Journal of Animal Ecology 2003
72, 691–697

Energy dynamics in a parasitoid foraging in the wild

JEROME CASAS*, GERARD DRIESSEN†¶, NICOLE MANDON*, SEBASTIAAN WIELAARD†, EMMANUEL DESOUHANT‡, JACQUES VAN ALPHEN†, LAURENT LAPCHIN§, ANA RIVERO*††, JEAN PHILIPPE CHRISTIDES* and CARLOS BERNSTEIN‡

**University of Tours, Institut de Recherches sur la Biologie de l'Insecte, IRBI, UMR CNRS 6035, Avenue Monge, F-37200 Tours, France; †Institute of Evolutionary and Ecological Sciences, University of Leiden, PO Box 9516, 2300 RA Leiden, the Netherlands; ‡Biométrie et Biologie Évolutive, UMR-CNRS 5558, Université Claude Bernard Lyon 1, 43 Bd. du 11 Novembre 1918, F-69622 Villeurbanne Cedex, France; §INRA, Centre de Recherches d'Antibes, Unité Mixte de Recherches 1112 R.O.S.E., 37, Bd du Cap, F-06606 Antibes Cedex, France; ¶Institute of Ecological Sciences, Vrije Universiteit, De Boelelaan 1085, 1081 HV Amsterdam, the Netherlands; and ††Centre d'Etudes sur le Polymorphisme des Microorganismes CNRS – UMR 9926, Institut de Recherche pour le Développement, 911 avenue Agropolis, BP 64501, 34394 Montpellier Cedex 5, France*

Summary

1. Although parasitoids are used widely as a biological models for understanding the evolution of animal behaviour, most studies have been constrained to the laboratory. The dearth of field studies has been compounded by the almost complete ignorance of the physiological parameters involved in foraging and dispersal, in particular of the energetic constraints imposed by resource limitation.

2. We estimated the dynamics of carbohydrates and lipids reserves of *Venturia canescen*s (Gravenhorst) females by releasing individuals of known nutritional status in a natural environment and recapturing them using host-containing traps. The recapture rate was around 30%. These results were compared with the reserves of caged animals kept under different experimental conditions (freshly emerged, starved to death, fed *ad libitum* and partially starved). Wild animals were also sampled in order to estimate the resource levels of the local population.

3. The results show that: (i) wasps are able to maintain a nearly constant level of energy over an extended foraging period; (ii) *V. canescens* takes sugars in the field; and (iii) the lipid reserves accumulated during the larval life may be limiting as lipogenesis does not take place in adults even under conditions of high sugar availability.

4. These results demonstrate that wasps can forage for hosts and food and disperse in this habitat for hours and days without running into a severe risk of energy limitation.

Key-words: carbohydrates, dispersal, energy budgets, host–parasitoid systems, lipids, *Venturia canescens*.

Journal of Animal Ecology (2003) **72**, 691–697

Introduction

Dispersal is a major process influencing life-history evolution (Roff 1984; Zera & Rankin 1989), population dynamics (Vance 1980; Hassell, Comins & May 1991; Amarasekare 1998), community structure (Holmes & Wilson 1998; Shurin & Allen 2001), population genetics (Lenormand & Raymond 2000) and speciation (Gavrilets, Li & Vose 2000). For many years, parasitoids (parasitic wasps that lay their eggs in or on the body of other arthropods, mainly insects) have been one of the preferred biological models in many of these fields, and also in the field of optimal foraging behaviour (Godfray 1994; Hassell 2000; Hochberg & Ives 2000). The small size of these animals, however, has hindered attempts to follow their movement patterns in the wild and has constrained studies to the laboratory (see Casas 2000 for a review). This problem has been compounded by the almost complete ignorance of the physiological parameters involved, in particular of the energetic constraints imposed by resource limitation under natural conditions.

