

The Influence of Food and Con-specifics on the Flight Potential of the Parasitoid *Ibalia leucospoides*

Deborah Fischbein · Juan C. Corley ·
José M. Villacide · Carlos Bernstein

Revised: 21 January 2011 / Accepted: 31 May 2011 /
Published online: 11 June 2011
© Springer Science+Business Media, LLC 2011

Abstract For insect parasitoids, knowledge of their flight capability is essential for a general understanding of the relationship with their hosts. For instance, flight capacity might partly determine their efficacy as biological control agents. *Ibalia leucospoides* Hochenwarch (Hymenoptera: Ibalidae) is a solitary, pro-ovigenic parasitoid of the woodwasp, *Sirex noctilio* Boidin (Hymenoptera, Siricidae), an economically important pest of softwood forestation. This study explores the flight capacities of *I. leucospoides* females and assesses the effects of a sugar-rich food supply and crowding on female flight performance, by using computer-linked flight mills. The present study shows: (1) a high variability in flight potential of *I. leucospoides* females, (2) no effects of food supply and grouping on wasp flight (flight distance and speed), (3) a significant effect of body size and wing loading on flight performance and, (4) a significant body mass loss during the flight dependent on the total distance flown. The lack of effect of food on a highly energy-demanding activity as flight may be related to the life-history traits and nutritional strategies of this parasitoid. The relevance of these observations for the use of *I. leucospoides* as a biological control agent is discussed.

Keywords Hymenoptera · *ibaliidae* · insect flight · flight mills · parasitoids feeding · *Sirex noctilio*

D. Fischbein · J. C. Corley · J. M. Villacide
Laboratorio de Ecología de Insectos, INTA EEA Bariloche CC 277, San Carlos de Bariloche 8400,
Río Negro, Argentina

D. Fischbein (✉) · C. Bernstein
Laboratoire de Biométrie et Biologie Evolutive UMR 5558, Université de Lyon Université Claude
Bernard Lyon 1, 43 Bd du 11 Novembre 1918, 69622 Villeurbanne, Cedex, France
e-mail: dfischbein@bariloche.inta.gov.ar

Introduction

Insects often engage in foraging flights in search for different resources, such as food, mating partners, nesting sites or hosts. Such movements can take place at very different scales, from moving between patches to long-distance displacements between distant populations (Johnson 1969; Desouhant et al. 2003). For parasitoids, insects that lay eggs in or on other arthropods, long distance dispersal may contribute to the stability and persistence of species interactions (Hassell and May 1973; Roland and Taylor 1997). In turn, among several attributes, the dispersal capability of parasitoids could affect success of biological control programs. High flight capability may encourage fast expansion from the initial release point, as well as colonization of uninhabited sites (i.e. isolated host patches) and re-invasion of areas where the parasitoids become extinct (Kidd and Jervis 2007).

For many insects, in metabolic terms, flight is the most costly of all activities (Chapman 1998). The large amounts of energy consumed in flight can be obtained from different sources such as carbohydrates, fat and protein. Generally, in the Diptera and the Hymenoptera, carbohydrates constitute the main fuel burnt during flight (Chapman 1998; Roff 1977; Vogt et al. 2000; Suarez et al. 2005), whereas to sustain flight Lepidoptera, Orthoptera and Hemiptera mainly burn lipids (Cockbain 1961; Beenackers 1969; Sappington et al. 1995; Rivero and Casas 1999). In parasitoids, adult metabolic resources originate from nutrients accumulated during larval development (the ‘teneral resources’) and from the food obtained as adults. Food can be obtained from the hosts themselves (in host-feeding species) or from non-host sources, such as extra-floral and floral nectar or honeydew (Jervis and Kidd 1996; Jervis et al. 1992; Rivero and Casas 1999).

In many agro-ecosystems where parasitoids are introduced as biological control agents, the availability of plant-derived food sources can be highly variable (Siekmann et al. 2001). In many cases food is unavailable where hosts are found (Jervis and Kidd 1996; Sirot and Bernstein 1996; Tenhumberg et al. 2006; Bernstein and Jervis 2008). Thus, it is widely held that sugar-rich food supplementation in target areas and/or prior to parasitoid release should improve the success of biological control (Jervis and Kidd 1996; Lewis et al. 1998; Bianchi et al. 2006). This is because adult feeding with sugar sources increases longevity and fecundity in many parasitoids species (Schmale et al. 2001; Siekmann et al. 2001). Furthermore, food provisioning may also increase flight capability (Wanner et al. 2006), allowing a faster spread of parasitoids and a higher host searching efficiency (Stapel et al. 1997; Lewis et al. 1998; Kidd and Jervis 2007). Consequently, the effects of sugar-rich food supply during rearing and in field conditions on life history traits should be carefully evaluated.

