calories which are, for him, irrelevant to the evolution of life-histories, unless it is transformed in units of *fitness*, and that the measurement of the reproductive effort is technically difficult. He proposed to base the analysis of life-histories on the concept of reproductive cost only, which he defined as: '*the deleterious effect of present reproduction on future survival or fecundity or both*' (Bell 1980). Bell's study aimed, in part, at providing a general framework for models investigating the evolution of iteroparity, assuming no age structure but costs of reproduction (Figure 3).

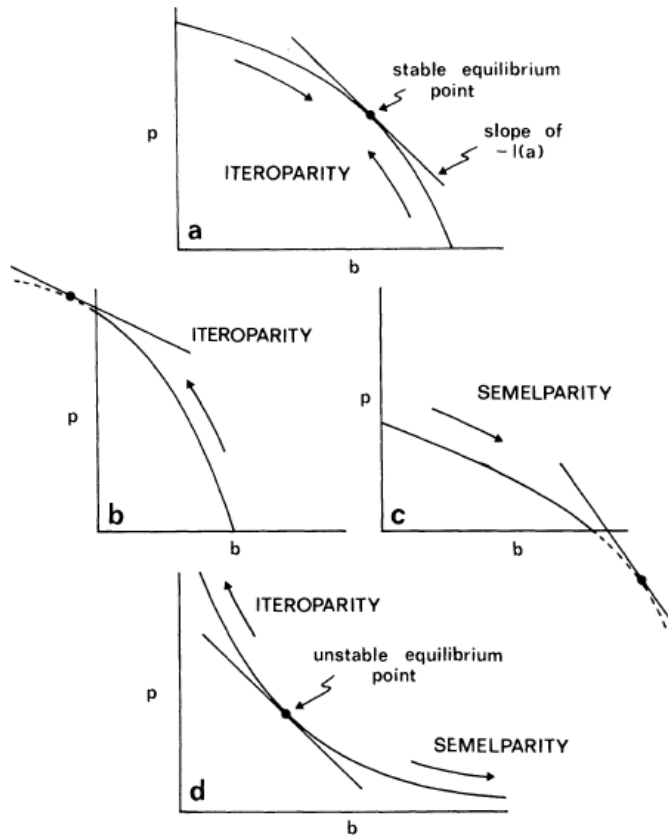


Figure 3. Bell's graphical analysis of the evolution of semel- and iteroparity. The arrows give the direction of evolution. The curves represent the functional relationship between fecundity b and adult survival p . For convex curves (a,b,c) either iteroparity or semelparity will be favoured, depending on the position of the stable equilibrium point. For concave curves (d) an unstable equilibrium point arises and either iteroparity or semelparity will evolve (from Bell (1980)).

2.1.3. Models incorporating the allocation of limited resources

Cody's 'Principle of Allocation' (Cody 1966) has stimulated a large number of theoretical studies considering the allocation of limited resources toward competing life-history traits, whose most influential ones are those of van Noordwijk and de Jong (van Noordwijk & de Jong 1986, de Jong & van Noordwijk 1992). Van Noordwijk and de Jong (1986) objective was to explain why so many positive correlations between traits that should theoretically trade-off, are recorded in field observations. This is the case, for instance, of Smith (1981), which recorded a positive correlation in the song sparrow *Melospiza melodia* between the number of fledglings produced per year and female survival the next breeding season. In van Noordwijk & de Jong's model, the total amount of energy available to an individual, A , has to be divided between two traits: R and S , which could correspond to reproduction and survival. We have therefore:

$$A = R + S . \quad (\text{Eq. 2})$$

The sign of the correlation between the two traits is given by the covariance between R and S which equals to:

$$\text{cov}(R, S) = \text{cov}(R, A - R) = \text{cov}(R, A) - \text{cov}(R, R) = \text{cov}(R, A) - \text{var}(R). \quad (\text{Eq. 3})$$

Since $\text{var}(R)$ is positive, $\text{cov}(R, S)$ will be negative when:

$$\text{cov}(R, A) < 0, \text{ or } \text{cov}(R, A) < \text{var}(R). \quad (\text{Eq. 4})$$

Yet, as the amount of energy available to an organism A increases, the amount of energy invested in reproduction R is expected to increase as well. $\text{Cov}(R, A)$ has therefore a high probability to be positive, which means that $\text{cov}(R, S)$, the sign of the observed relationship between the two traits, will also be positive. In their paper, van Noordwijk & de Jong also demonstrated that $\text{cov}(R, S)$ can be solely expressed as a function of the mean and variance of the acquisition and allocation of resources:

$$\text{cov}(R, S) = \bar{B}(1 - \bar{B})\sigma_a^2 - \bar{A}^2\sigma_b^2 - \sigma_a^2\sigma_b^2, \quad (\text{Eq. 5})$$

where \bar{B} and σ_b^2 are the average fraction of energy allocated to R and its variance, and \bar{A} and σ_a^2 the average amount of resources available to an individual and its variance. By taking $\text{cov}(R, S) = 0$ from equation 5 and plotting the variance in energy allocation σ_b^2 as a function of the variance in energy acquisition σ_a^2 , we can separate the areas where $\text{cov}(R, S)$ is positive and negative (Figure 4, original idea of Rigby and Moret (2000)). On this graph, it appears obvious that cases in which the observed relationship between the two traits is positive are most common, especially when the variance in energy allocation σ_b^2 is relatively low compared to the variance in energy acquisition σ_a^2 .

This model has proven useful to explain the occurrence of positive phenotypic correlations between traits. Glazier (2000), in a literature survey on correlations between storage and reproductive investment recorded in various taxa, put forward that laboratory studies, because they limit the range of variation in energy acquisition (σ_a^2) compared to field studies, most often reveal negative correlations. Individual differences in foraging ability or body condition should therefore be taken into account when seeking negative relationships between traits.

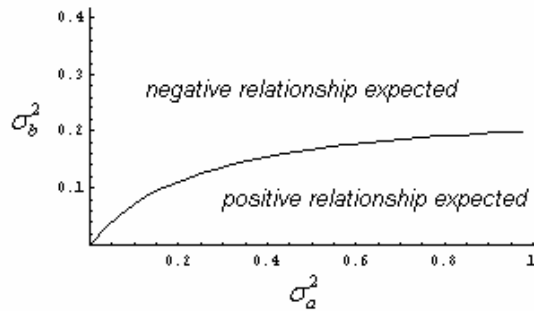


Figure 4. Graphical representation of the model of van Noordwijk and de Jong (1986). The x-axis gives the variance in energy acquisition and the y-axis the variance in energy allocation. Below the curve, the relationship observed between the two traits R and S (Eq. 2) that should theoretically trade-off is positive and is negative above. $\bar{B} = \bar{A} = 0.5$ (from Rigby and Moret (2000)).

Van Noordwijk and de Jong developed another model that became very popular: the ‘*Y-model*’ (de Jong & van Noordwijk 1992). This model considers that energy acquisition and allocation are each controlled by a single locus, and introduces covariances between traits at the levels of both phenotype and genotype. I will not go further into the rationale of the model, but only emphasise that this model unified the physiological view of life-history *trade-offs* and some concepts of quantitative genetics. The most decisive impact of this model lies in the idea of a single pool of resources that have to be allocated to two competing traits (Figure 5). The ‘*Y-model*’ has been shown to fit well for instance in the parasitoid wasp *Asobara tabida*, as in this species fat appears to be differentially allocated to survival and reproduction (Ellers & van Alphen 1997).

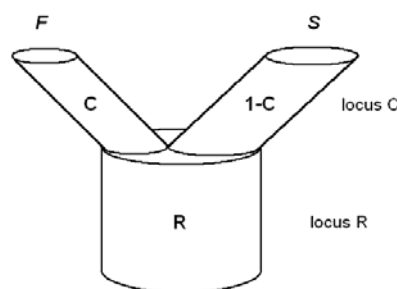


Figure 5. The ‘*Y-model*’, as imagined by de Jong and van Noordwijk in 1992. The fraction R of resources available, whose quantity is determined by the locus R , is divided in a fraction C toward the life-history trait F and $(1-C)$ toward the trait S . The strategy of energy allocation toward F and S is determined by the locus C (reproduced from de Jong and van Noordwijk (1992)).

Smith and Fretwell (1974) also developed an ingenious theoretical analysis based on the energy allocation principle to investigate the optimal investment of resources toward size and number of offspring. Their graphical analysis, which is also developed

analytically in their paper, proposed that a finite set of energy is available for reproduction. They therefore assumed that the *fitness* of each young is a direct function of the fraction of energy invested in increasing the size of the eggs, which is in itself inversely proportional to the energy invested in increasing the total egg number (Figure 6). The optimal allocation of resources toward the size and number of offspring will be the one that maximises offspring *fitness*.

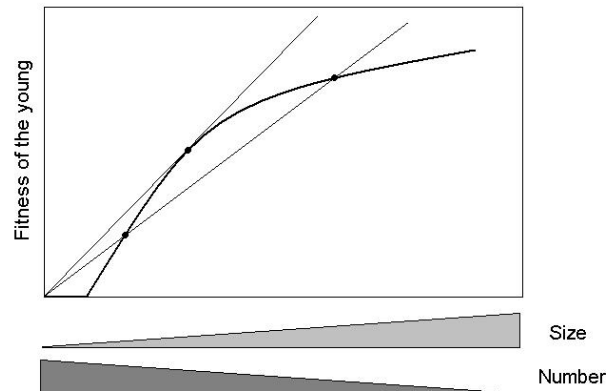


Figure 6. Smith & Fretwell's graphical analysis of the *trade-off* between size and number of offspring. The y-axis represents the *fitness* of each young. The x-axis gives the size of each young, *i.e.* the energy allocated into egg provisioning. This percentage of energy is inversely proportional to the number of offspring, since the energy allocated into egg provisioning is no more available to increase the number of eggs produced. The bold curved line is the set of all possible combinations of parental types, each of them investing a different proportion of energy into increasing either the size or the number of its offspring. The straight lines are the *adaptive functions*, *i.e.* the sets of parental types being equally successful in contributing to future generations. The intersections between the two lines give the strategies of energy allocation toward offspring size and number and their subsequent *fitness*, the optimal one lying at the intersection of the tangent with the curve (modified from Smith and Fretwell (1974)).

Explicit considerations of underlying physiological mechanisms as key factors that shape organisms' behaviour and reproductive success definitely came in theoretical modelling with the development of *Foraging Theory* (Stephens & Krebs 1986) and the application of *Dynamic Modelling* to the study of animal behaviour in the 80's (Houston & McNamara 1985, Mangel & Clark 1988). Foraging models usually define the optimal strategy as the one that maximises the net rate of energy gain while foraging. *Dynamic modelling* defines a set of optimal strategies according to time-dependent factors such as the level of energy reserves, the number of eggs carried or the probability of escaping predation. More precise descriptions of these models will be developed in the section '*Relations between foraging, environmental characteristics and energy allocation*' (p54), as they provide an explicit link between the strategies of energy allocation and foraging behaviours.

Recent developments in ecology put forward that instead of a common pool of energy that has to be divided to provide energy for maintenance *versus* growth, energy is profoundly compartmentalised. In the next section I will provide elements and examples in Insects to illustrate the compartmentalisation of energy observed in this taxa.

2.2. From the ‘*Y-model*’ of de Jong and van Noordwijk to an integrated compartmentalised model

In the previous section, we saw that the most classical theoretical models considering the allocation of nutritional resources toward competing functions deal with a common pool of resources that has to be separated between different life-history traits, as in the ‘*Y-model*’ (de Jong & van Noordwijk 1992). Modern empirical investigations of the processes of energy allocation toward biological functions however put forward that the energetic pool is compartmentalised. Different nutrients, which are not used for the same purposes, are commonly involved in energy allocation processes. Energy is also compartmentalised in stored resources and resources acquired from feeding. On the other hand, the processes of energy acquisition and allocation are not fixed, but highly dynamics along organisms’ lifetime.

In this section I will draw a general picture of the roles of the different nutrient classes in Insects to emphasise that competing functions such as reproduction and locomotion are not necessarily fuelled by the same nutrient pools.

2.2.1. Role and importance of the different energy sources

Instead of a common pool of nutrients, metabolic energy can be divided into several nutrients that are sometimes used for specific functions, not used equally and acquired similarly. It is of utmost importance to consider the different energetic compartments in studies of energy allocation because some nutrient classes may be limiting for specific functions (*e.g.* those that are not available in food and therefore not renewable) and others not. I will focus here on the three major and most classical nutritional sources of energy: carbohydrates (*i.e.* sugars), lipids and proteins, and describe some of the technical developments that allowed the quantification of these nutrients in Insects. A large literature exists on Insect metabolism (that can be defined as the sum of all chemical reactions occurring in an organism) that separates in more details the different

nutrient classes and takes into account the reactions linking them (*e.g.* Engelmann 1970, Nation 2002). However, our aim here, rather than to draw an exhaustive picture of Insect metabolism, is to provide basic concepts to understand nutrient mobilisation in Insects, as well as an overview of nutrient utilisation in maintenance and reproduction.

In Insects, the energy storage organ is the fat body, a relatively large, irregular and diffuse tissue that surrounds the gut. This organ is also the site of a large number of metabolic processes, such as yolk protein synthesis (Chapman 1969). Insect haemolymph – the equivalent of Vertebrate blood – also contain, but to a lesser extent, various energetic nutrients such as trehalose, that are mobilised faster than nutrients originating from the fat body (Nation 2002).

The most common carbohydrates can be divided in mono- or disaccharides such as glucose, trehalose (glucose-glucose dimer) and sucrose (glucose-fructose dimer), and in more complex sugars such as glycogen (glucose polymer). Glucose is the primarily molecule providing ATP when combined with oxygen. The other carbohydrate molecules have to be separated into their glucose or fructose elements, and fructose converted into glucose, before being used to provide energy. Trehalose is the most common sugar circulating in the haemolymph in Insects², and an easily and rapidly energy-converted molecule (Nation 2002). Sucrose is the most common nutrient acquired from sugary food. The glucose available in Insect gut directly diffuses into the haemolymph through the gut membrane without specific transport mechanisms. Glucose can be then readily used to provide energy. When glucose concentration reaches a certain threshold in the haemolymph, it is converted into trehalose or glycogen in the fat body. Conversely, when glucose concentration falls below this threshold, trehalose and glycogen are mobilised and converted into glucose (Nation 2002). Carbohydrates are the firsts and most easily energetic sources mobilised when needed. Their role in maintenance is generally accepted. Carbohydrates are known to fuel flights of several Insects (Vogt *et al.* 2000, Suarez *et al.* 2005). Carbohydrates reserves are theoretically sufficient, in fed Dipteran or Hymenopteran, to fuel flights for 30 min to 2 hours (Nation 2002). For longer flights, metabolism switches to lipid or proline

² HPLC analyses recently conducted on the Braconidae parasitoids *Cotesia glomerata* and *Microplitis mediator* however put forward that trehalose is absent from their sugar profiles (Steppuhn & Wäckers 2004). These authors emphasised the fact that our knowledge on Insect metabolism is based on a limited number of model systems.

mobilisation (Candy *et al.* 1997, Nation 2002). A more detailed description of Insect flight energetics will be given in the section ‘*The costs of locomotion*’ (p65).

While carbohydrates seem to be mobilised rapidly when needed, lipids and proteins appear to be used mainly for long and extensive needs of energy, or for specific functions such as egg manufacturing.

Lipids are mostly stored in the fat body together with glycogen, and to a lesser extent, also directly available in flight muscles. They may be synthesised from carbohydrates through lipogenesis (we will see in the section ‘*Lipogenesis*’ p41 that lipogenesis seems absent in parasitoids). They are less easily mobilised than carbohydrates, but provide much more energy than them (129 moles of ATP for one mole of lipids vs. 36 ATP for one mole of glucose, Nation (2002)). Lipids are sometimes presented as responsible of survival (*e.g.* Ellers 1996), and often referred as the critical source of energy for egg production (*e.g.* Ellers & van Alphen 1997, Giron & Casas 2003b, Bernstein & Jervis 2008). We need to separate here the energetic cost of building an egg with the expenditure associated with nutrient incorporation into eggs. The amount of nutrients incorporated into eggs should crucially depend on the nature of eggs. While yolk-rich – or anhydropic³ – eggs contain large amounts of proteins and lipids (Canavoso *et al.* 2001), some eggs – hydropic – do theoretically not (for more details, see section ‘*Lifetime egg dynamics*’ p47). To my knowledge, the energetic cost of building an egg has not been quantified precisely, but is expected to be relatively low for anhydropic eggs, as suggested by Wheeler (1996). Among other functions (see Canavoso *et al.* 2001 for a review), lipids are involved in the fuelling of long flights in Lepidopteran and Orthopteran Insects, and are known to play a great role in providing metabolic energy during diapause (Ellers & van Alphen 2002, Hahn & Denlinger 2007). Here I would like to mention an elegant study of lipid metabolic pathways, which demonstrated that the two flight morphs of *Gryllus firmus* differentially biosynthesise and allocate lipids to different purposes (Zhao & Zera 2002). While the ‘long winged’ morph, highly specialised for dispersal, synthesise a larger amount of total lipids and triglycerides – the main flight fuels – and preferentially allocate them toward somatic tissues, the ‘flightless’ morph, specialised for reproduction, synthesise a greater amount of phospholipids which are allocated to ovaries.

³ The term ‘hydropic’ reflects that hydropic eggs are small and increase in size after oviposition as they absorb water and nutrients from host tissues (Jervis & Kidd 1986).

Proteins are composed of amino acids and are generally stored in the fat body. Proteins seem to be used for various purposes. In butterflies, free amino acids and other nitrogen compounds (found in nectars and pollen) are known to play important roles in both somatic maintenance and oogenesis (Dunlap-Pianka *et al.* 1977, Boggs 1981b). Proteins are expected to play a decisive role in egg production in Insects, especially for species having anhydroptic eggs, since the process of vitellogenesis, the accumulation of yolk (=vitellogenin) into oocytes, is a major step into the process of oogenesis. Some Insects such as beetles, the tsetse fly and mosquito have been reported to use the amino acid proline to fuel their flights (Nation 2002). Large proteins, named ‘storage proteins’ provide metabolic energy during metamorphosis and supply amino acids for adult tissue building. Their concentration reaches high levels at the end of larval development, and then steadily decreases during adult stage (Hunt *et al.* 2003). Proteins are also involved in Insect diapause (Hahn & Denlinger 2007). Proteins, as lipids, have also been demonstrated to be differentially allocated to different functions in the two flight morphs of *Gryllus firmus* (Zera & Zhao 2006). In this study, the authors showed that precursor amino acids are preferentially converted into metabolic energy – lipids and triglycerides – in the ‘long winged’ morph, and that they are preferentially converted into ovarian materials (*e.g.* vitellogenin) in the ‘short winged’ morph.

The most energy-demanding activities in Insects are flight, diapause and oogenesis. Under the assumption of a limited supply of energy compared to the demand of these three functions, compromises are expected to arise between them. During flight, oxygen consumption may increase up to 70-fold compared to rest (Candy *et al.* 1997, see section ‘*The costs of locomotion*’ p65). On the other hand, diapause is a remarkable strategy during which insects generally stay for several months in reduced activity, and in a few cases several years, without eating (Hahn & Denlinger 2007). These two activities involve the utilisation of great amounts of nutrients. Even if it is sometimes possible, in some model Insects, to draw the precise dynamics of utilisation of one or another compound to fuel flight or diapause, no clear pattern of nutrient utilisation can be sorted out. Carbohydrates, lipids and proteins both appear to play decisive roles in flight and diapause.

Approximate quantifications of body lipids have been carried out in butterflies by visually determining the size and aspect of the fat body that is expected to reduce in size with time (Boggs 1986). There exist a simple method of lipid extraction, which consists

in assessing the difference between insect dry weight before and after ether extraction, that allowed lipid quantification in several organisms (*e.g.* May 1992, Ellers 1996, Ellers & van Alphen 1997), but the precision of the method might be questioned, regarding the small amounts of material weighed. The pioneering works of van Handel (van Handel 1985a, b), which aimed at quantifying body sugars and lipids in mosquitoes have been successfully applied in parasitoids by Olson *et al.* (2000), and followed by Rivero & West (2002), Casas *et al.* (2003), Giron and Casas (2003b), Pelosse *et al.* (2007). These methods are based on the use of sugar- and lipid-specific reagents that acquire coloration in presence of sugars or lipids. Nutrient concentrations are then assessed with the use of spectro-photometric analyses that measure the absorbance (*i.e.* a measure proportional to nutrient concentration) of solutions. Nutrient concentrations are then easily assessed by comparing the absorbance of the solutions of interest *versus* the absorbance of solutions of known concentrations. The reagent specific to sugars is anthrone. This molecule turns to green in presence of sugars. The interesting feature of anthrone is that its reactivity with glucose or fructose changes with temperature and therefore allows separating these two monosaccharides (van Handel & Day 1988). While at room temperature, anthrone specifically reacts with fructose, it reacts with both glucose and fructose when briefly heated at 90°C. This feature allows assessing the relative importance of sugars originating from sugar feeding, as fructose is specific to sucrose, the most common constituent of nectars, and body sugars. Because glycogen can be easily precipitated and thus separated from more simple sugars, the method of sugar quantification is able to separate glycogen, simple constitutive sugars and sugars originating from sucrose. In the section '*Determination of insect's dietary range*' (p59) we will see how these techniques have been used and extended to the determination of sugar feeding in Insects. The reagent for lipids is vanillin, which turns pink in presence of any lipid molecule. A method of estimation of sugars and lipids on the same individuals has been first presented by van Handel and Day (1988) and applied in Hymenopteran parasitoids by Olson *et al.* (2000). Proteins have been more classically assayed in various taxa, the most famous technique for their quantification being the Bradford assay (Bradford 1976). The Bradford reagent binds with the most classical proteins, and allows a global quantification of the total protein load. This technique should therefore be used with care, because the Bradford reagent does not detect every protein classes, and the proteins assayed may come from membranes or stored tissues. Other techniques based on enzyme activities allow a more detailed quantification of

different types of proteins and amino acids, but they will not be described here. Very recent developments make now possible to measure sugars, lipids and proteins in a single individual (D. Giron, unpublished results on the parasitoid *Eupelmus vuiletti*, Pelosse *et al*, in prep b on *Venturia canescens*, P.-F. Pelisson, unpublished results on beetles of the genus *Curculio*). The quantification of several nutrients on a single individual allows limiting the number of insects analysed and precisely investigating the individual compartmentalisation into different nutrients. On the other hand, because these methods significantly decrease the fraction of body parts used to assess each nutrient concentration, they are submitted to a greater sensibility. We will see in the section ‘*Determination of insect’s dietary range*’ (p59) that another analysis, the high-performance liquid chromatography (HPLC), allows a precise and simultaneous characterisation and quantification of several nutrients.

A first compartmentalisation of energy sources occurs at the level of metabolic nutrients. We will see in the next section that available resources in Insects may also be compartmentalised in stored resources and resources acquired from food.

2.2.2 Extension of the concepts of *income* and *capital breeders* to the study of the relative importance of stored and nutritional resources

Here I will develop an example to illustrate the concepts of *income* and *capital* breeding. As previously mentioned, several attempts have been carried out during the 1980’s to reveal *trade-offs* between current reproduction and survival, or current and future reproduction. An experiment conducted with the blue tit *Parus caeruleus* found evidence of a phenotypic *trade-off* between clutch size and adult survival (Nur 1984). Unexpectedly, when the same experiment has been carried out on the great tit *Parus major*, the *trade-off* has not been revealed (Tinbergen 1987). Further investigations put forward that the blue tit shows a high metabolic rate and is unable to store energy reserves, and that the great tit demonstrates the opposite characteristics. Sibly & Calow (1984) referred those organisms that do not have the capacity to store energy and therefore only rely on their incoming resources to fuel their reproduction as ‘*income breeders*’, and those that use their energy reserves as ‘*capital breeders*’. Stearns (1989) suggested that *income breeders* are less subject to the cost of reproduction, because it is

not paid from stored resources. Foraging for food is however an activity that inevitably incurs costs, either metabolic or in term of exposition to predators. Then, as we will see in the section ‘*Lipogenesis*’ (p41), food does generally not provide all nutrients essential for reproduction, and the depletion of specific classes of nutrients is inevitable.

More recently, the terms *capital* and *income* have been used to separate the energy, or more specifically, the nutrients, that are stored or acquired by an organism, respectively. Boggs (1997b) also proposed to use the term ‘*capital expenditure*’ to refer to the use of stored nutrients, and ‘*income expenditure*’ to the use of nutrients as they are acquired. The *capital resources* may correspond either to the resources that are stored by the adults and later used to fuel an energetic function, but also to the resources that come from the egg, the mother, or, in organisms with complex life cycles, from previous stages. When a nutrient not available in adult food is critical for adult reproduction (e.g. egg manufacture), the organism will only rely on the resources acquired during the larval stage for this nutrient. Casas *et al.* (2005) for instance demonstrated that the host-feeding⁴ parasitoid *Eupelmus vuilletti* critically depends on lipids for reproduction, but that this nutrient is present in limited quantities in adult food sources and cannot be synthesised from sugars. These authors therefore proposed to apply the concepts of *income* and *capital breeder* to separate the nutrient classes that can be renewed during the adult stage or not. *E. vuilletti* therefore appears *capital breeder* for lipids, because unable to get more than those stored during larval stage, *income breeder* for sugars, because this class of nutrients is largely acquired in adult food, and intermediate between *capital* and *income* breeder for proteins.

In this section, I will focus on holometabolous organisms, such as holometabolous Insects, that show different life-stages, and explain how the compartmentalisation in larval- and adult-derived resources may affect the processes of energy allocation toward life-history traits. In holometabolous organisms, the juvenile and adult stages may exploit different environments, or different food types. The energy acquired and stored by the juvenile and adult stages may therefore differ both qualitatively and quantitatively (Rivero *et al.* 2001). The nutrients stored during the larval stage and available at adult emergence are referred as the *teneral resources* (Rivero & Casas 1999a). At adult emergence, holometabolous Insects have generally already invested a

⁴ Some parasitoid species resort to host-feeding, *i.e.* they acquire metabolic nutrients through the consumption of host tissues (see section ‘*The role and importance of feeding*’ p56).

fraction of their metabolic resources to reproduction, for instance to build the reproductive materials (e.g. nurse cells). In some organisms, *capital* and/or *income resources* are then also allocated to reproduction during the adult stage (we will see later that this is not the case for all of them). Jervis *et al.* (2001) proposed a useful tool to measure the relative allocation of nutrients toward reproduction and maintenance at emergence: the *ovigeny index*, i.e. the fraction of the total egg production that is already matured at emergence (particular attention will be given to this topic in the section ‘*Lifetime egg dynamics*’ p47). To my knowledge, Boggs (1981a) has been the first to point out the importance of considering the relative importance of larval *versus* adult resources in the study of life-history strategies of organisms with complex life-cycles.

Boggs’s works provided an explicit framework which takes into account the fact that juvenile stages’ energy allocation strategies constitute a first step in the allocation process, and that the resulting energy allocation patterns observed at adult emergence will have broad implications for adult nutritional and life-histories (Boggs 1981a, 1990, 1997b). In her studies, Boggs especially focused on the evolutionary relationships between the initial patterns of energy allocation and (i) adult reliance on external food sources on the one hand, and (ii) adult reproductive output on the other hand. Because interactions between energy allocation strategies and foraging behaviour are involved here, I will develop other aspects in the section ‘*Relations between foraging, environmental characteristics and energy allocation*’ (p63). To investigate the relationships between resource allocation at metamorphosis and adult nutrient intake and outputs, Boggs considered in a first approach that total organisms’ metabolic resources are divided in resources originating from the larval stage that are available at adult emergence, and *income resources* that are acquired during the adult stage (Boggs 1981a). She proposed to link the potential reproductive effort *PRE* together with the proportion of larval and adult resources allocated to reproduction, and with the adult reproductive output. She therefore gave the following equation:

$$PRE = aB + bN_i = cN_r, \quad (\text{Eq. 6})$$

where *a* is the proportion of nutrients at adult emergence allocated to reproductive *versus* somatic reserves, *B* the total amount of available nutrients at emergence, *b* the proportion of *income* nutrients allocated to reproductive *versus* somatic reserves, *N_i* the

total adult nutrient intake, c a constant and N_r the total nutrient reproductive output of adult. From this equation follows:

$$aB = cN_r - bN_i, \quad (\text{Eq. 7})$$

which means that the initial allocation of larval resources toward reproduction is closely linked to the adult nutrient intake, the allocation of *income resources* toward reproduction, and reproductive output (Figure 7). To assess the impacts of N_r and N_i on a , Boggs compared three butterfly species that have similar larval foraging strategies – B is therefore assumed to be constant – but differ in adult reproductive outputs N_r and resource intake N_i . The results put forward that the initial allocation of resources toward reproduction increases at the expense of somatic maintenance as the reliance on *income resources* diminishes. In other words, when the expected availability of food sources is low, a large fraction of larval resources should be invested toward adult reproduction at metamorphosis. This study emphasised the importance of considering a sequential allocation of resources toward the different life-history traits in organisms with complex life-cycles.

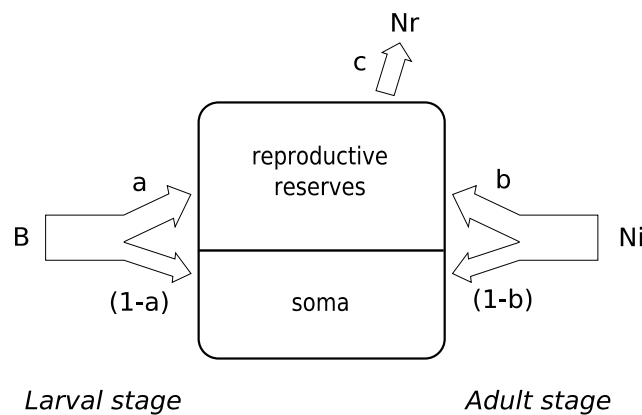


Figure 7. Schematic representation of the model of Boggs (1981a). Resources allocated to reproductive reserves *versus* soma may originate from larval or adult stages. Reproductive reserves are lost according to the reproductive output N_r . See the text for details.

In another study, Boggs suggested considering that the energy available to produce additional eggs during the adult stage may be derived from both *capital* and *income resources* (Boggs 1990). In many Insects, the male provides nutrients to the female at mating that can be considered as *income resources*. These nutrients may come directly from the sperm, from preys offered to the female or from spermatophores, *i.e.* masses containing spermatozoa and other compounds that are transferred to the female during

copulation. In butterflies, a radiotracer study demonstrated that females use male-derived amino acids included in the spermatophore for both oogenesis and maintenance (Boggs & Gilbert 1979). These male donations are expected to play a critical role in female reproductive success, especially when they provide nutrients that cannot be acquired otherwise by the female. To test the role of male-donated nutrients in female insect reproductive success, Boggs proposed a model in which the resources devoted to the manufacture of eggs, E , may come from the resources acquired during the larval stage, L , the *income* resources coming from male donations, M , and *income* resources originating from food, A (Boggs 1990). The resources used to make eggs, E , therefore equal:

$$E = L + A + M . \quad (\text{Eq. 8})$$

Some Insects (we will see later that it is not the case for all of them) have a fraction of yolked – or mature – eggs (yolk or vitellogenin is the classical protein that surrounds insect eggs) at emergence that are ready for reproduction, and a fraction of eggs that are immature and would need to be yolked – or matured – to be available for reproduction. To reflect the fact that the larval resources can be already fully invested in egg production at emergence through mature eggs, but also subsequently invested in egg production through the maturation of immature eggs, Boggs assumed that a fraction b of the larval resources L has been devoted to yolked eggs and $(1 - b)$ to immature eggs (Figure 8). The reproductive resources E can consequently be separated in her model in eggs that are already mature at emergence on the one side, and immature eggs + the energy subsequently invested in egg production on the other side:

$$E = bL + [(1 - b)L + A + M] . \quad (\text{Eq. 9})$$

Because larval resources, resources originating from food or male donations may differ qualitatively (for instance females that exclusively feed on sugar sources may acquire proteins through spermatophores), they can both be separated in several nutrient types i . The total energy invested into eggs is therefore the sum over all the i -types of nutrients:

$$E = \sum_i y_i b_i L_i + \sum_i z_i [(1 - b_i) L_i + A_i + M_i] , \quad (\text{Eq. 10})$$

where y_i and z_i are the fractions of nutrient i that are used for reproduction, during larval stage and adult stage, respectively. This model predicted that (i) the less eggs yolked at emergence, the more *income resources* should be gained during adult stage, and (ii) the nutrient composition of spermatophores and food sources exploited by females should be compensated. By combining data from the literature, Boggs indeed put forward that male-derived nutrients often differ in composition from the food acquired by females. This suggests that nutrients originating from males may be limiting for female reproduction. A comparison of two butterfly species differing in their mating frequency also suggested that the amount of male nutrients acquired *via* mating is inversely correlated with females' reliance on food (Boggs 1990).

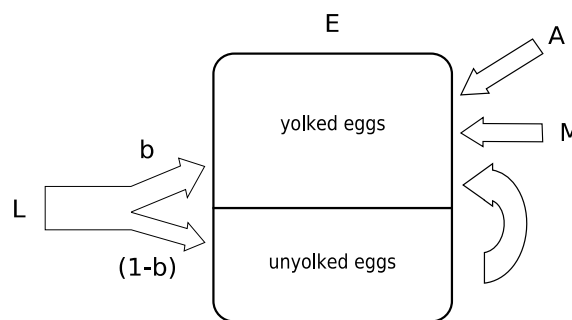


Figure 8. Schematic representation of Boggs model (1990). Resources from larval stage (L) are allocated either to the elaboration of yolked eggs or unyolked eggs. Resources may also come from adult food (A) and male-donations (M). Unyolked eggs will contribute during the adult stage to the elaboration of yolked eggs. See the text for details.

The two studies described above (Boggs 1981a, 1990) provided important advances in the understanding of the importance of the processes of energy allocation during juvenile stages for adult reproductive success, and also emphasised the fact that juvenile and adult food may differ qualitatively, and that some resources can be renewed during adult stage, and some other not. We will focus in the next section on lipids that are typically not renewable by the adult in parasitoid wasps.

2.2.3. Lipogenesis

Essential nutrients that cannot be acquired from adult food will have to be used with parsimony and may be limiting for reproductive success. Here I will focus on the case-study example of lipids. Lipids are often presented as critical for reproduction (but see section '*Role and importance of the different energy sources*' p31), and are completely

absent in sugary food sources such as nectars or honeydew. Lipid synthesis from sugars, lipogenesis, has been reported among some Insects: mosquitoes (Nayar & van Handel 1971, van Handel 1984), fruit flies (Warburg & Yuval 1996), Lepidoptera (Brown & Chippendale 1974). A relatively large number of investigations however suggested that lipogenesis is absent in Hymenopteran parasitoids. The absence of lipogenesis has also been observed in Diptera such as *Musca domestica* and *Anastrepha serpentina* (van Handel 1984, Jacome *et al.* 1995). These organisms therefore rely on their *teneral* lipid reserves only, which may limit reproduction.

The absence of lipogenesis has been suggested in different Hymenopteran parasitoid species from data where although adult parasitoids were provided with sugary food, their *teneral* lipid amounts never increased but rather decreased or stayed constant along their lifetime (Ellers 1996, Olson *et al.* 2000, Rivero & West 2002, Giron & Casas 2003a, Lee *et al.* 2004, Casas *et al.* 2005, Pelosse *et al.* in prep b (Section 2 – Chap I p81, and Table 1)). For instance, in the Braconidae parasitoid *Macrocentrus grandii*, free sugar and glycogen amounts increased at the beginning of life in females provided with sugars and decreased in unfed females, whereas lipid amounts decreased whatever the feeding treatment (Olson *et al.* 2000). Another study conducted on the parasitoid *Venturia canescens* put forward that lipid amounts all along lifetime never increase above the amount of *teneral reserves*, even in parasitoids provided with *ad libitum* access to sugars (Casas *et al.* 2003).

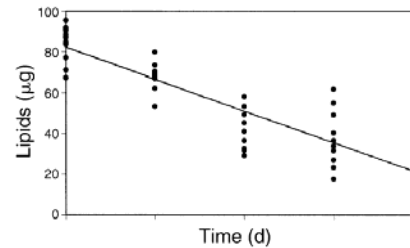
A causal relationship between the absence of lipogenesis and lipid decreases along lifetime has been provided by Giron and Casas (2003a). These authors provided wasps with radioactive carbon-marked glucose as adult food and recorded its incorporation into the hydrophilic body fraction, *i.e.* constituted with sugars, and into the hydrophobic one, *i.e.* constituted with lipids. The presence of radio-labelled carbon in the hydrophobic phase only proved that sugars were not converted into lipids after being ingested (Giron & Casas 2003a).

Table 1. (next page) Lifetime variations of lipid reserves in several Hymenopteran parasitoid species.

Species	Experimental setup	Main results	Conclusions, remarks	References
<i>Asobara tabida</i> Hydropic eggs, moderately <i>synovigenic</i> .	Agar-yeast + <i>ad libitum</i> honey <i>versus</i> agar only.		Lipid amounts decrease whatever the feeding treatment, and the decrease is more rapid in unfed wasps.	Ellers 1996
<i>Macrocentrus grandii</i> Non-host-feeding, egg resorption.	<i>Ad libitum</i> 50% sucrose + water <i>versus</i> water only. No oviposition.		Lipid amounts at death are higher in fed wasps. Lipids decline more rapidly in starved wasps.	Olson <i>et al.</i> 2000
<i>Nasonia vitripennis</i> Host-feeding, anhydropic eggs, <i>synovigenic</i> .	<i>Ad libitum</i> 30% honey solution <i>versus</i> water only. No host-feeding and oviposition.		Unfed wasps use larger amounts of lipids in the beginning of life.	Rivero & West 2002
<i>Eupelmus vuaeletti</i> Host-feeding, anhydropic eggs, extremely <i>synovigenic</i> .	<i>Ad libitum</i> 10% glucose solution <i>versus</i> water only. No host-feeding and oviposition.		Lipids stay constant during the first 72h of life, whatever wasps' feeding status.	Giron & Casas 2003a

Eupelmus vuiletti
Host-feeding,
anhydropic eggs,
extremely
synovigenic.

No hosts and no sugar.

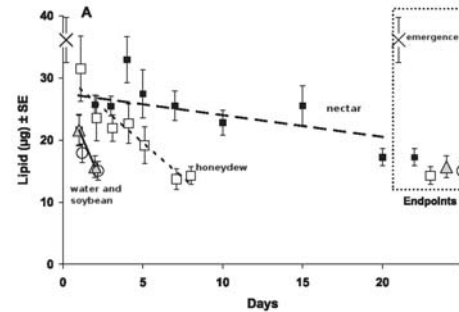


Lipids decrease all
along lifetime.

Casas *et al.*
2005

*Diadegma
insulare*
Non-host-
feeding,
Synovigenic.

Ad libitum naturally occurring
food sources: leaves with
aphids producing honeydew,
flowers, *versus* water.
No oviposition.

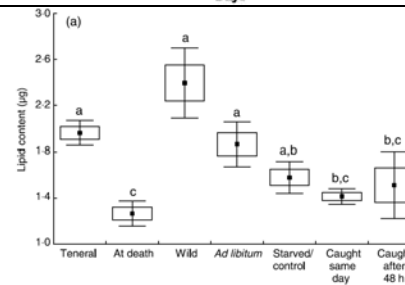


Lipid decrease is more
important in wasps fed
with honeydew, and
again more important in
wasps fed either with
soybean or water only.

Lee *et al.*
2004

*Venturia
canescens*
Non-host-
feeding,
synovigenic,
hydropic eggs.

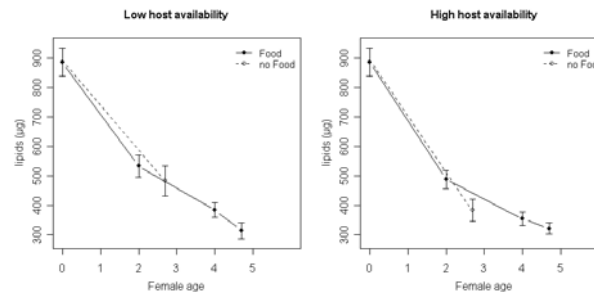
Measurements on emerging
wasps, dead wasps without
access to food and water, *ad
libitum* pure honey for 48h,
wasps starved during release,
and wasps recaptured in the
field the same day or after 48h.



The amounts of lipids
recorded at emergence
(*teneral*) are the
maximum amounts
recorded.

Casas *et al.*
2003

2 µL 20% sucrose solution
daily,
5 hosts *versus* 30 hosts per day.