This work is part of an effort to unravel the role of dispersal in population dynamics, life-history trait

Correspondence: Jérôme Casas, University of Tours, Institut de Recherches sur la Biologie de l'Insecte UMR CNRS 6035, 37200 Tours, France. Fax: + 33 2 47 36 69 66; E-mail: casas@univ-tours.fr

evolution and the genetic make-up of populations of *Venturia canescens* (Gravenhorst) in the field. *V. canescens* is a classical model for the study of life-history evolution, genetics and population dynamics of parasitic wasps (see Driessen & Bernstein 1999 and references therein). Furthermore, most recent studies have underlined the importance of dispersal in determining the genetic structure of the population in the wild (Schneider *et al*. 2002).

Knowledge of the energetics of dispersal and movement of parasitoids in the field requires information of two key parameters: the energetic input (food acquisition) and the energetic output (metabolic demands and flight costs). However, a simple combination of these values is not sufficient in itself to predict the dynamics of energetic reserves, as movement patterns and foraging decisions intervene. A direct way of solving this problem is to measure the energy reserves of foraging parasitoids at different time-points in the dispersal process.

Here we quantify the dynamics of energy in *V. canescens* females foraging in their natural environment. For this purpose we carry out a quantification of the energetic reserves (lipids and carbohydrates) of parasitoids issued from a series of release and recapture experiments. We compared these results with the reserves of caged animals kept under different experimental conditions (freshly emerged, starved to death, fed *ad libitum* and partially starved). Wild animals were also sampled in order to estimate the resource levels of the local population. To our knowledge, this is the first report on the energetics of foraging and dispersal in any parasitoid under field conditions.

Materials and methods

Venturia canescens is a solitary, koinobiont, partially synovigenic larval parasitoid of pyralid moths, which is known to thrive either in anthropogenic conditions such as granaries and mills, or under field conditions where it attacks different pyralid species in desiccated fruits such as carob, medlar, fig and date or husks of almond and walnut (Driessen & Bernstein 1999). In the conditions in which the experiment was performed, in the South of France, these tree species occur in small stands between which parasitoids disperse in search for hosts. *V. canescens* does not resort to host feeding but field and experimental evidence suggests that it uses other food sources (see Discussion).

All experiments were carried out with wasps from a thelytokous strain collected from a wild population in 1998 in Antibes in the south-east of France. They had been reared on larvae of the pyralid moth *Ephestia kuehniella* Zeller in a host medium consisting of semolina.

TENERAL RESERVES AND MINIMAL IRREDUCIBLE RESERVES

For these measurements, 69 wasps that had emerged between 07.30 and 08.30 in the morning were removed from the standard culture. Thirty-two of these were frozen immediately at –80 °C. Biochemical analysis of these animals (see below) allowed to estimate lipid and sugar contents of females at emergence (teneral reserves). The remaining 37 wasps were put into a cage (35 × 35 × 50 cm) at 25 °C and 16/8 h light/dark regime with water but no food. During daytime (08.00–17.00 h) the cage was checked hourly for dead wasps, and this was also conducted at 23.00 h. Wasps found dead in the cage were immediately frozen at –80 °C. These were used to estimate the reserve levels at death or the 'minimal irreducible reserves'. These are considered to be structural resources, such as lipids and carbohydrates forming cell walls, connecting tissues, etc. that cannot be burned.

DYNAMICS OF SUGAR AND LIPID RESERVES IN THE FIELD

On 7 and 9 September 1999 release–recapture experiments were carried out in the 'Jardin Thuret' botanical garden (Antibes, France), a 4-ha heterogeneous forest-like park with mainly exotic bushes and trees and small open lawns. On the study site, a grid was constructed consisting of 97 equidistant (10 m) wooden poles (recapture sites) of 1 m height. The grid was nearly circular with a diameter of 120 m. Traps for recapturing the wasps could be attached to the top of the poles. The traps consisted of 2 × 5 × 5 cm honeycomb-like structured pieces of cardboard containing fifth instar *E. kuehniella* larvae settled in their food medium (semolina). These traps have been shown to be very effective for recapture experiments with *V. canescens*. Previous field experiments have shown that these wasps are equally attractive to both well-fed wasps and wasps starved for 48 h, which is close to the lethal period.