Ibalia leucospoides Hochenwarth (Hymenoptera, Ibalidae) is a solitary, koinobiont and pro-ovigenic parasitoid of the woodwasp *Sirex noctilio* Boidin (Hymenoptera, Siricidae) (Spradbery 1977; Madden 1981). Woodwasps are primitive xylophages that attack pine trees. While *S. noctilio* is native to Mediterranean Europe, in the last century it has successfully invaded Australia, New Zealand, South Africa, South America and North America (Hoebeke et al. 2005). In most regions where *S. noctilio* has established, it has become an important pest of pine tree forestation, due to its reported outbreak population

dynamics during which tree mortality can be severe (Corley et al. 2007). *I. leucospoides* is one of several bio-control agents adopted for pest management purposes of woodwasp populations (Hurley et al. 2007). The parasitoid, also native to Europe, was introduced into Australasia in the early 1960's. *I. leucospoides* has established throughout the invasion range of *S. noctilio*, mostly through accidental introductions, together with its host (Madden 1988). Under field conditions, *I. leucospoides* may parasitize up to 40% of its hosts.

Because of its applied importance there is a growing research effort on *I. leucospoides*. Most work has focused on its hosts foraging behaviour (Chrystal 1930; Madden 1968; Spradbery 1970a, b; Fernández-Arhex and Corley 2005; Martínez et al. 2006; Fernández-Arhex and Corley 2010), but to date, no attempts to evaluate its flight capacity and its relationship with rearing conditions (i.e.: food provisioning; housing in groups) have been made. In cultivated forest systems, trees attacked by *S. noctilio* are spatially aggregated, especially during long-lasting endemic population phases, during which overall *S. noctilio* densities are typically low (Corley et al. 2007). Although host foraging and feeding behaviour of *I. leucospoides* are not known in its natural environment, in cultivated forests *I. leucospoides* emerge within host aggregates, where floral nectar is rare or absent. Given the importance of this parasitoid in *S. noctilio* management programs, knowledge on the effects of housing conditions (i.e.: food provisioning; crowding) on flight performance can be helpful in the context of mass rearing and release protocols.

The present study investigates whether sugar supply and crowding influence flight capacity in *I. leucospoides*. The study focuses on the effects of sugar-rich food supply and housing with con-specifics, on female flight performance, as measured in flight mill systems (Schumacher et al. 1997; Blackmer et al. 2004; Wanner et al. 2006; Senger et al. 2007; Bruzzone et al. 2009). Morphological traits such as size and wing loading which are likely contributors to flight abilities are also taken into account (Roff 1977; Byrne et al. 1988; Dudley and Srygley 1994; Shirai 1995; Cronin et al. 2000).

Materials and Methods

Ibalia leucospoides attacks eggs and first instar larvae of *Sirex noctilio* woodwasps. *I. leucospoides* life cycle is closely related to the development of woodwasp larvae, usually lasting 1 year (but see Corley et al. 2004). This species was first recorded in pine tree plantations in NW Patagonia in 1993, at the time woodwasps were first detected. Since, it has become established in most pine plantations in the region.

Parasitoids were reared from pine (*Pinus contorta*) logs collected in the field, from several heavily attacked plantations located in NW Patagonia (Argentina). Once felled, trees were cut into 1 m-long logs and kept individually in locker-type cages under ambient indoor conditions, at 21°C, until insect emergence occurred. Each morning newly emerged insects were collected from the cages and immediately placed in individual plastic containers with food or water (see below in “Experimental Design” section).

Experimental Design

The influence of two factors, food access (“*feeding*”) and crowding (“*conspecifics*”) was tested according to a factorial design. Feeding had two conditions: fed animals provided with 30% diluted honey solution ad libitum and unfed wasps with access only to distilled water. In turn, conspecifics also had two levels: isolated females (housed in individual containers, immediately after emergence) and grouped females (housed in the same container, in groups of four). The storage containers were of 251 cm³, a relatively small volume for four rather large individuals (13.41 mm, mean body length). Wasps to be tested of the grouped treatment were picked at random from the cage immediately before the experiment.

All tested animals were kept under the corresponding treatment for 7 days within a rearing chamber under semi-controlled temperature and humidity conditions (temperature $21 \pm 0.1^\circ\text{C}$; 54% r.h.), and a LD 16:8 h photoperiod. Flight trials began 4 h after to the onset of the photo-phase. Each female flew in the mills for 22 h and was weighed (Scientech SA210; Scientech, Boulder, Colorado, USA; to the nearest 0.0001 g.) immediately before and after flight. The differences in weight before flight were used as a measure of any interference between individuals while feeding in groups. In addition, the weight before flight and the weight after flight were used to calculate loss of body mass (see below). Seven days of food deprivation ensured that fed and unfed wasps differed in their carbohydrate energy reserves (D. Fischbein, unpublished data).