The decreases of lipids
are equivalent whatever
the host availability and
feeding treatments.

Pelosse *et al.* in prep b

The comparison of lipid decreases among fed and unfed wasps put forward, in the majority of cases, that lipid decrease is less pronounced in the presence of incoming carbohydrates (Ellers 1996, Olson *et al.* 2000, Rivero & West 2002, Lee *et al.* 2004). Some authors argued that organisms that acquire sugars from food rely less on lipids to fuel maintenance, and therefore spare lipids for both maintenance and reproduction. In *Venturia canescens*, we however put forward that the decrease in lipids is the same, in average, for fed and unfed wasps (Pelosse *et al.*, in prep b).

As reported by Giron and Casas (2003), the absence of lipogenesis seems to be the rule among parasitoids from the Aculeata group. Surprisingly, concerned organisms strongly differ in their egg maturation and nutritional strategies (see table 1). It is conceivable that lipogenesis may have been selected against in parasitoids feeding on lipid sources, such as host tissues⁵. On the other hand, it is more difficult to understand how lipogenesis has disappeared in parasitoids feeding on carbohydrates only, under the assumption that lipids are critical for reproductive success.

Although lipids have attracted all attention among behavioural eco-physiologists, proteins have been quite overlooked. They however play a primordial role in oogenesis and are not acquired in adult food in parasitoid feeding on sugary food sources only. Nectars contain free amino acids, but in small quantities (see section '*Food sources and their main properties*' p57). Casas *et al.* (2005) showed that in the host-feeding parasitoid *Eupelmus vuilletti*, protein amounts steadily decrease all along lifetime when only sugar is provided, and that they increase when the parasitoid also have the possibility to host-feed. In a recent study, we also revealed that the non host-feeding parasitoid *V. canescens* experiences similar decreases for lipids and proteins whatever the feeding treatment (Pelosse *et al.*, in prep b).

We saw that in holometabolous Insects, energy allocation operates during both juvenile and adult stages, and that the strategies adopted during the larval stage may have decisive impacts on adult reproductive success, particularly because some nutrients are only available to juvenile stages. We will see here that more general models have been designed to take into account any series of hierarchical energy allocation events.

⁵ Host-feeding has however been demonstrated to provide limited amounts of lipids (Giron *et al.* 2002). See section '*Food sources and their main properties*' (p57).

2.2.4. Hierarchical energy allocation

Extensions of the ‘*Y-model*’ of de Jong and van Noordwijk have been proposed to consider hierarchical energy allocation to different traits (de Laguerie *et al.* 1991, de Jong 1993, Worley *et al.* 2003). These quantitative genetic models overcome the simplifying assumption of the ‘*Y-model*’ that considers that energy is divided to reproduction and maintenance, and propose to consider that energy is first allocated to reproduction and maintenance, and that for instance, the energy allocated to reproduction is subsequently allocated to male and female production (Figure 9). The rationale of these models will not be developed here. Their main conclusion is that variations in allocation at the base of the hierarchy have the property to mask *trade-offs* that should theoretically take place further in the hierarchy.

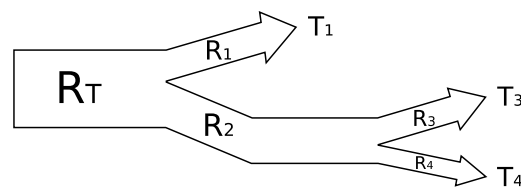


Figure 9. Schematic illustration of a hierarchical allocation. The total amount of resources R_T has first to be divided between R_1 , that gives the trait T_1 , and R_2 . The amount of resources R_2 has then to be divided between R_3 , that results in the trait T_3 and R_4 , that results in the trait T_4 . R_1 could for instance represent the energy devoted to maintenance and therefore T_1 the survival, and R_3 and R_4 the amounts of resource allocated to the production of males and females, and T_3 and T_4 the corresponding number of males and females (reproduced from Worley *et al.* (2003)).

From now, we considered a static allocation of resources. We will see in the next section that fluxes of energy losses and gains however take place during organisms' lifetime, and profoundly modify their energetic budgets.

2.3. Dynamic energy allocation

2.3.1. Models describing the dynamic allocation of nutrients

Dynamic models describing nutrient allocation processes assume that energy is allocated to reproduction, growth, storage and maintenance and that the allocation patterns can change with age (Perrin & Sibly 1993). They have been applied, among others, to the study of the evolution of longevity (*e.g.* Cichon 1997) and the study of the optimal distribution of reproductive effort along lifetime (Leon 1976). Here we will

focus on the dynamic model of energy allocation developed for parasitoids by Casas *et al.* (2005). In their paper, the authors built a comprehensive dynamical model of nutrient acquisition and allocation toward maintenance and reproduction in *Eupelmus vuilletti*, on a daily basis all along lifetime. The model has been parametrised with a large amount of data obtained in this species, ranging from the precise amounts of each nutrient contained into a single egg to estimations of daily nutrient expenditures. Their model allowed predicting nutrient decreases and increases along lifetime.

$$N_j(i) = N_j(i-1) - M_j(i-1) + \alpha_j \beta f(i-1) - \delta_j \gamma E(i-1) \quad (\text{Eq. 11})$$

where $N_j(i)$ is the amount of nutrient of class j at time i . This amount equals the amount of nutrient N_j at time $i-1$, minus the amount of nutrient used for maintenance M_j at time $i-1$, added to the amount of nutrient gained through host-feeding $\alpha_j \beta f$ – where α_j is the amount acquired with a single host-feeding event, β the nutrient conversion factor and f the number of host eaten – minus the amount lost through ovipositions $\delta_j \gamma E$ – where δ_j is the amount incorporated into a single egg, γ the inverse of the conversion factor β , and E the amount of eggs laid.

In the next section we will see that in some parasitoid Insects, a dynamics in egg number is observed during the adult stage.

2.3.2. Lifetime egg dynamics

Flanders (1950) was the first to propose a distinction between parasitoids that emerge with their full mature egg complement and are unable to mature additional eggs thereafter, referred as *proovigenic*, and parasitoids that mature additional eggs during their adult stage, referred as *synovigenic*. As previously mentioned, Jervis *et al.* (2001) later proposed the *ovigeny index (OI)*: the proportion of the total egg number produced which are mature at emergence, to measure the relative investments in reproduction between larval and adult stage. In Jervis and co-authors' paper, the *OI* of 67 parasitoid species is estimated, and a total of 638 species are classified in either as *proovigenic* or *synovigenic* (Jervis *et al.* 2001, Figure 10). *Proovigenic* species are characterised by $OI=1$ and strictly *synovigenic* species – those having no egg mature at emergence – by $OI=0$. The *OI* provides a more precise measure of the allocation of larval resources to reproduction than the dichotomy between *pro-* and *synovigeny*, since all values ranging

between 0 and 1 are possible. The first thinking that the percentage of mature eggs at emergence could help understanding organisms' life-histories, especially their reliance as adults on food sources, have initially been suggested by Boggs (1997b): '*Opportunity to use adult nutrients in reproduction is measured by the percentage of eggs fully mature at adult emergence; the fewer mature eggs, the greater the opportunity for use of adult nutrients.*' *Proovigenic* species can indeed be seen as species completely *capital breeders* for reproduction, as they do not need to incorporate *income resources* into their eggs. It could be tempting to link *synovigeny* to *income breeding*, but *synovigenic* organisms appear to use both adult and larval-derived nutrients for egg manufacture (O'Brien *et al.* 2000, Rivero *et al.* 2001, see section '*Dynamics of nutrient incorporation into eggs*' p51).

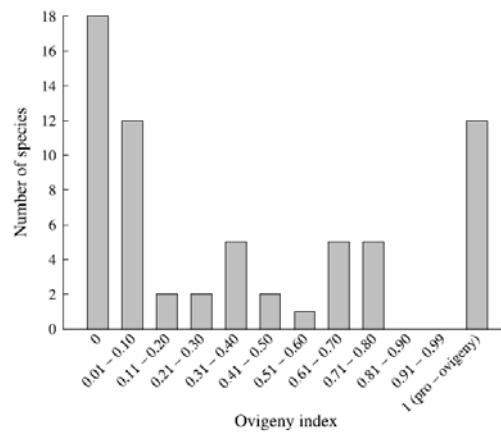


Figure 10. Estimation of the *ovigeny index* (OI) for 67 parasitoid species (from Jervis *et al.* (2001)).

Egg resorption occurs in response to resource shortage and theoretically allows re-allocating the nutrients invested into egg manufacture to maintenance (Jervis & Kidd 1986, Collier 1995b). Only anhydropic eggs are possibly submitted to resorption because they contain a lot of nutrients (Flanders 1950). Price (1975) suggested that providing the higher number of eggs in hydropic species, resorbing a large number of eggs could compensate the small fraction of yolk present in each egg. Jervis *et al.* (2001) argued that since this strategy has never been observed, it should not be a viable option. Although *egg resorption* is widely thought to provide nutrients for metabolic maintenance in parasitoids (e.g. Leius 1961) formal studies quantifying its role in extending female longevity are crucially lacking.

Since the *ovigeny index* has been proposed in 2001, a large number of life-history and nutritional traits have been correlated to this index (Jervis *et al.* 2001, Jervis *et al.* 2003, Jervis & Ferns 2004, Jervis *et al.* 2005, 2007). In their paper, Jervis *et al.* (2001) used a statistical method correcting for the phylogenetical relationships linking species and found significant correlations between *OI* and lifespan, nature of eggs, etc... (see Table 2, also reviewed in Jervis *et al.* (2007) for holometabolous Insects and in Jervis *et al.* (2005) for Lepidoptera). This approach directly follows the ‘dichotomous hypothesis’ (Godfray 1994) which attempted to correlate the developmental mode of parasitoids – koinobiont or idiobiont⁶ – to several life-history traits (*e.g.* Mayhew & Blackburn 1999). This approach is sometimes only based on hypotheses, or on limited results observed in a few species. When results are available from many species, they might be questioned, even if based on statistical methods correcting for phylogenetical relationships, as they involve comparisons of species differing in a large number of biological and ecological traits. On the other hand, this approach has the merit to provide a general framework for the study of *trade-offs* in energy allocation.

To maximise their reproductive success, parasitoids are expected to approach a good match between the number of eggs they carry and the environmental host availability. Habitat variability however necessarily precludes any perfect match between egg load and host availability (Rosenheim 1996, Sevenster *et al.* 1998). A large body of theory, developed for *proovigenic* species, investigated conditions in which parasitoid females are more likely to become time- or egg-limited, *i.e.* to die with remaining eggs or having no more eggs and being still alived, respectively (Mangel & Clark 1988, Rosenheim 1996, Mangel & Heimpel 1998, Rosenheim *et al.* 2008). These models have proven useful to understand the selective factors acting on egg load evolution in parasitoids. However, *proovigeny* seems to represent more the exception than the rule among parasitoids (Jervis *et al.* 2001). *Proovigenic* models predicting time- or egg-limitation in different contexts and their influence on host-parasitoid population dynamics are therefore not applicable most of the time. Several developments of dynamics methods considered that *synovigeny* can minimise both time- and egg-limitation (Ellers *et al.* 2000), but also results in transient egg limitation because of the delay taking place to mature additional eggs (Heimpel & Rosenheim 1998, Casas *et al.*

⁶ When attacked by a koinobiont parasitoid, the host continues to develop and remains active, but arrests development when attacked by an idiobiont one.

Section 1. Chap II. Literature analysis

Table 2. Expected and/or observed correlations between the *ovigeny index* (OI) and different life-history or nutritional strategies among parasitoids.

OI=1 <i>Proovigeny</i>	OI=0 <i>Synovigeny</i>	Explanation	Proven or not
Small body size	Large body size	Small organisms show a higher mortality probability and should consequently concentrate their reproduction early in life.	Proven by Ellers and Jervis (2003), Jervis <i>et al.</i> (2003), Jervis and Ferns (2004).
Low lifespan	High lifespan	The important initial allocation of resources to oogenesis in <i>proovigenic</i> organisms most likely occurs at the expense of metabolic energy storage.	Proven by Boggs (1986, 1997b), Jervis <i>et al.</i> (2001, 2003, 2007).
No host-feeding	Host-feeding (more generally, reliance on external nutrient input during adult stage)	In a <i>synovigenic</i> organism, a large amount of incoming nutrients may be required, since nutrients are needed for both reproduction and maintenance, whereas in a <i>proovigenic</i> one, only maintenance needs to be fuelled (Flanders 1950).	Not proven by Jervis <i>et al.</i> (2001).
No egg resorption	Egg resorption	Resorption should be associated with a long lifespan since it precludes oviposition and is a time-consuming process (Jervis & Kidd 1986).	Proven by Jervis <i>et al.</i> (2001).
Hydropic eggs	Anhydropic eggs	Only anhydropic eggs are useful to resorb, and are associated with host-feeding behaviour since they contain large amounts of nutrients.	Proven by Jervis <i>et al.</i> (2001), Jervis and Kidd (1986).
Koinobiont	Idiobiont	Koinobiont parasitoids typically have a low lifespan, a high oviposition rate and spend a longer period as pupae and have therefore more time to mature eggs (Mayhew & Blackburn 1999).	Proven by Jervis <i>et al.</i> (2001).
Certainty in reproductive opportunities	Uncertainty in reproductive opportunities	<i>Synovigeny</i> allows adjusting the reproductive output to the variation in host encounter (Ellers <i>et al.</i> 2000).	Jervis <i>et al.</i> (2001) argued that <i>proovigeny</i> is often associated with aggregated host distributions.

2000, Rosenheim *et al.* 2000). With a *Dynamic Programming* model (see the section ‘*Foraging Theory and Dynamic Modelling: Explicit links between physiology and behaviour*’ (p54) for the description of the method) assuming daily egg maturation and oviposition rates, Casas *et al.* (2000) for instance succeeded predicting the transient egg limitations observed at the end of each day in the parasitoid *Aphytis aonidiae* by Heimpel *et al.* (1998).

In this section we especially focused on parasitoid Hymenoptera. Lepidoptera also exhibit a wide range of ovarian dynamics: some species eclose as adults with the majority of their eggs already yolke, whereas other eclose with no eggs yolke (Dunlap-Pianka *et al.* 1977, Wheeler 1996). Boggs (Boggs 1986, 1997b) was actually the first to link the initial reproductive investment to the nutritional traits of adult butterflies. Jervis, Boggs and Ferns indeed published a paper to correlate butterflies’ *OI* to several of their life-histories (Jervis *et al.* 2005). The most striking parallel between Boggs’ studies and those of Jervis is found in the fact that *synovigenic* parasitoids should theoretically host-feed to sustain the protein demand of oogenesis, and that similarly, butterfly that have no eggs mature at emergence rely on pollen food sources in addition to the common nectar ones, which provide amino acids (see Jervis *et al.* (2001) p453 for a detailed comparison of Boggs’ predictions with parasitoids and section ‘*Relations between larval allocation and adult foraging*’ p63).

Egg maturation involves the incorporation of metabolic nutrients into eggs. Whether these nutrients originate from *income* or *capital* resources has been addressed in several studies.

2.3.3. Dynamics of nutrient incorporation into eggs

Boggs and Gilbert (1979) were the firsts, to my knowledge, to explore the dynamic allocation of *income* and *capital* nutrients in egg production. These authors used radioactive amino acids to test the assumption that in butterflies, male-donated nutrients contained in spermatophores are used by the female as metabolic substrates for both maintenance and reproduction. To label larval resources, they injected radioactive amino acids in parasitoid larvae, and to label the *income resources* from food, they provided adult females with a sugar solution containing radioactive proteins. They also labelled *income resources* originating from male-donated nutrients in spermatophores,

by providing adult males with a similar labelled food, and by mating them to females thereafter. They found that nutrients originating from spermatophores and larval-derived nutrients are both used for egg production. Because the radioactivity derived from spermatophores was still found throughout female body one week after mating, they hypothesised that male nutrients are also used for maintenance (Boggs & Gilbert 1979). In this study, different females were used to follow the incorporation of larval or *income* resources into the eggs, and only amino acids were considered. Later on, Boggs (1997a) explored the same issue, but combined the monitoring of larval and *income* nutrients in a same individual, and analysed both glucose and amino acid dynamics. To analyse on a single individual larval and *income* nutrient incorporation into eggs, either labelled carbon was provided in larval food or labelled hydrogen in adult food. This study revealed that for a nutrient available in adult food, such as glucose, *income reserves* are preferentially used over *capital reserves* for egg manufacture, and that for a nutrient that is scarce in adult food, larval reserves are used to a greater extent (Boggs 1997a). The biological realism of this study can however be criticised because amino acids were abundantly provided to adult females while they are not expected to find such large amounts in nectars on which they feed.

A radiotracer study has also been used in a host-feeding *synovigenic* parasitoid, *Dinarmus basalis*, to follow the incorporation of *income* proteins into eggs (Rivero & Casas 1999b). The authors provided adult females with a sugar solution containing radioactive amino acids and followed the dynamics of amino acids incorporation into eggs by sequentially providing hosts to the female and monitoring radioactivity in eggs laid. Their results demonstrated that the first egg laid by the female (the first host was provided immediately after the 1-hour feeding period) already contained *income* amino acids, and that every subsequent egg did as well, with a peak of incorporation occurring for the 10th egg, and a decline taking place thereafter (Rivero & Casas 1999b). In another study on the same species, both *capital* and *income resources* were followed (Rivero *et al.* 2001). The results suggested that larval resources are more used for growth and maintenance, and the nutrients acquired by the adults to produce eggs.

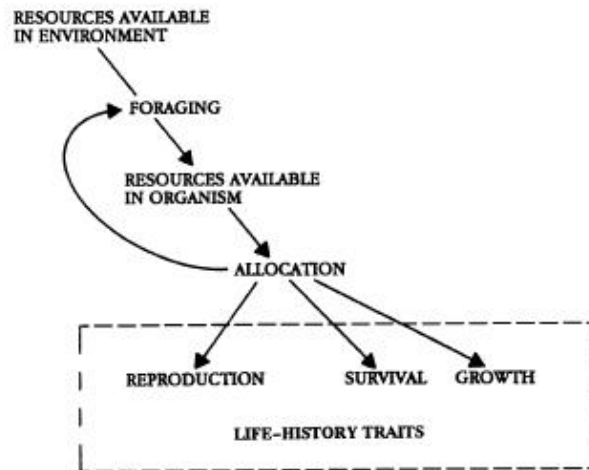


Figure 11. Boggs' synthetic linkage between foraging and energy allocation (from Boggs (1992)).

As we saw at different points in this section, the patterns of resource allocation cannot be considered independently of individual behaviour, foraging and environmental characteristics. The most direct evidence of a link between allocation strategies and behaviour is that food foraging profoundly modifies the amount of resource available, and therefore the amounts that will be allocated to reproduction and survival (Figure 11). As Boggs pointed out: *'[...] allocation of larval nutrient resources to reproductive reserves at metamorphosis may be predicted from knowledge of overall adult nutrient intake and reproductive output. This suggests an evolutionary interaction between patterns of resource allocation during metamorphosis and nutritional/life histories.'* (Boggs 1981a).

In the following section, we will explore the relationships between Insect energy allocation patterns and foraging and see how they may be affected by some environmental characteristics. We will see that foraging activities may incur costs and benefits, and generate *trade-offs* in term of current *versus* future reproduction.

3. Relations between foraging, environmental characteristics and energy allocation

We will see in this section that *Foraging Theory* and *Dynamic Programming* introduced explicit links between physiological variables such as the level of energy reserves, environmental characteristics and foraging behaviours. Then, I will present the benefits and costs associated with food foraging. Since foraging generally involves flight, which is the most expensive activity in Insects, I will also pay attention to the costs incurred by this activity. Lastly, we will see how these behaviours incur *trade-offs* between current and future reproduction in parasitoid Insects.

3.1. *Foraging Theory* and *Dynamic Modelling*: Explicit links between physiology and behaviour

Foraging Theory or *Optimal Foraging Theory* (or ‘*rate-maximization theory*’ according to Mangel 1989) broadly investigates how animals should forage so as to maximise their *fitness* (Bulmer 1994). This theory has mostly been developed by Emlen (1966), MacArthur and Pianka (1966) and Charnov (1976), and described in details in the book ‘*Foraging Theory*’ (Stephens & Krebs 1986). Classical models of *Foraging Theory* are of two types. In ‘Patch Models’, animals feed in patches that become depleted as they feed on and have to “decide” when it is most advantageous to leave the patch. These models come from the ‘Marginal Value Theorem’ which emphasised that animals should leave the patch when its energy gain falls below the average energy gain expected in the environment (Charnov 1976). The second types of models are the ‘Prey Models’. Here, animals have to decide which preys to include in their diet. In both model types, the optimal behaviour will be the one that maximises the net rate of energy gain.

Foraging Theory incorporated physiology in the sense that an individual gains a quantity of energy when a prey is consumed or a patch exploited, and losses energy by searching for preys or patches. In the most basic models presented above, animals are not constrained in their foraging activities. Several developments included different types of constraints (*e.g.* sequential prey encounter, prey recognition from varying

distances, incomplete information⁷, Stephens & Krebs 1986). Some nutrient types may contain essential nutrients, even if less profitable. A large number of foraging models also consider *trade-offs* between feeding and predator avoidance (e.g. Lima *et al.* 1985).

The foraging models described above are static in the sense that they consider constant probabilities of attack rate or patch leaving. The approach of *Dynamic Modelling* allows considering changes in animal state (e.g. energy reserves), animal experience or habitat characteristics. The assumption of a constant behaviour is therefore relaxed, and animals have the possibility to adjust their decisions regarding the change in these variables.

Dynamic Programming methods have been developed in 1975 by Bellman and applied to the study of foraging behaviour in the 80's (Houston & McNamara 1985, Mangel 1987, Houston *et al.* 1988, Mangel & Clark 1988, Mangel 1989). Dynamic models define a temporal set of optimal strategies by taking into account internal or external variables such as the level of energy reserves, the number of eggs carried or the probability of escaping from predation in the environment. They allow taking into account changes in animal and environment states – state variables – in response to foraging activities and foraging responses to state variables.

Dynamic foraging models commonly incorporate *trade-offs* since the choice between two activities is often a function of internal or external variables (Stephens & Krebs 1986). *Dynamic Modelling* has been for instance applied to the study of oviposition decisions in parasitoids. Host-feeding parasitoids feed from host materials that provide them with nutrients useful for both reproduction and maintenance (see section '*Effects of food*' p61). While in some species, the host used for feeding can be subsequently used for oviposition – feeding is '*non-concurrent*', in others it cannot, as host-feeding damages the host – here feeding is '*concurrent*' (Jervis & Kidd 1986). The latter species therefore face a *trade-off* between survival and reproduction: when a host is encountered, females have the options to feed on the host or to oviposit (see also section '*Trade-off between current and future reproduction*' p67). Theoretical investigations for instance put forward that females should host-feed when their energy reserves or egg load are low, or when the hosts are small (Houston *et al.* 1992, Chan &

⁷ Classical foraging models assume that foragers are omniscient, *i.e.* they have a perfect knowledge of prey encounter rates, profitability, *etc.*

Godfray 1993, Collier *et al.* 1994, Collier 1995a). The fact that *host-feeding* might provide nutrients only for reproduction, maintenance or for both has been taken into account by Chan and Godfray (1993) and Collier (1995a) and tested experimentally by Collier (1995b). The time delay in conversion of nutrients for egg maturation has been incorporated in the models of Collier *et al.* (1994) and Collier (1995a) and estimated empirically by Collier (1995b) and Rivero and Casas (1999b). A large number of experiments have also been designed to test the influence of physiological state and environmental variables on *host-feeding* behaviour (*e.g.* Heimpel & Rosenheim 1995, Heimpel *et al.* 1996, Ueno 1999). We will see in the section '*Trade-off between current and future reproduction*' (p67) that models have recently been applied to the study of the optimal choice between host and food foraging in non-host-feeding parasitoids.

Another set of questions addressed with *Dynamic Programming* methods is the optimal choice between accepting or rejecting a host that is already parasitised, and therefore of low quality, as eggs laid will have a reduced survival probability (*e.g.* Mangel 1989, Sirot & Bernstein 1997, Sirot *et al.* 1997).

We saw that internal variables such as the amount of energy reserves affect individual's foraging behaviours. In turn, foraging behaviours, mainly food foraging, influence both quantitatively and qualitatively animal's energetic budgets.

3.2. The role and importance of feeding

Feeding profoundly affects lifetime energy allocation patterns since it allows gaining *income resources* to counterbalance energy losses. In a first section, we will see that different food sources are available for Insects. Because their constitutions differ, they will allow replenishing different energetic compartments and will have different consequences in term of longevity, maintenance or reproduction. In a second section, we will see that some techniques allow determining Insects' dietary range, *i.e.* characterising the food sources exploited. Then, I will focus on the main effects of food. In a last section, we will see how feeding generally occurs at the expense of reproduction in parasitoids and explore associated *trade-offs* between current and future reproduction.

3.2.1. Food sources and their main properties

Here we will focus on the main food sources exploited by Insect parasitoids in the field: hosts, nectars and Homopteran honeydew (Jervis & Kidd 1986, Jervis *et al.* 1992), discuss and compare their main nutritional properties. We will also examine the potential role of pollen and leachates. Parasitoids can be separated in two groups regarding their nutritional life-history. Some of them resort to *host-feeding*, *i.e.* feed upon their hosts, and other do not and only rely on sugary food sources. The diet of *host-feeding* species is generally not limited to host materials, but also includes sugary food sources (Jervis & Kidd 1986).

Honeydew and floral nectar especially contain glucose, fructose and sucrose (Petanidou 2007). As mentioned in the section '*Role and importance of the different energy sources*' (p31), ingested sucrose, a fructose-glucose dimer, can be directly used to provide energy to the organism or stored into trehalose or glycogen for later use. According to some authors, sugar-feeding only provides energy for body maintenance (Rivero & Casas 1999a, see section '*Effects of food*' p61). Nectars and honeydew also contain free amino acids (Baker & Baker 1973).

Mevi-Schütz and Erhard (2005) works suggested that amino acids contained in nectars enhance butterfly fecundity and longevity. This view has been criticised by Jervis and Boggs (2005) and O'Brien *et al.* (2002), which emphasised the fact that essential amino acids utilised for oogenesis are for the most part derived from the larval stage. Both sugar and amino acid concentration extremely varies according to the plant species and seems to be related to the pollinator type (Baker & Baker 1973, Gardener & Gillman 2002, Petanidou 2007). It has been shown that plants pollinated by butterflies have high concentrations of free amino acids compared to plants pollinated by birds or bees (Gardener & Gillman 2002). Gardener and Gillman (2002) put forward a positive effect of amino acids in attracting pollinators and emphasised their contribution to the taste of the nectar rather than their nutritional value.

Honeydew and nectar sugars contain, in addition to the most common sugars: maltose, melibiose, melezitose, raffinose and erlose (Petanidou 2007). These sugars are

more common in honeydew and can reduce its suitability⁸ (Wäckers 2000). Empirical studies showed that these oligosaccharides do not elicit a feeding response in parasitoids (Wäckers 1999), and that they quickly crystallise compared to sucrose, making it difficult for parasitoids to feed on (Wäckers 2000). Lee *et al.* (2004) found that floral nectar increased life expectancy of *Diadegma insulare* up to three-fold more than aphid honeydew.

Here I would like to mention a potential food source for Insects that is rarely considered: plant leachates, *i.e.* exudates secreted on the surface of foliage in a large number of plants (Tukey 1971). Leachates may contain large amounts of carbohydrates (Tukey 1971, Mercier & Lindow 2000), and could thus provide a potential widespread food source for Insects. Sisterson and Averill (2002) observed Braconidae *Phanerotoma franklini* parasitoids feeding on leachates produced by cranberry leaves in the field. However, experiments designed to test the influence of leachates in *P. franklini* (Sisterson & Averill 2002) and *Rhagoletis pomonella* (Hendrichs *et al.* 1993) maintained wasps in presence or absence of foliage and did not clearly succeed demonstrating their role in enhancing longevity, probably because wasps were more active in presence of foliage.

Host-feeding is widespread among parasitic wasps. Most of the time, the host is punctured with the ovipositor or the mouthpart, and in some cases a feeding tube is constructed with the ovipositor to attain host haemolymph (Jervis & Kidd 1986). *Host-feeding* especially provides proteins and amino acids, and has been shown to provide limited amounts of lipids (Giron *et al.* 2002). *Host-feeding* is generally recognised to provide the nutrients used to mature additional eggs in *synovigenic* parasitoids (Jervis & Kidd 1986). It is also admitted that *host-feeding* provides nutrients for maintenance and enhances longevity in some parasitoids (Leius 1961, Jervis & Kidd 1986, Collier 1995b, see section '*Effects of food*' p61).

A parallel between sugary food sources on the one side, and protein and lipid-rich food sources on the other side is observed among butterflies. Butterflies' most common food sources are nectars which provide mainly carbohydrates, pollen which especially provides amino acids and spermatophore nutrients which are obtained by females

⁸ We will see in the next section '*Determination of insects' dietary range*' (p59) that melezitose has been used as a 'signature sugar' to assess if insects have fed upon honeydew, even if this has been recently criticised.

through copulation and provide lipids and amino acids. According to Jervis *et al.* (2001), pollen feeding is rare among parasitoid wasps and bears several disadvantages (Jervis 1998).

We will see in the next section that some techniques make now possible to precisely characterise the nutrients ingested by Insects.

3.2.2. Determination of insect's dietary range

Observations carried out in the field demonstrated that parasitoids acquire nectars by feeding on flowers (*e.g.* Jervis *et al.* 1993). *In natura* observations are somehow difficult to carry out, especially owing to the fact that parasitoids are small. Recent advances in nutrient detection with biochemical analyses now allow a precise characterisation of the feeding status of caught insects (Heimpel *et al.* 2004). We will focus in this section on sugar feeding for the main reason that it is relatively most difficult to characterise and quantify, and less documented compared to *host-feeding*.

As already mentioned in the section '*Role and importance of the different energy sources*' (p31), simple biochemical methods can be used to assess the concentration of sugars. The anthrone reagent specifically reacts with fructose when the reaction takes place at room temperature (van Handel & Day 1988). Because fructose originates from sucrose, which is specifically acquired from nectars or honeydews in the field, this technique allows assessing if feeding occurred (Jervis *et al.* 1992, Heimpel *et al.* 2004). If fructose is assayed just after a sugar meal, and before its potential conversion into glucose or more complex sugars, a precise estimation of the quantity of fructose acquired is possible.

Steppuhn and Wäckers (2004) criticised the use of these classical biochemical techniques to determine if feeding occurred and/or to explore its impact on nutrient dynamics (*e.g.* Olson *et al.* 2000, Casas *et al.* 2003, Lee *et al.* 2006). They argued that these techniques provide only limited information on the overall sugar composition and do not provide information on the food sources used because unable to identify every sugar. In their study they propose to use high-performance liquid chromatography (HPLC) to analyse parasitoids' sugar profiles (Steppuhn & Wäckers 2004). They proposed two parameters that, in combination, allow characterising the nutritional state and feeding history in the two Braconidae parasitoids *Cotesia glomerata* and *Microplitis*

mediator: the overall sugar level and the ratio of glucose to fructose. Indeed, they observed that overall sugar levels (glucose, fructose, sucrose, sorbitol, mannitol) were 5 to 10-fold higher in wasps *ad-libitum* fed on 70% water-diluted sucrose than in wasps only provided with water. In addition, they reported that the ratio glucose/(glucose+fructose) in newly emerged and unfed wasps was high, *i.e.* glucose was the most abundant sugar. This ratio dropped to lower levels because fructose levels increased, in fed females whatever their feeding history, *i.e.* fed during different periods or fed and subsequently starved (Steppuhn & Wäckers 2004, Figure 12). Similar results regarding the relative importance of fructose and glucose have been observed in Braconidae *Macrocentrus grandii* parasitoids *ad libitum* fed on 50% water-diluted sucrose or starved in the laboratory (Olson *et al.* 2000), and in *Venturia canescens* wasps that were food deprived, released in the field and recaptured (Desouhant *et al.* in prep). Whether sugar levels recorded in the laboratory realistically illustrate sugar contents of wild insects could be questioned, as in the studies previously mentioned, wasps were given *ad libitum* access to highly concentrated sugars. In their attempt to compare laboratory with semi-field conditions, Steppuhn and Wäckers (2004) maintained wasps into cages in the field but also provide them with *ad libitum* highly concentrated sugars. Casas *et al.* (2003) nevertheless recorded similar sugar levels in wasps fed with *ad libitum* pure honey and wasps released in the field and recaptured the same day in the parasitoid *Venturia canescens*.

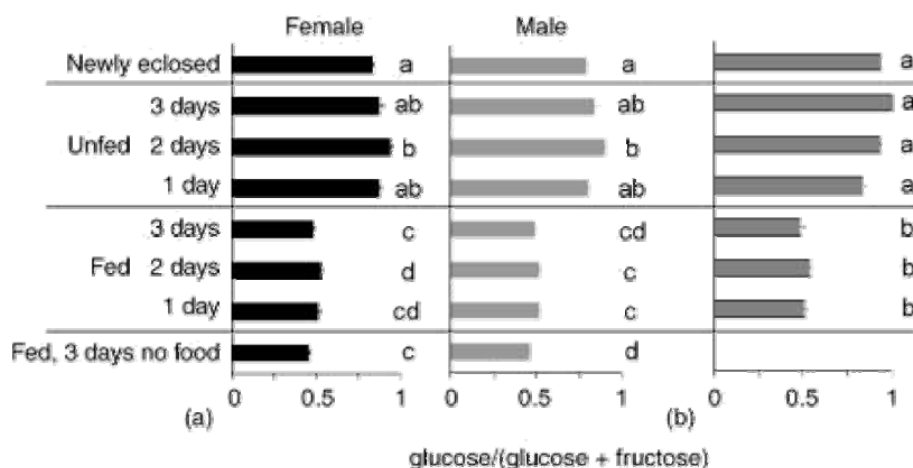


Figure 12. Ratio glucose/fructose in (a) *Cotesia glomerata* males and females and (b) *Microplitis mediator*, according to different feeding histories. Fed females were given *ad libitum* 70% water-diluted sucrose during 3, 2 or 1 days or during 2 days and were then starved during 3 days. Unfed ones were given only water. Graphs reproduced from Steppuhn & Wäckers (2004).

As previously mentioned, honeydew contains specific oligosaccharides such as melezitose that are synthesised by Homopteran, which have been used as ‘signature sugars’ until recently to determine if honeydew feeding occurred (Heimpel *et al.* 2004). However, a recent analysis of sugar profiles conducted on sucrose-fed Hymenopteran parasitoids *Diadegma semiclausum* and *D. insulare* revealed that these parasitoids are also able to synthesise melezitose (Wäckers *et al.* 2006). Because the ability to synthesise oligosaccharides seems absent in other parasitic wasps such as Braconidae (Steppuhn & Wäckers 2004), the authors hypothesised that *Diadegma* species have specific enzymes adapted to metabolise honeydew. Because Lee *et al.* (2006) put forward that the ratio glucose/(glucose+fructose) is higher in *Diadegma insulare* fed on honeydew compared to those fed on nectar, one may nevertheless use this ratio to determine if honeydew feeding occurred.

We saw that several food sources can be potentially used and that insect feeding status can be relatively easily assessed. In the following section, we will see what are the main effects of feeding on survival and reproduction.

3.2.3. Effects of food

Food influence on reproductive success has been widely investigated among several Insect taxa. In parasitoids, the influence of non-host food has been extensively studied to test whether the presence of food sources would improve parasitoids’ efficiency in the field and the success of biological controls (Jervis & Kidd 1996, Lewis *et al.* 1998). It is commonly assumed that non-host foods are mainly used for maintenance and host materials for egg production (Engelmann 1970, Jervis & Kidd 1986). According to Jervis and Kidd (1986), the fact that both sexes of *host-feeding* species consume non-host food (Leius 1961), but only females consume host materials (Onagbola *et al.* 2007), provides an evidence that non-host foods are used for maintenance and host materials for egg production. Indeed *host-feeding* is often associated with *synovigeny* and thought to be absent in most of the *proovigenic* parasitoids that do not need to mature additional eggs (Jervis & Kidd 1986).

A large number of investigations suggested that the main effect of the consumption of sugary foods is to enhance survival (*e.g.* Leius 1961, Fletcher *et al.* 1994, Heimpel *et al.* 1997, Ellers *et al.* 1998, Olson & Andow 1998, Olson *et al.* 2000, Sisterson &

Averill 2002, Tylianakis *et al.* 2004). For instance, the *host-feeding* parasitoid *Aphytis melinus* maintained without sugars has a life expectancy of approximately 3 days, even if allowed to host-feed, and of 17 days when provided with sugars (Heimpel *et al.* 1997). The non-host-feeding females *Venturia canescens* live approximately 3 days when deprived of food and 27 days when provided *ad libitum* or every 48h with 50 % water-diluted honey (Desouhant *et al.* 2005).

Studies clearly demonstrating a positive effect of sugars on egg maturation rates in parasitoids are scarce (but see Tylianakis *et al.* 2004, Bezemer *et al.* 2005).

In several studies, sugary food sources are presented as responsible of higher fecundities or oviposition rates. Most of these results should however be considered with care since they compare lifetime fecundities among fed and unfed wasps that differ in their life expectancy (Heimpel *et al.* 1997, Olson & Andow 1998, Bezemer *et al.* 2005). Tylianakis *et al.* (2004) nevertheless put forward that parasitism rates of the non-host-feeding aphid parasitoids *Aphidius rhopalosiphi* and *Diaretiella rapae* are positively affected by both floral resources in the field and sugary food sources in the laboratory. A similar observation has been reported in the parasitoid *Microplitis croceipes* in semi-field (Stapel *et al.* 1997) and field conditions (Takasu & Lewis 1995) and in the parasitoid *Diadegma insulare* in the field (Lee *et al.* 2006, Lee & Heimpel 2008).

To test and compare the suitability of naturally occurring sugars as food sources in parasitoids, Hausmann *et al.* (2005) provided 40% water diluted sugar solutions to Braconidae wasps *Cotesia glomerata* which have been starved, and measured their recovering time and longevity. Glucose, fructose, sucrose and melezitose provided the highest benefits, maltose, raffinose, galactose or mannose provided intermediate benefits, and melibiose, trehalose and rhamnose only limited benefits.

Host-feeding materials are used for maintenance in some parasitoid species, since they have the property to increase longevity (Leius 1961, Jervis & Kidd 1986, Collier 1995b, Onagbola *et al.* 2007). It has been suggested that *host-feeding* has the property to enhance longevity only in the presence of sugars (Bai & Smith 1993, Heimpel *et al.* 1997).

As previously mentioned, *host-feeding* mainly appears to provide nutrients that are not found in sugary food sources such as proteins and lipids, and that are generally useful for egg maturation. Among host-feeding parasitoids, a distinction can be made between parasitoids that need to host-feed to mature eggs and therefore to oviposit, the ‘*anautogenous*’, and those that are able to lay eggs without feeding on hosts first, the ‘*autogenous*’ (Jervis & Kidd 1986). In *anautogenous* parasitoids, it seems obvious that the nutrients derived from hosts are used for egg maturation.

Host-feeding has been positively linked to the egg maturation rate in several studies (e.g. Heimpel *et al.* 1997, Rivero & West 2005). Heimpel *et al.* 1997 for instance observed that among wasps fed with honey, those that had the possibility to host-feed matured more eggs than those that had not.

In this section I focused on the benefits incurred by feeding. Feeding nevertheless also incurs costs. Parasitic wasps feeding on sugars have been shown to subsequently demonstrate a period of inactivity (Lee & Heimpel 2007, Desouhant personal observation). It is therefore most probable that feeding exposes wasps to a higher probability of predation, as suggested by Sirot and Bernstein (1996). Feeding on a host may also be costly when host-feeding is *non-concurrent*, i.e. the host used to feed is used for oviposition (Rivero & West 2005).

We saw that food availability may have important consequences on reproductive success, since it can affect both reproduction and longevity. In the next section we will see how food foraging may affect the patterns of energy allocation.

3.2.4. Relations between energy allocation and food foraging

To my knowledge, few studies directly investigated the relationships between food foraging and energy allocation. A body of literature focused on the relationships existing between the initial patterns of allocation observed at adult emergence in holometabolous Insects and the nutrient intake of adults. Other evidences come from the effects of resource shortage on reproduction and longevity.