Wasps that had emerged over a half-day from the standard culture were put individually into glass tubes (2 × 7 cm) with a drop of honey on the plug and kept at 25 °C and 16/8 h light/dark regime. These animals were divided into two groups. One group (n = 22) remained in these conditions for 48 h, after which they were frozen at –80 °C to measure reserves after *ad libitum* feeding. The remaining wasps were kept for the release experiments. On the second day they were colour-marked with a dot of water-soluble acrylic paint on the thorax. After marking, these wasps were put individually in tubes again with a drop of honey on the plug. Twelve hours before release the plugs were replaced by clean ones without food.

On the morning of the third day after their removal from the culture, the wasps were released into the centre of the grid. Releases started at 0900 h by removing the plugs gently from the tubes. The wasps always left their tubes calmly and there were no indications of any disturbance during the wasps' departure. In 15 min 90% of the wasps had left the tubes. Two release–recapture experiments were carried out, one in which the traps

were put out 1 h after release (dispersal period) and another in which the traps were put out 5 h after release. It took 10–15 min to equip all poles with traps. Using two dispersal periods enabled us to expand the time interval over which reserve dynamics could be studied on the day of release to around 8 h (see Results). Recapturing started 15 min after all traps were set out. Every 15 min, all traps in the grid were checked for *V. canescens*. If present, they were caught with a exhauster, frozen within 15 min at –80 °C and the time and place of recapture were recorded. Recapture continued until 1800 h. For the two experiments 82 and 84 wasps were prepared, respectively, but only 75 were released in each experiment. The remaining animals (n = 16) were frozen immediately before release to serve as controls. These wasps had been starved for 12 h (see above). Hence, they are used not only for measuring the initial condition of the released wasps, but also for comparisons with the other feeding treatments. Weather conditions on both experiment days were very similar: sunny, light winds (around 1 m/s) and temperatures ranging between 23 °C and 32 °C (mean 26·6 °C) and 22 °C and 29 °C (mean 24·9 °C), respectively.

During the second of our experiments, 10 wasps were recaptured with a colour mark of the preceding experiment. These wasps had thus been out in the field for about 48–54 h after release, and were included to study long-term reserve dynamics.

During these experiments, 36 unmarked wild wasps were caught on the traps. These wasps were also frozen to provide an estimate of sugar and lipid reserves in the wild population from which the experimental wasps originated.

BIOCHEMICAL AND STATISTICAL ANALYSIS

Sugars, glycogen and lipids were quantified using the methods of van Handel & Day (1988). It is important to note that we use the term 'sugars' for all carbohydrates excluding glycogen. The energy level was calculated by adding the contribution of lipids and sugars, assuming 16·74 J per milligram carbohydrate and 37·65 J per milligram lipid (Clement 1992). Data on sugar and lipid reserves of freshly emerged, starved to death, wild-caught, *ad libitum*-fed, partially starved and recaptured wasps were not all normally distributed and hence analysed using a Kruskall–Wallis one-way ANOVA, followed by pairwise comparisons (with significance levels corrected for the number of comparisons) to determine which populations differed significantly (Conover 1980). The data of both experiments were pooled.

Results

For both sugars and lipids the null-hypothesis that all sample distributions were identical was rejected (for both cases, $P < 10^{-10}$, d.f. = 6, one-way ANOVA). This allowed a more detailed analysis by pairwise comparisons (Fig. 1). We start by comparing teneral reserves and reserves at death (minimal irreducible amounts). Wild females caught during the release experiments and of unknown nutritional status are subsequently analysed. These results are compared in turn with the lipid and sugar contents of females previously fed *ad libitum*, and with the contents of females that had been starved for 12 h after *ad libitum* feeding (i.e. the control group of the field experiment). As wild females were smaller than the laboratory reared ones, all measurements on lipid and sugar contents were corrected for hind tibia length and are given in µg per 0·02 mm tibia length. The mean tibia length of all wasps was 1·88 mm.

Finally, lipid and sugar dynamics during foraging in the field were analysed. Thirty (40%) and 18 (24%) wasps were recaptured for the two experiments, respectively. Fifteen of each group were analysed biochemically. The average recapture distance was 30·6 m (range 0–60 m).