As mentioned in the section ‘*Extension of the concepts of income and capital breeders to the study of the relative importance of stored and nutritional resources*’ (p36), the allocation strategies adopted during the larval stage in holometabolous Insects

may reflect adult reliance on food sources. When the probability to get additional resources to fuel reproduction during adult stage is low, a large amount of energy is expected to be allocated to reproduction. We saw in the section ‘*Lifetime egg dynamics*’ (p47) that the *ovigeny index (OI)* – the proportion of the total number of eggs produced that are mature at emergence – has been linked to adult energy intake. In parasitic wasps, *proovigenic* species emerge with their full egg complement mature upon emergence. These species are generally those that do not resort to *host-feeding*, since they theoretically do not need *income resources* to mature additional eggs (Jervis *et al.* 2001). In the same manner, both pollen feeding – which provides amino acids that are scarce in nectars – and mating rate – mating allowing females to incorporate spermatophore-derived nutrients – are positively correlated with low *OI* in butterflies (Boggs 1997b, Jervis *et al.* 2005).

The relationships between larval energy allocation and adult food intakes have been tested and confirmed by comparing butterfly species showing distinct *OI* and adult diets (Boggs 1981a, 1990, May 1992, Boggs 1997b). They have also been linked to the lifetime age-specific fecundity patterns by Boggs (1986, 1997b) (Figure 13). The idea is that when a large number of mature eggs is available at emergence and no food can be used by the adult to mature additional eggs, fecundity should be concentrated in the first days of life and should rapidly decline. On the other hand, when few mature eggs are available and food is acquired by the adult to mature additional eggs, fecundity is expected to be spread all along lifetime. These predictions have been confirmed by the comparative analysis of three butterfly species differing in their *OI* and adult diets (Boggs 1997b). It has also been demonstrated in a butterfly species having no mature eggs at emergence that longevity is favoured at the expense of fecundity when the quantity of food is reduced (Boggs & Ross 1993).

By limiting the amount of resources available at metamorphosis, Stevens *et al.* (2000) put forward that in caddis flies, the patterns of energy allocation at metamorphosis are different in short- and long-lived species. The short-lived species appears to favour the allocation of resources to the abdomen, and therefore to the reproductive apparatus, and the long-lived species to somatic maintenance in the thorax. This result suggests that short-lived species favour the maximisation of early reproduction at the expense of longevity. Interestingly, larval and adult food limitation may have different impacts on reproductive success. In a study investigating energy

allocation patterns in a butterfly, it has been shown that larval food limitation has the sole effect of reducing adult longevity, and adult food limitation the effect of reducing fecundity (Boggs & Freeman 2005).

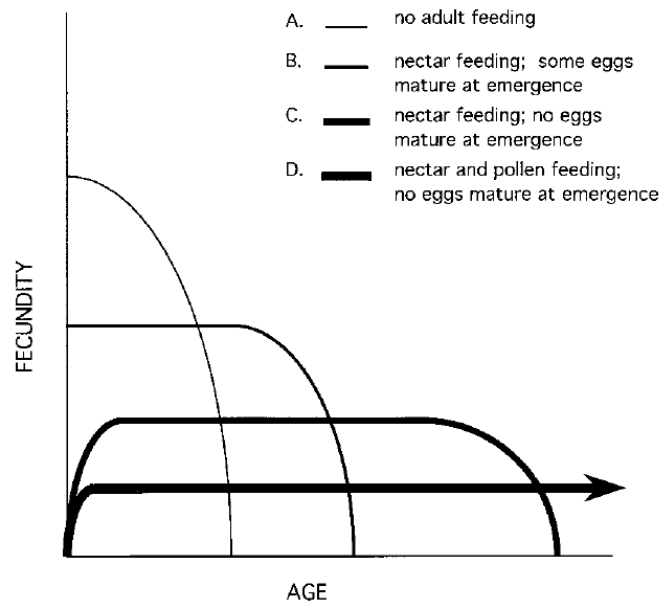


Figure 13. Boggs synthesis on age-specific fecundity in Lepidoptera species (Boggs 1986). The shape of the fecundity function is assumed to be the result of the potential importance of adult nutrients into reproduction, defined as the relative quality of adult diet and the proportion of eggs mature at adult emergence (graphs reproduced from Boggs (1997b)).

We saw in this section that several benefits may be associated with food foraging. Nevertheless, foraging in the field generally involves flight, which is a highly expensive activity.

3.4. The costs of locomotion

Flight is the most expensive activity in Insects. Flight is often under-considered in studies of energy allocation, while large amounts of metabolic energy have to be directed to flight. The metabolic rate of a honeybee, corrected by its mass, is for instance 3 times higher than the metabolic rate of a hovering hummingbird, and 30 times higher than in a human in maximum activity (Nation 2002). Flight is primarily made possible in Insects by their tracheal system: oxygen is rapidly and directly provided to the muscles through the trachea. The highly specialised mitochondria also allow supporting high metabolism rates (Candy *et al.* 1997).

It is generally assumed that Dipteran and Hymenopteran mainly use carbohydrates to fuel their flights, and that Lepidopteran and Orthopteran that fly over longer distances use lipids (*e.g.* Candy *et al.* 1997, Nation 2002).

Trehalose appears to be the main flight fuel used by Insects (Candy *et al.* 1997). Trehalose can originate from the glycogen stored in the fat body. In Hymenopteran such as the ant *Solenopsis invicta* or the orchid bee *Euglossa imperialis*, carbohydrates like glycogen are used (Vogt *et al.* 2000, Suarez *et al.* 2005). When performing 3 minutes-flights, the parasitoid females *Cotesia rubecula* mainly use carbohydrates (Siekman 2002). During longer flights of 17 min, the Coleopteran *Decapotoma lunata* uses proline and glycogen (Auerswald & Gäde 1995). In the mosquito *Aedes aegypti*, flying over several kilometres induces a 30 %-diminution of glycogen reserves and 9 % of lipids (Briegel *et al.* 2001).

Proline, a common free amino acid circulating in Insect haemolymph seems to play a major role in flight. Proline allows the transfer of energy from the fat body through the haemolymph to the flight muscle (Scaraffia & Wells 2003). Proline appears to play a role in flight in beetles or tsetse fly (Bursell 1963, Nation 2002). Proline has also been demonstrated to fuel flights in the mosquito *Aedes aegypti* (Scaraffia & Wells 2003).

It has been suggested that parasitoid females *Asobara tabida* fed with honey use lipids to fuel their flights. In a field experiment, the level of lipid reserves appeared to be positively correlated with flight capabilities and the females caught in the furthest recapture sites were the one showing the lowest lipid levels (Ellers *et al.* 1998). In *Aphis fabae*, flight performances also appear to be positively correlated to lipid levels (Cockbain 1961). In the Hemipteran *Holopterna alata*, lipids also seem to be used during 3 minutes-flights (Gäde *et al.* 2006). Lipids as well as triglycerides also play critical roles in flight in *Gryllus firmus*, since they are present in higher quantities in the long-wing morph (Zhao & Zera 2002, Zera & Zhao 2006). The inconvenient of using lipids to fuel flight is that lipids that are stored in the fat body have to be transported through the haemolymph to the flight muscles. Because the haemolymph is aqueous, lipoproteins available in the haemolymph, the lipophorins, are mobilised to transport lipids (Nation 2002).

In *Aphis fabae*, a switch in the substrate used has been recorded: aphids appear to use first their carbohydrate reserves, and to switch to lipid reserves after 1 hour of flight (Cockbain 1961).

Even if the utilisation of specific flight fuels seems well documented in several Insect species, O'Brien (1999) suggested that it may be sometimes hazardous to draw generalities. The nutritional and life-histories most likely affect flight metabolism. In a study of flight in the Lepidopteran *Amphion floridensis*, butterflies fed with nectars indeed appear to preferentially use carbohydrates for flight, and starved ones lipids. Some Hymenopteran parasitoid species are for instance known to disperse over important distances (Godfray 1994). This species may need to switch from carbohydrate to lipid or protein metabolism.

While food foraging allows enhancing survival and therefore future reproduction, foraging for hosts allows enhancing current reproduction. We will see in the next section that these two activities are often mutually exclusive in parasitoids and that compromises in the investment to each of them are most likely to arise.

3.5. *Trade-off* between current and future reproduction

We saw that to increase their future reproductive output, parasitoids need to successfully find and exploit food sources. On the other hand, to gain immediate *fitness* rewards, they have to successfully find and attack hosts. These two activities – host and food foraging – are mutually exclusive since the time allocated to one activity is lost for the other, and will be referred as the *trade-off* between host and food foraging. The intensity of this *trade-off* is different whether we consider *host-feeding* or *non-host-feeding* parasitoids. Food and host foraging are intimately linked for *host-feeding* parasitoids, since the hosts may constitute food resources. Nevertheless, as previously mentioned, feeding on a host may either mean losing an opportunity to oviposit, or decreasing host quality and therefore potentially reducing offspring *fitness*. In parasitoids feeding on sugary substances, food sources are sometimes associated to hosts. For instance, parasitoids attacking aphids may have the possibility to feed on the honeydew produced by their hosts (Jervis & Kidd 1996). But in the majority of cases, food and host sources are spatially separated in *non-host-feeders* (Jervis & Kidd 1995). In such cases, the time allocated to food searching can clearly not be allocated to host

searching. The time spent exploiting food sources may be important. *Phanerotoma franklini* parasitoids have for instance been reported to spend 25% of their time grazing on leachates at the surface of plant foliage (Sisterson & Averill 2002).

The *trade-off* between host and food foraging has been relatively largely investigated in *host-feeding* parasitoids (see section '*Foraging Theory and Dynamic Modelling: Explicit links between physiology and behaviour*' p54). By modelling the optimal decision between host-feeding or ovipositing, Mangel and Clark (1988), Houston *et al.* (1992), Chan and Godfray (1993), Collier *et al.* (1994) and Collier (1995a) suggested that depending on the costs and benefits of host-feeding, the female will either lay an egg or feed on the host. All these models for instance predict that hosts should be used for oviposition when female energy reserves or egg load are high or when the host is of good quality. These predictions have been tested and confirmed in the laboratory and in the field (Collier 1995b, Heimpel & Rosenheim 1995, Heimpel *et al.* 1996, Rivero & Casas 1999b, Ueno 1999).

Dynamic modelling approaches have also been used to investigate the factors affecting the optimal decision between host and food searching in *non-host-feeding* parasitoids (Sirot & Bernstein 1996, Tenhumberg *et al.* 2006, Bernstein & Jervis 2008). These models suggest that the optimal decision between these two activities is in part affected by the level of energy reserves: females are predicted to search for food when their energy reserves fall below a certain threshold (Sirot & Bernstein 1996, Tenhumberg *et al.* 2006, Bernstein & Jervis 2008).

This prediction has been largely verified experimentally. *Non-host-feeding* parasitoids are known to learn and preferentially respond either to host- or food-associated cues depending on their nutritional state (Lewis & Takasu 1990, Wäckers 1994, Lewis *et al.* 1998). Lewis and Takasu (1990) for instance designed an experiment in which wasps were trained to associate odours with hosts and food, and were then given the choice between the two odours in a flight tunnel. This work demonstrated that hungry wasps preferentially respond to the odour associated with food, and fed wasps to the odour associated with hosts (Figure 14). Desouhant *et al.* (2005) have shown that *V. canescens* females are also able to respond to both food- and host-associated cues depending on their nutritional state, in the laboratory and in the field. In particular, they appeared to prefer cues associated with both host and food sources to cues indicating a

single resource, probably because the association of the two resources allows minimising travel costs.

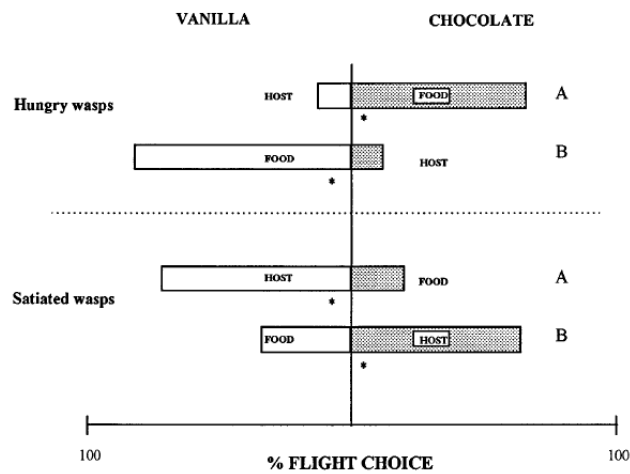


Figure 14. Responses of hungry and satiated wasps *Microplitis croceipes* in a flight tunnel to vanilla and chocolate odours. Females were trained to associate one of the two odours to host and food sources (from Lewis & Takasu 1990).

Dynamic models suggested that the second preponderant factor affecting the optimal choice between host and food foraging is food availability. While Tenhumberg *et al.* (2006) suggested that parasitoids should always feed when their energy reserves are low, even if the probability to find food in the environment is very low, Sirot and Bernstein (1996) put forward that parasitoids should not feed if they have no chance to find food in the environment. Tenhumberg *et al.* (2006) suggested that these differences might come from the fact that they introduced more biological realism in their model compared to Sirot and Bernstein (1996). For instance, rather than considering a constant energetic gain associated with feeding, as in Sirot and Bernstein (1996), they considered a probability function giving the energetic values of energy sources. To test this assertion, Bernstein and Jervis (2008) incorporated in a model comparable to Sirot and Bernstein (1996) model the parameter values chosen by Tenhumberg *et al.* (2006). As Tenhumberg *et al.* (2006), they predicted that parasitoids should search for food even when the probability to find food is low. The differences between the two models therefore seem more attributable to the model parametrisation than to the model structure in itself. Bernstein and Jervis (2008) underlined that in Tenhumberg *et al.* (2006) model, a single meal for instance allows parasitoids sustaining a six times-longer period of activity than in Sirot and Bernstein (1996) model.

I am aware of a single study suggesting that when the probability to find food in the field is low, parasitoids should invest extra time into host foraging. In a field study, *Microplitis croceipes* females provided with honeydew have been demonstrated to invest more time into host foraging compared to females provided with sucrose or nectar (Stapel *et al.* 1997). The authors emphasised that honeydew is typically a low quality-food source which is more scattered than other food sources in the field. This observation strengthens Sirot and Bernstein (1996) assumption that parasitoids should only forage for hosts if the probability to find food in the environment is low.

Bernstein and Jervis (2008) considered egg dynamics as another variable susceptible to influence host and food foraging behaviours (Figure 15). They particularly compared situations reflecting either *proovigeny* or *synovigeny*. They assumed that parasitoid energy reserves can be separated into *metabolic reserves* (*MRs*, sugars and glycogen) and *egg production reserves* (*EPRs*, lipids and proteins). In their model, food allows replenishing *MRs* only, *MRs* can be used for maintenance purposes only, *EPRs* can not be synthesised from *MRs* and *EPRs* can be used for both maintenance and reproduction. In the *proovigenic* model, *EPRs* are not considered because assumed to have been completely converted into eggs during the larval stage. On the other hand, *EPRs* and eggs are pooled in the *synovigenic* model, which allows wasps allocating their *EPRs* either to the maturation of additional eggs or to sustain their metabolic needs. The comparison of the two models suggests that food searching is less likely in *synovigenic* wasps, because in this case, parasitoids can resort to a ‘last resort’ strategy by converting their *EPRs* in maintenance. This observation seems at odd with the prediction made in the section ‘*Lifetime egg dynamics*’ (p47) that *synovigenic* parasitoids should rely more on external nutrients – are more prone to be *host-feeders* – compared to *proovigenic* parasitoids. The difference comes from the fact that in Bernstein and Jervis (2008) model, a *non-host-feeding* situation in which *income nutrients* can be used for maintenance only is depicted, while in the section ‘*Lifetime egg dynamics*’ we considered that *income nutrients* are directed to both maintenance and egg maturation in *synovigenic* parasitoids, and to maintenance only in *proovigenic* ones.

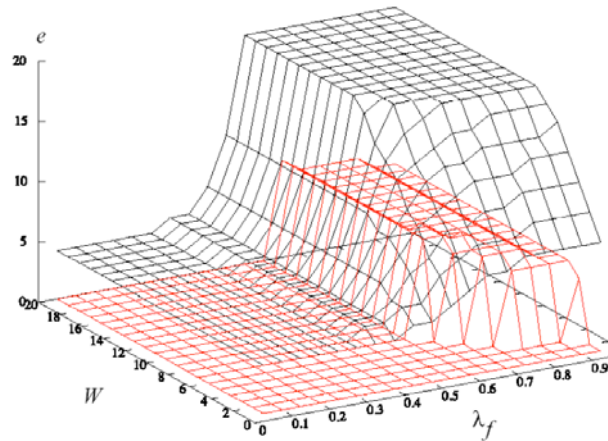


Figure 15. Optimal decisions between host and food foraging as a function of the level of energy reserves e , the number of eggs W and the probability to find food in the environment λ_f . When their energy reserves are above the upper surface, parasitoids should search for hosts. When the energy reserves fall between the two surfaces, the parasitoid should keep on with their activity (either searching food or hosts), and when they fall below the lower surface, parasitoids should start searching food (from Bernstein & Jervis (2008)).

Here I would like to add that the three models previously described assume that foragers are omniscient: they are aware of the probability to find food in their environment for example. This assumption appears consistent with the fact that *Venturia canescens* females are able to perceive the presence of food in their environment when they are foraging for hosts, and that they modify their host-patch exploitation behaviour in response to these cues (Lucchetta *et al.* 2007).

From now, this literature analysis mainly focused on the mechanisms underlying *trade-offs* in energy allocation and on how *trade-offs* can be used to assess the optimal strategies that should be adopted at the individual level. In the following section, we will see that *trade-offs* may also play important roles in the structuring of populations and communities, and may facilitate species coexistence.

4. Role of *trade-offs* in population dynamics and community structuring

In this section, I will briefly review the role of *trade-offs* in population dynamics and community structuring. Because the literature on this topic is vast, I chose to focus first on the consequences of *trade-offs* on the dynamics of host-parasitoid populations. Because the question of the influence of *trade-offs* on coexistence has been relatively overlooked in host-parasitoid systems, I will then give more general examples on the role life-history *trade-offs* or *trade-offs* in resource exploitation can have on species coexistence.

4.1. The role of the *trade-off* between current and future reproduction in host-parasitoid population dynamics

A relatively large body of literature has focused on the factors affecting host-parasitoid population stability. For instance, *interference*, *i.e.* a process by which parasitoid females become less efficient as their density on a patch increases, is well-known to have the property to stabilise host-parasitoid systems (*e.g.* Hassel & May 1973). More generally, a vast number of density-dependent factors that lessen the attack rate of parasitoids when hosts are scarce, has been assumed to play a role in the stabilisation of host-parasitoid populations (Bonsall & Bernstein 2008).

The role of the *trade-off* between current and future reproduction in the stabilisation of populations has been relatively well studied in *host-feeding* parasitoids. The effect of the behaviour of *host-feeding* in host-parasitoid population dynamics has been first investigated by Kidd and Jervis (1989). These authors, followed by Kidd and Jervis (1991) and Briggs *et al.* (1995) put forward that *host-feeding* in itself does not affect population stability. Host-parasitoid population models incorporating *synovigeny* and *egg resorption* however provide evidence that the fact that nutrients acquired through host-feeding are directed to parasitoid maintenance and has a destabilising effect on populations (Kidd & Jervis 1989, Briggs *et al.* 1995). This effect may come from the fact that when hosts become scarce, parasitoids have the possibility to resorb their eggs to increase their longevity. By introducing the optimal host-feeding behaviour in a host-

parasitoid population model, Krivan (1997) nevertheless suggested that non-destructive *host-feeding*, *i.e.* when the host does not die after *host-feeding*, may have a stabilising effect on population dynamics.

The stabilising effect of the *trade-off* between current and future reproduction has been largely less explored in *non-host-feeding* parasitoids, the only exception being the works of Sirot and Bernstein (1996) and Krivan and Sirot (1997). Sirot and Bernstein (1996) modelled a ‘State-Dependent Ideal Free Distribution’ (SDIFD, McNamara & Houston 1990) based on their dynamic programming results (see section ‘*Foraging Theory and Dynamic Modelling: Explicit links between physiology and behaviour*’ p54) and suggested that the presence of parasitoids on the food patch has a stabilising effect on the host-parasitoid population. Krivan and Sirot (1997) designed a host-parasitoid population model and confirmed that sharing time between host and food searching may have a stabilising effect on the dynamics of populations. The stabilising effect may come from the fact that when hosts are abundant, most of the parasitoids search for hosts, and when hosts become scarce, parasitoids prefer searching for food (Sirot & Bernstein 1996, Krivan & Sirot 1997).

In this section we saw that *trade-offs* in behaviour can affect the structure of populations. Here, only *trade-offs* at the intraspecific level has been considered. We will see in the next section that *trade-offs* can also play a role in community dynamics at the interspecific level. More precisely, we will see that adopting different strategies regarding *trade-offs* in life-history traits or resource utilisation may have the property to reduce interspecific competitive interactions and therefore to favour species coexistence.

4.2. Role of *trade-offs* in community structuring

Understanding how species interact and the factor facilitating their coexistence is the core of community ecology. At a regional spatial scale, the most studied mechanisms allowing species coexistence are *trade-offs* between competition and dispersion or colonisation of empty patches (*e.g.* Levins & Culver 1971, Hastings 1980, Nee & May 1992, Tilman 1994). The idea is that a spatial niche separation directly limits interspecific competitive interactions. Here we will focus on the mechanisms facilitating

coexistence at a local spatial scale. Locally, coexistence can typically take place when the competitors exploit different resources. When the same resource is utilised by both competitors, differences in foraging behaviours or life-history traits, for instance between competition and longevity, may favour coexistence. Because in such cases, one species maximises a specific trait and the other species another trait, Kneitel and Chase (2004) referred to this mechanism as *interspecific trade-offs*.

The mechanisms of species coexistence can be investigated with *Adaptive Dynamics* theory. In the following section, I will provide a few elements to understand the most basic concepts of the theory (for a detailed explanation of the method, see the paper of Geritz *et al.* (1998)).

4.2.1. Adaptive Dynamics: A powerful approach to explore evolutionary stability and coexistence

Adaptive Dynamics is a powerful approach to explore the dynamics of phenotypic changes on the long term (Geritz *et al.* 1998). This theory has been developed in the 90's by Metz *et al.* (1996) and Geritz *et al.* (1997, 1998). *Adaptive Dynamics* is based on game theory concepts such as the Evolutionary Stable Strategy (ESS, Maynard Smith 1982), as well as concepts of population genetics and population dynamics. The basic principle of the method is that if a resident population constituted of individuals showing a strategy x can be invaded by a mutant showing a strategy x' with $x' > x$, then the strategy will tend to increase over the course of evolution. To determine if a mutant is able to invade the resident population, the *invasion fitness*, *i.e.* the growth rate of the mutant in the resident population, is computed (Metz *et al.* 1992). *Adaptive Dynamics* typically makes the assumption that mutations are rare and that the evolutionary timescale – in which changes in the value of the strategy are observed – is very large compared to the ecological timescale – in which variations in the density of the population are observed. In practical, this means that mutants will be assumed to arise in the resident population which is at its demographic equilibrium. The *Adaptive Dynamics* approach allows finding fixed points in the evolution, or *evolutionary singular strategies*, and precisely characterising their evolutionary properties. The necessary information to assess the properties of *evolutionary singular strategies* can be summarised in *pairwise invisibility plots* (Geritz *et al.* 1998). These graphs represent the sign of the *invasion fitness* according to the values of the resident and mutant strategies

(Figure 16). *Adaptive Dynamics* for instance allows assessing whether an ESS can be reached or not over the course of evolution (property of convergence-stability), which is an advantage over classical game theory.

The success of *Adaptive Dynamics* theory is for the most part attributable to its ability to find events of *evolutionary branching*, which are defined as processes of phenotypic divergence in an initially monomorphic resident population (Geritz *et al.* 1998). *Evolutionary branching* suggests that coexistence is evolutionary stable and is attainable through the process of evolution. This powerful tool is the focus of the majority of the applications of *Adaptive Dynamics*. The property of *evolutionary branching* is verified when an evolutionary singular strategy is convergent-stable: evolution will converge to this point, but not ESS-stable: when the point is reached, mutants have the possibility to invade and a polymorphism therefore arises (Figure 17).

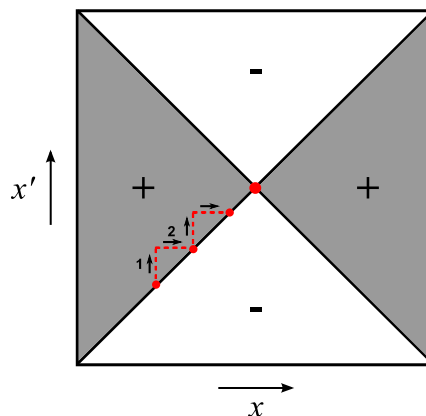


Figure 16. *Pairwise invasibility plot*: Sign of the *invasion fitness* according to the resident and mutant traits x and x' . Grey areas correspond to positive *invasion fitness* and white areas to negative *invasion fitness*. Since mutations are assumed to be small, the main diagonal $x=x'$ will be considered. Mutants can invade only in areas where the *invasion fitness* is positive. 1: A mutant having $x' > x$ successfully invades. 2: The resident strategy therefore increases. Step by step, the trait will evolve toward the evolutionary singular strategy represented by a large red dot. This strategy cannot be invaded by any mutant since when the resident trait is at this point, the *invasion fitness* is negative whatever the mutant strategy. This evolutionary singular strategy is therefore both ESS- and convergent-stable.

In the following section, we will see how *trade-offs* in resource exploitation or life-history *trade-offs* have the property to facilitate species coexistence. Most of the examples depicted below used the *Adaptive Dynamics* framework and sought *evolutionary branching* to assess if evolutionary stable coexistence can take place. I would not go further into the details of the methods employed because they involve

relatively complicated mathematical techniques. For a detailed illustration of the method, see Section 2 – Chap III (p157).

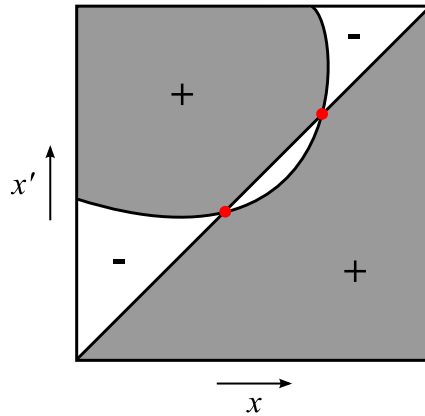


Figure 17. *Pairwise invasibility plot* illustrating *evolutionary branching*. The evolutionary singular strategy on the right is convergent-stable and will therefore be reached over the course of evolution through small step-mutations. Contrary to the example depicted in Fig 16, this singular strategy is not ESS-stable, which means that every nearby mutant can invade. A dimorphism or *evolutionary branching* will therefore arise at this point.

4.2.2. *Trade-offs in resource exploitation, life-history trade-offs and coexistence*

When the nutritional resource is structured, and when competitors demonstrate different acquisition strategies for this resource, coexistence is likely to occur (Vincent *et al.* 1996, Abrams & Holt 2002, Kisdi & Liu 2006). The most famous example of such coexistence comes from a gastropod – microalgae system where two gastropod species differ in their foraging behaviours. While ‘diggers’ thoroughly exploit resources and therefore show a higher food intake at low resource availability, ‘grazers’ exploit a larger area of resources per unit of time but only partially deplete them, which would favour them at high resource densities (Schmitt 1996). The models of Wilson *et al.* (1999), Richards *et al.* (2000) and Wilson and Richards (2000) have suggested that such a *trade-off* in foraging behaviour, together with spatial variations in the density of food patches, might explain the coexistence of the two competitors. Differences in predator handling time, *i.e.* time needed to handle and consume a prey, because they result in differences in the level of resource extraction, have also been suggested to favour coexistence of predators in predator-prey systems (Abrams & Holt 2002, Kisdi & Liu 2006).

Consumer – resource models, that is models in which consumers generally compete for two substitutable nutritional resources, have been vastly used to explore the evolution of specialists and generalists, and the conditions favouring their coexistence. Levins (1962) was the first to exploit this idea. As previously described (see section ‘*Levins’ fitness set and Cody’s ‘Principle of Allocation’*” p21 of the literature analysis), Levins considered that the competitor efficiencies in the two habitats are negatively correlated in a *fitness set* and that the shape of this function determines if evolution will tend to produce one generalist or two specialists (Levins 1962, 1968). This approach has been applied to the study of the impact of various *trade-offs* in foraging efficiency in the two habitats (*e.g. trade-offs* in searching efficiency, in carrying capacity, in capture probability or handling time) on the coexistence of generalists and specialists on two resources (Figure 18). The main results deriving from this large literature are that: (i) variability in consumer carrying capacities may favour coexistence (*e.g.* Kisdi 2002, Egas *et al.* 2004), (ii) coexistence seems facilitated by strong *trade-offs* (*e.g.* Egas *et al.* 2004, Diekmann *et al.* 2005, Rueffler *et al.* 2006), and (iii) coexistence may be mediated by the nature of the *trade-off*, *trade-offs* in capture probability or search efficiency being good candidates to facilitate coexistence (Vincent *et al.* 1996, Rueffler *et al.* 2006).

Trade-offs involving competitive ability and other life-history traits, such as attack rate or longevity, have also been suggested to play a key role in species coexistence. Amarasekare (2000) for instance empirically investigated the coexistence of two competing parasitoid species in the field and suggested that it could be favoured by the higher ability to find unparasitised hosts of the inferior competitor. How *trade-offs* involving competitive ability affect species coexistence has been theoretically investigated by Bonsall *et al.* (2002), Bonsall *et al.* (2004), Bonsall and Mangel (2004) and Bonsall and Bernstein (2008). For instance, interspecific competition between two parasitoid species sharing a common host has been suggested to be reduced by *trade-offs* between larval competitive ability and adult longevity or ability to paralyse hosts (Bonsall *et al.* 2002).

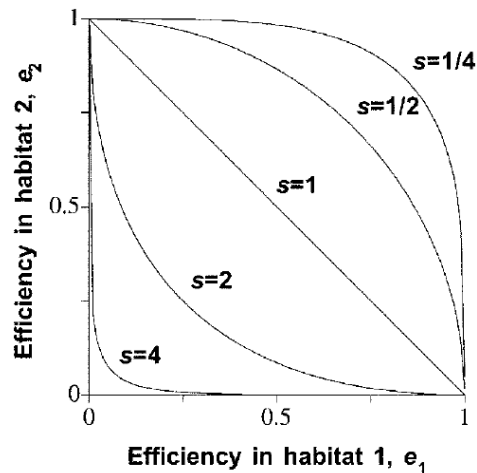


Figure 18. *Trade-off* shape for different values of the *trade-off* strength s . The *trade-off* function is given by: $(e_1)^{1/s} + (e_2)^{1/s} = 1$. Convex *trade-offs* with $s < 1$ are termed *weak*, and concave *trade-offs* with $s > 1$ *strong* (from Egas *et al.* 2004).

This literature analysis addressed the questions of how *trade-offs* have been considered in studies of adaptation, what are the main mechanisms underlying *trade-offs* in energy allocation and their relationships with foraging behaviours, and how *trade-offs* may affect the structure of populations and communities. In the second section of the manuscript, I will describe the results obtained in my PhD thesis. The first chapter will be devoted to the study of the relationships between energy allocation strategies, foraging behaviours and environmental characteristics at the intraspecific level. In the second chapter, we will explore the role of environmental characteristics in shaping energy allocation strategies and see how these strategies could favour species coexistence. In a third chapter, we will go further into the mechanisms allowing species coexistence and present a study examining the role of the *trade-off* between current and future reproduction in the structuring of communities.

Section 2. Results

Chap I. *Trade-offs* in resource allocation as a response to environmental characteristics at the intraspecific level

In this chapter, we experimentally explore the relationships between energy allocation, life-history *trade-offs* and environmental characteristics at the intraspecific level.

This manuscript is in preparation as: *Pelosse P., Bernstein C. and Desouhant E. 'Adjustment of resource allocation strategies as a response to environmental conditions and consequences on fitness-related traits in a parasitic wasp'* (Pelosse *et al.* in prep b).

1. Introduction

As a consequence of a limited pool of energy available, organisms are often constrained to make 'choices' in allocating their metabolic resources to reproduction, growth and survival (Roff 1992). Energy allocation toward traits associated with animal reproductive success thus trades off and shapes both intra and inter specific differences between individuals. Energy acquisition and allocation strategies, because they rely on individuals' reproductive and feeding behaviours, are also expected to play an important role in population structuring. Integrated studies on processes of acquisition and allocation of nutrients are therefore needed to understand the physiological processes underlying population dynamics and community structuring (Strand & Casas 2008).

Insect parasitoids develop at the expense of their hosts, generally other insects, as larvae, and are free as adults. Their reproductive success is primarily linked to their available eggs, their longevity and efficiency in locating suitable hosts. Parasitoid females generally rely on food sources as well, to achieve a maximal life expectancy (*e.g.* Heimpel *et al.* 1997, Ellers *et al.* 1998) and higher fecundities (reviewed by Jervis & Kidd 1986). Host and food foraging are energetically costly since these activities may involve flight, the most expensive activity in Insects (Harrison & Roberts 2000). Energy allocation toward these energy-demanding processes is expected to be under strong

selective pressure, and shaped by environmental availability and spatial distribution of hosts and food (Ellers & van Alphen 1997). Parasitoids constitute therefore interesting biological models to explore energy acquisition and allocation strategies, their link with foraging activities and reliance on environmental characteristics.

In holometabolous organisms, distinct processes and strategies of energy acquisition and allocation may take place during larval and adult stages (Boggs 1997b, a, Rivero *et al.* 2001). Energy gained and stored during juvenile stages constitutes the ‘teneral resources’ available at emergence (Rivero & Casas 1999). For parasitoids not feeding on hosts, some nutrients, such as lipids, cannot be acquired by adults feeding on sugary substances, and cannot usually be synthesized from sugars (Olson *et al.* 2000, Rivero & West 2002, Giron & Casas 2003a). They are therefore critical for parasitoids’ reproductive success, especially if needed for egg production and/or maintenance. During adult stage, energy allocation is expected to be dynamic, as a result of energy gains, losses and fluxes from maintenance to reproduction, and vice-versa. Synovigenic parasitoids, as opposed to proovigenic ones that emerge with their full egg complement, have the ability to mature additional eggs as adults (Flanders 1950). They should consequently be able to adjust the number of eggs they carry to the host availability in the environment (Rosenheim 1996, Sevenster *et al.* 1998, Ellers *et al.* 2000). On the other hand, egg resorption theoretically allows parasitoids re-allocating energy invested in eggs toward maintenance when the metabolic balance is negative, even if studies showing its influence on longevity are lacking (King & Richards 1968, Jarvis & Kidd 1986).

The influence of food presence and/or host richness on egg load dynamics and/or egg maturation strategies over parasitoid adult stage have been documented and linked to animal reproductive success in several studies (*e.g.* Bai & Smith 1993, Harvey *et al.* 2001, Eliopoulos *et al.* 2003, Roberts & Schmidt 2004). Integrated studies of reproductive success at the level of both egg and energy dynamics are however scarce (but see Casas *et al.* 2005), and comprehensive studies on their dependence on habitat characteristics are lacking, while needed to understand how nutrients are invested toward life-history and behavioural traits and predict how animal respond to climate change.

Our general hypothesis is that parasitoids should modify their resource allocation in response to environmental host and food availability, in order to maximize their lifetime reproductive success. Previous works on the dependence of allocation strategies on environmental characteristics already suggested that under conditions of high host availability, parasitoid females preferentially allocate their metabolic energy toward reproduction, and under conditions of low host availability toward maintenance (e.g. Ellers & van Alphen 1997). The patterns of energy allocation also critically depend on the quantity of energy available, and therefore in the most part, to the availability of food. We expect that without food, wasps should modify their resource allocation toward reproduction and maintenance in response to host availability to maintain a high reproductive success. Because synovigenic wasps are expected to adjust their egg maturation rate to the availability of hosts, parasitoids should have a large number of offspring but die early in conditions of high host availability, and a low number of offspring and a good longevity in conditions of low host availability. Because egg maturation is known to require the incorporation of lipids and proteins (Dunlap-Pianka *et al.* 1977, Ellers & van Alphen 1997, Giron & Casas 2003b), parasitoids should rely on these nutrients to a greater extent in conditions of high host availability. With food, we expect that wasps should be able to maximize both reproduction and longevity, especially when oviposition opportunities are numerous. When sugary food sources are available, parasitoids are known to replenish their carbohydrates reserves. Because lipogenesis is absent in parasitic wasps studied so far, food availability should allow a relative saving of lipids and proteins for reproduction.

We studied in the laboratory the plasticity in energy allocation strategies in response to host and food availability in the thelytokous parasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae), and its ability to achieve a good reproductive success in different environmental conditions. *V. canescens* is synovigenic and should have the potential ability to adjust its egg production rate to the habitat quality. Thelytokous *V. canescens* mainly thrive in anthropogenic habitats (e.g. granaries) where host density is relatively high and food absent, but are also found in natural habitats where hosts are more scattered and food sources present (Schneider *et al.* 2002, Amat 2004). The potential switches between these two habitats are expected to have selected for a flexible energy allocation in this species.

This study is, to our knowledge, the first to address the question of the influence of both food and host richness on both egg and energy allocation dynamics, and to link them to parasitoid reproductive success.

2. Material and methods

2.1. Biological material

Venturia canescens Gravenhorst (Hymenoptera: Ichneumonidae) is an endoparasitoid of Pyralidae larvae (Salt 1976). *V. canescens* is a solitary parasitoid, *i.e.* only one offspring can develop per host, and is koinobiont (Corbet 1968), *i.e.* hosts continue to grow when parasitized. *V. canescens* females are synovigenic, which means that they emerge with mature and immature eggs, and can produce, when provided with sugar, up to 100 eggs during their lifetime (Trudeau & Gordon 1989, Harvey *et al.* 2001, Roberts & Schmidt 2004). *V. canescens* eggs are small and yolk-deficient (=hydropic), and do not therefore contain large amounts of nutrients. Egg resorption does not occur in this species (Eliopoulos *et al.* 2003). *V. canescens* does not feed on host tissues, but on sugary substances in natural conditions (Casas *et al.* 2003, Desouhant *et al.* 2005). The parasitoids used in this experiment are thelytokous, and thus only constituted by females. They have been obtained in the field near Valence, southern France, during the summer 2004. The hosts *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) are maintained in the laboratory on biological wheat semolina. Development and experiments has been performed from October to December 2006 in a controlled environment ($24 \pm 1^\circ\text{C}$, $80 \pm 5\%$ RH and 13 hL:11 hD).

2.2. Experimental set up

The general purpose of the experiment was to evaluate whether *V. canescens* females allocate their energy reserves in accordance to two fundamental environmental variables: host availability and food presence. The experiment consisted in providing each day to females either a high or a low density host patch, and either food or not. To investigate the lifetime energy allocation dynamics, the nature and amount of energy reserves (carbohydrates, lipids and proteins), egg load and daily number of offspring have been recorded on wasps at emergence, after two or four days of the experimental treatment, or at death. Longevity has also been recorded on wasps followed until death.

Because without access to food, *V. canescens* survive only 2-3 days (see results and Desouhant *et al.* 2005), measurements on wasps not provided with food were only done at death.

Each day, approximately 15 emerging females, collected at their emergence from our rearing stock between 09:00 and 10:30, were transferred into a cage (30×30×30 cm) without food. After 24 h, at 09:30 am, 2 randomly chosen females were frozen to halt metabolic processes, in order to evaluate the initial energy allocation patterns. Among the remaining females, 8 were randomly assigned to one of the 8 combinations of the different treatments: *Host availability: low or high; Food presence: presence or absence; Egg-laying days: 2, 4 or until death (Figure 1).*

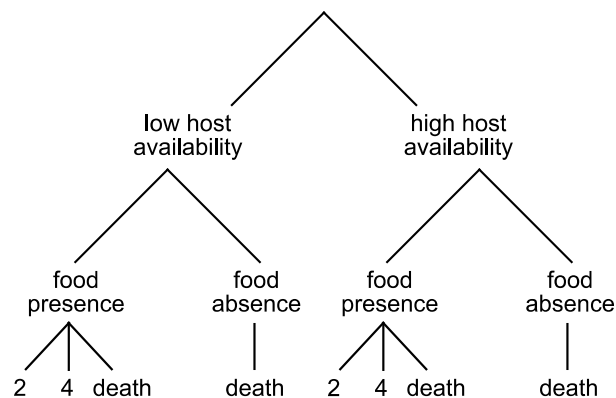


Figure 1: Experimental design. Each day, either one high or low availability host patch, followed by food or not, was provided to females. Energy allocation was recorded either after 2, 4 egg-laying days or at death for females provided with food, and at death for females that did not have access to food.

The females were individually placed into a clear cylindrical plastic box (8×5 cm) closed with a net to allow ventilation, in a room free of host odors. They were daily provided either with a high host-density patch at 11:00 am for 2 hours or with a low host-density patch at 11:15 am for 15 min, depending on if they were assigned to the treatments *high* or *low host availability*. *High* and *low host availability* patches were made up of 30 and 5 third-instar hosts, respectively, in 7 mm deep 55 cm-diameter dishes filled with 13 g of wheat semolina, and covered with a net to prevent the host larvae from escaping. Patches were prepared 7 days before being exploited by parasitoids, to let host larvae impregnate the semolina with mandibular secretions attractive for parasitoid females. Each day at 01:30 pm, Petri dishes containing 2 μ L of 20% sucrose solution or empty Petri dishes were provided during 30 min to the females assigned to the treatments *presence* and *absence of food*, respectively. We chose a

relatively low quality food – sugar concentration of nectars remarkably varies in the field, depending on the plant species (Petanidou 2007) – compared to most of the laboratory experiments which provide *ad libitum* access to high concentrated sugar sources.

The females assigned to the treatments *egg-laying during 2 days* and *4 days* were frozen at 09:30 am on the day following their last egg-laying day. The death of the females assigned to the treatment *egg-laying until death* was controlled at least every 2 h from 09:00 am to 18:00 pm and the females frozen immediately.

2.2.1. Longevity

The date and time of death were recorded for the females of the treatment *egg-laying until death*. The time of death was always estimated as the median time between the time at which the female was found dead and the preceding control time.

2.2.2. Daily number of offspring

Host patches were collected after being parasitized and larvae transferred into clear plastic tubes (7×3 cm) containing semolina. High host density patches were divided in two to avoid high levels of larval competition that may disturb development. The daily number of emerging wasps and butterflies were then determined for each female.

2.2.3. Wasp size and egg load

The left hind tibia length has been considered as an index of adult body size, given that a positive correlation occurs between dry body mass and hind tibia length in *V. canescens* (Harvey & Vet 1997, Roberts & Schmidt 2004), and that energy reserves, egg load and longevity are known to be strongly affected by tibia length in numerous parasitoids (*e.g.* Harvey *et al.* 1994, Ellers *et al.* 1998, Eliopoulos *et al.* 2003). Frozen females were held with a thin pair of forceps, dipped and gently shake for 10 s in physiological water to remove eventual traces of sugar and/or semolina. The left hind tibia was then removed, the reproductive apparatus dissected on a glass slide in 2 µL of physiological water, and a cover slip laid on the reproductive system. Pictures of eggs and tibia were captured with the Motic® M100 Digital Camera adapted on a microscope and connected to a computer. The cover slip was gently removed and the

reproductive materials collected into an Eppendorf tube together with wasp body and tibia, by washing the slide with 50 μL of physiological water. Dissections were done on an ice tray and dissected wasps were immediately put in the freezer to avoid the proteins to be degraded by proteases. The total dissection procedure never lasted more than 4 min. Tibia length and the number of mature and immature eggs were subsequently determined from pictures with the software Motic Images Plus® 2.0 ML. Eggs were considered mature when present in oviducts and calyx, and immature in ovaries.

2.2.4. Quality and quantity of energy reserves

The reproductive apparatus and wasp body were analyzed together. Colorimetric assays originally designed for mosquitoes (van Handel 1985a, b, van Handel & Day 1988), and modified from Giron *et al.* (2002), were carried out on wasps to measure their energy contents. This new method allows quantifying total lipids, proteins, and carbohydrates – fructose originating from ingested sucrose (glucose–fructose dimer), glucose from trehalose (glucose–glucose dimer) and glucose from glycogen (glucose polymer) – for the same individual. Each day, 15-20 females were simultaneously analyzed. A small metal ball and 300 μL of methanol were added into the Eppendorf tubes containing dissected females and the samples were simultaneously crushed with a Quiagen Retsch Tissue Lyser® mixer mill for 30 s at 25 beats/s. Balls were then removed from the tubes with a magnet to avoid handling the solution, and tubes were centrifuged 15 min at 1400 rpm. For the protein assay, 200 μL of supernatant was collected and 800 μL of Bradford reagent added (Bradford 1976). After 5 min at ambient temperature, absorbance was read at 595 nm. 100 μL of methanol, 100 μL of chloroform and 40 μL of 2 % sodium sulfate were added into the remaining samples, the tubes vortexed and centrifuged 15 min at 1400 rpm. For lipid assay, 150 μL of the supernatant was collected and heated at 90°C until complete evaporation. Then, 40 μL of 98 % sulfuric acid was added; the tubes were heated for 2 min at 90°C and cooled in ice. 960 μL of vanillin reagent (68 % phosphoric acid + 1.2 g/L vanillin, van Handel 1985b) was added; the tubes were vortexed and after 20 min at ambient temperature, absorbance was read at 525 nm. 150 μL of the supernatant was then collected for glucose and fructose assays. The samples were almost fully evaporated at ambient temperature for approximately 2 hours; 1 mL of anthrone reagent (70 % sulfuric acid + 1.4 g/L anthrone, van Handel 1985a) was added, and after 20 min at ambient temperature,

absorbance was read at 625 nm to estimate fructose concentrations. Tubes were then heated 15 min at 90°C and cooled in ice, and absorbance was read at 625 nm to estimate glucose concentrations. Pellets were finally used to assay glycogen concentrations. To remove traces of dimeric sugars, pellets were washed with 400 µL of 80 % methanol, vortexed and centrifugated 5 min at 1400 rpm. Supernatants were removed; 1 mL of anthrone reagent added, and the tubes were vortexed and heated 15 min at 90°C. Samples were cooled in ice, collected in plastic syringes and filtered with Durapore® PVDF membranes to remove cuticle fragments. Absorbance was then read at 625 nm. Because glucose assayed originated from both trehalose and sucrose, trehalose concentrations were assessed by calculating the difference between total glucose and fructose concentrations (van Handel & Day 1990). All nutrient concentrations were estimated from absorbance curves of solutions of known concentrations of glucose, fructose, sunflower oil for lipids, and Bovine Serum Albumin for proteins. To assess actual per-wasp nutrient levels, nutrients amounts were multiplied according to how the solutions were diluted.

2.3. Statistical analyses

To investigate the combined effects of the variable *wasp size*, the qualitative variables *food presence* and *host availability*, and interactions on parasitoids' longevities, we used a Cox proportional hazards regression model (Cox 1972).

The influence of *wasp size*, *age* (*i.e. number of egg-laying days*), *host availability* and *food presence*, on egg loads and nutrients levels has been assessed with linear models. *Wasp age* was considered as a qualitative variable to account for non-monotonous variation of eggs or energy contents over lifetime. Transformations were applied (square root for glycogen, glucose, fructose and lipids) when residuals were not normally distributed or when the residual variance was not constant over the response variable. To investigate the effects of *wasp age* on egg loads and nutrients levels, we included in the analyses the females stopped at emergence. Because it was not possible to take into account the effect of the host availability since females at emergence did not experience any, we performed two distinct analyses for *high* and *low host availability*. Then, to accurately explore the effects of *host availability* on egg and energy measurements, we removed from analyses the females stopped at emergence for the same reason, and did not consider the females that had no access to food to avoid a

confounded effect of the fact that they have been measured at death only, in contrast to females provided with food. Finally, to investigate the effect of *food presence*, only the females followed until death have been considered, since measurements on females without food access have been carried out at death only.

Data on daily number of offspring contain clusters of data since parasitoid females were allowed to lay eggs during several days. The number of offspring is hence repeated for each female. As a consequence, to investigate the influence of *wasp age*, *wasp size*, *host availability* and *food presence* on females' daily offspring production, we used a Mixed Effects Model accounting for time series data (Crawley 2002). Number of offspring was considered as the response variable, *wasp age* (that is the egg-laying day), *wasp size*, *host availability* and *food presence* as explanatory variables of fixed effects, and the female as a random effect. In the model, intercepts and slopes of offspring number along time were initially assumed to vary between females. To find the more accurate model, a backward procedure of model selection, together with maximum likelihood model comparisons – were likelihood-ratio (LR) are χ^2 -distributed with a number of degrees of freedom given by the difference between the degrees of freedom of the two models compared – has been computed.

For all analyses, *wasp size* was incorporated as the first explanatory variable to remove any effect of animal size from the measurements. We always followed a backward procedure to sequentially remove variables and assess the more parsimonious model, and examined residuals. Data analyses as well as graphs have been realized with the *R* free software environment (R Development Core Team 2008, <http://www.R-project.org>). Survival analyses were performed using the *R* “survival” package (S original by Terry Therneau and ported by Thomas Lumley) and mixed effect models using the *R* “nlme” package (Pinheiro *et al.* 2008).

3. Results

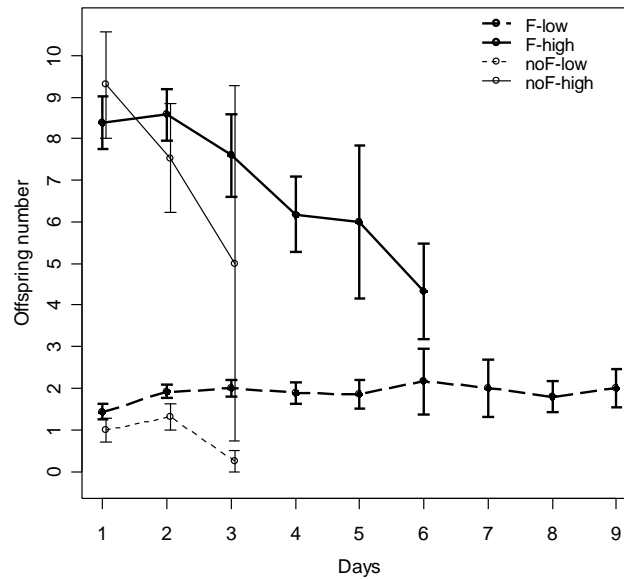


Figure 2: Daily number of offspring (\pm SE) according to 4 treatments: food presence and low host availability (F-low), food presence and high host availability (F-high), no food and low host availability (noF-low) and no food and high host availability (noF-high).

3.1. Lifetime reproductive success

3.1.1. Offspring production

In the Mixed Effects Model, intercepts and slopes of offspring number along time were initially assumed to vary between females. Indeed, slopes did not significantly differ ($LR=0.94$; $d.f.=2$; $P=0.6$), which means that offspring production variation was globally similar among females. Conversely, the average number of offspring produced greatly differed among females, as intercept variations explained 28% of the variability of offspring number in the final model. The interaction between *host availability* and *wasp age* strongly influenced offspring production ($t=-5.5$; $d.f.=302$; $P<0.0001$; **Figure 2**). While at *high host availability*, the number of offspring tended to decrease with female age, it remained constant at *low host availability*. The interaction between *host availability* and *wasp size* also played a great role in prediction the number of offspring ($t=3.4$; $d.f.=137$; $P<0.001$). Size positively affected offspring number when host availability is high, but does not when host availability is low. Finally, as expected,

parasitoids get globally higher numbers of offspring in conditions of *high host availability*, compared to *low host availability* (d.f.=137; P=0.048).

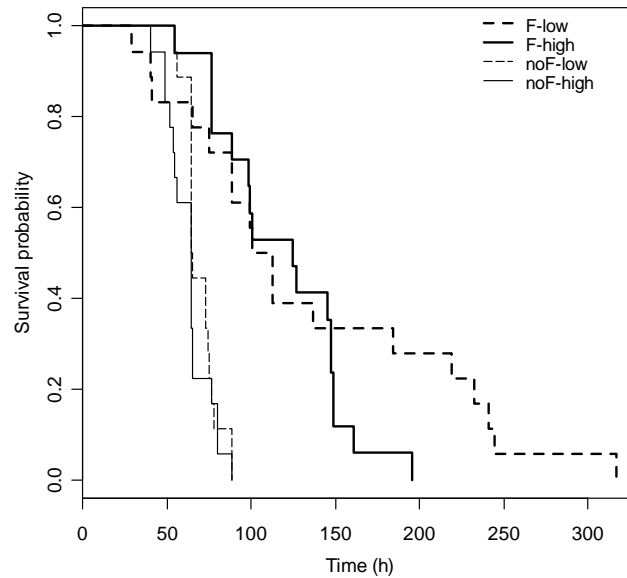


Figure 3: Kaplan-Meier curves for survival probabilities according to 4 treatments: food presence and low host availability (F-low), food presence and high host availability (F-high), no food and low host availability (noF-low) and no food and high host availability (noF-high).

3.1.2. Longevity

As expected, parasitoids longevity has been significantly affected by *food presence* ($z=5.76$; $P<0.0001$; **Figure 3**), fed wasps living approximately twice longer than unfed ones. Longevity was, in average, 66.3 h (SE: 1.9; Median: 64.5) without and 126.9 h (SE: 11.1; Median: 112.5) with food. While we expected that energy saved from reproduction in conditions of *low host availability* would be devoted to enhance longevity, *host availability* neither directly affected life expectancy ($z=1.35$; $P=0.2$), nor indirectly through its interaction with *food presence* ($z=-0.3$; $P=0.8$). *Wasp size* ($z=-1.06$; $P=0.3$) did not influence longevity, but its interaction with *food presence* did ($z=-2.5$; $P=0.01$). Graphical analyses suggested that size positively affected longevity in absence of food, but did not with food (results not shown).

3.2. Underlying processes

3.2.1. Egg load

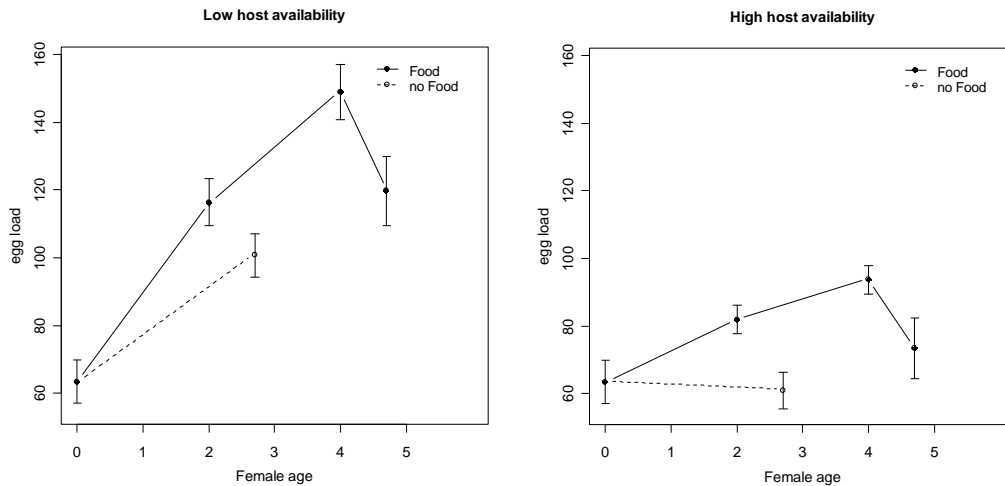


Figure 4: Egg load number variation (\pm SE) over lifetime for low (left) and high (right) host availability, according to 4 treatments: food presence and low host availability (F-low), food presence and high host availability (F-high), no food and low host availability (noF-low) and no food and high host availability (noF-high).

We considered only the number of mature eggs, since the number of immature eggs was constant for all treatments (results not shown). *Host availability* had a strong effect on parasitoids' egg loads: females showed higher egg numbers at low than at high host availabilities ($F(1,97)=80$; $P<0.0001$). For the two host availabilities, the number of mature eggs significantly varied according to *wasp age* (low host availability: $F(3,56)=25$; $P<0.0001$; high host availability: $F(3,63)=3.8$; $P=0.01$; **Figure 4**; c.f. **Annex** for details): after a strong increase until day 4, a small decrease is observed at the end of life. The interaction between *wasp size* and *age* also played a significant role in predicting the egg load at high host availabilities ($F(3,56)=3.1$; $P=0.03$). Indeed, graphical analyses revealed that the relation between egg number and size was weak at emergence and death and strong for intermediate ages (results not shown). *Food presence* significantly affected egg loads, as the number of mature eggs at death was lower for wasps that did not have access to food compared to those who did ($F(1,57)=4.2$; $P=0.05$).

At day 2, females at low host availability have approximately 35 eggs more than at high host availability, and 55 eggs at day 4. The difference in the total number of

offspring produced among the two host availabilities is however only 14 at day 2 and 23 at day 4. The differences in egg load recorded between the two host availabilities cannot thus only reflect the differences in the number of eggs laid but to egg maturation differences. Contrary to our expectation, egg maturation rates were most likely higher in conditions of low host availability.

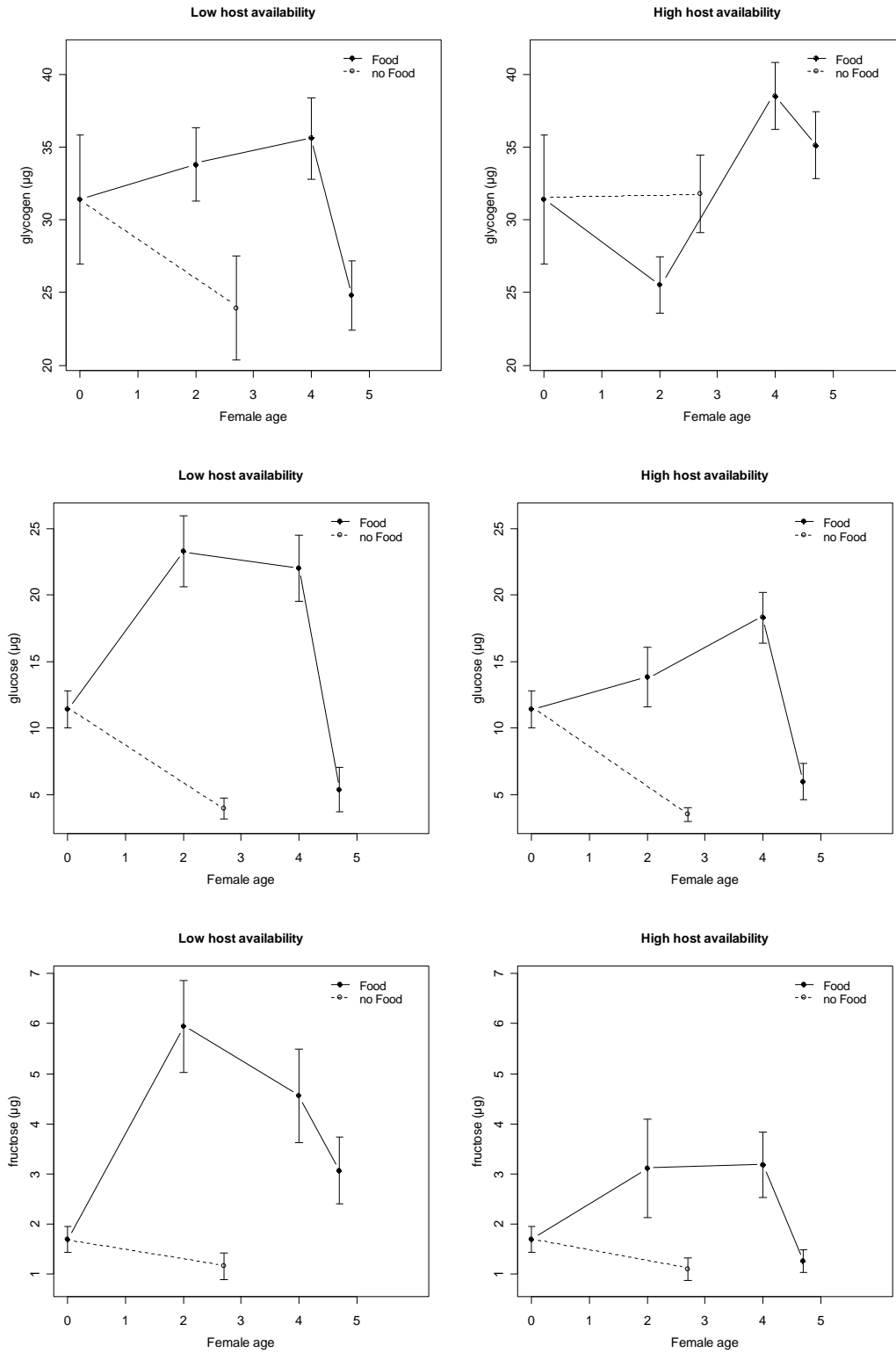
3.2.2. Energy reserves

Glycogen contents were not significantly affected by *wasp age* at low host availability ($F(3,61)=2.4$; $P=0.08$), but by the interaction between *wasp size* and *age* ($F(3,61)=2.8$; $P=0.05$; **Figure 5**; c.f. **Annex** for details). Conversely, a significant effect of *wasp age* ($F(3,64)=4.1$; $P=0.01$) and no effect of the interaction ($F(3,61)=0.02$; $P=1$) has been recorded at high host availability. Indeed, glycogen contents did not vary at low, compared to high host availability. Glycogen contents at death were similar regardless of *food presence* ($F(1,63)=0.9$; $P=0.3$). Furthermore, *host availability* ($F(1,99)=0.4$; $P=0.5$) did not have a significant effect on glycogen reserves, but the interaction between *wasp age* and *host availability* did ($F(2,99)=7.8$; $P<0.001$). At low host availability, glycogen levels remained relatively constant until the age of 4 days and then strongly decreased at the end of life, while they decreased in the early life and strongly increased from day 2 to 4 at high host availabilities.

At low host availability, glucose contents were significantly influenced by *wasp age* ($F(3, 61)=20.4$; $P<0.0001$) and by the interaction between *wasp size* and *age* ($F(3, 61)=3.6$; $P=0.02$) (**Figure 5**). On the other hand, at high host availability, only *wasp age* affected glucose contents ($F(3, 64)=11.4$; $P<0.0001$). *Food presence* ($F(1, 63)=1.1$; $P=0.3$), as well as *host availability* ($F(1, 98)=3.4$; $P=0.07$) did not significantly affected glucose contents. As for glycogen, the interaction between *wasp age* and *host availability* allowed, to some extent, predicting glucose contents ($F(2, 98)=3.1$; $P=0.05$): while at low host availability, glucose levels strongly increased in early life, stay constant at intermediary ages and strongly decreased at the end of life, they slowly increased until day 4 at high host availability and decreased at the end of life.

Fructose contents were affected by *wasp age* ($F(3,61)=5.5$; $P<0.01$) and by the interaction between *wasp age* and *size* ($F(3,61)=4.3$; $P<0.01$) at low host availability, and only by the interaction ($F(3,60)=3.5$; $P=0.02$) at high host availability (**Figure 5**).

Indeed, fructose concentrations strongly increased at the beginning of life and decreased until death at low host availability, and remained more constant at high host availability.



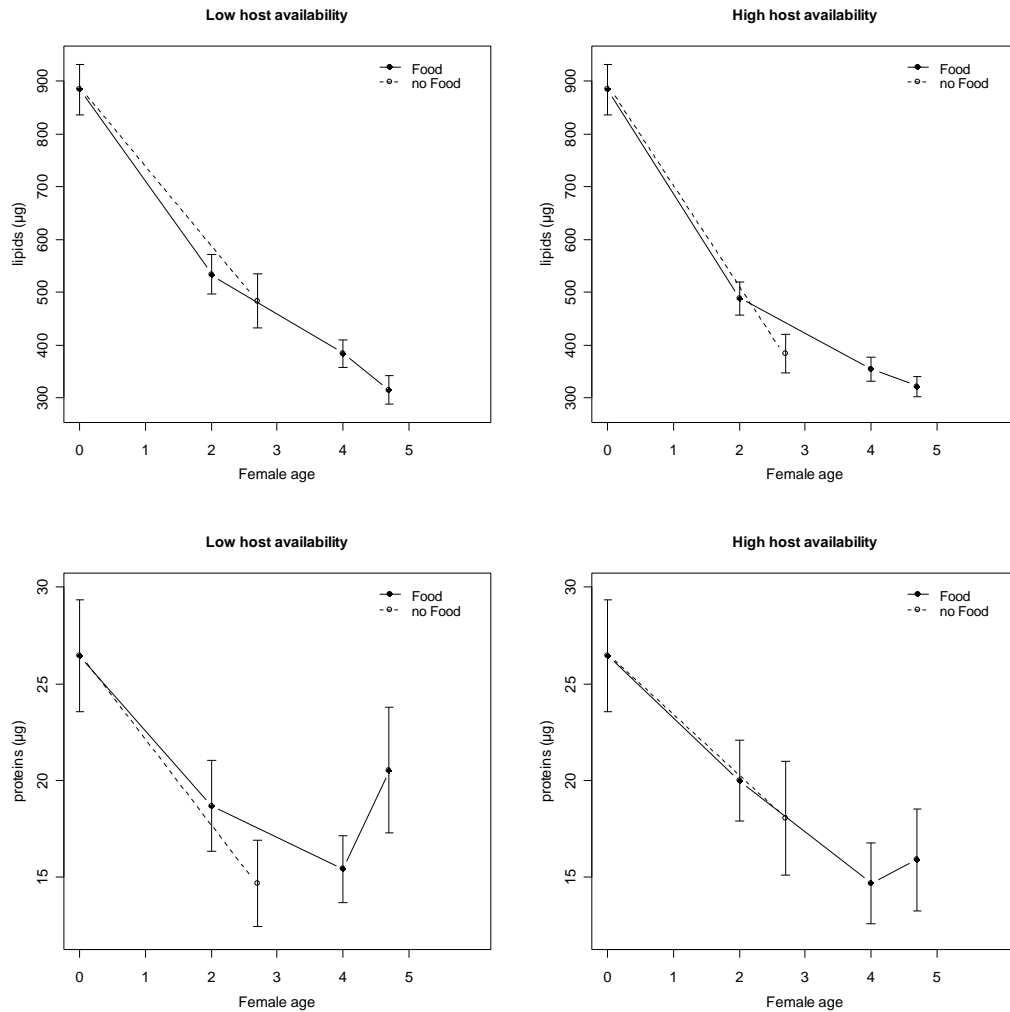


Figure 5: Energy amounts variation (\pm SE) over lifetime for low (left) and high (right) host availability, according to 4 treatments: food presence and low host availability (F-low), food presence and high host availability (F-high), no food and low host availability (noF-low) and no food and high host availability (noF-high).

The interaction between *wasp age* and *size* reflects that fructose levels are not affected by size at emergence, then positively affected from day 2 to 4 and negatively affected at death (results not shown). Females that did not have access to food showed lower amounts of fructose at death ($F(1,68)=8.5$; $P=0.005$), especially at low host availability. In addition, *host availability* influenced parasitoids' fructose levels ($F(1,95)=14.1$; $P<0.001$), wasps experiencing low host availabilities having globally higher fructose levels than those experiencing high host availabilities. Finally, the interaction between *wasp age*, *size* and *host availability* had an effect on the fructose contents ($F(2,95)=4$; $P=0.02$).

Lipid levels were significantly affected by *wasp age* ($F(3,61)=77$; $P<0.0001$) and by the interaction between *wasp size* and *age* ($F(3,61)=4.1$; $P=0.01$) at low host availabilities. On the other hand, *wasp age* ($F(3,64)=78$; $P<0.0001$) was the only variable that significantly affected lipid contents at high host availabilities (**Figure 5**). Lipid levels were not noticeably different for *high* and *low host availabilities* ($F(1,96)=2.5$; $P=0.1$). At high host availability, lipids were expected to be used more as a result of a potential higher egg maturation rate. Whatever the host availability, lipid reserves however monotonically decreased all along lifetime. *Food presence* did have an effect on lipid reserves ($F(1,68)=11.1$; $P=0.001$), as females provided with food generally showed higher levels of lipids at death than those that were not. This observation is in accordance with our expectation that lipids could be saved when carbohydrates are acquired.

Proteins levels significantly differ according to *wasp age* (low host availability: $F(3,51)=4.1$; $P=0.01$; high host availability: $F(3,50)=6.8$; $P<0.001$): they showed a continuous decrease until the age of 4 days, remained then constant for high host availabilities and seemed to increase for low host availabilities (**Figure 5**). On the other hand, both *food presence* ($F(1,48)=0.4$; $P=0.6$) and *host availability* ($F(1,73)=0.6$; $P=0.4$) did not affect protein reserves.

4. Discussion

This study provides evidence that parasitoid's allocation strategies are profoundly affected by environmental characteristics, but that reproductive success is crucially constrained by food acquisition. In an environment providing a large number of reproductive opportunities and without food, parasitoids maximize their offspring number and suffer from a reduced longevity. While we expected that at low host availability, parasitoids would maximize their longevity at the expense of reproduction, by reducing their egg maturation rate, the absence of food prevents them enhancing their longevity. Conversely, our results counter-intuitively suggest that egg maturation rate is higher for a reduced number of oviposition opportunities. Lipid and protein reserves were not differentially affected by the egg maturation rates, which suggests that they are not extensively incorporated into eggs in this species.

Our results suggest that parasitoids' reproductive success is first decisively constrained by the availability of hosts. Regardless of food presence, females get more offspring when provided with large number of hosts. As expected, in the absence of food, the females provided with high host availabilities seemed to face a trade-off between reproduction and longevity, since they maximized their offspring number but suffered from reduced longevity. In contrast, parasitoid females in conditions of low host availability showed a reduced fecundity and appeared not able to allocate energy to maintenance without food, since they also suffer from a reduced longevity. At emergence, thelytokous *V. canescens* have a relatively high number of mature eggs – approximately 60 in our experimental conditions – and their incapacity to resorb eggs (Eliopoulos *et al.* 2003) make them unable to reallocate energy already invested in reproduction to maintenance. Synovigenic wasps are nevertheless expected to adjust their egg maturation rate to the environmental host availability (Ellers *et al.* 2000). Surprisingly, while at high host availabilities, synovigenic wasps should mature more eggs to achieve a maximal reproductive success (Rosenheim 1996, Sevenster *et al.* 1998), we observed the opposite pattern: they seemed to have matured more eggs at low host availability. Wasps experiencing high host availabilities probably met competing needs: under these conditions they had lower glucose and fructose reserves (see below), which were most likely used to sustain the metabolic costs of egg-laying behaviour and thus lacked free carbohydrates to fuel egg maturation process. Whatever the availability of hosts, a decrease of egg number is observed at the end of life. This decrease partially avoids wasting energy invested in the elaboration of eggs, and therefore dying with remaining eggs. It should not be attributed to egg resorption that does not take place in *V. canescens*, but to a decrease of egg maturation rate, probably resulting from the reduction of available metabolic energy. Wasps experiencing low host availabilities nevertheless suffer from an important time limitation since they die with 100-120 remaining eggs. With a daily supply of 500 hosts, Eliopoulos *et al.* (2003) suggested that *V. canescens* females have only few eggs remaining. Here we would like to emphasize that time limitation is probably less detrimental in species having hydropic eggs such as *V. canescens*, because eggs do not contain large amounts of nutrients.

As expected, food influenced parasitoid survival, and indirectly affected reproduction through a positive effect on egg maturation rates. While environmental host availability did not influenced wasps' survival (result similar to Harvey *et al.*

2001), food availability strongly did. The positive effect of sugar feeding on parasitoid longevity observed in our experiment has been documented by several studies (*e.g.* Leius 1961, Jervis & Kidd 1986, Heimpel *et al.* 1997, Eijs *et al.* 1998). Here a relatively low quality food was provided, which was however sufficient for wasps to survive twice as longer than without food. Yet, with *ad libitum* access to sugar, *V. canescens* females can survive up to 36 days (Ahmad 1936). In our study, food did not directly allow parasitoid females achieving higher fecundities. The average number of offspring produced per day is 4.7 (SE=0.4) for wasps provided with food and 4.6 (SE=0.7) for those that were not. Sugar is however known to increase female motivation to search for hosts in the field (Takasu & Lewis 1995, Stapel *et al.* 1997). As already demonstrated in *V. canescens* (Eliopoulos *et al.* 2003), our results suggest that sugars played a role in egg maturation: regardless of host availability, wasps without access to sugars died with substantially less eggs than those that had access to sugar. In parasitoids not resorting to host-feeding, similar observations has been reported in Aphidiidae (Olson & Andow 1998, Tylianakis *et al.* 2004), but no effect of sugar on egg maturation rate as been observed in *Phanerotoma franklini* (Sisterson & Averill 2002). Feeding most probably allowed allocating large quantities of sugars to the energy-demanding egg maturation process. This study also provides evidence that host exploitation and egg-laying behaviours are metabolically costly in terms of carbohydrates: an early-life glycogen reserve decrease occurred only when wasps laid more eggs in conditions of high host availability.

As expected, carbohydrate reserves globally increased when wasps were provided with food. Non-host-feeding parasitoids feed on floral nectar or honeydew in the field (Jervis *et al.* 1993). The nutrients gained by adults – the *incoming* resources, *sensu* Rivero & Casas 1999) – are therefore mainly constituted of carbohydrates (*i.e.* sugars). When ingested, sucrose is separated in glucose and fructose, and fructose is rapidly converted into glucose, the most easily mobilized source of energy. Indeed, while lipid and protein reserves were not affected by feeding, glucose and fructose contents were multiplied by a maximum of 2.2, compared to emergence levels, in wasps provided with sugar. Yet, when having *ad libitum* access to honey, or recaptured after a release of 8 to 48 h in the field, *V. canescens* females increase their sugar levels by an order of magnitude of 10 (Casas *et al.* 2003). In our study, fructose levels were low compared to glucose ones, probably because a relatively low quality food has been used. Indeed,

Braconidae parasitoids fed upon 50-70 % sucrose solutions show similar glucose and fructose amounts (Olson *et al.* 2000, Steppuhn & Wäckers 2004). In insects, glucose is easily converted into trehalose (glucose-glucose dimer), the first mobilized storage source of energy. Glycogen storage or utilization is closely linked to glucose concentration in haemolymph: at low concentrations, glycogen is hydrolyzed in glucose, and at high concentrations, stored in glycogen (Nation 2002). Accordingly, glycogen levels globally fluctuate in the same manner as glucose levels in our study. Casas *et al.* (2005) nutrient budget in *Eupelmus vuilletti* suggested that carbohydrate levels determine wasps' survival. We observed here a similar pattern for glucose: their levels at death were close to zero for all treatments. A different scenario however occurred for glycogen levels at death: for low host availabilities, they were relatively low, but surprisingly remained very high at high host availabilities, regardless of food presence. The fact that wasps died without using their entire energy reserves, while theoretically needed to a greater extent when oviposition opportunities are numerous, is quite unexpected. Two hypotheses can be put forward. First, since egg maturation rate was lower at high host availabilities, wasps may have rely less on their glycogen reserves to mature eggs, especially if glycogen is needed for egg provisioning. Secondly, flight, the most energy-demanding activity in Insects (Harrison & Roberts 2000), is expected to affect nutrient allocation strategies in a decisive manner. In the literature, it is generally adopted that Hymenopteran that do not fly on long distances rely on carbohydrates – especially glycogen – to fuel their flights, and Lepidopteran and Orthopteran that perform long distance flights on lipids (Candy *et al.* 1997, Vogt *et al.* 2000, Nation 2002, Suarez *et al.* 2005). At low host availabilities, it is possible that wasps have been more active because they tried to leave the experimental environment in search of other reproductive opportunities, which resulted in glycogen reserve depletion. More detailed investigations are however needed to understand the potential roles of egg maturation and/or flight in glycogen mobilization.

As expected, food acquisition did not allow *V. canescens* enhancing its lipid and protein reserves. As previously reported by Casas *et al.* (2003), the most abundant reserve nutrient in *V. canescens* are lipids. Since lipids cannot be acquired in adult food by non-host-feeding parasitoids, the teneral resources accumulated during larval stage are the only resources available for adults. In several insects, sugar feeding increases first glycogen storage, and then switches to lipid storage (Nation 2002). We have

however evidences that in parasitoids studied so far, including *V. canescens*, lipogenesis, *i.e.* lipid synthesis from sugar, is absent (Ellers 1996, Olson *et al.* 2000, Rivero & West 2002, Casas *et al.* 2003, Giron & Casas 2003a). Whatever the experimental conditions, we observed a steadily decrease in lipid levels all along lifetime, as already reported in various parasitic wasps (Ellers 1996, Lee *et al.* 2004, Casas *et al.* 2005). This result suggests that lipids are not involved in egg maturation. Ellers (1996) and Lee *et al.* (2004) recorded lower decline rate of lipids for wasps having access to sugar, and suggested that sugar feeding reduces parasitoids' reliance on lipid reserves. Here, we only observed lower lipid levels at death in wasps provided with sugar, as reported by Olson *et al.* (2000), but no consistent difference in decrease rates. Our results may differ because parasitoids were given access to hosts in our study, while otherwise not. Lipids are most probably used to sustain maintenance needs, since they provide far much energy than carbohydrates (Canavoso *et al.* 2001). Indeed, fat reserves have already been linked to parasitoids' survival in several studies (Ellers 1996, Ellers & van Alphen 1997). The same decrease as lipids which was observed for proteins in our study may come from the fact that proteins were not available, as lipids, in the food source provided. In the field, different scenarios may take place since amino acids are prevalent in nectars (Petanidou 2007) and have been suggested to play a role in butterfly reproductive success (Jervis & Boggs 2005, Mevi-Schütz & Erhardt 2005). In our experimental conditions, both lipids and proteins seemed limiting for wasp survival, as the levels at death were very low compared to those at emergence. The increase of protein amounts at end of life, especially remarkable for low host availability is surprising. Proteins cannot be synthesized from carbohydrates or lipids. Some Insects are known to hydrolyze their flight muscle at the end of life to provide metabolic energy (Karlsson 1994). Since the Bradford reagent used to assay proteins specifically binds to hydrophobic amino acids, it is possible that changes in the nature of proteins rendered some of them more accessible to the reagent.

To conclude, this study of resource allocation from physiology to life history traits shows that environmental characteristics have critical effects on resource allocation strategies. It provides evidence that animals are not always able to properly allocate their energy resource and achieve high reproductive success, as a result of competing needs for limiting nutrients. Our investigation therefore appeals for explicit

considerations of underlying mechanisms to understand the impact of environmental changes on animal reproductive success.

5. References

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6. Annexes

Annex 1: Effectives for measurements of egg load, energy reserves and longevity, according to Host availability (*low* or *high*), Egg-laying days (*0*: at emergence; *2*: after 2 days of egg-laying; *4*: after 4 days) and, for measurements performed at death, Food presence (*death food*: at death with food access; *death no food*: at death without food access).

MEASUREMENT	HOST AVAILABILITY	EGG-LAYING DAYS			FOOD PRESENCE	
		<i>0</i>	<i>2</i>	<i>4</i>	<i>DEATH FOOD</i>	<i>DEATH NO FOOD</i>
EGG LOAD	<i>LOW</i>	15	18	18	13	16
	<i>HIGH</i>		17	19	17	15
FRUCTOSE	<i>LOW</i>	15	18	18	18	18
	<i>HIGH</i>		18	18	17	18
GLUCOSE	<i>LOW</i>	15	18	18	18	18
	<i>HIGH</i>		18	18	17	18
GLYCOGEN	<i>LOW</i>	15	18	18	18	18
	<i>HIGH</i>		18	19	17	18
LIPIDS	<i>LOW</i>	15	18	18	18	18
	<i>HIGH</i>		18	19	17	18
PROTEINS	<i>LOW</i>	13	14	15	14	14
	<i>HIGH</i>		14	14	14	14
LONGEVITY	<i>LOW</i>	-	-	-	18	18
	<i>HIGH</i>	-	-	-	17	18

Annex 2: Effectives for daily offspring number measurements, according to Host availability (*low* or *high*), Food presence (*food* or *no food*) and wasp age (Day).

	HOST AVAILABILITY	FOOD PRESENCE	DAY								
			1	2	3	4	5	6	7	8	9
OFFSPRING NUMBER	<i>LOW</i>	<i>FOOD</i>	53	51	31	27	7	6	6	5	5
		<i>NO FOOD</i>	17	16	4	-	-	-	-	-	-
	<i>HIGH</i>	<i>FOOD</i>	51	49	32	28	8	6	-	-	-
		<i>NO FOOD</i>	17	15	4	-	-	-	-	-	-

Annex 3 (next page): Statistical results of linear models. Energy reserves and egg load are the response variables, and wasp size (*size*), age (*age*, *i.e.* Egg-laying days), Host availability (*density*), Food presence (*food*) and their interactions, the explanatory variables. “Wasp age” gives results of the analyses performed to test the influence of wasp age, either for *low* or *high* host availability. “Food presence” and “Host availability” give results of the analyses performed to test the influence of food presence and host availability (see section ‘statistical analyses’). Explanatory variables highlighted in bold have a significant influence over the response variable.