COMPARISONS BETWEEN TREATMENTS

At birth, females had an average of 1·96 (SE = 0·06) µg lipids (Fig. 1a, n = 30, two lipid measurements were lost) and 0·15 (SE = 0·01) µg sugars (Fig. 1b, logarithmic scale). The mean minimal irreducible amount of lipids was 1·27 (SE = 0·06) µg (Fig. 1a) and 0·06 (SE = 0·002) µg for sugars (Fig. 1b). Thus the decline between birth and death is 35% for lipids and 60% for sugars. Expressed in terms of total energy (not corrected for size), teneral females had a mean of 7·6 J, while the minimum irreducible amount was of 4·9 J. Therefore, at birth on average 2·7 J of energy reserves was available to the wasps, of which only 6% was in the form of sugars.

The mean lipid content of the 36 wild females caught in the field experiments was somewhat higher than the teneral lipid level, but not significantly so (2·39 with SE = 0·16 µg vs. 1·96 with SE = 0·06 µg, Fig. 1a). The sugar content of the wild wasps, on the other hand, was more than five times the teneral level (0·83 (SE = 0·12) µg vs. 0·15 (SE = 0·01) µg, $P < 0·05$ (Fig. 1b), which shows that wild wasps do feed on sugars in the field. The mean total energy level of the wild wasps was 8·4 J. Correcting for the minimum irreducible amount of reserves (4·9 J), this means that wild animals on average had 3·5 J to spend.

Ad libitum access to honey for 48 h increased the sugar levels significantly ($P < 0·05$) to an average of 3·12 (SE = 0·33) µg, which was more than 20 times above the teneral level and around four times above the wild level (Fig. 1b). In contrast, the mean lipid level in the *ad libitum*-fed wasps (1·86 µg, SE = 0·10, Fig. 1a) was not significantly different from that in teneral and wild wasps. Twelve hours of starvation after *ad libitum* conditions had a significant effect on the sugar levels ($P < 0·05$). Sugar levels dropped 82% to an average of 0·57 (SE = 0·07) µg (Fig. 1b). Lipid levels decreased non-significantly to 1·58 (SE = 0·07) µg (Fig. 1a).