RESPONSE		WASP AGE	FOOD PRESENCE	HOST AVAILABILITY
GLYCOGEN (SQRT)	LOW	SIZE: A=5.5 ; F(1,61)=10.4 ; P=0.002 AGE: F(3,61)=2.4 ; P=0.08 SIZE:AGE: F(3,61)=2.8 ; P=0.05	SIZE: A=7.5 ; F(1,67)=1 ; P=0.3 DENSITY: A=7.2 ; F(1,67)=13.4 ; P<0.001 FOOD: A=-5.4 ; F(1,63)=0.9 ; P=0.3	SIZE: A=7.4 ; F(1,99)=17.8 ; P<0.0001 AGE: F(2,99)=5.6 ; P<0.01 DENSITY: A=0.7 ; F(1,99)=0.4 ; P=0.5
	HIGH	SIZE: A=5.3 ; F(1,64)=14.3 ; P<0.001 AGE: F(3,64)=4.1 ; P=0.01 SIZE:AGE: F(3,61)=0.02 ; P=1	SIZE:DENSITY: A=-9.1 ; F(1,67)=5.2 ; P=0.03 SIZE:FOOD: A=5.9 ; F(1,63)=0.05 ; P=0.8 DENSITY:FOOD: A=6 ; F(1,63)=0.2 ; P=0.9 SIZE:DENSITY:FOOD: A=-6.7 ; F(1,63)=0.6 ; P=0.5	SIZE:AGE: F(2,99)=3.1 ; P=0.05 SIZE:DENSITY: A=4.7 ; F(1,96)=0.1 ; P=0.8 AGE:DENSITY: F(2,99)=7.8 ; P<0.001 SIZE:AGE:DENSITY: F(2,96)=2.1 ; P=0.1
GLUCOSE (SQRT)	LOW	SIZE: A=3 ; F(1,61)=9.4 ; P<0.01 AGE: F(3,61)=20.4 ; P<0.0001 SIZE:AGE: F(3,61)=3.6 ; P=0.02	SIZE: A=-3 ; F(1,63)=1.4 ; P=0.2 DENSITY: A=-0.4 ; F(1,63)=0.9 ; P=0.4 FOOD: A=-3 ; F(1,63)=1.1 ; P=0.3	SIZE: A=11.7 ; F(1,98)=6.2 ; P=0.01 AGE: F(2,98)=42.1 ; P<0.0001 DENSITY: A=0.9 ; F(1,98)=3.4 ; P=0.07
	HIGH	SIZE: A=3 ; F(1,30)=1.4 ; P=0.2 AGE: F(3,64)=11.4 ; P<0.0001 SIZE:AGE: F(3,60)=2.4 ; P=0.08	SIZE:DENSITY: A=-0.1 ; F(1,63)=0.08 ; P=0.8 SIZE:FOOD: A=2.9 ; F(1,63)=0.001 ; P=1 DENSITY:FOOD: A=3.3 ; F(1,63)=0.4 ; P=0.5 SIZE:DENSITY:FOOD: A=-3.3 ; F(1,63)=0.1 ; P=0.8	SIZE:AGE: F(2,98)=5.9 ; P<0.01 SIZE:DENSITY: A=-1.1 ; F(1,95)=0.5 ; P=0.5 AGE:DENSITY: F(2,98)=3.1 ; P=0.05 SIZE:AGE:DENSITY: F(2,95)=1.3 ; P=0.3
FRUCTOSE (SQRT)	LOW	SIZE: A=-0.05 ; F(1,61)=1.3 ; P=0.3 AGE: F(3,61)=5.5 ; P=0.002 SIZE:AGE: F(3,61)=4.3 ; P=0.008	SIZE: A=-3.2 ; F(1,68)=8.8 ; P=0.004 DENSITY: A=1.8 ; F(1,63)=2.1 ; P=0.2 FOOD: A=-0.4 ; F(1,68)=8.5 ; P=0.005	SIZE: A=-6.0 ; F(1,95)=0.09 ; P=0.8 AGE: F(2,95)=4.5 ; P=0.01 DENSITY: A=3.2 ; F(1,95)=14.1 ; P<0.001
	HIGH	SIZE: A=-0.05 ; F(1,60)=0.05 ; P=0.8 AGE: F(3,60)=1.7 ; P=0.2 SIZE:AGE: F(3,60)=3.5 ; P=0.02	SIZE:DENSITY: A=-1.5 ; F(1,63)=0.1 ; P=0.7 SIZE:FOOD: A=0.3 ; F(1,63)=0.3 ; P=0.6 DENSITY:FOOD: A=-1.1 ; F(1,63)=2.8 ; P=0.1 SIZE:DENSITY:FOOD: A=0.6 ; F(1,63)=0.01 ; P=0.9	SIZE:AGE: F(2,95)=5.9 ; P<0.01 SIZE:DENSITY: A=-2.8 ; F(1,95)=0.6 ; P=0.4 AGE:DENSITY: F(2,95)=0.6 ; P=0.6 SIZE:AGE:DENSITY: F(2,95)=4.0 ; P=0.02
LIPIDS (SQRT)	LOW	SIZE: A=17.5 ; F(1,61)=37 ; P<0.0001 AGE: F(3,61)=77 ; P<0.0001 SIZE:AGE: F(3,61)=4.1 ; P=0.01	SIZE: A=14.1 ; F(1,68)=5.2 ; P=0.03 DENSITY: A=9.3 ; F(1,63)=2.5 ; P=0.1 FOOD: A=2.8 ; F(1,68)=11.1 ; P=0.001	SIZE: A=23 ; F(1,104)=37 ; P<0.0001 AGE: F(2,104)=32 ; P<0.0001 DENSITY: A=-19.3 ; F(1,96)=2.5 ; P=0.1
	HIGH	SIZE: A=18.7 ; F(1,64)=1.5 ; P=0.2 AGE: F(3,64)=78 ; P<0.0001 SIZE:AGE: F(3,61)=0.06 ; P=1	SIZE:DENSITY: A=-10 ; F(1,63)=0.3 ; P=0.6 SIZE:FOOD: A=-45 ; F(1,63)=0.01 ; P=0.9 DENSITY:FOOD: A=-52 ; F(1,63)=1.6 ; P=0.2 SIZE:DENSITY:FOOD: A=61 ; F(1,63)=4.1 ; P=0.05	SIZE:AGE: F(2,96)=3.0 ; P=0.05 SIZE:DENSITY: A=22.5 ; F(1,96)=1.1 ; P=0.3 AGE:DENSITY: F(2,96)=0.2 ; P=0.9 SIZE:AGE:DENSITY: F(2,96)=2.0 ; P=0.1
PROTEINS	LOW	SIZE: A=47 ; F(1,51)=6.3 ; P=0.02 AGE: F(3,51)=4.1 ; P=0.01 SIZE:AGE: F(3,48)=2 ; P=0.1	SIZE: A=25 ; F(1,48)=0.5 ; P=0.5 DENSITY: A=95 ; F(1,48)=0.09 ; P=0.8 FOOD: A=-14 ; F(1,48)=0.4 ; P=0.6	SIZE: A=55 ; F(1,73)=2.6 ; P=0.1 AGE: F(2,73)=2.4 ; P=0.1 DENSITY: A=-19 ; F(1,73)=0.6 ; P=0.4
	HIGH	SIZE: A=51.3 ; F(1,50)=6.3 ; P=0.02 AGE: F(3,50)=6.8 ; P<0.001 SIZE:AGE: F(3,47)=0.2 ; P=0.9	SIZE:DENSITY: A=-103 ; F(1,48)=0.03 ; P=0.9 SIZE:FOOD: A=19 ; F(1,48)=2.1 ; P=0.2 DENSITY:FOOD: A=-108 ; F(1,48)=1.9 ; P=0.2 SIZE:DENSITY:FOOD: A=113 ; F(1,48)=.08 ; P=0.4	SIZE:AGE: F(2,73)=1.8 ; P=0.2 SIZE:DENSITY: A=19 ; F(1,73)=0.4 ; P=0.6 AGE:DENSITY: F(2,73)=1.1 ; P=0.3 SIZE:AGE:DENSITY: F(2,73)=0.9 ; P=0.4
EGG LOAD	LOW	SIZE: A=24.5 ; F(1,56)=20 ; P<0.0001 AGE: F(3,56)=25 ; P<0.0001 SIZE:AGE: F(3,56)=3.1 ; P=0.03	SIZE: A=116 ; F(1,57)=1.6 ; P=0.2 DENSITY: A=46 ; F(1,57)=33 ; P<0.0001 FOOD: A=-16 ; F(1,57)=4.2 ; P=0.05	SIZE: A=188 ; F(1,97)=17 ; P<0.0001 AGE: F(2,97)=8 ; P<0.001 DENSITY: A=48 ; F(1,97)=80 ; P<0.0001
	HIGH	SIZE: A=82 ; F(1,63)=5.1 ; P=0.03 AGE: F(3,63)=3.8 ; P=0.01 SIZE:AGE: F(3,60)=0.7 ; P=0.5	SIZE:DENSITY: A=67 ; F(1,53)=0.7 ; P=0.4 SIZE:FOOD: A=-163 ; F(1,53)=0.2 ; P=0.7 DENSITY:FOOD: A=-126 ; F(1,53)=0.5 ; P=0.5 SIZE:DENSITY:FOOD: A=129 ; F(1,53)=0.2 ; P=0.7	SIZE:AGE: F(2,90)=1.4 ; P=0.3 SIZE:DENSITY: A=62 ; F(1,90)=2.1 ; P=0.2 AGE:DENSITY: F(2,90)=1.9 ; P=0.2 SIZE:AGE:DENSITY: F(2,90)=0.4 ; P=0.7

This first chapter explored how *trade-offs* in energy allocation strategies are adjusted in response to environmental quality at the intraspecific level, and has suggested that nutrients can differentially affect parasitoid reproductive success. In the following chapter, we will experimentally explore the influence of environmental characteristics in shaping energy allocation strategies, and investigate the potential role of differences in these strategies in the coexistence of competing species. In the first part of this chapter, we will focus on the energy allocation strategies adopted during parasitoid juvenile stage, and in the second part, we will test whether the energy allocation strategies adopted during the larval stage are maintained over adult stage despite feeding activity.

Chap II. *Trade-offs* in resource allocation, adaptations to different habitats and their potential roles in coexistence

1. Differential energy allocation as an adaptation to different habitats in the parasitic wasp *Venturia canescens*.

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Perrine Pelosse, Carlos Bernstein & Emmanuel Desouhant

Laboratoire de Biométrie et Biologie Evolutive (UMR 5558); CNRS; Univ. Lyon 1, 43 bd 11 nov, 69622, Villeurbanne Cedex, France.

Running title: Differential energy allocation as an adaptation to habitat characteristics.

Corresponding author: Perrine Pelosse; pelosse@biomserv.univ-lyon1.fr; Laboratoire de Biométrie et Biologie Evolutive (UMR 5558); CNRS; Univ. Lyon 1, 43 bd 11 nov, 69622, Villeurbanne Cedex, France.

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1.1 Abstract

Environmental pressures are expected to favor organisms that allocate optimally metabolic resources to reproduction and survival. We studied the resource allocation strategies and the associated trade-offs in the parasitoid wasp *Venturia canescens*, and their adaptation to the characteristics of the environment. In this species, individuals of two reproductive modes coexist in the same geographical locations but occur mainly in

distinct habitats. Thelytokous (asexual) wasps are mostly found in anthropogenic habitats, where hosts tend to aggregate and food is absent. Arrhenotokous (sexual) wasps are exclusively found in natural habitats, where hosts are scattered and food is present. We analysed (i) the quantity of energy stored during ontogeny, (ii) the trade-off between reproduction and survival by measuring egg load and longevity and (iii) the host patch exploitation behaviour of the wasps at emergence. Arrhenotokous wasps emerge with more metabolic resource than thelytokous ones, especially glycogen, nutrient that could be used to fly, in searching for food and/or hosts. Thelytokous wasps allocate more energy than arrhenotokous wasps to egg production: this would allow parasitism of numerous hosts. The trade-off between egg production and longevity was not revealed within reproductive modes, but when comparing them. At emergence, arrhenotokous wasps tend to exploit host patches less thoroughly than thelytokous wasps, suggesting that by leaving the host patch, they search for food. The results clearly show adaptations to the characteristics of habitats preferentially inhabited by the two reproductive modes, and suggest a mechanism that facilitates their coexistence in natural conditions.

1.2 Introduction

The anatomical, physiological and behavioural traits of organisms have evolved through the process of natural selection, resulting in an increase in their reproductive success (Roff 1992, Stearns 1992). A perfect matching between traits of an organism and environmental factors is however never attained because organisms must cope with constraints, changing environments and contradictory needs (Roff 1992). For instance, the limited energy supply does not allow maximizing all traits associated with fitness. As a result, energy allocation toward different ecological functions trades-off, resulting in habitat specializations at the species level (*e.g.* Ellers & van Alphen 1997).

Parasitoids are good biological models to study energy allocation strategies because a female reproductive success is directly related to its fecundity and its efficiency in locating suitable hosts. Since these two processes are both energy-demanding and linked to fitness, energy allocation to each of them should be under strong selective pressure (Ellers *et al* 2000). A high reproductive success will be attained by female parasitoids if they approach a perfect matching between the number of eggs they carry and the number of hosts encountered during adult life (Rosenheim 1996, Sevenster *et al*

1998). Consequently, the availability and spatial distribution of the hosts might determine how the resources should be invested toward survival and reproduction (Ellers & van Alphen 1997).

In parasitoids, the nutritional resources provided by the host and stored by the parasitoid during ontogeny constitute the only energy reserves available at emergence (the 'teneral resources', Rivero & Casas 1999a). These resources are of utmost importance if adults do not feed or if some required nutrients cannot be obtained or synthesized from adult food (Boggs 1997a). When the host provide few resources, parasitoid larvae are particularly expected to make 'choices' in allocating energy to different functions (*e.g.* larval growth, energy storage, egg production).

In this paper, we studied energy allocation strategies in relation to habitat characteristics in the solitary endoparasitoid *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae). In this species, closely related asexual (thelytokous) and sexual (arrhenotokous) strains occur in the same geographical locations (Beukeboom *et al* 1999, Schneider *et al* 2002). Extensive sampling in the South of France revealed that (i) arrhenotokous wasps exclusively live in natural conditions where they predominate and (ii) thelytokous wasps develop both in natural and anthropogenic environments (*i.e.* granaries and mills) but are mostly found in the latter (Schneider *et al* 2002, Amat 2004).

Table 1. Main characteristics of the two habitats inhabited by the two reproductive modes of *Venturia canescens*.

ANTHROPOGENIC HABITATS (granaries, mills)	NATURAL HABITATS
Closed environments	Open environments
No food	Relatively frequent food sources (Casas <i>et al</i> 2003)
Relative stability of thermal factors (<i>e.g.</i> temperature)	Variability of thermal factors
Hosts at the surface of the stored flour or grain (Ahmad 1936, Waage 1979)	Hosts in desiccated fruits (Salt 1976); Most often 1 host / fruit (Driessen & Bernstein 1999)
Hosts tend to aggregate and may attain high densities	Hosts scattered, scarce and homogeneously distributed

Assuming that thelytokous and arrhenotokous wasps are adapted to their preferred habitats, we expect that they would adopt different energy allocation strategies and host exploitation behaviours. In natural habitats, *V. canescens* attacks several species of pyralid moth larvae in dried fruits (Salt 1976), where most often, a single host develop (Driessen & Bernstein 1999, Table 1). Consequently, arrhenotokous wasps have to fly in search for scattered hosts and/or for feeding sites (Desouhant *et al* 2003, Desouhant *et al* 2005). In addition, they must find mates to reproduce. Indeed, arrhenotokous females left release points sooner than thelytokous ones in a mark-release-recapture experiment (Amat 2004), and were, in average, faster flyers on a flight mill (Lukas *et al* in prep.). Since flying is one of the most energy-demanding activities in insects (Harrison & Roberts 2000), we hypothesized that, during ontogeny, arrhenotokous wasps would allocate a non-trivial part of their available energy to the elaboration of energy reserves. Carbohydrate glycogen is the main flight fuel used by Hymenoptera (Wolf *et al* 1999, Vogt *et al* 2000, Harrison & Fewell 2002). Moreover, as food is present in natural habitats (Casas *et al* 2003), arrhenotokous wasps should leave host patches earlier than thelytokous ones, in search for food (Sirot & Bernstein 1996). Conversely, in anthropogenic habitats, hosts tend to aggregate and may attain high densities because they develop at the surface of the stored flour or grain (Ahmad 1936, Waage 1979, Bernstein personal observation, Table 1). Under such conditions, thelytokous wasps might initiate fewer flights and find more hosts. Thus, we hypothesized that they allocate more energy to egg production than arrhenotokous wasps. Furthermore, as food is most often absent in anthropogenic habitats, they probably exploit host patches more thoroughly than arrhenotokous wasps. For wasps of the two reproductive modes, the energy allocated to the energy reserves must trade-off with the energy allocated to egg production (for empirical evidence on a parasitoid: Ellers & van Alphen 1997; for a review in holometabolous insects: Jervis *et al* 2005).

Here, to test the above-mentioned hypotheses, we studied the energy allocation strategies adopted during ontogeny and the host patch exploitation behaviour at emergence of thelytokous and arrhenotokous females *V. canescens*. Parasitoids were compelled to develop in hosts that provide either a high or a low quantity of nutritional resources. This enabled us (i) to assess the effect of the amount of resources provided by the host on the energy allocation and behavioural strategies, (ii) to control the quantity of nutritional resources acquired by parasitoids and (iii) to create conditions of resource

limitation under which energy allocation toward survival and reproduction should trade-off. We used two approaches to assess the energy allocation strategies adopted by the female parasitoids. First, the fraction of resources allocated during ontogeny to energy storage was assessed by a colorimetric analysis (van Handel 1985a, 1985b). This analysis enables to appraise both the quality (carbohydrates or lipids) and the quantity of energy reserves. Then, to determine the quantity of energy allocated to reproduction and to test whether this energy trades-off with the energy devoted to survival, we focused on the trade-off between reproduction and survival. Egg load and longevity were measured on females that had access to neither food nor hosts. Finally, we characterized the host exploitation behaviour adopted at emergence by female parasitoids by considering two key variables of foraging behaviour: the patch residence time and the number of ovipositions (van Alphen *et al* 2003).

1.3. Materials & Methods

1.3.1. Biological material and cultures

Venturia canescens Gravenhorst (Hymenoptera: Ichneumonidae) is an endoparasitoid of lepidopteran larvae, mainly Pyralidae (Salt 1976). *V. canescens* females emerge with mature and immature eggs (Trudeau & Gordon 1989) that mature during adult lifetime (synovigeny). Energy transfer from eggs to survival by egg resorption does not occur in *V. canescens* (Eliopoulos *et al* 2003). *V. canescens* is a solitary parasitoid i.e. only one offspring can develop per host. Hosts are attacked from their second to fifth instar (Harvey *et al* 1995). *V. canescens* is koinobiont (Corbet 1968), i.e. hosts continue to grow when parasitized. The mandibular gland secretions released by hosts on the substrate, when they feed, act as kairomones and enable *V. canescens* to locate hosts, and to estimate host density (Corbet 1971, Driessen & Bernstein 1999). It is easy to assess in *V. canescens* whether an attack results in an oviposition: a characteristic movement of the abdomen, the “cocking”, is performed by the animal in order to place a new egg at the tip of its ovipositor, ready for the next attack (Rogers 1972, Amat *et al* 2003). *V. canescens* does not practice host-feeding, but feeds on sugar in natural conditions (Casas *et al* 2003, Desouhant *et al* 2005).

Thelytokous and arrhenotokous strains used in this experiment were obtained from the same location in natural conditions near Valence, Southern France, during summer

2004. Hosts used for parasitoid development, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), are maintained in laboratory on wheat semolina. Hosts and parasitoids are reared in a controlled, constant environment ($24 \pm 1^\circ\text{C}$, $80 \pm 5\%$ RH and 13hL: 11hD). All experiments were performed in those conditions during March and April 2005.

1.3.2. Method

General design

We compared the energy allocation strategies adopted during ontogeny and the host exploitation behaviour at emergence, between thelytokous and arrhenotokous females of *Venturia canescens*. To assess the influence of the amount of nutritional resources available during ontogeny, we compelled parasitoids to develop in two host densities (Harvey *et al* 1995, Bernstein *et al* 2002, Lane & Mills 2003): low (condition hereafter called High Resource Availability: HRA) and high (condition hereafter called Low Resource Availability: LRA). Female parasitoids that emerged from either of these two conditions were assigned to one of the 3 following experiments: (1) *energy reserves at emergence*, (2) *trade-off between reproduction and longevity* and (3) *host exploitation behaviour* (see Table 2 for number of tested wasps).

The hosts providing large amounts of resources were obtained by introducing 20 second instar (25 ± 2 days old) *Ephestia kuehniella* larvae in cylindrical plastic boxes (8×5 cm) containing 10 g of semolina. The hosts providing limited resources were obtained by introducing in similar boxes, within the same quantity of semolina, 300 host larvae. The two host densities were chosen according to Bernstein *et al* (2002). On each of 6 consecutive days, one high-density and four low-density boxes were prepared for each reproductive mode. Host larvae developed in these conditions during 7 days. Then, each day and for each reproductive mode, 9 females were introduced in each high-density box and 3 females in each low-density box, to parasitize the hosts. A smaller number of females was used in the low-density boxes in order to minimize superparasitism. Several females per box were used in order to limit maternal effects on emerged female characteristics. Thus, a statistical effect of the box on measurements of offspring females is most unlikely. Parasitoid females used to parasitize the hosts were individually collected at emergence from our rearing stock. Arrhenotokous females were transferred to cages containing males (nearly 25 females for 50 males each day)

and mating was checked. Thelytokous and mated arrhenotokous females were maintained in different cages (with constant numbers of 25 females) during 24 hours with access to food (1:2 water diluted honey on a piece of cotton wool). Then, they were placed in the host boxes during 72 hours with access to similar food.

Table 2. Number of tested wasps for each combination of the two experimental factors: reproductive mode (arrhenotokous or thelytokous) and resource availability during ontogeny (HRA: High Resource Availability or LRA: Low Resource Availability), for each experiment (1: energy reserves at emergence; 2: trade-off between reproduction and longevity; 3: host exploitation behaviour; size: size of the wasps).

Resource availability during ontogeny	ARRHENOTOKOUS				THELYTOKOUS			
	1	2	3	size	1	2	3	size
HRA	21	24	18	45	20	28	18	48
LRA	24	22	16	46	26	23	17	49

Newly emerging females were collected each day and assigned alternatively to either of the two experiments “*energy reserves at emergence*” and “*trade-off between reproduction and longevity*”. We interrupted female collection 14 days after the first emergences.

A specific treatment was used for the “*host exploitation behaviour*” experiment. We randomly extracted from the host boxes some parasitoid pupae before emergence, 15 days after parasitization, and placed them individually in plastic tubes (7×3 cm). Thus, the females emerged in an environment free of cues on host availability that could influence behaviour.

Energy reserves at emergence

Our aim was to test whether thelytokous and arrhenotokous wasps store the same quantity of energy during ontogeny and to characterize the nature of the reserves.

We assessed, on the whole females, the levels of lipids and carbohydrates at emergence with a colorimetric analysis (van Handel 1985a, 1985b, van Handel & Day

1988). This method has already been used for *V. canescens* (Casas *et al* 2003). It allows quantification, for the same individual, of total lipids, fructose, glucose from trehalose (glucose-glucose dimer) and glucose from glycogen (glucose polymer) (van Handel & Day 1988). As sucrose (glucose-fructose dimer) traces might be present in the boxes (the mothers were fed with honey), we removed the eventual effects of feeding from the determination of glucose contents. We determined for each female the concentration of fructose and total glucose, and considered the difference to assess the concentration of constitutive glucose (van Handel & Day 1990).

Newly emerged females were frozen after collection to halt metabolic processes. As an index of individual size, the left hind tibia was removed and measured with a graduated scale, under a microscope. To remove any size effect from our measurements, we divided them by individual tibia length. The total amount of energy available at emergence was assessed using the following equivalences: 16.74 Joules per mg carbohydrates and 37.65 Joules per mg lipids (Rivero & Casas 1999a, Casas *et al* 2003).

Trade-off between reproduction and longevity

To investigate the effects of resource availability during ontogeny and of the reproductive mode, on the trade-off between reproduction and longevity, we recorded on the same individuals both longevity and egg load at death.

Parasitoids were isolated at emergence in plastic tubes (7×3 cm) with a water-imbibed piece of cotton wool and without access to food and hosts. The tubes were inspected at 2 hours intervals from 9:00 am to 7:00 pm to register the time of death. We considered the wasps dead in the night to have died at 2:00 am (the median time between 7:00 pm and 9:00 am, Desouhant *et al* 2005). After death, wasps were dissected and eggs from the whole egg complement were counted under microscope. The left hind tibia was measured.

Host exploitation behaviour

To analyse the behaviour of thelytokous and arrhenotokous females on a host patch at emergence, we recorded patch residence time and number of ovipositions on newly emerged females.

Newly emerged females from isolated pupae were placed in plastic tubes (7×3 cm) with a water-imbibed piece of cotton wool. During 3 hours before trials, arrhenotokous females were provided with 3 males (1-3 days old and fed with honey) to mate, while thelytokous were kept isolated. Two of the males came from the low-density host boxes and one from the high-density host boxes. Host patches used in the trials consisted of 6 third instar hosts in 5 mm deep 50 mm-diameter dish filled with semolina and covered with a fine netting, to prevent the host larvae from escaping. Patches were prepared 1 week before trials to let the host larvae contaminate the semolina with mandibular gland secretions. Just before a trial, a patch was placed at the centre of a larger dish (25 cm diameter) filled with semolina (Driessen & Bernstein 1999). Patch surface and semolina level were adjusted to the large dish rim. Each trial started with the introduction of one female at the patch edge. The female parasitoid was free to leave the large dish. No food was available in the environment. The behaviour was continuously recorded, until the wasp left the large dish, with an event recorder. We defined the patch residence time as the total time between the first entry into the patch and the last departure, i.e. the last crossing of the patch edge before leaving the large dish. As the number of ovipositions corresponds to the number of cockings (Rogers 1972, Amat *et al* 2003), we tested after each trial whether an egg had been laid after the last cocking, by providing female with host-contaminated semolina, and checking for an additional cocking.

1.3.3. Statistical analysis

The effects of resource availability during ontogeny (HRA and LRA) and reproductive mode (thelytokous or arrhenotokous) on parasitoid size, lipid, glucose and energy contents per mm tibia were investigated in 2-way ANOVAs. The variables “glucose from trehalose per mm tibia” and “lipids per mm tibia” were first square root transformed, as the residuals were not normally distributed.

In the behavioural experiment, some females stayed on the host patch without displaying any host searching behaviour. The egg-laying rate (number of ovipositions / patch residence time) was null both for females that stayed a long time on the patch without laying any egg and for females that left early the host patch before laying any egg. To discriminate between these two kinds of females, we considered two variables: patch residence time and number of ovipositions. To analyse the effects of resource availability during ontogeny and of reproductive mode on these variables, we used

generalised linear models assuming a Gamma or a Poisson distribution of the residuals (log link), for patch residence time and for the number of ovipositions, respectively. Resource availability and reproductive mode were introduced in the models as explanatory variables.

To assess the effects of resource availability and reproductive mode on the relation between egg load and longevity, we used a generalization of the analysis of variance: the Multivariate Analysis of Variance (MANOVA) that allows the response variable to be multi-dimensional (Tomassone *et al* 1988). Here, the response variable: “egg load and longevity” was bi-dimensional. Egg load and longevity were also fitted separately to linear models of analysis of variance. In all the models, we introduced the parasitoid size as the first explanatory variable, in order to remove any size effect.

We used a backward stepwise procedure to remove non-significant factors and interactions between factors, and to select the final models. Residuals were examined to confirm that models accurately fitted the data. All data analyses and graphics were performed with the *R* free software environment (Ihaka & Gentleman 1996, <http://cran.at.r-project.org>), and some of the figures with the “ade4” package (Chessel *et al* 2004).

1.4. Results

1.4.1. Size

Data on parasitoid size, measured on wasps assigned to the “*energy reserves at emergence*” and “*trade-off between reproduction and longevity*” experiments, were pooled in the analysis (Table 2).

Parasitoid adult size was strongly affected by resource availability during ontogeny ($F=227.6$, d.f.=1 and 186, $P<0.001$). Females were larger when they developed in conditions of HRA (tibia length: 1.91 ± 0.01 mm (mean \pm s.e.), against 1.66 ± 0.01 mm for females developed in conditions of LRA). Neither the interaction of reproductive mode with resource availability during ontogeny ($F=0.06$, d.f.=1 and 184, $P=0.81$) nor reproductive mode ($F=0.6$, d.f.=1 and 185, $P=0.43$) significantly affected wasp size.

1.4.2. Energy reserves at emergence

The overall energy content at emergence, corrected for size, was significantly higher for arrhenotokous than for thelytokous females (Figure 1a, $F=4.65$, d.f.=1 and 88, $P=0.03$). The energy content at emergence was higher for individuals developed in conditions of HRA, irrespective of their reproductive mode ($F=14.3$, d.f.=1 and 88, $P<0.001$). The effect of the interaction between resource availability and reproductive mode was not significant ($F=0.005$, d.f.=1 and 87, $P=0.94$).

Lipid content at emergence was neither affected by resource availability (Figure 1b, $F=0.42$, d.f.=1 and 88, $P=0.52$) nor by reproductive mode ($F=0.99$, d.f.= 1 and 88, $P=0.32$). The effect of the interaction between these two factors was not significant ($F=0.009$, d.f.= 1 and 87, $P=0.93$).

The amount of glucose at emergence, originated from trehalose, was higher for females developed in conditions of HRA (Figure 1c, $F=11.1$, d.f.=1 and 89, $P=0.001$). This amount did not differ between arrhenotokous and thelytokous wasps ($F=0.63$, d.f.=1 and 88, $P=0.43$), and was not affected by the interaction between reproductive mode and resource availability ($F= 0.07$, d.f.=1 and 87, $P=0.79$).

Glycogen-stored glucose was influenced both by resource availability during development and by reproductive mode. Arrhenotokous wasps had significantly more glycogen than thelytokous wasps at emergence ($F=7.7$, d.f.=1 and 88, $P=0.007$). The glycogen content of female parasitoids decreased significantly when they developed in conditions of LRA (Figure 1d, $F=35.7$, d.f.=1 and 88, $P<0.001$), in the same way for the two reproductive modes ($F= 0.04$, d.f.=1 and 87, $P=0.84$).

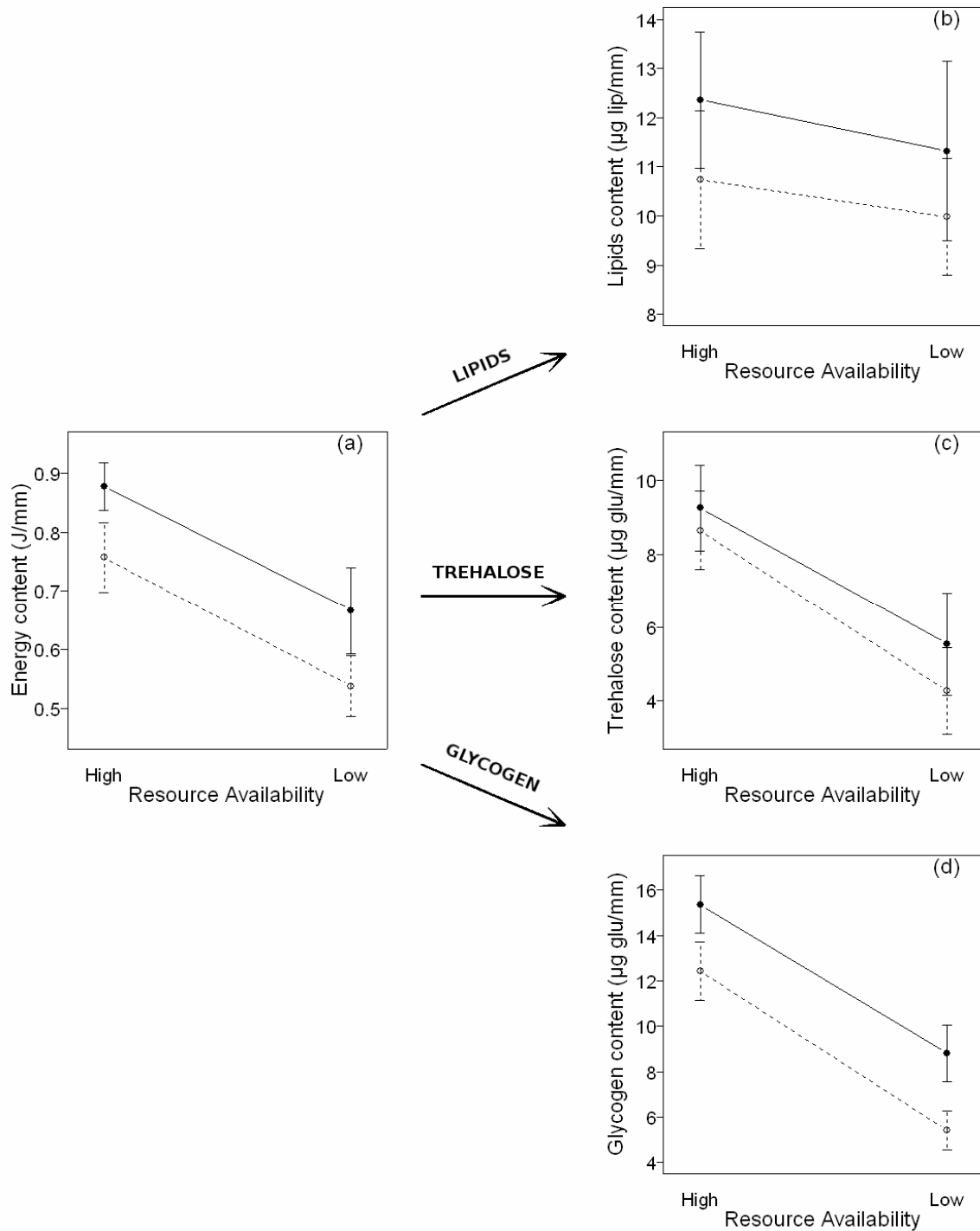


Figure 1. Energy reserves of arrhenotokous (solid lines and filled circles) and thelytokous (dashed lines and opened circles) females at emergence, according to resource availability during ontogeny (either Low or High Resource Availability: LRA and HRA). (a) Total energy supply (mean \pm s.e.) (joules / mm hind tibia length). (b) Lipid contents (mean \pm s.e.) (μg / mm hind tibia length). (c) Glucose from trehalose contents (mean \pm s.e.) (μg glucose / mm hind tibia length). (d) Glucose from glycogen contents (mean \pm s.e.) (μg glucose / mm hind tibia length).

1.4.3. Trade-off between reproduction and longevity

Parasitoid size, introduced as the first explanatory variable in the Multivariate Analysis of Variance, had a significant influence on the relation between egg load at death and longevity ($F=114.6$, $d.f.=2$ and 91 , $P<0.001$). After considering this size effect in the model, both resource availability ($F=7.5$, $d.f.=2$ and 91 , $P<0.001$) and reproductive mode ($F=44.9$, $d.f.=2$ and 91 , $P<0.001$) significantly affected the relationship between egg load at death and longevity. This result indicates that arrhenotokous and thelytokous females differed significantly both in egg load and longevity (Figure 2): arrhenotokous wasps lived longer (HRA: 85 ± 2 h (median: 89 h) and LRA: 61 ± 4 h (median: 65 h); against HRA: 74 ± 2 h (median: 75 h) and LRA: 48 ± 4 h (median: 41 h) for thelytokous females), and had fewer eggs (HRA: 72 ± 3 eggs and LRA: 50 ± 3 eggs; against HRA: 98 ± 3 eggs and LRA: 64 ± 4 eggs for thelytokous females) than thelytokous females. When the wasps developed in conditions of LRA, they decreased both in fecundity and longevity (Figure 2). The interaction between resource availability and reproductive mode was nearly significant ($F=2.9$, $d.f.=2$ and 91 , $P=0.059$).

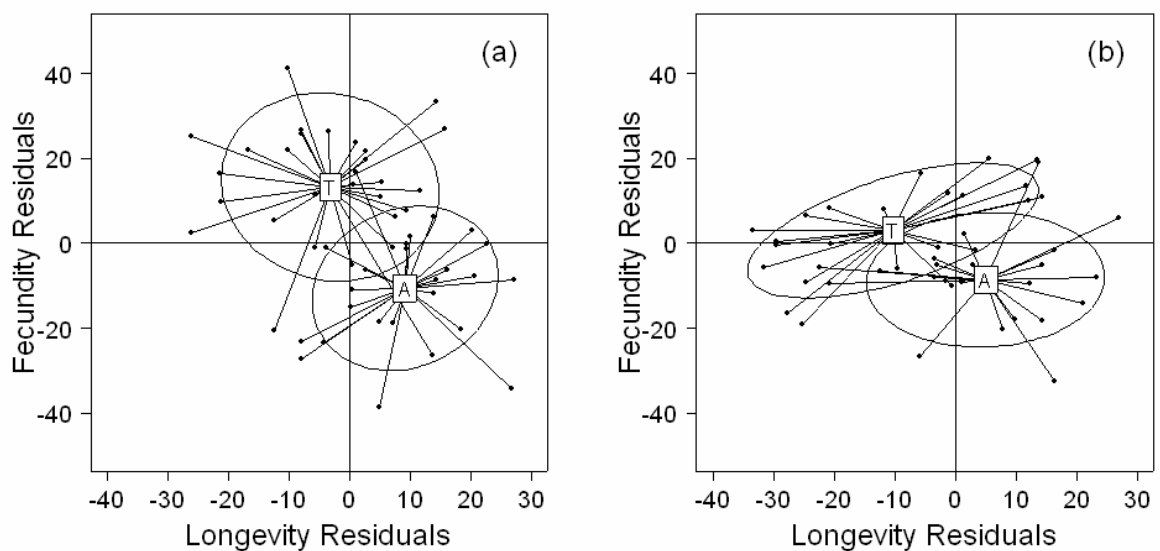


Figure 2. Arrhenotokous (A) and thelytokous (T) individual positions in accordance with egg load at death (fecundity) and longevity, both corrected by size. (a) Parasitoids developed in conditions of HRA, or (b) in conditions of LRA. Axes show the residual values from linear regressions of both fecundity and longevity as a function of female body size. Each point represents an individual, and is connected to the mean point of its group (A or T) by a segment. The ellipses are used to point out the dispersion of individuals within each group.

To investigate more precisely the differences between arrhenotokous and thelytokous wasps in their responses to resource availability during development, longevity and egg load were analyzed separately. The interaction between resource availability and reproductive mode significantly influenced the egg load at death ($F=5.84$, d.f.=1 and 92, $P=0.018$), but not the longevity ($F=0.29$, d.f.=1 and 92, $P=0.6$) of the wasps. Thus, the longevity of arrhenotokous and thelytokous wasp was similarly reduced in conditions of LRA. Conversely, the decrease in egg load in conditions of LRA was larger for thelytokous than for arrhenotokous females.

1.4.4. Host exploitation behaviour

Patch residence time was significantly affected by the interaction between resource availability and reproductive mode ($t=3.3$, d.f.=65, $P=0.002$). Arrhenotokous wasps stayed longer on the host patch when they developed in conditions of HRA (504 ± 85 s), compared with LRA (158 ± 41 s, Figure 3a). The overall time spent on the host patch by thelytokous females was long, independent of resource availability during development (HRA: 377 ± 65 s, and LRA: 467 ± 68 s, Figure 3a).

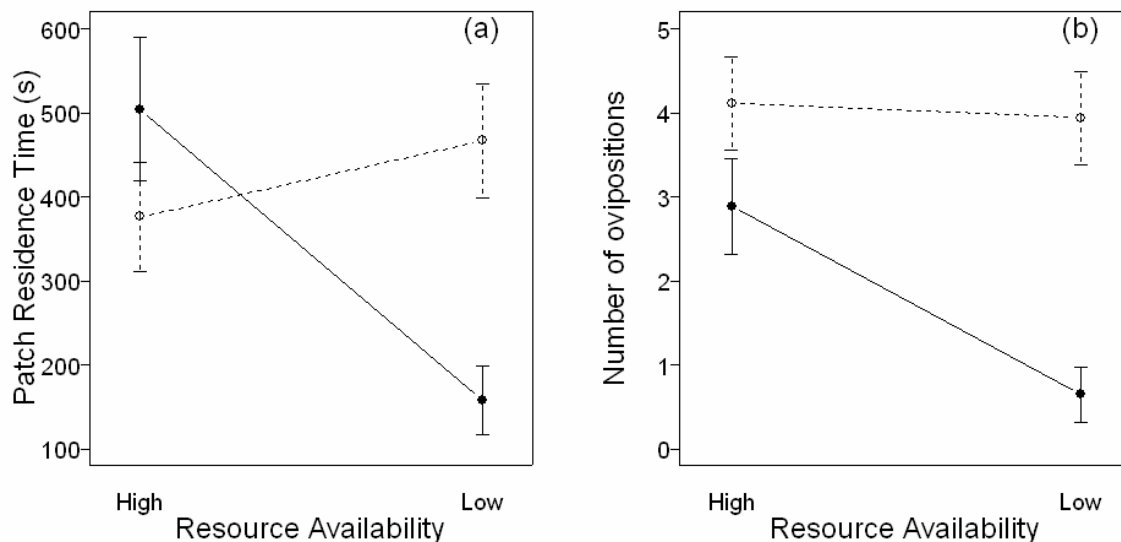


Figure 3. Host exploitation behaviour of arrhenotokous (solid lines and filled circles) and thelytokous (dashed lines and opened circles) females at emergence, according to resource availability during ontogeny (either LRA or HRA). (a) Patch residence time (mean \pm s.e.) (in s). (b) Number of ovipositions on a patch (mean \pm s.e.).

As the number of eggs laid strongly depends on patch residence time, a similar pattern was observed for the number of ovipositions. The number of eggs laid was influenced by the interaction between reproductive mode and resource availability during development ($t=-3.9$, $d.f.=66$, $P<0.001$). The number of eggs laid remained high and relatively constant for thelytokous females (HRA: 4.1 ± 0.6 eggs, and LRA: 3.9 ± 0.6 eggs, Figure 3b) but decreased for arrhenotokous ones when they developed in conditions of LRA (HRA: 2.9 ± 0.6 eggs, and LRA: 0.6 ± 0.3 eggs, Figure 3b).

1.5. Discussion

In this work we revealed physiological, life-history and behavioural adaptations to habitat for conspecific wasps differing in reproductive mode. As expected, wasps adopt specific energy allocation strategies during ontogeny, in accordance to their reproductive mode. While arrhenotokous wasps store more energy, mainly as glycogen, during ontogeny, thelytokous wasps allocate more energy to egg production. Resource availability during ontogeny did not affect the energy allocation patterns, but influenced differently the host patch exploitation behaviour for wasps of the two reproductive modes. Thelytokous wasps laid a relatively high number of eggs whatever the developmental conditions. Conversely, arrhenotokous wasps left the host patches earlier and laid fewer eggs when developed under resource shortage.

The allocation and behavioural patterns strengthened our initial hypothesis, i.e. environmental conditions (natural and anthropogenic for arrhenotokous and thelytokous modes, respectively; Table 1) operate as strong selective pressures, modelling both the allocation of resources and the behaviour.

1.5.1. Energy allocation strategies in relation to host quality

By varying the level of resources provided by the host *Ephestia kuehniella*, we investigated the effect of an intraspecific variation of host quality on *V. canescens*. Whatever the reproductive mode, developing in a small host results in a decrease of adult size (as estimated by tibia length) and size-related components of fitness (energy content, egg load and longevity). Bernstein *et al* (2002) made the same observation for thelytokous *V. canescens*.

The biochemical assay revealed that arrhenotokous wasps have more energy reserves at emergence, especially glycogen, than thelytokous ones, independently of resource availability during ontogeny. In Hymenoptera, glycogen is usually allocated to flight (Wolf *et al* 1999, Vogt *et al* 2000, Harrison & Fewell 2002). As a consequence, our results may partially provide a proximate explanation of the fact that arrhenotokous wasps are faster flyers than thelytokous ones, as reported by previous workers (Amat 2004, Lukas *et al* in prep.). With more energy available for flight activity, arrhenotokous wasps should have an advantage over thelytokous ones in searching for scattered hosts and food sources in natural habitats. For each reproductive mode, the carbohydrate stock (free glucose and glycogen) undergoes a larger decrease than the lipid stock when the wasps developed in conditions of low resource availability (48.0 against 8.2%). In such conditions, arrhenotokous and thelytokous *V. canescens* tended to maintain a high lipid storage, to the detriment of carbohydrate storage. This could be explained by the absence of lipogenesis (lipids synthesis from carbohydrates) in adults of this species (Casas *et al* 2003), as is generally the case in parasitic wasps (Giron & Casas 2003a). Moreover, carbohydrates are found in adult food sources (nectar, fruit exudates) on which *V. canescens* feeds in natural conditions (Casas *et al* 2003, Desouhant *et al* 2005), while lipids are absent. This observation underlies the importance of host-derived nutrient storage, in species that feed on different substrates as juveniles and adults (Boggs 1997a).

Egg load and longevity did not trade-off within each reproductive mode, in spite of the fact that we controlled experimentally the level of resources acquired by parasitoid larvae, as suggested by van Noordwijk and de Jong (1986). It is possible that life-history traits not considered here (*e.g.* egg quality) are involved in the trade-off between reproduction and survival. Nevertheless, the trade-off occurs between the two reproductive modes. Ellers & van Alphen (1997) recorded such a trade-off between northern and southern populations of *Asobara tabida*. Without access to hosts and food, arrhenotokous wasps lived longer and had fewer eggs at death than thelytokous ones. The larger glycogen stock of arrhenotokous wasps might be involved in their higher longevity because the experimented wasps were not allowed to fly. Indeed, a model considering the ectoparasitoid *Eupelmus vuilletti* suggested that carbohydrate levels determine wasp survival (Casas *et al* 2005). The role of lipids in the trade-off remains unclear because the two reproductive modes have the same amount of lipids. Insects

incorporate lipids into eggs (Giron & Casas 2003a). Consequently, since thelytokous wasps have more eggs, lipids might be located differently for thelytokous and arrhenotokous wasps, the former having more lipids in eggs and the latter in fat body. A precise quantification, and comparison between the two reproductive modes, of amounts of lipids in reproductive organs is thus needed. The difference in egg load at death between the two reproductive modes was observed also at emergence (results not shown and Schneider 2003), and could not be attributed to a difference in egg maturation rate. Thelytokous wasps produce thus more eggs before emergence. Owing to the relative high host availability in anthropogenic habitats, thelytokous wasps might have been selected to produce a high number of eggs during ontogeny.

When experiencing conditions of low resource availability during ontogeny, the longevity was identically affected for the two types of wasps, but the number of eggs was significantly more reduced for thelytokous wasps than for arrhenotokous ones (29.8 against 34.3%). Arrhenotokous wasps thus seem to maintain a higher egg production rate than thelytokous ones when developing in a low-quality host. This suggests that arrhenotokous wasps tolerate higher variation in host quality (*e.g.* size). As a result, they might be able to develop in more host species, *i.e.* might be more generalist, than thelytokous ones. Salt (1976) reported numerous natural host species in which thelytokous *V. canescens* were able to develop, but no comparisons have been made yet between the two reproductive modes.

1.5.2. Toward a dynamic energy allocation

In synovigenic wasps, energy allocation by adults is expected to be dynamic, allowing wasps to adjust their egg load to the oviposition opportunities. Both thelytokous and arrhenotokous *V. canescens* females mature eggs during adult stage, reaching at death nearly twice the egg load at emergence (Schneider 2003). In anthropogenic habitats, the relative high host availability should select thelytokous wasps that mature additional eggs. Nevertheless, egg maturation is energy-demanding and thelytokous wasps have few energy reserves at emergence and cannot acquire additional resources by feeding in anthropogenic habitats. Conversely, with a higher energy supply at emergence and access to food, arrhenotokous wasps are expected to mature eggs when needed, allowing them to adjust their egg load to the variation of host availability. Egg resorption (the transfer of metabolic reserves from eggs to maintenance) does not occur

in *V. canescens* (Eliopoulos *et al* 2003). Consequently, the quantity of energy allocated during ontogeny to egg production by thelytokous wasps cannot be shifted then to survival.

1.5.3. Behavioural strategies at emergence

The behaviour at emergence of *V. canescens* females of both reproductive modes was differently affected by resource availability. Thelytokous females did not modify their host patch exploitation behaviour (patch residence time and number of ovipositions) depending on the developmental conditions, exploiting intensively the host patch. Conversely, arrhenotokous wasps thoroughly exploited the host patch when they developed in conditions of high resource availability, but left it early when they experienced a resource shortage. The food availability in the preferred habitats could explain such distinct behaviours: the presence of food in the immediate environment affects the patch residence time in *V. canescens*, by decreasing it (Lucchetta *et al* in prep.). With a limited life expectancy, thelytokous wasps probably do not waste time by searching for food that is absent in anthropogenic habitats. Conversely, with a reduced number of eggs and a high longevity, arrhenotokous wasps might prefer to search for food that is present in natural habitats, than exhaust their egg supply. In a multi-patch experiment, when experiencing a high patch encounter rate, they show indeed a reduced oviposition rate whereas thelytokous wasps increased it (Thiel *et al* 2005). By modelling the optimal time allocation between sugar and host-searching in the non-host-feeding parasitoid *Cotesia rubecula*, Tenhumberg *et al* (2006) suggested that wasps should always search for food, if available, once their energy reserves drop to low levels. Thelytokous wasps are known to leave anthropogenic habitats when their energy reserves decline (Beling 1932). The threshold below which *V. canescens* search for food seems to be lower for thelytokous wasps, as a result of a low probability of finding food in anthropogenic habitats.

1.5.4. Differential energy allocation: a mechanism that facilitates the coexistence of sexual and asexual reproductions in *V. canescens*?

At the community level, interspecific trade-offs, i.e. species specialization for different ecological functions, is one of the most common explanations for coexistence of

potentially competing species (Kneitel & Chase 2004). As thelytokous and arrhenotokous individuals are distinct genetic entities (Beukeboom *et al* 1999, Schneider 2003), we can regard them as two competing species. Indeed, the individuals of the two reproductive modes are known to co-occur locally in natural habitats from June to September (Beukeboom *et al* 1999, Schneider *et al* 2002, Amat 2004). Asexual forms benefit theoretically of a higher multiplication rate than sexual ones because sex requires producing males that only indirectly contribute to the next generation ("the two-fold cost of sex", Maynard Smith 1978). In the laboratory, the displacement of sexual *V. canescens* by asexual ones occurs in 4-5 generations (Amat, unpublished data). The differences in flight capability and host exploitation behaviour between wasps of the two reproductive modes should allow sexual wasps to maintain with their asexual counterparts at a local scale (Levins & Culver 1971, Hastings 1980, Tilman *et al* 1997). More investigations are however needed to make sure that the differences recorded here at emergence are maintained over adult stage in natural habitats. For instance, in *V. canescens*, access to food increases female longevity (Harvey *et al* 2001, Desouhant *et al* 2005). With frequent access to food in natural habitats, both arrhenotokous and thelytokous females are thus expected to increase their flying capacity and/or longevity.

1.5.5. Differential energy allocation as an adaptation to habitat

To compensate the two-fold cost of sexual reproduction, all else being equal between arrhenotokous and thelytokous females, one would expect that arrhenotokous wasps evolved larger egg supplies than thelytokous ones. However, we observed the opposite. This suggests that the adaptations we revealed result from specializations for specific environments and are not a response to the reproductive mode.

This study clearly shows adaptations to habitat through a differential energy allocation toward reproduction and survival in *V. canescens*, arrhenotokous wasps allocating more energy to resource storage and thelytokous wasps to reproduction. Such an interspecific trade-off opens unique perspectives to understand the coexistence of the two reproductive modes, and to a larger extent, two species.

1.6. References

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In this section we revealed that the patterns of energy allocation adopted during the larval stage differ among arrhenotokous and thelytokous individuals in *Venturia canescens*. In the next section we will explore their maintenance over parasitoid adult stage to test whether *trade-offs* in energy allocation could account for the maintenance of sexual individuals in this species.

2. Are initial patterns of energy allocation maintained over adult stage in thelytokous and arrhenotokous *Venturia canescens*?

This manuscript is in preparation as: Pelosse P., Amat I., Bernstein C. and Desouhant E. ‘*Comparison of lifetime resource allocation strategies in thelytokous and arrhenotokous Venturia canescens. Does food presence weaken the initial advantages of arrhenotokous wasps?*’ (Pelosse *et al.* in prep a).

2.1. Introduction

The study of the strategies of allocation of energy resources to competing needs such as reproduction and maintenance is of great importance for understanding the factors determining organisms’ reproductive success (Strand & Casas 2008). Energy allocation strategies have been partly shaped by natural selection to cope with the characteristics of the environment. In organisms with complex life-cycles, such as holometabolous insects, the selective pressures acting on nutrient acquisition and allocation may differ between life stages. Adults, because they rely on the resources gained and stored during the juvenile stage, the *teneral resources* (Rivero & Casas 1999), should depend, especially in the beginning of their lives, on the resource allocation strategies adopted during larval stage. Compromises are known to arise from juvenile stages to adjust the patterns of nutrient allocation to the environmental conditions faced by the adult. For instance, butterflies that cannot acquire proteins from food during their adult stage allocate a relatively large amount of proteins to build reproductive materials during their larval stage (Boggs 1981, 1997). Of course, the patterns of energy allocation toward reproduction and maintenance resulting from juvenile stages are generally not fixed. The acquisition of *income resources* (Boggs 1997, *sensu* Sibly & Calow 1984) through adult feeding, as well as energy expenditures associated with locomotion, reproduction or maintenance, profoundly modify adult energetic budgets. Energy allocation during the adult stage is therefore expected to be dynamic, allowing, to a certain extent, the adjustment of the metabolic resources to the requirements.

Parasitoids, *i.e.* holometabolous insects that are parasite during their juvenile stages and free-ranging as adults, provide interesting models to explore the mechanisms of energy allocation and their reliance on environmental characteristics (Jervis *et al.* 2008). Parasitoid females' reproductive success is directly linked to their efficiency in locating hosts and food sources and to the number of eggs available (Lee & Heimpel 2008). Energy allocation to maintenance and reproduction is thus expected to critically depend on the availability and spatial distribution of food and hosts, and to be under strong selective pressure (Ellers & van Alphen 1997). Some specific processes allowing re-allocating energy from maintenance to reproduction, and vice-versa, are known to occur in parasitoids. Synovigenic wasps, as opposed to proovigenic ones, are for instance able to mature additional eggs during their adult stage to adjust the number of eggs they carry to the environmental host availability (Flanders 1950, Ellers *et al.* 2000). In some species, females also resort to egg resorption when facing resource shortages, which allows them partly recovering energy allocated to reproduction to maintenance (King & Richards 1968).

In this paper, we explore the ability of adult parasitic wasps to adjust their energy allocation to an environment for which their initial pattern of energy allocation seems not well adapted. Our model system is the solitary parasitoid *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae). In this species, closely related thelytokous and arrhenotokous strains occur in the same geographical locations but preferentially thrive in distinct habitats (Beukeboom *et al.* 1999, Schneider *et al.* 2002). While arrhenotokous wasps exclusively live in natural conditions where they predominate, thelytokous wasps preferentially thrive in anthropogenic environments (*i.e.* granaries and mills), but are also found in natural habitats (Schneider *et al.* 2002, Amat 2004). These habitats strongly differ in host and food availabilities and spatial distributions (see *Table 1* of Pelosse *et al.* 2007 for a summary). In a previous study, we found that the strategies of resource allocation adopted during the larval stage are in line with the selective pressures experienced in the two habitats, and strongly differ between the two reproductive modes (Pelosse *et al.* 2007). As a result of the relative low host availability in natural habitats and the scattering of both hosts and food sources for which an extensive flight activity is most likely needed, arrhenotokous wasps emerge with relatively few eggs and large resources of glycogen. Since glycogen is the main flight fuel used by Hymenoptera (Vogt *et al.* 2000, Suarez *et al.* 2005), arrhenotokous wasps

are thus expected to have higher flight capabilities over thelytokous ones. In contrast, thelytokous wasps experience relatively high host availabilities in anthropogenic habitats and do not have to disperse much since hosts are relatively aggregated. They therefore emerge with a large egg complement and lower glycogen reserves.

The different energy allocation patterns observed among *V. canescens* reproductive modes may give insights into the issue of the maintenance of sex in natural habitats (Pelosse *et al.* 2007). Thelytokous and arrhenotokous wasps are found together in natural habitats from June to September (Amat 2004). Because sexual individuals suffer from the “two-fold cost of sex” (Maynard Smith 1978), we expect that without a short-term advantage, arrhenotokous wasps would be displaced by thelytokous ones. Our hypothesis is that the initial energy allocation patterns observed in arrhenotokous wasps: their relatively high level of energy reserves and their low number of eggs, would give them an advantage in natural habitats to counterbalance the “two-fold cost of sex” (Maynard Smith 1978). Yet, in natural habitats, sugary food sources are widely available from floral nectars and leave exudates (Desouhant *et al.* 2005) and thelytokous wasps are known to acquire sugars in field conditions (Casas *et al.* 2003, Desouhant *et al.* in prep). Thelytokous wasps may therefore potentially benefit from natural food sources to increase their metabolic reserves, which would weaken the initial differences in energy allocation patterns between the two reproductive modes.

Our aim is to test whether the initial advantage of arrhenotokous *V. canescens* females in term of energy allocation strategies is maintained over the adult stage in an environment providing a relatively low host number and food. This work is part of other studies on the two reproductive modes of *Venturia canescens*, which found out advantages of arrhenotokous wasps in natural habitats in term of responses to deteriorating conditions (Amat *et al.* 2006, Thiel *et al.* 2006) and flight (Lukas *et al.* submitted). We expect first that conditions of low host availability would constrain thelytokous wasps to lay few eggs, and that the two reproductive modes will show similar fecundities. Then, with access to sugary food sources, thelytokous wasps should acquire and store carbohydrates and therefore increase their longevity. Finally, because thelytokous *V. canescens* females have numerous eggs at emergence and are incapable of egg resorption (Eliopoulos *et al.* 2003), we expect that they would die with many remaining eggs when limited by the number of oviposition opportunities, and therefore waste energy allocated to reproduction.

To test thelytokous females' abilities to adjust their allocation strategies to conditions close to those encountered in natural habitats, we carried out a laboratory experiment in which thelytokous and arrhenotokous *V. canescens* experienced low host availabilities and were provided with food. Adult females were provided daily with a low availability host patch and a given quantity of food. To follow the dynamic processes of energy allocation toward somatic maintenance and reproduction, egg loads, stored and free carbohydrates, daily number of offspring and longevity were assessed on groups of females of different ages. We chose to focus our analysis on carbohydrates because (i) they reflect and allow quantifying the acquisition of food, (ii) glycogen can be used to indirectly assess flight capabilities, and (iii) carbohydrates are the main compartment affected by environmental variables such as food and host availability, at least in thelytokous *V. canescens*, while lipids and proteins show monotonous decreases over lifetime (Pelosse *et al.* in prep). To test whether the differences observed between the two reproductive modes do not come from different abilities to find food in our experimental conditions, we conducted an additional experiment in which we monitored the feeding behaviors of the wasps.

2.2. Material and methods

2.2.1. Biological material

Venturia canescens Gravenhorst (Hymenoptera: Ichneumonidae) is a koinobiont endoparasitoid of lepidopteran larvae, mainly Pyralidae (Salt 1976). *V. canescens* is a solitary parasitoid, which means that only one offspring can develop per host. Kairomones produced by hosts provide attractive substances for *V. canescens* (Corbet 1971, Castelo *et al.* 2003). *V. canescens* females emerge with mature and immature eggs (Trudeau & Gordon 1989, Harvey *et al.* 2001, Roberts & Schmidt 2004) that mature during adult lifetime (synovigeny). With continuous sugar access, thelytokous *V. canescens* can produce up to 100 eggs over their lifetime (Harvey *et al.* 2001, Roberts & Schmidt 2004). Eggs are small and yolk-deficient (=hydropic). *V. canescens* does not feed on hosts, but feeds on sugary food sources in natural conditions (Casas *et al.* 2003, Desouhant *et al.* 2005). Thelytokous and arrhenotokous strains used in this experiment were obtained from the same location in natural conditions near Valence, southern France, during the summer of 2004 for thelytokous wasps, and 2005 for arrhenotokous

ones. Hosts used for parasitoid development, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), were maintained in the laboratory on wheat semolina medium. Hosts and parasitoids were reared in a controlled environment ($24 \pm 1^\circ\text{C}$, $80 \pm 5\%$ RH and 13 hL:11 hD). Experiments have been carried out in the same conditions from March to July 2006.

2.2.2. Experimental design

The general aim of the experiment was to assess if the initial differences in energy allocation patterns between thelytokous and arrhenotokous *V. canescens* maintain during the adult stage in an environment with food and low host availability. To limit the variations in parasitoid size, the larval development of all experimented parasitoids has been conducted at controlled host densities, so as each parasitoid larva has a similar amount of nutritional resources available. Emerging females were then daily provided with a few hosts and with controlled amounts of food. We investigated their lifetime energy allocation dynamics by measuring variables reflecting either the somatic or reproductive compartments at emergence, at two days, four days or at death.

Development of experimented parasitoids

In a previous study we showed that the competition between host larvae affected the energy allocation strategies of parasitoids during their larval stage (Pelosse *et al.* 2007). The larval development of the females used here therefore occurred at a constant host density, in a controlled quantity of medium. Host density was chosen to be intermediate between those used in our previous experiment, as the high density (300 hosts in 10g semolina) corresponded to a strong level of competition, with high mortality rates and wasps emerging with few metabolic reserves, and the low density (20 hosts in 10g semolina) to a very low level of competition with excess of food (Bernstein *et al.* 2002, Pelosse *et al.* 2007).

The females used in the experiment developed in clear cylindrical plastic boxes (8×5 cm) containing 100 second instar *Ephestia Kuehniella* and 20g of wheat semolina. Hosts developed in those conditions during 7 days before being parasitized. The females used to parasitize the hosts were collected at emergence from the rearing stock. After their emergence, approximately 25 thelytokous females were introduced into a cage (30×30 cm), and approximately 25 arrhenotokous females and 25 males were

transferred into another cage for 3 hours, to allow mating (mating rate recorded during 2 hours is approximately 80%, Pelosse personal observation). While males were removed, food was supplied in each cage (1:2 water diluted honey on cotton wool). After 24 h, 5 females were transferred into each host box for 72 h. Each week during 12 weeks, 2 boxes were parasitized by thelytokous females and 4 by arrhenotokous females to allow collecting a sufficient number of arrhenotokous females that emerge together with males. A drop of honey was supplied on nets closing the boxes, and nets were changed while females were removed from host boxes, to prevent the offspring from feeding. After approximately 27 days of larval development, emerging parasitoids were collected for 12 days for each box.

Egg-laying experiment

Each day at 9:00 a.m., parasitoids already present in host boxes were removed, so as every parasitoids emerged between 9:00 and 10:30 a.m.. Ten thelytokous emerging females were transferred into a cage (30×30 cm), and 6 arrhenotokous ones into another cage containing 6 males (0-3 days old, emerged from the same boxes), to limit the global density differences between thelytokous and arrhenotokous cages. After a period of 4 hours, during which we expected that every arrhenotokous females mated, the males and 4 randomly chosen thelytokous females were removed from cages. Arrhenotokous females were mated because almost all of them are mated in natural conditions (Metzger *et al.* 2008). Mating does not induce strong costs, as mated and unmated females have similar longevities (Metzger 2008). Females were maintained in cages without food during 24 h.

Each day at 9:30 a.m., 2 females of each reproductive mode, randomly chosen from the cages (see above), were frozen and therefore constituted the females controlled at emergence. Remaining arrhenotokous and thelytokous females were randomly assigned to one of the three treatments: controlled at the age of 2 days, controlled at the age of 4 days or controlled at death. The females were individually placed in clear cylindrical plastic boxes (8×5 cm) closed with nets to allow ventilation, on a clean white desk and in a room free of host odours. Each female was daily provided with a host patch at 11:15 a.m. for 15 min. Host patches were made up of 5 third instar hosts in 7 mm deep 55 cm-diameter dishes filled with 13 g of wheat semolina, and covered with a net to prevent the host larvae from escaping. Patches were prepared 7 days before being

exploited by parasitoid females to let the host larvae impregnate the semolina with kairomones. At 1:30 p.m., 2 μ L of 20% sucrose solution were provided to females for 30 min on trays.

The females constituting the groups controlled at the age of 2 and 4 days were frozen at 10:30 a.m. on the day following their last egg-laying and feeding day. The females controlled at death were frozen at 10:30 a.m., 11:15 a.m., 11:30 a.m., 1:00 p.m. or 2:00 p.m., depending on when death occurred.

Energy allocation analysis

To investigate and compare how wasps of the two reproductive modes allocated their energy to reproduction and maintenance we recorded for every female the number of offspring, the longevity, the size, the egg load and the amount of stored (glycogen) and free (glucose and fructose) carbohydrates.

- (i) *Offspring number.* Host patches were collected each day after being parasitized, and host larvae transferred into ventilated clear plastic boxes (9×9 cm) containing approximately 50g of semolina. The daily number of emerging adult offspring was subsequently determined for each female.
- (ii) *Longevity.* The date and time of death were recorded on the females controlled at death. The time of death was calculated as the median time between the time at which the female was found dead and the preceding controlled time.
- (iii) *Wasp size and egg load.* Since the hind tibia length is strongly positively correlated to dry body mass in *V. canescens* (Harvey & Vet 1997, Roberts & Schmidt 2004), it was considered as an index of adult body size. The left hind tibia was measured under the microscope with a graduated scale. Wasps were dissected in 3 μ L of demineralized water on a glass slide, a cover slip was laid on the ovaries and mature and immature eggs were counted under the microscope. Eggs were considered as mature when available in wasp oviducts and calyx, and immature eggs in ovaries. The cover slip was gently removed to keep the reproductive materials on the slide. To collect the reproductive materials into the Ependorf tube together with wasp body, the slide was

washed with 40 μ L of 2% Sulfate Sodium, a solution used for carbohydrate assay (see below).

(iv) *Amount of carbohydrates.* The reproductive apparatus (collected as above) and whole body wasp were analysed together. A colorimetric analysis was carried out to assess females' carbohydrate levels (van Handel 1985, van Handel & Day 1990). This method quantifies fructose from ingested sucrose (glucose-sucrose dimer), glucose from trehalose (glucose-glucose dimer) and glucose from glycogen (glucose polymer) in the same individual. To determine the concentration of glucose originating from trehalose, the concentration of fructose deriving from sucrose is removed from the total glucose concentration that combines glucose originating from both sucrose and trehalose (van Handel & Day 1990). Nutrient concentrations were assessed from absorbance curves of known concentrations of glucose and fructose.

Feeding behaviour monitoring

To test whether the differences in resource allocation patterns recorded in the two reproductive modes (see results) come from different abilities to find food or to different processes of energy allocation, a complementary experiment was carried out with supplementary females. The abilities of the two reproductive modes to locate and ingest the food were compared. Parasitoid wasps were collected at emergence from the rearing stock and transferred in cages as previously, in order to allow arrhenotokous females to mate. Host patches, made of 20 hosts in 13 g of semolina, were provided to the wasps between 11:30 a.m. and 1:00 p.m., and 2 μ L of 20 % sucrose solution was provided between 1:00 p.m. and 1:30 p.m.. The following variables were then recorded by two observers, each of them simultaneously monitoring 10 wasps: the time needed to locate and start feeding on the drop of food, the total number and the duration every feeding bout during 30 min.

2.2.3. Statistical analyses

The time needed to locate food has been considered as survival data. To investigate the effects of wasp size, reproductive mode (factor with two modalities: thelytokous and arrhenotokous) and their interaction on wasps' longevities, as well as the effect of

reproductive mode on time needed to locate food, we used Cox proportional hazards regression models (Cox 1972). Model comparisons were computed using likelihood-ratio (LR) tests.

Linear models have been used to investigate (i) the effects of wasp size, female age (factor with four modalities: 0, 2, 4 and death) and reproductive mode on egg loads and on carbohydrates levels, (ii) the effect of reproductive mode on total duration of feeding and number of feeding bouts. Transformations were applied (square root for glycogen, glucose and fructose, and logarithm for number of feeding bouts) when residuals were not normally distributed or when the residual variance was not constant over the response variable. To remove any effect of animal size from the measurements, wasp size was incorporated as the first explanatory variable in the models. A backward procedure of variable elimination has been used to find the model having the minimum number of explanatory variables.

To analyse the daily number of offspring produced by females, we initially used a Mixed Effects Model which allows taking into account the pseudoreplication originating from measurement repetitions among females. Nevertheless, because offspring variations occurring between females were not statistically significant, linear models assuming no random effect in the data have been finally computed (see results). The daily number of offspring has been considered as the response variable and wasp size, age, reproductive mode and their interactions as explanatory variables. Mixed Effects model comparisons have been computed using likelihood-ratio (LR).

All analyses and graphs have been computed using the *R* free statistical software (R Development Core Team 2008, <http://www.R-project.org>). Survival analyses were performed using the *R* ‘survival’ package (S original by Terry Therneau and ported by Thomas Lumley) and mixed effect models with the *R* ‘nlme’ package (Pinheiro *et al.* 2008).

2.3. Results

2.3.1. Size

Wasp size, measured on females at emergence, was different for the two reproductive modes ($F(1,47)=6.8$; $P=0.01$). Tibia length was in average 1.83 mm ($n=24$; $SE=0.02$) for thelytokous wasps and 1.75 mm ($n=25$; $SE=0.02$) for arrhenotokous ones.

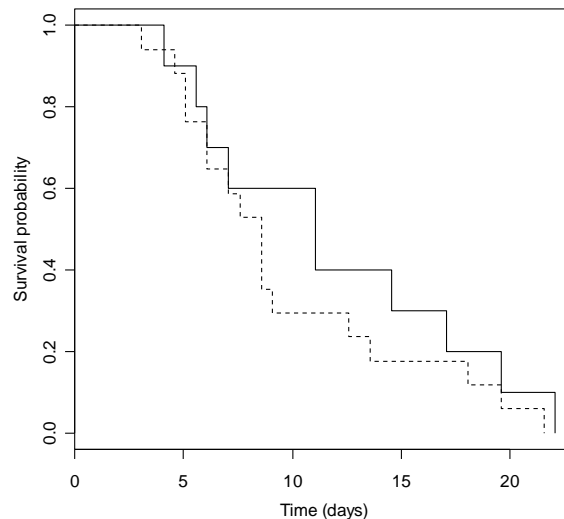


Figure 1: Kaplan-Meier curves for survival probabilities according for thelytokous (dashed lines) and arrhenotokous (solid lines) wasps. For effectiveness, see **Annex 3**.

2.3.2. Longevity

Parasitoids' size ($LR=1.7$; $d.f.=1$; $P=0.1$), reproductive mode ($LR=1.9$; $d.f.=1$; $P=0.1$), as well as their interaction ($LR=0.2$; $d.f.=1$; $P=0.8$) did not significantly influence wasp longevity (**Figure 1**). Longevities averaged 11.8 days (Median: 11.1; $SE=2.0$) for arrhenotokous wasps, and 9.7 days (Median: 8.6; $SE=1.3$) for thelytokous ones.

2.3.3. Daily offspring number

A random effect coming from repetitions of offspring measurement among females was initially taken into account in a Mixed Effects Model. Neither slopes ($LR=0.01$; $d.f.=1$; $P=1$) nor intercepts ($LR<0.0001$; $d.f.=1$; $P=1$) of offspring number along time significantly differ between females. Daily offspring number was neither significantly affected by wasp size ($F=1.8$; $d.f.=4$ and 452 ; $P=0.1$), nor by reproductive mode ($F=0.09$; $d.f.=1$ and 457 ; $P=0.8$; **Figure 2**) and nor by female age ($F=1.2$; $d.f.=1$ and 458 ; $P=0.3$). Indeed, no particular trend for daily number of offspring was observed on **Figure 2**. Offspring variance tended to increase with female age because offspring data

on females controlled after 2 and 4 egg-laying days have been considered, and the effectives are thus more consequent for ages inferior to 4.

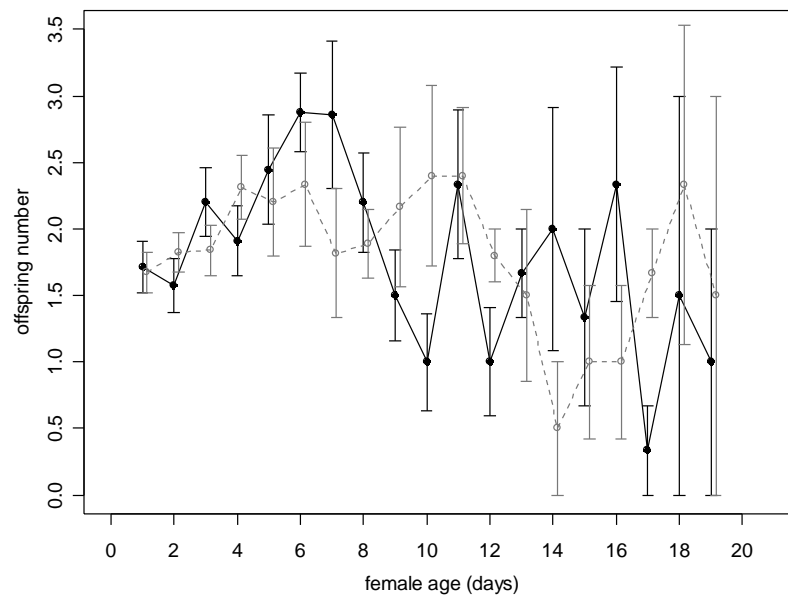


Figure 2: Mean daily number of offspring (\pm SE) of thelytokous (grey dashed lines) and arrhenotokous females (black solid lines). For effectives, see **Annex 2**.

2.3.4. Egg load

As the number of immature eggs was similar for all treatments (results not shown), only mature eggs number has been considered for analyses. Wasp size positively affected egg loads ($F(1,138)=21.2$; $P<0.0001$). After removing the effect of wasp size, egg loads were still significantly different between the two reproductive modes ($F(1,138)=39.2$; $P<0.0001$; **Figure 3**; *c.f.* **Annex 1** for detailed statistical results), thelytokous females having globally more eggs than arrhenotokous ones, regardless of parasitoid age. Moreover, significant egg number variations occurred along lifetime ($F(3,138)=15.3$; $P<0.0001$), in the same manner for both reproductive modes. The number of mature eggs was approximately multiplied by two during the first two days of life, and then decreased until death.

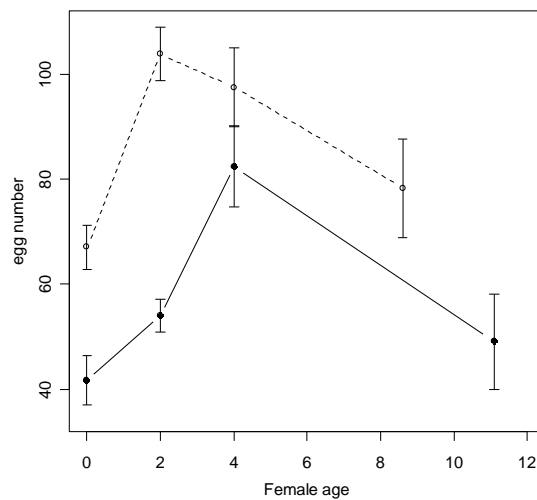


Figure 3: Egg load variation (mean \pm SE) over arrhenotokous (solid line) and thelytokous (dashed line) lifetimes. (Median longeivities are 8.6 days for thelytokous and 11.1 days for arrhenotokous). For effectives, see **Annex 3**.

2.3.5. Quantity and quality of carbohydrate reserves

Fructose levels were neither directly modified by wasp size ($F(1,128)=2.6$; $P=0.1$), nor by reproductive mode ($F(1,128)=3.1$; $P=0.08$; **Figure 4a**; *c.f.* **Annex 1** for detailed statistical results). However, they showed important variations over lifetime ($F(3,128)=54.5$; $P<0.0001$), reaching very high values at two days and then decreasing toward initial levels until death. The interactions between female size and age ($F(3,128)=5.5$; $P=0.001$), and between female size, age and reproductive mode ($F(3,128)=3.6$; $P=0.02$) played a significant role in predicting the amounts of fructose. A graphical analysis showed that fructose contents were not affected by wasp size at emergence for both reproductive modes, were then positively correlated to size at 2 days in thelytokous wasps but surprisingly negatively correlated to size at 2 days in arrhenotokous wasps, and then negatively correlated to size at 4 days and at death, regardless of the reproductive mode (results not shown).

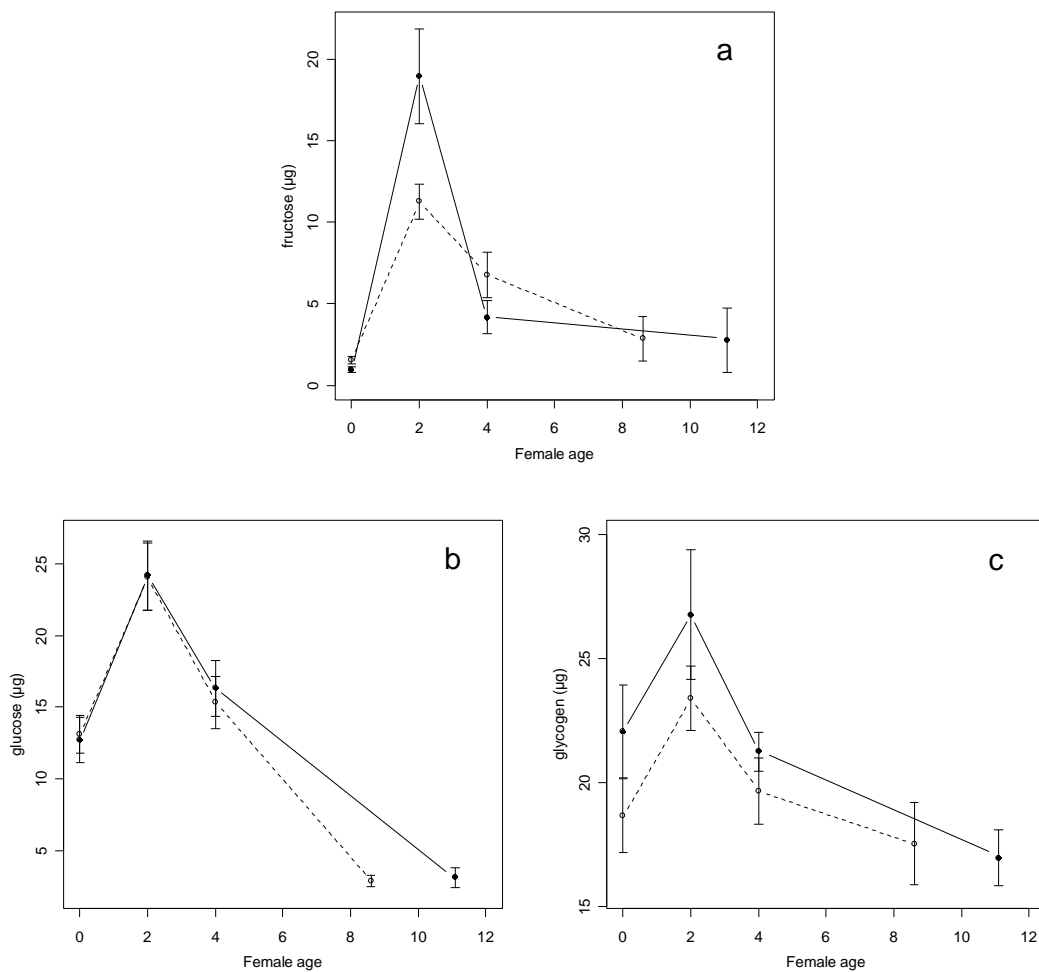


Figure 4: Fructose (a), glucose (b) and glycogen (c) amounts (mean in $\mu\text{g} \pm \text{SE}$) of arrhenotokous (solid line) and thelytokous (dashed line) wasps over lifetime. For effectives, see **Annex 3**.

Glucose levels were positively affected by wasp size ($F(1,136)=9.6$; $P<0.01$), and greatly differed depending on female age ($F(3,136)=51.3$; $P<0.0001$; **Figure 4b**). They significantly increased in the beginning of life, then decreased from day 2 until death and reached very low levels compared to emergence. Glucose content was not statistically different between the two reproductive modes ($F(1,135)=0.3$; $P=0.6$).