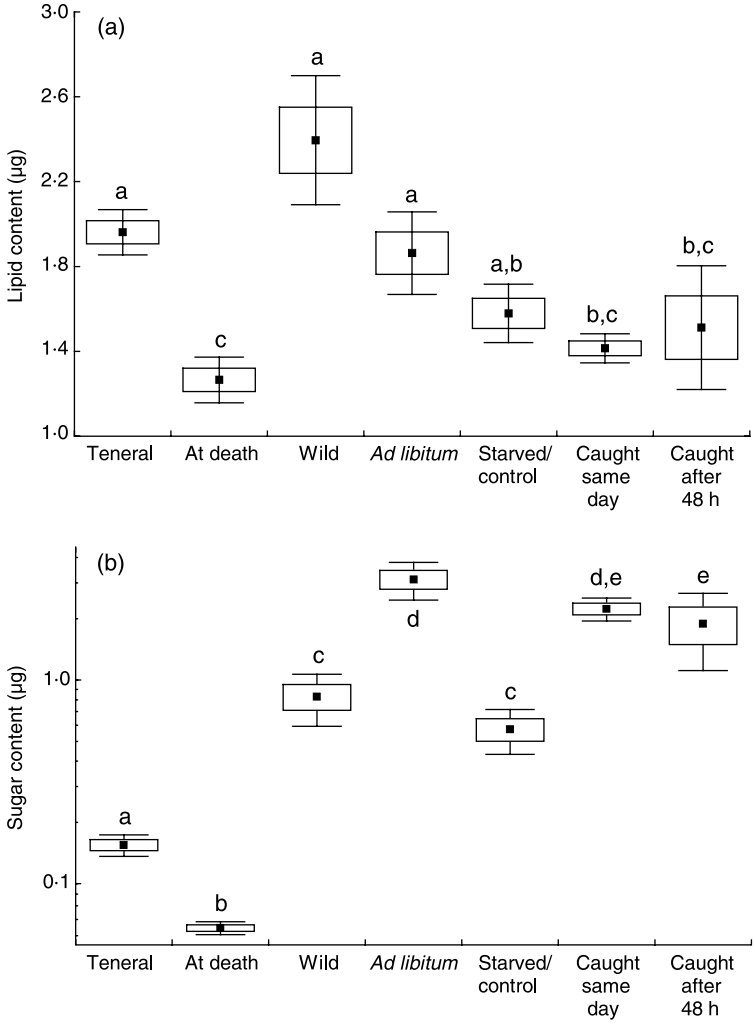

Fig. 1. Total lipids (a) and sugars (b) contents (in µg/0·02 mm hind tibia length) of freshly emerged wasps (teneral), wasps that had just died, wild wasps, wasps fed *ad libitum*, wasps starved for 12 h (= control group of release experiment), wasps recaptured within 500 min (on the day of the release experiment) and wasps recaptured on the third day after release (> 48 h). Dots indicate means, boxes indicate the standard errors of the means and whiskers indicate the 95% confidence intervals of the means. Homologous groups are indicated by identical characters.

DYNAMICS OF LIPID, SUGAR AND GLYCOGEN LEVELS IN THE FIELD

The mean hind tibia length of the recaptured wasps was not different from that of those that were kept for control ($P = 0{\cdot}413$, d.f. = 38, *t*-test). Figure 2a shows the changes in lipid (solid line and filled circles) and sugar levels (dashed line and open circles) of the wasps recaptured on the same day in the field experiments. The points at $t = 0$ are from the control sample that was frozen just before release. The regressions of lipids and sugars against time were nearly horizontal when the control data were omitted from the analysis ($y = 1{\cdot}25 + 0{\cdot}0005x$, $n = 30$, $P = 0{\cdot}14$; $y = 2{\cdot}20 + 0{\cdot}0001x$, $n = 30$, $P = 0{\cdot}93$, respectively). Compared to the control sample the mean lipid level of the recaptured wasps decreased slightly but significantly (from 1·57 µg to 1·41 µg, $P = 0{\cdot}024$, d.f. = 44, *t*-test, Figs 1b and 2a), while the sugar levels increased fourfold (from 0·57 µg to 2·24 µg, $P < 10^{-6}$, d.f. = 44, *t*-test, Figs 1a and 2a). The net result of this was that the energy level from lipids and sugars increased significantly during the first 100 min after release, from 0·069 J to an average of 0·091 J ($P = < 10^{-5}$, d.f. = 44, *t*-test, Fig. 2b) after which it remained constant throughout the day ($y = 0{\cdot}084 + 0{\cdot}0002x$, $n = 30$, $P = 0{\cdot}435$). We analysed a subset of our samples for glycogen and found an increase over time (for the control group at release time: mean = 0·18 µg, SE = 0·04, $n = 10$, for the group recaptured after 6 h: mean = 0·307 µg, SE = 0·18, $n = 9$).

The mean lipid content of the individuals that were caught 48 h or more after their release was 1·51 (SE = 0·15) µg (Fig. 1a), while their mean sugar content was 1·89 (SE = 0·40) µg (Fig. 1b). Both values were not significantly different from the ones of the wasps recaptured during the first 500 min on the day of release (i.e. 1·41 (SE = 0·04) µg for lipids and 2·24 (SE = 0·15) µg for sugars) leading to similar total energy levels in both groups: 0·089 J for the wasps recaptured after 48 h and 0·091 J for those recaptured on the same day ($P = 0{\cdot}70$, d.f. = 38, *t*-test).