After removing the effect of wasp size ($F(1,118)=12.2$; $P<0.001$), the reproductive mode significantly affected glycogen levels ($F(1,118)=7.1$; $P<0.01$; **Figure 4c**), arrhenotokous wasps having globally more glycogen than thelytokous ones. Glycogen reserves significantly varied according to female age ($F(3,118)=5.4$; $P<0.01$): after an

initial increase from emergence to day 2, they declined until death and reached values slightly lower than those recorded at emergence.

2.3.6. Feeding behaviour

Neither the time needed to locate the food ($z=0.26$; $P=0.8$; Arrhenotokous: mean=2.8 min, SE=0.6 min, $n=13$; Thelytokous: mean=3.6 min, SE=1.2 min, $n=25$), nor the total duration spent by wasps feeding on the drop of food during 30 min ($F(1,35)=2.9$; $P=0.1$; Arrhenotokous: mean=8.9 min, SE=1.2 min, $n=13$; Thelytokous: mean=6.8 min, SE=0.7 min, $n=25$), nor the total number of feeding bouts observed ($F(1,36)=1.7$; $P=0.2$; Arrhenotokous: mean=3.8 min, SE=0.5 min, $n=13$; Thelytokous: mean=5.4 min, SE=0.6 min, $n=25$) significantly differed between thelytokous and arrhenotokous wasps.

2.4. Discussion

Thelytokous wasps appear to have been selected in anthropogenic habitats, where the availability of hosts is relatively high and food absent, and show patterns of energy allocation at adult emergence in line with these conditions (Pelosse *et al.* 2007). Our results show that they are nevertheless globally able to adjust their allocation strategies when faced with an environment in which host availability is low and food present, since they achieved fecundities and longevities comparable to arrhenotokous wasps. The initial advantage of arrhenotokous wasps in term of energy allocation strategies was nevertheless maintained during the adult stage in our experimental conditions. Arrhenotokous wasps maintained higher glycogen reserves which could give them higher flight capabilities in natural habitats, and died with less remaining eggs than thelytokous ones.

As expected, the two reproductive modes get similar offspring numbers over their lifetimes, as a result of the low experimental host availability. They nevertheless differed regarding their underlying egg loads: in our experimental conditions, thelytokous wasps carried 30 eggs more than arrhenotokous ones in average, regardless of female age. For such low host densities, the smaller egg number of arrhenotokous females was however sufficient to achieve a maximal fecundity. Parasitoid females are known to have evolved mechanisms to avoid being alive and having no more eggs, *i.e.*

being egg limited, or dying with remaining eggs, *i.e.* being time limited (Heimpel *et al.* 1996, Rosenheim 1996, Rosenheim *et al.* 2008). Synovigenic organisms are expected to adjust the number of eggs they carry to the environmental host availability (Ellers *et al.* 2000, Rosenheim *et al.* 2000). While in the experimental conditions of host scarcity, parasitoid females were not expected to mature additional eggs, the number of eggs approximately increased of 40 for both reproductive modes in the beginning of life. The processes of egg maturation most likely subsequently slowed down, since egg loads decreased continuously until death, which means that the number of eggs laid was superior to the number of eggs matured. The decrease of egg loads cannot result from egg resorption which is absent in *V. canescens* (Eliopoulos *et al.* 2003). Nevertheless, both reproductive modes appeared limited by time as they died with still some eggs remaining, which mean that they invested too much energy toward reproduction compared to the number of oviposition opportunities. As initially expected, thelytokous wasps died with more extra eggs: nearly 80 against 50 for arrhenotokous wasps. Here, the process of egg maturation clearly appears not to be the result of the high number of oviposition opportunities encountered, but more a passive physiological process that arises because metabolic energy is available to fuel egg maturation. While completely deprived of hosts and with *ad libitum* access to food, thelytokous *V. canescens* were already known to mature large amounts of eggs in excess (Roberts & Schmidt 2004). In species having hydropic eggs, *i.e.* small and containing few nutritional materials, such as *V. canescens*, egg maturation is not expected to require the incorporation of many nutrients (Wheeler 1996). *V. canescens* eggs contain very few lipids and proteins, but relatively large amount of carbohydrates (Schneider 2003, Pelosse *et al.* in prep) which were not limiting in our experimental setup. Then, as proved by glycogen storage that took place at least during the first days of life, the energetic budget of both reproductive modes was probably positive in our experiment (see below). Indeed, food was provided, the number of ovipositions performed by wasps was relatively limited and no flights were allowed. In the non-host-feeding parasitoid *Leptomastix dactylopii* provided with *ad libitum* sugary food, egg maturation rates have indeed been shown to be independent of the host availability experienced in the beginning of life (Rivero-Lynch & Godfray 1997). With metabolic reserves in excess, egg maturation may be adaptive as it would prevent wasps to be limited by the number of eggs in case of a sudden change of reproductive opportunity number. To our knowledge, this assumption has never been tested theoretically.

As expected, the food provided in our experiment allowed thelytokous wasps achieving a good life expectancy. The longevities of the two reproductive modes did not significantly differ one from another, but a trend aroused from the results: the median longevities were 8.6 and 11.1 days for thelytokous and arrhenotokous wasps, respectively. This result demonstrates that thelytokous wasps exploited a sufficient amount of food, even if we provided a small quantity of food every day, to sustain their maintenance requirements. Sugar feeding is recognized to positively affect parasitoid survival (*e.g.* Leius 1961, Heimpel *et al.* 1997, Eijs *et al.* 1998). Here, food allowed thelytokous wasps increasing their lower initial metabolic resource levels: their carbohydrate amounts significantly increased at the beginning of their lives, as arrhenotokous ones. Insects feeding on sugary substances mainly acquire sucrose, a glucose-fructose dimer, which is divided in the haemolymph in its two components (Nation 2002). Fructose cannot be then directly used to provide energy, but is rapidly converted into glucose in the haemolymph. As a result of sucrose ingestion, fructose amounts deeply increased during the first two days of life in both reproductive modes, but this increase was far much pronounced in arrhenotokous wasps. This divergence does not result from different abilities to exploit food in our experimental conditions, since neither the time needed to locate the drop of food, nor the total duration of feeding significantly differed between the two types of wasps. Because thelytokous wasps stored the same quantity of glycogen than arrhenotokous ones in the beginning of their lives, their lower fructose levels could then theoretically not be attributed to a higher storage of glucose into glycogen. Thelytokous females might have experienced a similar peak of fructose than arrhenotokous ones not recorded in our experiment if it took place before the measurement realized at the age of two days. It is also possible that thelytokous wasps have burn more energy, and therefore used more glucose than arrhenotokous wasps, during host patch exploitation. As thelytokous wasps globally demonstrate higher oviposition rates on host patches (Thiel *et al.* 2006, Pelosse *et al.* 2007), it is most likely that they performed more active energy-demanding host seeking behaviors in the patches.

We observed in a previous study that arrhenotokous wasps stored more glycogen during their larval stage than thelytokous wasps, which would give them an advantage for flight in natural habitats where host and food sources are relatively scattered (Pelosse *et al.* 2007). This pattern is here reinforced as glycogen levels of arrhenotokous wasps

remained higher than thelytokous ones during the adult stage. Glycogen reserves increased at the beginning of life, as a result of feeding, for both reproductive modes. Glycogen storage or utilization is closely linked to the concentration of glucose in the haemolymph: when the concentration is low, glycogen is hydrolyzed in glucose, and when this concentration is high, glucose is stored in glycogen (Nation 2002). Glycogen reserves consequently globally fluctuate in the same manner as glucose levels in our experiment. As already reported in the parasitoid *Macrocentrus grandii*, carbohydrates are stored into glycogen in the beginning of life, and glycogen is subsequently mobilized since its levels critically fall down (Olson *et al.* 2000). The energetic balance of intakes and outputs is thus positive in the first two days of life, and negative thereafter. Carbohydrates levels seemed to determine parasitoid survival in our experiment, as they reached very low values at death, probably close to the minimum irreducible constitutive levels, for both reproductive modes (Olson *et al.* 2000, Casas *et al.* 2003, Casas *et al.* 2005).

In this experiment, thelytokous wasps demonstrated a similar reproductive success than arrhenotokous wasps. While the total number of offspring was similar for both reproductive modes, arrhenotokous females produced females and males, the latter indirectly contributing to future generations, and thelytokous produced only females. As a consequence, thelytokous wasps have a demographic advantage over arrhenotokous ones. Other parameters should nevertheless be considered to account for the maintenance of sex in *V. canescens*. First, thelytokous wasps succeed, in our experimental conditions, gaining as much food as their arrhenotokous counterparts. Thelytokous females are able to acquire food in the field (Casas *et al.* 2003, Desouhant *et al.* 2005) and are known to increase their patch leaving tendency as food availability increase in their environment (Lucchetta *et al.* 2007). Detailed comparisons of the foraging behavior of the two reproductive modes in the field would be feasible and needed (Heimpel & Casas 2008), to assess their abilities to find food in natural conditions. Then, we expect that in natural habitats, arrhenotokous superiority in term of carbohydrate resources would provide them a dispersal advantage over thelytokous wasps, since Insect flight, which has not been considered in our study, is extremely metabolically costly (Canavoso *et al.* 2001). In the field, released arrhenotokous wasps are known to initiate dispersal faster than thelytokous wasps (Amat 2004), and are recaptured less easily which suggests that they disperse more efficiently (Amat 2004,

Lukas *et al.* submitted, Pelosse unpublished results). We also have evidences that the constitution of flight muscles provide arrhenotokous wasps with higher flight capabilities over thelytokous wasps (Bernstein, personal communication). Arrhenotokous wasps are also known to respond to deteriorating conditions when foraging on a host patch, while thelytokous are not (Amat *et al.* 2006).

When provided with limited host quantities and with food, thelytokous wasps that have been selected in environments where hosts are numerous and food absent are globally able to adjust their resource allocation patterns and achieve good longevity and lifetime fecundity. These findings emphasizes the fact that other mechanisms such as flight performance or response to abiotic factors should be consider together with energy allocation strategies to explore the co-occurrence of arrhenotokous and thelytokous wasps in natural habitats.

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2.6. Annexes

Annex 1: Statistical results of linear models. Energy reserves and egg load are the response variables, and wasp size (size), reproductive mode (repro) and wasp age (age, *i.e.* if females were controlled at emergence, after 2, 4 days or at death), and their interactions, the explanatory variables. Variables indicated in bold have a significant influence over the response variable.

Response	Explanatory variables	Response	Explanatory variables
Glycogen	size: F(1,118)=12.2; P<0.001 repro: F(1,118)=7.1; P<0.01 age: F(3,118)=5.4; P<0.01 size:repro: F(1,108)=0.3; P=0.6 size:age: F(3,108)=2.3; P=0.08 repro:age: F(3,108)=1.9; P=0.13 size:repro:age: F(3,108)=0.05; P=1	Glucose	size: F(1,136)=9.6; P<0.01 repro: F(1,135)=0.3; P=0.6 age: F(3,136)=51.3; P<0.0001 size:repro: F(1,125)=0.05; P=0.8 size:age: F(3,125)=1.7; P=0.2 repro:age: F(3,125)=0.1; P=1 size:repro:age: F(3,125)=0.2; P=0.9
Fructose	size: F(1,128)=2.6; P=0.1 repro: F(1,128)=3.1; P=0.08 age: F(3,128)=54.5; P<0.0001 size:repro: F(1,128)=2.0; P=0.16 size:age: F(3,128)=5.5; P=0.001 repro:age: F(3,128)=1.8; P=0.16 size:repro:age: F(3,128)=3.6; P=0.02	Egg load	size: F(1,138)=21.2; P<0.0001 repro: F(1,138)=39.2; P<0.0001 age: F(3,138)=15.3; P<0.0001 size:repro: F(1,128)=0.4; P=0.5 size:age: F(3,128)=2.0; P=0.1 repro:age: F(3,128)=0.4; P=0.8 size:repro:age: F(3,128)=0.3; P=0.8

Annex 2: Effectives for daily offspring number measurements, according to the reproductive mode (*A*: arrhenotokous; *T*: thelytokous) and female age (**day**).

Day	1	2	3	4	5	6	7	8	9	10
<i>A</i>	35	33	20	22	9	8	7	5	6	6
<i>T</i>	58	56	37	35	15	12	11	9	6	5
Day	11	12	13	14	15	16	17	18	19	20
<i>A</i>	6	4	3	4	3	3	3	2	2	-
<i>T</i>	5	5	4	2	3	3	3	3	2	-

Annex 3: Effectives for measurements of egg load, energy reserves and longevity, according to the reproductive mode (*A*: arrhenotokous; *T*: thelytokous) and the day females have been controlled (**0**: at emergence; **2**: after 2 days of egg-laying; **4**: after 4 days; **death**: at death).

		0	2	4	Death
Egg load	<i>A</i>	25	12	14	11
	<i>T</i>	24	20	21	17
Fructose	<i>A</i>	25	12	14	12
	<i>T</i>	24	20	21	16
Glucose	<i>A</i>	25	12	14	11
	<i>T</i>	24	20	21	14
Glycogen	<i>A</i>	23	12	13	7
	<i>T</i>	22	20	17	10
Longevity	<i>A</i>	-	-	-	10
	<i>T</i>	-	-	-	17

In this chapter, we were interested by *trade-offs* in energy allocation strategies, how they are shaped by environmental characteristics, and how they could contribute to the coexistence of competing species. In the following chapter, we will focus on the *trade-off* between current and future reproduction and explore its role in the dynamics of populations and communities.

Chap III. Role of *trade-offs* in population dynamics and community structuring: Example of the *trade-off* between host and food foraging

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Pelosse Perrine ^{1,2}, Van Dooren Tom J M ^{3,4}, Desouhant Emmanuel ^{1,5} & Bernstein Carlos ^{1,6}.

¹ Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

³ Institute of Evolutionary and Ecological Sciences, Leiden University, PO Box 9516, 2300 RA Leiden University, The Netherlands.

² Corresponding author: Pelosse Perrine; pelosse@biomserv.univ-lyon1.fr; Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

⁴ t.j.m.van.dooren@biology.leidenuniv.nl

⁵ desouhan@biomserv.univ-lyon1.fr

⁶ carlosbe@biomserv.univ-lyon1.fr

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1. Introduction

Understanding why there is such a vast number of species, what controls their densities and how they interact, is the core of community ecology. It has been suggested that the main mechanism promoting species coexistence is niche partitioning along temporal or spatial ranges, *i.e.* exploitation of different resources or different parts of the environment (Chesson 1994). Specialization in resource utilization (demographic trade-offs, *sensu* Vincent *et al.* 1996) has been suggested to promote species coexistence at a local scale, due to the reduction of interspecific competitive interactions. For instance, theoretical models predict that specialists exploiting a unique nutritional resource are able to coexist with generalists that use a wider range of resources (Egas *et al.* 2004, Abrams 2006, Rueffler *et al.* 2006). Species showing differences in their handling time, by exploiting either thoroughly or partially food sources, also have the possibility of persisting together (Schmitt 1996, Wilson *et al.* 1999, Richards *et al.* 2000, Kisdi & Liu 2006).

The role of trade-offs in resource utilization in species coexistence has been widely investigated. Conversely, the influence on coexistence of the trade-off between current and future reproduction has not been so far considered, in spite of being decisive for animal's reproductive success (Stearns 1992). In many insect parasitoids, *i.e.* insects that develop at the expense of another insect as larvae and are free-ranging as adults, this trade-off depends on the choice between host and food foraging (Collier *et al.* 1994, Sirot & Bernstein 1996). While foraging for hosts provides immediate gains in fitness, food foraging provides further survival and future fitness gains. Hosts and food resources are associated for parasitoids having the ability to feed on hosts, the host-feeding parasitoids, but are most often spatially separated for parasitoids feeding on sugary substances (Jervis & Kidd 1995). In the latter case, the two activities are mutually exclusive: the time invested in food foraging cannot be spent in host foraging, and vice versa. Several authors explored theoretically the cost/benefit balance to feed on a host rather than to oviposit on (*e.g.* Mangel & Clark 1988, Houston *et al.* 1992, Chan & Godfray 1993, Collier *et al.* 1994, Collier 1995). Conversely, few theoretical investigations focused on the trade-off between host and food foraging in parasitoids not resorting to host-feeding. The state dynamics models of Sirot and Bernstein (1996), Tenhumberg *et al.* (2006) and Bernstein and Jervis (2008) make an exception. These

authors suggest that individual's decisions to forage for food or hosts are mediated by internal variables such as energy reserves or egg load, as well as environmental variables such as host and food availabilities. The individual strategy of sharing time between host and food searching has been suggested to play a role in the stabilization of host-parasitoid populations by Krivan and Sirot (1997).

While the question of the influence of the compromise between host and food searching in the stabilization of host-parasitoid populations has already been addressed, its potential role in the coexistence of competing parasitoids remains largely unknown. More generally, the question of the evolutionary consequences of individual foraging decisions in host-parasitoid populations remains largely unexplored (but see Bonsall & Bernstein 2008). Different strategies of time allocation to host and food searching could however lead to a differential exploitation of host and food resources and consequently limit the competitive interactions between individuals. Then, they are expected to influence the timing of reproduction. Whereas favoring host foraging over feeding would result in a maximization of early reproduction, favoring food foraging at the expense of host exploitation would lead to the diffusion of reproduction over lifetime. Since both strategies are potentially equally advantageous, they may coexist under some conditions.

Our aim is to investigate, from a theoretical perspective, the evolutionary dynamics of the trade-off between host and food searching, and to seek its implication in species coexistence. To do so, we consider as Krivan and Sirot (1997) a host-parasitoid system in which parasitoids divide their time between host and food foraging, the total time being fixed. To introduce the trade-off, we assume that the reproductive rate of parasitoids is proportional to their time investment in host foraging, and that their mortality rate is a decreasing function of the investment in food foraging. Krivan and Sirot (1997) considered that the mortality rate of parasitoids decreases linearly with their investment in food searching. This needs not to be the case and we explore the influence of the shape of this function, which correspond to different nutritional effects of food on survival. The idea is that searching for food could be favored when food is of good quality.

To test under which conditions different investments in food and host searching would evolve, and if species adopting such different strategies could coexist, we use

evolutionary dynamics modeling techniques such as the framework of adaptive dynamics (Metz *et al.* 1996, Geritz *et al.* 1997, Geritz *et al.* 1998). The existence of cycles in host-parasitoid populations, by modifying the densities of hosts and parasitoids, may affect host and food foraging strategies. To take into account such an effect, we compare the evolution of the trade-off and seek conditions for coexistence under equilibrium and non-equilibrium dynamics conditions. This study shows that the evolutionary outcome of the investment in food searching is closely linked to the physiological effect of feeding on survival. In particular, when the quality of food is relatively low, the optimal strategy consists in searching for hosts only. We also demonstrate that parasitoids showing a different investment in food searching are able to coexist on an evolutionary timescale under non-equilibrium dynamics.

2. Model

We use a continuous model of a host-parasitoid system adapted from the model of Krivan and Sirot (1997, referred as K&S). The strategy submitted to selection in our model is the proportion of time invested in food searching, denoted by u . For parasitoids that feed on sugary substances, hosts and food sources are most frequently spatially separated (Jervis & Kidd 1995). Thus, to reflect the fact that host and food foraging are two mutually exclusive behaviors, it is assumed in our model that the investment in host searching is $(1-u)$. The more time allocated to host searching, the more hosts are expected to be found and parasitized. As a consequence, we assume, as K&S, that the parasitizing rate is proportional to the investment in host searching $(1-u)$. Since numerous studies suggest that sugar consumption allows parasitoids to reach an extended life expectancy (*e.g.* Heimpel *et al.* 1997, Desouhant *et al.* 2005), parasitoid mortality rate is assumed to be a decreasing function of the time invested in food searching. Food quality is expected to vary between food sources, as well as during the season (Jervis *et al.* 1993), and depending on the nutritional value of food, feeding would differentially affect parasitoid longevity (Siekman *et al.* 2001, Hausmann *et al.* 2005). As a consequence, while K&S stated that parasitoid mortality rate decreases linearly with the investment in food searching, we test three different shapes of mortality functions $f(u)$ to enhance the biological realism of the model (FIG 1). The first one is linear, with m being the minimum mortality rate, *i.e.* the mortality rate of a parasitoid spending all its time feeding ($u = 1$), and $m+M$ the maximum mortality rate

attained by parasitoids when they do not feed at all ($u = 0$). The second mortality function is convex and may correspond to a high-quality food type: feeding for a short time is sufficient to significantly decrease mortality rate. The third function is sigmoid and would reflect a situation in which the nutritional value of food is relatively low, as parasitoids need to feed for quite a long time to markedly decrease their mortality rate. For the two latter mortality functions, M gives the maximum mortality rate when parasitoids do not feed ($u = 0$) and b the mortality decreasing rate.

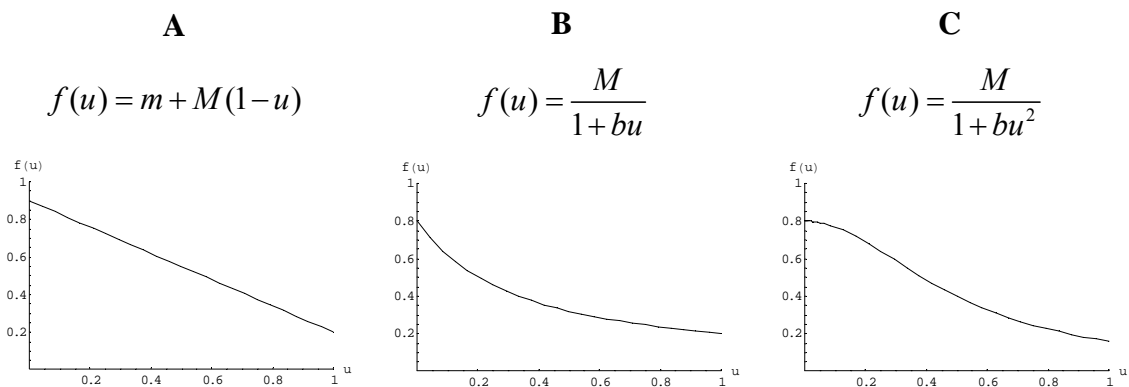


FIG 1. The three types of mortality functions $f(u)$. **A:** Linear ($m = 0.2$; $M = 0.7$); **B:** Convex ($M = 0.8$; $b = 3$); **C:** Sigmoid ($M = 0.8$; $b = 4$).

The general formulation of the model considers that several parasitoid species are competing for the same host population:

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{k}\right) - \sum_i (1-u_i) \frac{aP_i}{1+adH} H \quad (1)$$

$$\frac{dP_i}{dt} = (1-u_i) \frac{aH}{1+adH} P_i - f(u_i)P_i, \quad (2)$$

H and P_i being respectively the number of hosts and parasitoids of type i , r the host growth rate, k the carrying capacity, a the parasitoid attack rate, d the handling time or time needed to parasitize one host, and $f(u_i)$ the mortality rate of parasitoid of type i . We assume that several parasitoids, only differing in their investment in food searching, compete for the same host population. Competition between parasitoids occurs therefore indirectly through parasitism of the same host population. While K&S considered that the host's growth rate is exponential in the absence of parasitoids, we consider that it is density dependent (logistic), thus enhancing the biological realism of the model. The functional response, *i.e.* the number of hosts attacked per parasitoid, is a Holling type II,

which means that as the host density increases, parasitoids' attack rate increases with a decreasing speed, hence reaching a plateau for high host densities. This type of functional response is known to realistically represents the attack rate of many parasitoids in field conditions (Fernandez-arhex & Corley 2003).

Whatever the mortality function $f(u_i)$, it can be shown that H and P_i are positive when:

$$f(u_i) < \frac{ak(1-u_i)}{1+adk}, \quad (3)$$

and reach a stable equilibrium point under the following condition:

$$f(u_i) > \frac{(u_i-1)(1-adk)}{d(1+adk)}. \quad (4)$$

When the last condition is not verified, the host-parasitoid population reaches a stable limit cycle. For the specific case of the sigmoid mortality function, FIG 2 shows the combined effects of parasitoids' attack rate a , parasitoids' handling time d , mortality decreasing rate b and investment in food searching u on the population dynamical properties of the host-parasitoid system. Analogous patterns are observed for the two other mortality functions.

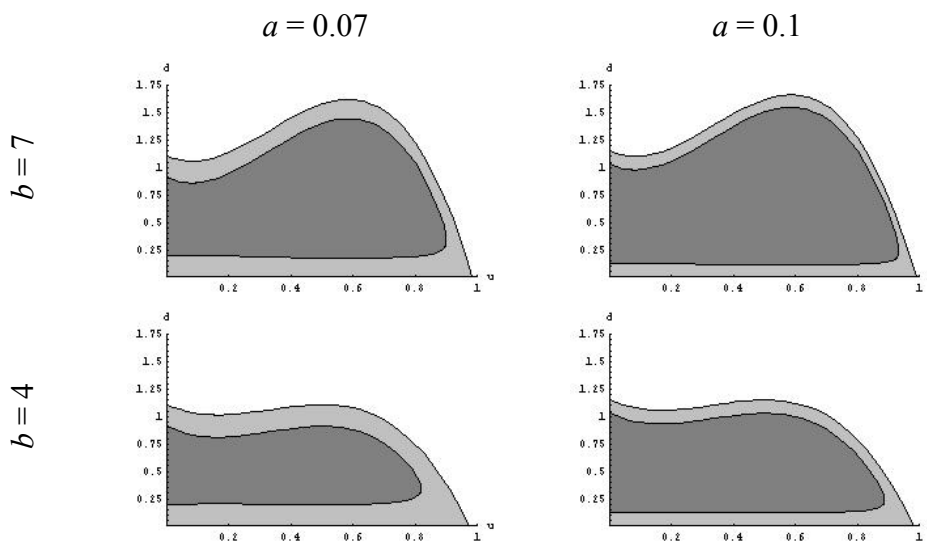


FIG 2. Combined effect of the handling time d , the investment in food searching u , the attack rate a and the mortality decreasing rate b , on the dynamical properties of the host-parasitoid population, for a sigmoid mortality function. In the white area, the population is not viable, in the grey light area the population converges to a stable equilibrium point, and in the grey dark area, the population reaches a stable limit cycle ($M = 0.8$; $k = 100$).

3. Evolution of the investment in food searching: Does food quality matter?

We test here whether food quality – represented by the shape of the mortality function $f(u_i)$ – affects the optimal investment in host and food searching. To investigate the evolutionary dynamics of parasitoids' investment in food searching, we consider a 1 host – 1 parasitoid system ($i = 1$). To assess if the strategy u_i will tend to decrease or increase over the course of evolution, a mutant parasitoid using a different strategy than the resident is introduced in the host-parasitoid resident population. Its ability to invade or not will determine the direction of evolution. In a first approach, we will use the methods of adaptive dynamics (Metz *et al.* 1996, Geritz *et al.* 1997, Geritz *et al.* 1998). Within this framework, the ecological timescale in which variations in host and parasitoid densities are observed is assumed to be very short compared to the evolutionary timescale in which the value of the trait submitted to selection, the investment in food searching, changes. As a matter of fact, the resident host-parasitoid population densities are assumed to be fixed, *i.e.* to have reached a stable equilibrium point, when the mutant arises. In a second approach, we will relax this assumption and look at the combined dynamics of host-parasitoid densities and investment in food searching. Non-equilibrium evolutionary dynamics will be investigated by introducing the mutant while the densities of the resident host-parasitoid population cycles.

To investigate the evolutionary dynamics of the investment in food searching u , the fitness of a mutant showing a different investment in food searching than the resident u' , that is, the invasion fitness (Metz *et al.* 1992), is determined. This currency corresponds to the per capita growth rate of the mutant in the resident population. Its sign determines which strategies are able to invade the resident population. Whether we consider that the population has already reached a stable equilibrium point when the mutant arises (adaptive dynamics framework), or that it cycles, the host density in the resident population will be represented either by the density at equilibrium or by the actual density of hosts. If we denote the host density by $h(u_i)$, the invasion fitness of a mutant devoting a proportion of time u' to feeding is:

$$w(u_i, u') = \frac{dP_i}{dt} \frac{1}{P_i} = (1 - u') \frac{ah(u_i)}{1 + adh(u_i)} - f(u') \quad (5)$$

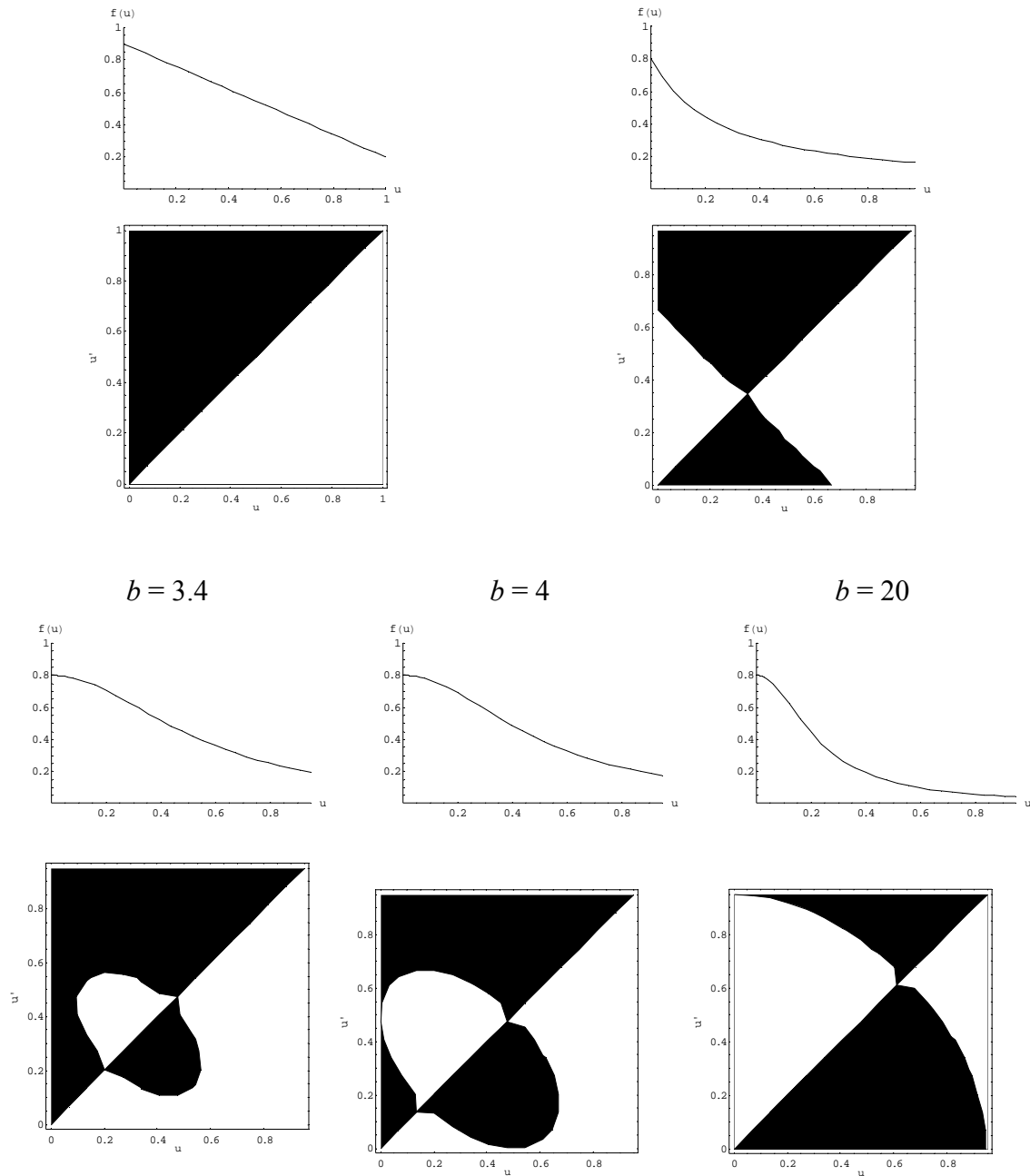


FIG 3. Mortality functions and corresponding Pairwise Invasibility Plots. The black areas correspond to negative invasion fitness. u is the resident value of the proportion of time invested in food searching, and u' the mutant trait value. For the linear mortality function, the CSS lies at $u = 0$ ($m = 0.2$ and $M = 0.7$). For the convex one, the CSS lies at $u = 0.5$ ($M = 0.8$; $b = 4$). For the sigmoid one, the repeller strategy lies at $u = 1/3$ and the CSS strategies at $u = 0$ and $u = 1/2$ ($M = 0.8$).

The direction of evolution, *i.e.* whether u_i , the proportion of time invested in food searching, tends to increase or decrease, is given by the first derivative of the invasion

fitness according to mutant trait, when the mutant is set to the resident value, *i.e.* the fitness gradient:

$$\left. \frac{\partial w(u_i, u')}{\partial u'} \right|_{u_i=u'} \quad (6)$$

The fixed points in the evolution, or evolutionary singular strategies, are the values under which the fitness gradient is null. In adaptive dynamics, to investigate the evolutionary properties of such singular strategies, the sign of the invasion fitness is plot according to the resident and mutant trait values in pairwise invasibility plots (PIPs, Geritz *et al.* 1998). A strategy will be ESS-stable (Evolutionary Stable Strategy, Maynard Smith 1982) when it cannot be invaded by any other strategy. Adaptive dynamics theory has the advantage over classical game theory of characterizing when a strategy is convergent-stable (Christiansen 1991), *i.e.* attainable in the course of evolution through small mutational steps. When both ESS- and convergence-stability are satisfied, the strategy is an evolutionary attractor and said to be a Continuously Stable Strategy (CSS, Eshel & Motro 1981). A strategy which lacks both ESS- and convergence-stability is in contrast an evolutionary repeller. In FIG 3, in which mortality functions and corresponding PIPs are represented, we show how the shape of the mortality function affects the evolutionary dynamics of the investment in food searching. For a linear mortality function, the investment in food searching evolves toward the CSS $u^* = 0$, that is, no investment in food searching (proofs are given in appendix). For the convex mortality function, the trait evolves toward a CSS given by:

$$u^* = \frac{b-1}{2b}. \quad (7)$$

This strategy is at an intermediate value between 0 and 1, which suggests that when food sources provide relatively high rewards in terms of survival, the best option is to divide time between host and food foraging. For the sigmoid mortality function, three evolutionary singular strategies arise. The first one is a repeller strategy given by:

$$u^* = \frac{\sqrt{b} - \sqrt{b-3}}{3\sqrt{b}}, \quad (8)$$

and depending on which side of the repeller evolution starts, u will evolve toward either:

$$u^* = 0 \text{ or } u^* = \frac{\sqrt{b} + \sqrt{b-3}}{3\sqrt{b}}, \quad (9)$$

which are both CSS. When faced with a relatively low food quality, the strategies of not feeding or dividing time between host and food searching therefore appear to be equally advantageous for parasitoids.

So far we investigated dynamical equilibrium situations: the mutant was introduced in a resident host-parasitoid population which has reached a stable equilibrium point. Here we explore situations of non-equilibrium dynamics in which simultaneous variations in the host-parasitoid densities and the investment in food searching may be observed. To do so we use the framework formalized by Vincent and Brown (2005) as ‘Darwinian dynamics’ (Vincent & Brown 1984, Brown & Vincent 1987, Rosenzweig *et al.* 1987, Abrams 1992, Brown & Vincent 1992). It is possible here to relax the adaptive dynamics assumption of small step evolution through mutations of little effect on fitness. Bigger mutations may indeed occur when an individual belonging to another population arises in the resident population. The evolutionary dynamics of the strategy is computed by multiplying the fitness gradient by an additive genetic variance σ^2 :

$$\frac{du_i}{dt} = \sigma^2 \left. \frac{\partial w(u_i, u')}{\partial u'} \right|_{u_i=u'} \quad (10)$$

Simulations of the dynamics of both host and parasitoid densities (given by equations 1 and 2, respectively) and investment in food searching (given by equation 10) suggested the following results. When the parasitoids’ mortality rate is a linear function of the proportion of time spent searching for food, the investment in food searching always evolves toward 0, in the same manner as for equilibrium dynamics. For the convex and sigmoid functions, different patterns are observed: when the trait does not reach 0 but an intermediate value, the investment in food searching cycles along with host-parasitoid densities, around the same values than in equilibrium dynamics (FIG 4).

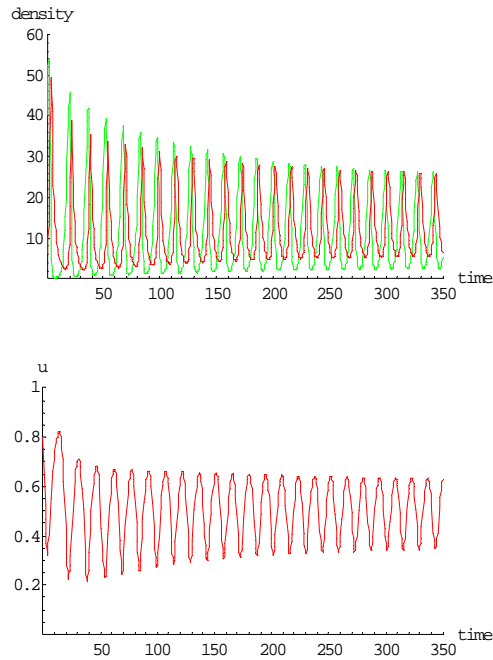


FIG 4. Combined dynamics of host and parasitoid densities (upper panel) and investment in food searching (lower panel), for a sigmoid mortality function and in conditions of non-equilibrium dynamics. Red: parasitoid density and trait value, Green: host density ($d = 0.25$; $M = 0.8$; $b = 4$; $a = 0.1$; $k = 100$; $r = 0.6$; $\sigma^2 = 0.1$; $H(0) = 40$; $P(0) = 6$ and $u(0) = 0.8$).

4. Coexistence of parasitoid species showing different investments in food searching

Our aim here is to test whether two parasitoid species investing different proportion of time to food foraging can persist together. We consider here a system in which two parasitoid species compete for the same host population ($i = 2$). As already mentioned, the invasion fitness of the mutant is an increasing function of the host density in our model. Consequently, the optimal strategy in equilibrium dynamics conditions will always be the one that minimize host density at equilibrium. This minimization principle prevents any evolutionary branching, *i.e.* a process of phenotypic divergence (Geritz *et al.* 1998), to occur (Mylius & Diekmann 1995, Metz *et al.* 1996, Kisdi 1998). We therefore investigate coexistence as a coalition, with the addition of another parasitoid – still considered as a mutant – differing in its investment in food searching in the one host-one parasitoid system at a very low density, once the equilibrium of the other species has been reached (whether fixed or cyclic). We focus on the sigmoid mortality function, since only in this case two distinct evolutionary stable strategies

were found. When the mutant is introduced while the resident population is at a non-cyclic equilibrium, there is no possibility for a stable coexistence of two feeding strategies to take place (see appendix).

In situations of non-equilibrium dynamics, host and parasitoid densities are not fixed. The mutant can thus appear at different moments in the cycle. Here, under some conditions of parameters a stable coexistence of two strategies takes place, with one parasitoid sharing time between host and food searching, and the other one searching hosts only (FIG 5). Interestingly, when the mutant evolves to an intermediate value of u , *i.e.* when the mutant spends a fraction of its time searching for food, both population and evolutionary dynamics stabilize after some time.

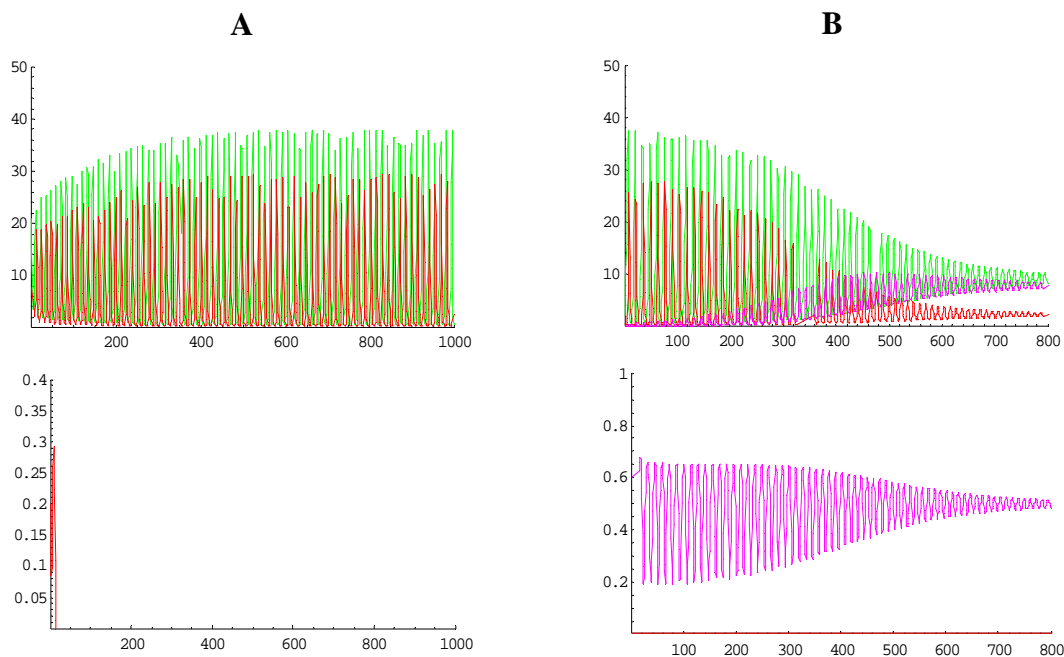


FIG 5. Dynamics of hosts (green) and parasitoids (red and purple) populations (upper panels) and evolution of the investments in food searching (red and purple, lower panels). **A**: One host – one parasitoid system. u evolves toward 0 and the population dynamics cycles. **B**: One host – two parasitoids system. A second parasitoid investing a different proportion of time to food searching (u_2 , purple) is introduced in the population depicted in **A** at $t = 1000$. **A**: $d=0.15$; $M=0.8$; $a=0.1$; $b=4$; $k=100$; $r=0.6$; $\sigma^2=0.1$; $H(0)=21$; $P(0)=8$; $u(0)=0.2$; **B**: $H(0)=0.8$; $P1(0)=2.5$; $P2(0)=0.1$; $u1(0)=0$; $u2(0)=0.6$.

5. Discussion

This study is the first to address the question of the role of the trade-off between host and food searching on the coexistence of competing parasitoid species. We show that under some conditions, two parasitoid species feeding on sugary substances might coexist when one of them share its effort between host and food foraging, and the other one forage for hosts only, providing that the host-parasitoid population cycles. The originality of our work lies in the exploration of the influence of physiological constraints on both population and evolutionary dynamics of a host-parasitoid system. We put forward that the nutritional value of food ingested by parasitoids, because of its intimate link with parasitoids' reproductive success, may have a strong influence on the optimal food foraging strategy adopted by parasitoids. When a small quantity of food is sufficient to sustain the energy requirements and to enhance longevity, dividing time between host and food foraging seems to represent the best option available for parasitoids. On the other hand, if to gain future fitness rewards, a large quantity of food has to be ingested, it may be more advantageous not to feed, and concentrate effort on foraging for hosts.

Our investigations suggest that the coexistence of two parasitoid species on the basis of the trade-off between host and food searching is not possible in a simple modelling framework, especially if it excludes temporal variability of the host resource. The fact that one species maximizes host exploitation and the other one invests some time in food searching seems not sufficient to reduce competitive interspecific interactions. We expect that in the presence of two host populations, coexistence would be possible, each species specializing on one host type. Our results nevertheless suggest that coexistence is possible in situations of cyclic host-parasitoid population dynamics. Temporal variability is known to promote polymorphism, with the two strategies specializing on one part of the cycle (Levins 1979, Chesson 1994, Egas *et al.* 2004, Abrams 2006, Kisdi & Liu 2006). Variations in host densities most likely allow the parasitoid species that shares its time between host and food foraging being advantaged at the lowest host densities, and inversely, the species favoring host foraging being advantaged at the highest host densities. The introduction of the parasitoid that forages for food nevertheless results in the stabilization of both population and evolutionary dynamics. Krivan and Sirot (1997) also suggested that the strategy of sharing time between food

and host searching has a stabilizing effect on host-parasitoid population dynamics. The understanding of the implications of this result will require further investigations.

The two strategies emerging from our model lie at different positions on the trade-off between current and future reproduction, and reflect two distinct life histories that may be adopted by parasitoids. The strategy of not feeding, which is suggested by our model when food exploitation does not allow significantly decreasing mortality, is quite unexpected since all parasitoid species studied so far appear to feed frequently in the field (Jervis *et al.* 1993). This strategy would definitely be advantageous in environments that provide scarce food sources, or that provide food of low nutritional value. By modeling the optimal behavior between host and food searching in non-host-feeding parasitoids, Sirot and Bernstein (1996) and Bernstein and Jervis (2008) suggested that when the travel time between food and host sources is high and when the probability of finding food in the environment is low, parasitoids should not search for food. The parasitoid species *Venturia canescens* is known to thrive in mills or granaries in which the probability to find food is low (Schneider *et al.* 2002). In such habitats, that contain, in addition, numerous hosts, the maximization of early-life reproductive output, and therefore the concentration on host foraging, appears to have been selected for (Pelosse *et al.* 2007). Aphid honeydew, a food source exploited by some parasitoid species, has already been proposed as a low nutritional food source compared to floral nectars, due to its high viscosity (Stapel *et al.* 1997, Wäckers 2000, Lee *et al.* 2004). The strategy of not feeding appears particularly pertinent for pro-ovigenic parasitoids, *i.e.* parasitoids that have their full egg complement mature at the beginning of their adult life, as opposed to synovigenic parasitoids that mature additional eggs during their adult lifetime (Flanders 1950). One may expect that pro-ovigenic parasitoids are less limited by food, since synovigenic parasitoids rely on food for both egg production and maintenance during the adult stage, but pro-ovigenic ones for maintenance only.

Neither spatial distribution of hosts and food sources nor fluctuations in food availability has been considered in our model, and this factor would significantly modify the results. Food foraging would be definitely selected for when food and hosts are closed to each other, because in such conditions the travel costs between the two resources are minimized (Bernstein & Jervis 2008). It has been shown that *V. canescens* prefers combinations of host- and food-related odors over odors indicating the presence of a single resource (Desouhant *et al.* 2005). On the other hand, if the two types of

resources are spatially separated, or if a high mortality probability is associated to food foraging, as proposed by Sirot and Bernstein (1996), then foraging for food would not be advantageous. We focus in this study on the evolution of parasitoid investment in food searching. As a consequence, we assume that evolution occurs in the parasitoid only. Moreover, we assumed here that the only trait submitted to evolution is the investment in food searching. Of course, others parameters such as parasitoids' attack rate could be considered as evolutionary variables as well, but the modeling techniques employed would be more complex, and the interpretations most likely more difficult. In non-equilibrium dynamics, we expect for instance that when the host density is high, higher attack rates would be favored, and conversely when host density is low.

This study provides evidence that the trade-off between host and food searching may have broad implications on parasitoid community assemblage. This work is part of a new area of research in behavioral ecology that links physiology, foraging and dynamics (Bonsall & Bernstein 2008), and open exciting and challenging questions.

6. Appendix: Properties of the evolutionary singular strategies in equilibrium dynamics

For simplicity, $F(H)$ will represent the functional response, *i.e.* the function giving the number of hosts attacked per parasitoid. In our host-parasitoid system, the non trivial population dynamical equilibria \hat{H} and \hat{P}_i are given by:

$$\frac{dH}{dt} = 0 \qquad g(\hat{H}) = \sum_i (1-u_i)F(\hat{H})\hat{P}_i \qquad (1)$$

\Leftrightarrow

$$\frac{dP_i}{dt} = 0 \qquad \frac{dP_i}{dt} = 0 \Leftrightarrow (1-u_i)F(\hat{H}) = f(u_i) \qquad (2)$$

At equilibrium, equation (2) holds for all P_i simultaneously.

If we consider that the system is at equilibrium when the mutant arises in the resident population, the evolutionary singular points u^* must verify:

$$\left. \frac{\partial w(u_i, u')}{\partial u'} \right|_{u'=u_i=u^*} = \left. \frac{\partial \left((1-u')F(\hat{H}) - f(u') \right)}{\partial u'} \right|_{u'=u_i=u^*} = 0, \quad (3)$$

$$\text{that is, } \left. \frac{\partial \left((1-u')F(\hat{H}) \right)}{\partial u'} \right|_{u'=u_i=u^*} = \left. \frac{\partial \left(f(u') \right)}{\partial u'} \right|_{u'=u_i=u^*}. \quad (4)$$

This means that the line $(1-u)F(\hat{H})$ should be tangential to the curve $f(u)$, u^* lying at the tangential points. We plotted below $(1-u)F(\hat{H})$ and a sigmoid mortality function $f(u)$ as a function of u (FIG 6).

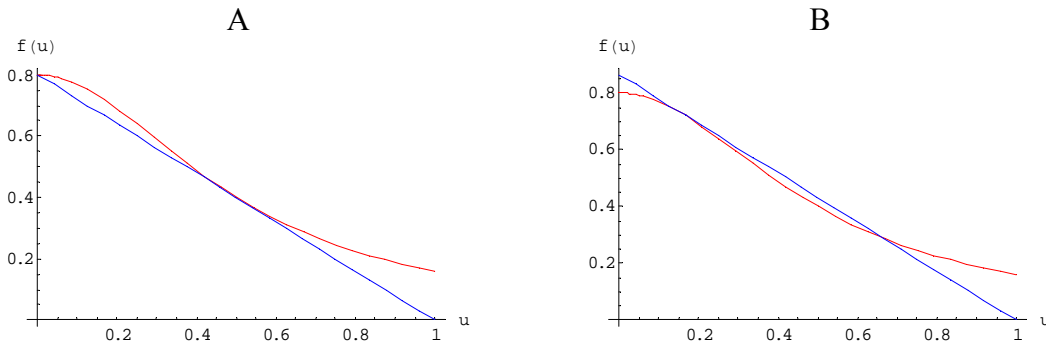


FIG 6. $(1-u)F(\hat{H})$ (blue) and $f(u)$ (red). The points where the straight line touches the curve are: $u_1^* = \frac{1}{3} \left(1 + \sqrt{1 - \frac{3}{b}} \right) = 0.5$ for A and $u_2^* = \frac{1}{3} \left(1 - \sqrt{1 - \frac{3}{b}} \right) = 1/6$ for B if $b=4$.

To get an ESS-stable singular strategy we have to verify:

$$\left. \frac{\partial^2 w(u_i, u')}{\partial u'^2} \right|_{u'=u_i=u^*} < 0, \quad (5)$$

$$\text{that is, } \left. \frac{\partial^2 f(u')}{\partial u'^2} \right|_{u'=u_i=u^*} > 0. \quad (6)$$

The singular strategies will therefore be ESS-stable when the mortality function is convex (second derivative positive).

To get a convergent-stable singular strategy we need to verify:

$$\left. \frac{\partial^2 w(u_i, u')}{\partial u' \partial u} \right|_{u'=u_i=u^*} + \left. \frac{\partial^2 w(u_i, u')}{\partial u'^2} \right|_{u'=u_i=u^*} < 0, \quad (7)$$

$$\text{that is, } \left. \frac{\partial^2 f(u')}{\partial u'^2} \right|_{u'=u_i=u^*} > 0. \quad (8)$$

In the same manner, the singular strategies will be convergent-stable when the mortality function is convex.

7. Acknowledgments

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Section 3. General discussion

Life-history *trade-offs* have a central position in the study of animal adaptation since they constrain and limit the range of observed life-history strategies. The understanding of the mechanisms underlying life-history *trade-offs* is of utmost importance to point out the proximal factors limiting animal reproductive success. In this PhD thesis, we explored the physiological mechanisms of nutrient allocation toward life-history traits, investigated how phenotypic *trade-offs* are affected by and adjusted in response to environmental characteristics and their role in the dynamics of population and communities.

In the first part of this discussion, I will summarise our objectives and the main results obtained during this PhD thesis. In the following parts of the discussion, I will discuss the main contributions of this work into the understanding of (i) the relationships between lifetime nutrient dynamics, reproductive success and environmental characteristics, (ii) the potential role of *trade-offs* in energy allocation in the coexistence of competing species, and (iii) the role of *trade-offs* between current and future reproduction in the structuring of populations and communities. Throughout this discussion, I will provide a critical analysis of our results and depict several perspectives appealed by this work.

1. Main results

Our first objective has been to explore the relationships between energy allocation, life-history *trade-offs* and environmental characteristics at the intraspecific level (Pelosse *et al.* in prep b, Section 2 – Chap I p81). In an experimental approach, we submitted adult parasitoids to different environmental conditions regarding the availability of hosts and food, and measured lifetime nutrient dynamics and reproductive success. Our main prediction was that parasitoids should be able to allocate their resources toward reproduction and maintenance to maximise their reproductive success according to the characteristics of the environment. Our results showed that reproductive success was strongly affected by food and host availability. Food particularly acted as a strong constraint on longevity: in conditions of low host availability, parasitoids seemed not able to favour energy allocation to maintenance at the expense of reproduction. Our

analysis of lifetime nutrient dynamics allowed us assessing which nutrients are limiting for animal reproductive success. Importantly, parasitoids appeared to store carbohydrates into glycogen and mature fewer eggs in presence of a large number of hosts, which suggested that glycogen could be used under these conditions for other activities such as flight. Then, our results showed that lipid and protein reserves are constantly depleted over lifetime, as it is the case in other parasitoids (Ellers 1996, Olson *et al.* 2000, Lee *et al.* 2004, Casas *et al.* 2005). Originally, we observed a similar decrease regardless of food consumption and number of egg-laying bouts. This result questions the utilisation of lipids for egg maturation and the idea that carbohydrate acquisition allows saving lipids for reproduction (see below).

Our second aim was to investigate the role of *trade-offs* in resource allocation in the coexistence of competing species (Pelosse *et al.* 2007, Pelosse *et al.* in prep a, Section 2 – Chap II p109). To do so, we adopted an experimental approach in which we compared energy allocation strategies and life-history *trade-offs* adopted by two strains that can be apprehended as two closely related species and that co-occur, at least partly, in the field. Our main hypothesis was that the different selective pressures experienced in the environments preferentially used by the two strains have selected for differences in resource allocation that should result in differences in life-history and behavioural traits. The first step of the study was to explore the patterns of resource allocation adopted during ontogeny. The results confirmed our initial hypothesis and particularly pointed out that energy can be differentially allocated, during parasitoid larval stage, toward the storage of energy reserves and the elaboration of eggs (Pelosse *et al.* 2007). In a second step, we investigated if the differences recorded at adult emergence were maintained during adult stage, especially in conditions of food presence. The results showed that food acquisition lessens the initial differences in resource allocation and suggested that other mechanisms have to be considered to account for the coexistence of the two strains (Pelosse *et al.* in prep a, see below).

Our third objective has been to investigate the role of the *trade-off* between current and future reproduction in population and community structuring (Pelosse *et al.* in prep c, Section 2 – Chap III p157). We adopted here a modelling approach of adaptive dynamics. We assumed that in parasitoids, current and future reproductions are respectively linked to the investments in host and food searching, and included this assumption in a simple host-parasitoid population model. Our first hypothesis was that

the extent at which food allows decreasing mortality rate should select for different strategies regarding the sharing of time between host and food foraging. Our results indeed suggested that when food does not allow significantly enhancing survival, parasitoids should not search for food and invest their entire time in host foraging. This finding questions the common thought that parasitoids generally feed in the field and opens interesting questions regarding the factors affecting parasitoid feeding behaviour (see below). Our simulations of the evolution of the investment in food searching and host-parasitoid population dynamics suggested that the fact that two parasitoids species showing different strategies regarding the *trade-off* between host and food foraging compete for a single host population (i) have a potentially stabilising effect on population dynamics, and (ii) might favour the coexistence of competing parasitoid species (see below).

2. The relationships between lifetime nutrient dynamics, animal reproductive success and environmental characteristics

While initially considered as a common pool of energy that has to be divided between several competitive functions, recent advances in the understanding of energy allocation suggested that energy is compartmentalised into different nutrients and that the lifetime patterns of energy acquisition and allocation are highly dynamics. The understanding of the factors affecting nutrient acquisition and allocation and their relationships with life-history traits is strongly needed to clarify what are the main constraints acting on animal reproductive success.

The results obtained in this PhD thesis demonstrated that in a *synovigenic* species not resorting to *host-feeding*, reproductive success is intimately linked to the environmental food and host availabilities (Pelosse *et al.* in prep b, Section 2 – Chap I p81). Our comprehensive analysis of lifetime nutrient dynamics mainly showed that two important classes of nutrients could be distinguished depending on how they are affected by environmental characteristics. The first type of metabolic nutrients, carbohydrates, shows dynamic patterns of variation strongly dependent on whether the environment provides sugary food sources, and whether a limited or large number of

oviposition opportunities is encountered. In contrast, a second type of metabolic nutrients, lipids and proteins, shows a continuous and constant decrease over lifetime whatever the feeding and egg-laying activities. These results raise several interesting questions that will be discussed below: What are the advantages of a fixed energy allocation?; Are lipids systematically utilised to mature eggs in parasitoids?; Do studies of energy allocation should consider more explicitly other factors such as flight?

What are the advantages of a fixed energy allocation?

Our results demonstrate that in *Venturia canescens*, lipid and protein reserves steadily and constantly decrease all along lifetime whatever the environmental conditions and the feeding activities. The absence of lipogenesis, *i.e.* lipid synthesis from sugars, has already been suggested in different Hymenopteran parasitoid species including *V. canescens* (Ellers 1996, Olson *et al.* 2000, Rivero & West 2002, Giron & Casas 2003a, Lee *et al.* 2004, Casas *et al.* 2005, and for *V. canescens*: Casas *et al.* 2003). Some of these studies also demonstrated that lipid decreases over lifetime are less pronounced when *income* carbohydrates are acquired in species exhibiting various life-histories (Ellers 1996, Olson *et al.* 2000, Rivero & West 2002, Lee *et al.* 2004, Casas *et al.* 2005, see table 1 p42). It is generally admitted that without food, lipids are utilised for both maintenance and reproduction, which results in a rapid decrease of lipid reserves, and that with food, carbohydrates acquired from sugary food (nectars, honeydews...) – or proteins acquired from host-feeding – can help sustaining maintenance and saving lipids for reproduction (Casas *et al.* 2005, Strand & Casas 2008). This idea has been incorporated into the Dynamic Programming model of Bernstein and Jervis (2008) which explored the optimal strategy regarding the mutually exclusive activities of food and host searching in non-host-feeding parasitoids. These authors assumed that parasitoid energy reserves are divided into ‘metabolic reserves’ (MRs, sugars and glycogen) and ‘egg production reserves’ (EPRs, lipids and proteins), that sugary food allows replenishing MRs which can be used for maintenance purposes only, that EPRs can not be synthesised from MRs due to the absence of lipogenesis and can be directed either to the maturation of additional eggs or to maintenance (Figure 19 **A**).

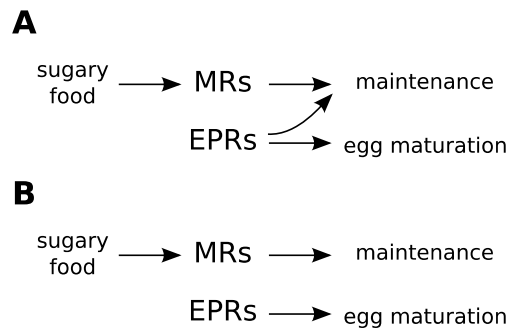


Figure 19. Allocation of ‘metabolic reserves’ (MRs) and ‘egg production reserves’ (EPRs) to maintenance and reproduction. A: Classical allocation pattern in Hymenopteran parasitoids; B: Hypothesised pattern in *V. canescens*.

If we follow the idea that egg production is typically fuelled by lipids, we can propose a novel hypothetical scenario on the allocation of MRs and EPRs from our results. In some parasitoid species including *V. canescens*, lipids seem to behave as a fixed and close energetic compartment that cannot be differentially directed toward maintenance and reproduction in response to the environmental quality (Figure 19 **B**). We propose below two factors that should have favoured the absence of a flexible lipid allocation in parasitoids: the degree of *synovigeny* and the environmental availability of hosts and food.

In contrast to what is often stated, *V. canescens* is highly *synovigenic*. Thelytokous *V. canescens* females have approximately 60 mature eggs at emergence, and show maximum numbers of mature eggs in their ovarioles of 100 or 150, without and with food access, respectively (Pelosse *et al.* 2007, Pelosse *et al.* in prep b). Some studies have suggested that with constant access to hosts and food, thelytokous *V. canescens* can have a lifetime production of up to 560 eggs (Harvey *et al.* 2001, Roberts & Schmidt 2004). This could mean that lipids are a critical and determinant resource for fecundity. Indeed, *V. canescens* appears to store very large amounts of lipids during ontogeny (Casas *et al.* 2003, Pelosse *et al.* in prep b), and to favour lipid utilisation for egg maturation rather than maintenance. Here I would like to mention that highly *synovigenic* Insects have high lipid and/or protein requirements to fuel egg maturation and are generally expected to feed on lipid- and/or protein-rich food – such as hosts – as adults (Jervis *et al.* 2001, Jervis *et al.* 2005). *Non-host-feeding* parasitoids that are highly *synovigenic* may have evolved mechanisms to derive large amounts of lipids from their hosts during the larval stage to counterbalance the absence of lipids in adult

food. These mechanisms may involve either a selective choice of hosts having relatively large lipid reserves or direct modifications of host metabolism (see Strand & Casas 2008). They could be investigated in a comparative analysis of species differing in their nutritional life-history and *ovigeny index*. As we demonstrated in this work, such a fixed energy allocation pattern may incur strong costs in term of longevity, and therefore costs in term of lifetime fecundity, when food is not available (Pelosse *et al.* in prep b, Section 2 – Chap I p81). This strategy would be advantageous in the field when hosts are aggregated in patches of high density: metabolic energy would be less needed to disperse in search of hosts and a high egg maturation rate early in life could be sustained. The dynamic programming model of Bernstein and Jervis (2008) could be used in a modified version to investigate more precisely the influence of both host and food availabilities and of the fixed and flexible patterns of allocation on food and host foraging strategies.

Are lipids systematically utilised to mature eggs in parasitoids?

Lipids are often referred as the critical source of energy for egg production. Our results nevertheless suggest that egg maturation rates are higher in conditions of low host availability, but do not provide evidence that lipid utilisation is higher under these conditions. Our data suggest more that egg maturation is favoured at the expense of glycogen storage, since in conditions of high host availability, glycogen storage is higher and egg maturation rate lower. A similar pattern is observed during larval stage when comparing the two reproductive modes of *V. canescens*: whereas arrhenotokous wasps appear to favour the storage of glycogen, thelytokous ones appear to favour egg maturation. Results obtained on the host-feeding parasitoid *Eupelmus vuiletti* suggested that *anhydropic* eggs contain relatively large amounts of glycogen and smaller amounts of lipids (Casas *et al.* 2005). Preliminary results suggest that *V. canescens hydropic* eggs contain fewer lipids than proteins and glycogen (less than 1.10^{-5} %, 12 % and 20 % of teneral lipid, protein and glycogen reserves, respectively, Pelosse unpublished results). Tracking studies demonstrating the incorporation of *income* nutrients into eggs have solely demonstrated that amino acids are incorporated into eggs (Boggs & Gilbert 1979, Boggs 1997a, Rivero & Casas 1999b, Rivero *et al.* 2001). To my knowledge, the rate of utilisation of lipid or carbohydrate reserves has never been precisely correlated to egg maturation rate. A comparison of nutrient utilisation among different parasitoid

species having *hydropic* or *anhydropic* eggs could help assessing which nutrients limit egg maturation.

Do studies of energy allocation in Insects should consider more explicitly other factors such as flight?

Carbohydrates are typically acquired from feeding on sugary substances and are generally thought to be the main nutrient contributing to Insect maintenance. Indeed, by modelling the lifetime nutrient dynamics based on real data acquired in the *synovigenic* host-feeding parasitoid *Eupelmus vuiletti*, Casas *et al.* (2005) suggested that carbohydrate levels should determine wasp survival. The data we obtained in *V. canescens* suggest that carbohydrate reserves are not systematically allocated to survival, and that others nutrients such as proteins and lipids may limit longevity. Carbohydrates reserves are entirely utilised during adult stage when a low number of oviposition opportunities are encountered. In contrast, when the host availability is high, simple sugars like fructose and glucose are entirely utilised but glycogen is stored. The understanding of glycogen storage in conditions of high host availability would require further investigations. Glycogen is generally thought to be the main flight fuel used by Hymenopteran (Candy *et al.* 1997, Vogt *et al.* 2000, Suarez *et al.* 2005). Flight, which is often overlooked in studies of energy allocation, is a highly energy-demanding activity (see section ‘*The costs of locomotion*’ of the literature analysis p65), and is expected to strongly affect Insect lifetime nutrient dynamics. To my knowledge, there exists only one study that assessed the metabolic costs of flight in a parasitic wasp. *Cotesia rubecula* females appear to use glycogen but not lipids to fuel short flights of 3 min (Siekmann 2002). Confirming the reliance of Hymenopteran parasitoids on glycogen to fuel their flights, and designing studies examining in more details the dynamics of nutrient utilisation during longer flights would allow a significant increase of our knowledge on nutrient dynamics and nutrient allocation in parasitoids. Such studies should be relatively easy to carry out and the methodology is already available from various other model systems such as Dipteran or Coleopteran (for references, see section ‘*The costs of locomotion*’ p65). Non-destructive micro-samples of haemolymph at different flight periods and determination of enzyme activity and/or metabolite concentrations would provide a good assessment of the dynamics of nutrient utilisation during flight (see Gäde *et al.* (2006) for an exemple on a Hemipteran).

3. *Trade-offs* in energy allocation and their potential role in promoting species coexistence

Different strategies regarding *trade-offs* in resource utilisation or life-history *trade-offs* have been suggested to play a role in the reduction of local interspecific interactions and therefore in coexistence (see section ‘*Role of trade-offs in population dynamics and community structuring*’ of the literature analysis p72). We investigated in this PhD thesis *trade-offs* in energy allocation, life-history and behavioural traits in the two strains of *Venturia canescens* (Pelosse *et al.* 2007, Pelosse *et al.* in prep a, Section 2 – Chap II p109).

The choice of our model system, the two reproductive modes of *Venturia canescens* may appear surprising and requires here some explanations. First, thelytokous and arrhenotokous individuals are distinct genetic entities (Beukeboom *et al.* 1999) and can therefore be regarded as two closely related species. Then, even if they preferentially thrive in distinct habitats – natural for arrhenotokous wasps and anthropogenic for thelytokous ones (Schneider *et al.* 2002, Amat 2004) – it has been shown that they co-occur in the field from June to September (Beukeboom *et al.* 1999, Schneider *et al.* 2002, Amat 2004). They are therefore expected to share common host and food resources during approximately 6 generations in the field. Under these conditions, arrhenotokous wasps that suffer from the costs associated with their sexual reproduction (*e.g.* they produce males that indirectly participates to future generations and are potentially submitted to mating costs) are expected to have evolved mechanisms to avoid being displaced by their thelytokous counterparts. Even if the model system considered in this PhD thesis can be criticised, mainly on the grounds that coexistence in this system is only partial, we argue that our study can nevertheless suggest mechanisms involved in the coexistence of closely related species.

The main question I handled during this PhD thesis regarding the unexpected co-occurrence of two reproductive modes in *V. canescens* is: Do arrhenotokous and thelytokous wasps show distinct strategies regarding *trade-offs* in resource allocation? Because the two habitats preferentially used by the two reproductive modes differ in a set of biotic and abiotic factors, they allow us making predictions about the strategies that should be adopted by the two types of wasps. As a first step, we explored the

patterns of resource allocation adopted by the reproductive modes during ontogeny, and to confirm that the initial patterns recorded maintain in the field, especially when food is available, we investigated in a second step the adult lifetime patterns of energy allocation. Our results suggest that during the larval stage, energy is differentially allocated to reproduction and survival in the two reproductive modes (Pelosse *et al.* 2007, Section 2 – Chap II – 1 p109). Particularly, thelytokous individuals appear to favour egg maturation during the larval stage, since they show a relatively large egg complement at adult emergence. In contrast, arrhenotokous wasps appear to favour the storage of metabolic reserves, especially glycogen. These initial differences have been suggested to favour arrhenotokous wasps in conditions of low host availability that are most likely prevalent in the field, especially because they would be less time-limited, *i.e.* less limited by the time available to lay their entire egg complement, than thelytokous wasps. Our measurement of life spans without food among both reproductive modes accordingly suggested that arrhenotokous females use their glycogen reserves to enhance their longevity (Pelosse *et al.* 2007, Section 2 – Chap II – 1 p109). Nevertheless, we also revealed that food acquisition, which has been shown to take place in the field in thelytokous *V. canescens* (Casas *et al.* 2003, Desouhant *et al.* in prep), seems to weaken the potential advantages of arrhenotokous females in the field (Pelosse *et al.* in prep a, Section 2 – Chap II – 2 p133). Even if time-limitation costs remained higher in thelytokous wasps, the two reproductive modes achieved a comparable reproductive success. This result clearly suggests that the *trade-off* in energy allocation alone is not sufficient to understand the maintenance of arrhenotokous individuals in the field, and appeals further investigations.

The most important factor that has not been considered in our study is space. In the field, wasps have to fly in search of hosts and food. The higher glycogen reserves recorded in arrhenotokous females might result in higher flight capabilities, which would favour them in the field where hosts are relatively scattered (Driessen & Bernstein 1999). A study has already been conducted to compare the flight capabilities of arrhenotokous and thelytokous *V. canescens* on a flight mill (Lukas *et al.* in prep). The results suggest that arrhenotokous wasps do not fly during longer periods or on longer distances, but that they are faster fliers than their thelytokous counterparts. A precise comparison of the dynamics of nutrient utilisation during flight could provide

insights into the question of the flight energetic advantage of arrhenotokous wasps (see above).

Experiments in the laboratory are easier to design and allow controlling a large number of parameters, but field experiments would permit to assess more realistically the critical factors affecting animal reproductive success (Heimpel & Casas 2008). Experiments of release and recapture in the field are well mastered on *Venturia canescens* (Casas *et al.* 2003, Amat 2004, Desouhant *et al.* in prep). Assessing egg maturation rates in the field has also proven doable (Casas *et al.* 2000, Lee & Heimpel 2008). An interesting perspective of this work would be to explore in the field the ability of the two reproductive modes to find food and hosts, compare their reproductive success, and link them with their energetic lifetime dynamics. The major technical difficulty is that arrhenotokous wasps are less easily recaptured in the field compared to thelytokous ones (Amat 2004, Pelosse personal observation). The factors that might be involved are arrhenotokous higher dispersal abilities or lower attractiveness to the traps containing *Ephestia kuehniella* that are used to recapture the wasps. Greenhouse experiments could help to circumvent this difficulty.

4. Role of *trade-offs* between current and future reproduction in the structuring of populations and communities

Lastly, I would like to focus on the *trade-off* between current and future reproduction and its potential role in population and community structuring. During my PhD thesis, I adopted a modelling approach to investigate the population and evolutionary dynamics of a host-parasitoid system in which parasitoids divide their time between host and food foraging (Pelosse *et al.* in prep c, Section 2 – Chap III p157). The three main results obtained are that the strategy of dividing time between host and food foraging may have a stabilising effect on host-parasitoid population dynamics, that under some conditions, the strategy of not feeding may be adaptive, and that two parasitoids adopting different strategies regarding their investment in host and food searching may have the possibility to coexist, provided that the host-parasitoid population cycles. I will focus on the two last results only, since the first one has already been discussed by Sirot and Bernstein (1996) and Krivan and Sirot (1997).

Feeding or not?

Our results suggest that when food does not allow to significantly enhance survival, the strategy of not feeding and concentrating investment in host foraging is a viable option. This finding is unexpected since it questions the common thought that parasitoids generally feed in the field (Jervis *et al.* 1993). Food foraging may have a limited effect on parasitoid longevity if food is of low quality. Low quality-food types such as honeydew have already been suggested to have limited effects on parasitoid survival (*e.g.* Wäckers 2000, Lee *et al.* 2004). To test the hypothesis that parasitoids should not respond to low quality-foods but concentrate their effort in host foraging, simple laboratory olfactometer experiments in which parasitoids would have the choice between foods of different qualities and hosts could be easily designed. How parasitoid respond to different food concentrations has been tested by Wäckers (1999). Different sugar solutions at different concentrations were proposed to starved *Cotesia glomerata* wasps and the gustatory response, *i.e.* if feeding for more than 5 seconds occurred, was recorded. The results suggest that at low concentration, common sugars such as fructose or sucrose still elicit a gustatory response (Figure 20).

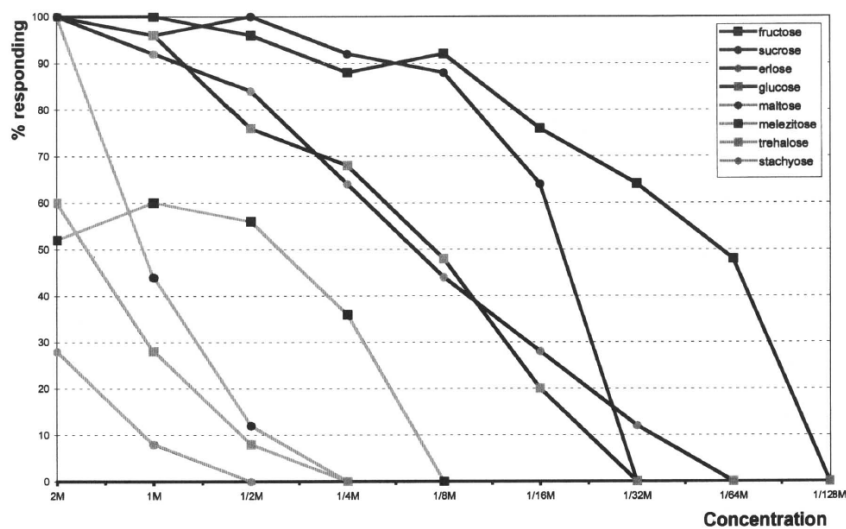


Figure 20. Percentage of food-deprived *Cotesia glomerata* responding to sugar solutions of different concentrations (from Wäckers (1999)).

The effect of feeding on survival will also be limited if food foraging incurs more costs than benefits. This could happen if food sources are spatially separated from hosts and important travel costs are involved. Dynamic programming approaches predict that

parasitoids should not feed when the probability to find food is low (Sirot & Bernstein 1996, Bernstein & Jervis 2008). In the field, *Microplitis croceipes* females appear to invest extra time in host foraging when provided with honeydew that is of lower quality and more scattered compared to nectar (Stapel *et al.* 1997). In field or semi-field conditions, low probabilities to find food could be mimicked by reducing the number of food sources or increasing the travel costs between host and food sources.

Here I would like to mention that the model of Bernstein and Jervis (2008) suggests that *non-host-feeding synovigenic* species should rely less on food compared to *proovigenic* species because they have the possibility to use their ‘egg production reserves’ (EPRs) as a last resort-strategy to fuel their maintenance (see Figure 19). Our results on *Venturia canescens* suggest that EPRs cannot systematically be re-directed toward maintenance (Pelosse *et al.* in prep b, Section 2 – Chap I p81). Under the assumption that sugary food is directed toward maintenance and egg maturation, *synovigeny* should be associated with a higher degree of dependence on food sources (Boggs 1981a, 1990, Jervis *et al.* 2001). A dynamic programming model comparing these different scenarios would be interesting in predicting the dependence on food of *proovigenic* and *synovigenic* parasitoid species.

In our model, we assumed that food is always available, and that the environment is not structured. These simplifying hypotheses could be modified by assuming that the environment is constituted of host and food patches. Stochasticity in food availability or in costs associated with feeding, which would more realistically illustrate the conditions encountered in the field, could strongly affect our predictions.

Coexistence on the basis of the trade-off between host and food foraging?

Our simulations of the evolution of the investment in food searching and host-parasitoid population dynamics suggested that the coexistence of a species maximising host foraging and a species sharing its time between host and food foraging is likely to occur under some conditions. Because this result is only based on numerical simulations, the short-term perspective of the work is to analytically investigate the conditions favouring species coexistence. This will be addressed by the computation of the *invasion fitness* in non-equilibrium dynamics, and the representation of its sign in *pairwise invasibility*

plots. This will allow determining if *evolutionary branching*, *i.e.* a process of phenotypic divergence in an initially monomorphic resident population, is likely to occur in our model, and therefore assessing if the coexistence of the two strategies would be evolutionary stable.

As emphasised by Bonsall and Bernstein (2008), studies of *behavioural ecology* of parasitoids have vastly investigated the role of individual behaviours in the dynamics of populations, but largely overlooked their influence in community dynamics (but see Bonsall *et al.* 2002, Bonsall *et al.* 2004, Bonsall & Bernstein 2008). While the development of *Adaptive Dynamics* allows linking individual behaviours, population and community dynamics in an efficient way, this theory has rarely been applied to the study of host-parasitoid community assemblages. The work carried out during this PhD thesis significantly contributed to make this link. Applications of host-parasitoid population dynamics models, for instance largely developed for *host-feeding* parasitoids, to the study of the evolution of various *trade-offs* (*e.g.* between current and future reproduction, competitive ability and longevity) and of their role in community structuring could be relatively easy to do and open an interesting field of investigations in *behavioural ecology*. Furthermore, the recent advances in the understanding of the physiological factors affecting parasitoid behaviours give now the possibility to include more physiological realism into population dynamics models (Strand & Casas 2008).

The ‘optimal’ approach in my PhD thesis would have consisted in designing experiments to test the predictions of the model I explored. Unfortunately I did not, for the main reason that shifts between theory and experiment are time consuming – learning the modelling techniques employed in this PhD thesis has not been an easy task – and not systematically obvious, especially when foraging behaviours are involved.

I handled during my PhD thesis several concepts that belong to several different fields – life-history theory, eco-physiology, behavioural ecology, population dynamics and community ecology – and both theoretical and empirical approaches. This experience has some drawbacks in the sense that I did not have enough time to thoroughly explore all the questions I addressed during the thesis, and to provide links between the theory

and experiments. This approach has nevertheless been interesting in the sense that it provided me with backgrounds in complementary fields. I hope that I would have the opportunity in the future to go further and to make links between different approaches.

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RÉSUMÉ

Les compromis évolutifs ou *trade-offs* occupent une place centrale dans l'évolution des traits d'histoire de vie car ils contraignent l'univers des possibles. Les *trade-offs* dans l'allocation d'énergie vers la reproduction et la maintenance sont essentiellement liés, chez les insectes parasitoïdes, à la disponibilité en hôtes et en nourriture de l'environnement et au nombre d'œufs dont disposent les femelles. Nos expériences relevant de l'écologie comportementale et de l'éco-physiologie démontrent, chez le parasitoïde *Venturia canescens*, (i) que les caractéristiques de l'environnement sélectionnent une allocation différentielle des ressources vers la fabrication des œufs et la mise en place des réserves énergétiques pendant la phase larvaire ; et (ii) qu'un ajustement des stratégies d'allocation d'énergie en réponse à la disponibilité en hôtes existe pendant la phase adulte. Nos travaux théoriques révèlent le rôle central de la qualité de la nourriture dans l'évolution du *trade-off* entre recherche d'hôtes et de nourriture, et suggère son importance dans la structuration des communautés de parasitoïdes.

TITLE

Role of trade-offs in the specialisation and coexistence of competing species. Theoretical and empirical developments in parasitoid insects.

ABSTRACT

Trade-offs have a central place in the evolution of life-history traits since they bound the universe of possibilities. Trade-offs in energy allocation toward reproduction and maintenance are essentially linked, in parasitoid insects, to the host and food availability of the environment and to the number of eggs carried by females. Our experiments in behavioural ecology and eco-physiology show, in the parasitoid *Venturia canescens*, that (i) environmental characteristics select for a differential energy allocation toward egg manufacture and energy storage during the larval stage; and (ii) that an adjustment of the energy allocation strategies in response to the host availability takes place during the adult stage. Our theoretical investigations put forward that food quality has a central role in the evolution of the trade-off between host and food searching, and suggest its importance in the structuring of parasitoid communities.

DISCIPLINE

Écologie, Biométrie.

MOTS-CLÉS

Trade-off ; compromis évolutif ; allocation d'énergie ; écologie comportementale ; éco-physiologie ; trait d'histoire de vie ; parasitoïde ; *Venturia canescens* ; dynamique adaptative ; approvisionnement optimal ; spécialisation à l'habitat ; mode de reproduction.

KEYWORDS

Trade-off; energy allocation; behavioural ecology; eco-physiology; life-history trait; parasitoid; *Venturia canescens*; adaptive dynamics; optimal foraging; habitat specialisation; reproductive mode.

INTITULÉ ET ADRESSE DU LABORATOIRE

Laboratoire de Biométrie et Biologie Évolutive, CNRS UMR 5558, Université Claude Bernard Lyon 1, 43 bd du 11 novembre 1918, 69622 Villeurbanne Cedex.