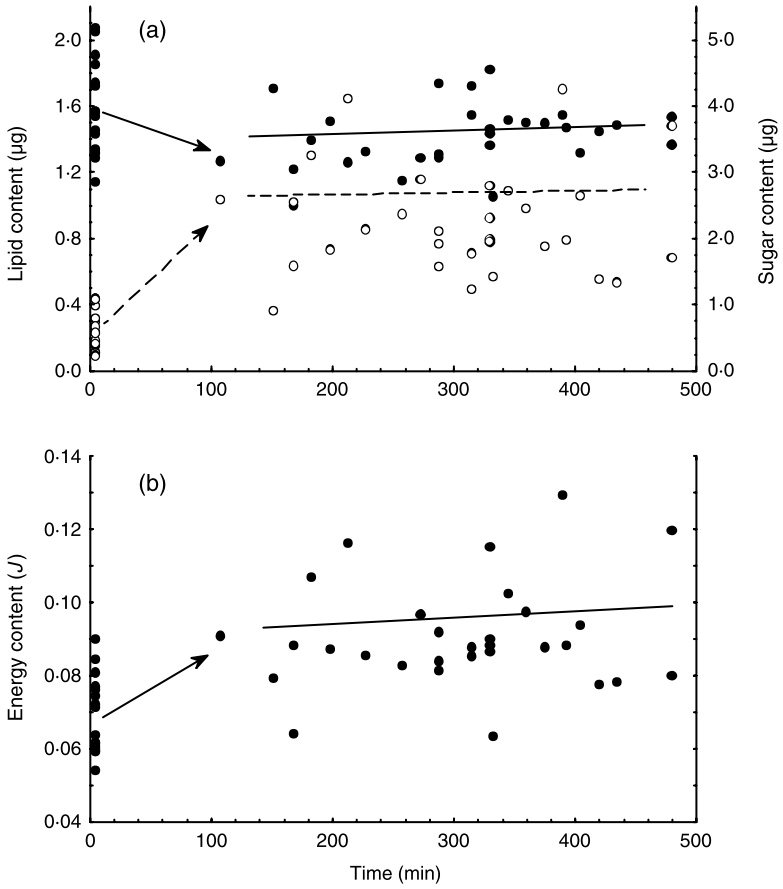

Fig. 2. Lipid (left *y*-axis, black dots, solid line) and sugar (right *y*-axis, open dots, dashed line) contents (a) and total energy contents (b) of control wasps (at $t = 0$) and wasps recaptured on the same the day of the release experiment (units in µg/0·02 mm hind tibia length). Regression lines are for recaptured wasps only. Arrows launch from the mean values of the controls.

Discussion

V. canescens emerges from its host with a limited amount of energy reserves which are stored mainly in the form of lipids (94%). This value is probably close to the available amount for survival and movement, because the whole reproductive system, including eggs, contains less than 2% of the usable lipids (M. V. Schneider, unpublished observations). We based our analyses on carbohydrates and lipids only. Our energy budget is therefore not quite complete, as the biochemical essays do not enable us to analyse protein contents in the same individuals. Proteins are used by a few insects as a flight fuel (Colorado beetle and the tsetse fly in particular) and for maintenance by other insects when they exposed to long periods of starvation (Chapman 1998). However, the only fuel for flight in all hymenopterans studied so far (ants, bumble bees and bees) are carbohydrates (Wolf *et al.* 1999; Vogt *et al.* 2000; Harrison & Fewell 2002) and the time span of this study is too short for muscle degeneration to take place.

Sugar levels rapidly increased fourfold during the first hour after release and remained constant over a period of 48 h. This rapid increase is concomitant with a significant decline in lipids. We believe that there is no causal relationship between the two processes because neoglucogenesis from lipids is rare among insects (Candy *et al.* 1997) and because the net gain in energy is positive (Fig. 2b). An alternative hypothesis could have been that we recaptured a subsample made of particularly strong individuals (measured using tibia length), but we did not find statistical evidence for this. Another alternative explanation for the increase of the sugar levels could be that the recaptured wasps mobilized sugars from their glycogen reserves. However, the analysis of glycogen reserves in a subsample of both control and released wasps showed that glycogen levels were far too low at release time to account for this increase and in fact increased markedly after 6 h. From these elements, we conclude that the wasps must have obtained sugars in the field.

Potential sugar sources for *V. canescens* in the wild are honeydew, nectar, extra floral nectar, leaf exudates and some of the host substrates (figs, carobs, dates). Flowering plants and host natural substrates were absent in the botanical garden. Due probably to the exotic nature of the vegetation, honeydew producing aphids were virtually absent. However, honeydew produced by the generalist planthopper *Metcalfa pruinosa* (Say) was

abundantly present. In the laboratory *V. canescens* feeds and survives well on this exudate (S. Wielaard, unpublished observations) and it may have served as the main food source to the wasps in the field experiment.

Lipid levels never increased significantly above the teneral levels, neither in wild females that had foraged in the environment for an unknown period, nor in the wasps that had *ad libitum* access to food during 48 h immediately after emergence. This suggests that teneral lipid levels correspond to the maximum available amount of lipids. In addition, the lipid level of released wasps did not increase over a period of 2 days. The possible absence of lipogenesis in *V. canescens* is, however, in agreement with the findings in all adult parasitic wasps studied so far (Giron & Casas 2003). If lipid reserves are indeed set at birth, a prudent use of lipids is required to keep them as a spare fuel to survive periods of low sugar intake and for reproduction.

A steady state in energy reserves is quickly attained and lasts from several hours up to 2 days. This suggests that wasps strive for a specific target level of energy reserves that, in turn, might be adjusted with sugar intake. This adjustment is achieved by allocating time between searching for food and searching for hosts. We do not know the energetic status of the uncaptured wasps nor the time spent searching for food by the recaptured ones. Different theoretical models have studied how parasitoids should trade off between using hosts for oviposition or as a food source (Kidd & Jervis 1991; Collier 1995; Jervis & Kidd 1995) or between searching for food or for hosts in different locations (Sirot & Bernstein 1996). The main assumption of these models is that foraging for food and hosts are competing behaviours with respect to time and reserve expenditure. In a recent study, Sisterson & Averill (2002) showed that starved wasps spent a quarter of their time searching for food once released in the environment. Obviously, our study cannot assess conclusively the energetic constraints experienced by the wasps nor the compromise achieved between searching for food and hosts. In contrast, our results demonstrate that wasps can forage for hosts and disperse within this habitat for days without running into a severe risk of energy limitation.

This study is the first to quantify the strategies of energy acquisition and use of parasitoids foraging in the wild. This kind of work is a prerequisite for understanding the physiological basis for dispersal and decision-making by foraging animals. An increase in experimental efforts in estimating the physiological rules and parameters and in validating models is required. Otherwise, models of growing complexity will continue to lack an experimentally well-founded physiological basis, as they tend to do so far (Roitberg & Friend 1992; Collier 1995; Sirot & Bernstein 1996). Tracking dynamic changes in the energetics of small insects foraging freely is obviously a challenge, but one which is feasible today given the rapid advances in microanalytical measurements.

Acknowledgements

We kindly thank Roger Boll, Michèle Salles, Emile Franco and Thierry Spataro for their assistance in the field, Guillaume Lopin for his help with the biochemical analysis, Jeanne Daumal for keeping the *Venturia canescens* culture, Catherine Ducatillon for permission to use 'Jardin Thuret' for the field experiment and David Giron and Jacintha Ellers for comments on the MS. This work was supported by the French PICS-CNRS grant no. 745 and the Dutch 'van Gogh' programme (NWO grant no. 01377UH).

References

Amarasekare, P. (1998) Interactions between local dynamics and dispersal: insights from single species models. *Theoretical Population Biology*, **53**, 44–59.

Candy, D.J., Becker, A. & Wegener, G. (1997) Coordination and integration of metabolism in insect flight. *Comparative Biochemistry and Physiology*, **117B**, 497–512.

Casas, J. (2000) Host location and selection in the field. *Parasitoid Population Biology* (eds M. Hochberg & T. Ives), pp. 17–26. Princeton University Press, Princeton.

Chapman, R.F. (1998) *The Insects: Structure and Function*. Cambridge University Press, Cambridge.

Clement, A.N. (1992) *The Biology of Mosquitoes*, Vol. 1. *Development, Nutrition and Reproduction*. Chapman & Hall, London.

Collier, T.R. (1995) Adding physiological realism to dynamic state-variable models of parasitoid host feeding. *Evolutionary Ecology*, **9**, 217–235.

Conover, W.J. (1980) *Practical Nonparametric Statistics*. John Wiley, New York.

Driessen, G. & Bernstein, C. (1999) Patch departure mechanisms and optimal host exploitation in a insect parasitoid. *Journal of Animal Ecology*, **68**, 445–459.

Gavrilets, S., Li, H. & Vose, M.D. (2000) Patterns of parapatric speciation. *Evolution*, **54**, 1126–1134.

Giron, D.& Casas, J. (2003) Lipogenesis in an adult parasitic wasp. *Journal of Insect Physiology*, **49**, 141–147.

Godfray, H.C.J. (1994) *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton University Press, Princeton.

van Handel, E. & Day, J.F. (1988) Assay of lipids, glycogen and sugars in individual mosquitoes: correlations with wing length in field collected *Aedes vexans*. *Journal of the American Mosquito Control Association*, **4**, 549–550.

Harrison, J.F. & Fewell, J.H. (2002) Environmental and genetic influences on flight metabolic rate in the honey bee, *Apis mellifera*. *Comparative Biochemistry and Physiology A*, **133**, 323–333.

Hassell, M.P. (2000) *The Spatial and Temporal Dynamics of Host–Parasitoid Interactions*. Oxford University Press, Oxford.

Hassell, M.P., Comins, H.N. & May, R.M. (1991) Spatial structure and chaos in insect population dynamics. *Nature*, **353**, 255–258.

Hochberg, M. & Ives, T. (2000) *Parasitoid Population Biology*. Princeton University Press, Princeton.

Holmes, E.E. & Wilson, H.B. (1998) Running from trouble: long-distance dispersal and the competitive coexistence of inferior species. *American Naturalist*, **151**, 578–586.

Jervis, M. & Kidd, N. (1995) Incorporating physiological realism into models of parasitoid feeding-behavior. *Trends in Ecology and Evolution*, **10**, 434–436.

Kidd, M. & Jervis, N. (1991) Host-feeding and oviposition strategies of parasitoids in relation to host stage. *Researches on Population Ecology*, **33**, 13–28.

Lenormand, T. & Raymond, M. (2000) Analysis of clines

with variable selection and variable migration. *American Naturalist*, **155**, 70–82.

Roff, D.A. (1984) The cost of being able to fly: a study of wing polymorphism in two species of crickets. *Oecologia*, **63**, 30–37.

Roitberg, B.D. & Friend, W.G. (1992) A general theory for host seeking decisions in mosquitos. *Bulletin of Mathematical Biology*, **54**, 401–412.

Schneider, V., Beukeboom, L.W., Driessen, G., Lapchin, L., Bernstein, C. & Van Alphen, J.J.M. (2002) Geographical distribution and genetic relatedness of sympatrical thelytokous and arrhenotokous populations of the parasitoid *Venturia canescens* (Hymenoptera). *Journal of Evolutionary Biology*, **15**, 191–200.

Shurin, J.B. & Allen, E.G. (2001) Effects of competition, predation, and dispersal on species richness at local and regional scales. *American Naturalist*, **158**, 624–637.

Sirot, E. & Bernstein, C. (1996) Time sharing between host searching and food searching in parasitoids: state-dependent optimal strategies. *Behavioural Ecology*, **7**, 189–194.

Sisterson, M. & Averill, A.L. (2002) Costs and benefits of food foraging for a braconid parasitoid. *Journal of Insect Behavior*, **15**, 571–588.

Vance, R.R. (1980) The effect of dispersal on population size in a temporally varying environment. *Theoretical Population Biology*, **18**, 343–362.

Vogt, J.T., Appel, A.G. & West, M.S. (2000) Flight energetics and dispersal capability of the fire ant, *Solenopsis invicta* Buren. *Journal of Insect Physiology*, **46**, 697–707.

Wolf, T.J., Ellington, C.P. & Begsely, I.S. (1999) Foraging costs in bumblebees: field conditions cause large individual differences. *Insectes Sociaux*, **46**, 291–295.

Zera, A.J. & Rankin, M.A. (1989) Wing dimorphism in *Gryllus rubens*: genetic basis of morph determination and fertility differences between morphs. *Oecologia*, **80**, 249–255.

Received 22 November 2002; accepted 11 April 2003