Two morphological variables were measured: hind tibia length (TL, in cm) and wing loading ($\text{WL} = \text{body mass (g)}/\text{wing area (cm}^2\text{)}$). The left and right wings of each wasp were digitally scanned and with the aid of an image processing software (HOJA Software, Verga A.R., INTA IFIVE Argentina, 2001) the forewing and hind wing areas measured.

Flight Mills

To study the effects of food consumption and grouping on the flight performance of *I. leucospoides*, flight mills were used based on the model of Bruzzone et al. (2009). Four mills were run simultaneously on each day of experimentation. Each female was anesthetized with CO₂ for 20 s (Bruzzone et al. 2009; Yu et al. 2009) and the dorsal side of the thorax was glued to one end of an L shaped insect pin, using cyanoacrylate glue. The pin was shaped in order to create a suitable flight angle and greater surface area of contact between the pin and the insect thorax. Finally, the opposite free end of the pin was attached to one end of a wooden, horizontal rod. Wasps were left to recover for 15 min before flight tests.

The rotation of the mills was detected by infrared optical sensors connected through a circuit to the parallel port of a microcomputer. A Python script was designed to collect data from the interface board. Each spin made by the wasp was recorded when the beam of light generated by a LED was interrupted by the end of the wooden rod opposite to the one where the insect was held. The computer recorded each revolution (48.7 cm) as the wasp propelled the wooden rod (15.5 cm long). For each flight mill, the programme recorded every spin, speed rotation ($\text{m}\cdot\text{s}^{-1}$) and accumulated flight distance (km). The data series, which

consisted of a series of irregularly separated events (records of each time the wasp activated the sensor), were re-sampled to a series of speed data uniformly separated by 1 s. On this basis, the following flight parameters were estimated: total distance flown in kilometres, maximum 30 min-running mean speed throughout the whole flight (V_{30min} , $m.s^{-1}$) and maximum 60 s-running mean speed, also through the duration of flight (V_{60s} , $m.s^{-1}$).

The running mean speed is a mean obtained from a speed data set using a fixed time interval (i.e.: 60 s and 30 min). This running mean speed reduces the noise and reveals the speed tendencies. As new data were added to the series, the first data is eliminated, enabling the period to remain constant. As aforementioned, we calculated the running mean speed using two different periods (short and long time intervals) to ensure better quality information. The short periods (60 s) result in a closer and more sensitive tracking of speed changes while long intervals (30 min) enable us to track a long term tendency in speed variation. *I. leucospoides* females started to fly soon after they were introduced in the flight mills. Wasps flew for several hours and stops of variable periods were frequently observed (D. Fischbein, pers. obs). Again, the use of moving intervals allowed us to cope with inactivity periods, reducing the noise produced by them.

Statistical Analysis

For the analyses of the influence of feeding, conspecifics and morphological variables on the different flight parameters, a linear model assuming a normal distribution of residuals was used. Flight parameters and morphological variables were log transformed to take into account allometric relationships. The data were first fitted to an initial model and then least significant variables were progressively removed from the model until a minimal appropriate model was obtained (i.e. a simplified model in which all terms are significant). We tested the effect of removing successive factors and variables by means of ANOVA. Single factors or variables incorporated into significant interactions were maintained in the minimum adequate model (Crawley 2007). The initial model fitted to the data was $\log_e(\text{flight parameter}) = \log_e(\text{WL}) * \text{feeding} * \text{conspecifics} + \log_e(\text{TL}) * \text{feeding} * \text{conspecifics}$, where * represents the sum of the influences of three-way interactions, two-way interactions and the four single variables. Inspection of residuals confirmed the fit to a normal distribution.

To assess whether the presence of conspecifics would cause interference while feeding, the effects of feeding, conspecifics and hind tibia length on the weight before flight were analyzed. A linear model assuming a normal distribution of residuals was used and the weight and hind tibia length were log transformed. A backward procedure was used to remove non-significant factors and interactions between factors, and to select the final models. Residuals were examined to confirm that the final models accurately fitted the data.

To further compare the effect of access to food on metabolic expenses in flight, the loss of body mass during flight as a function of log-transformed total distance flown and feeding was examined. The total body mass change was estimated as $\log(\text{initial mass} - \text{final mass}) / \text{initial mass}$. All data analyses were done using the R statistical environment (R Development Core Team 2008).

Results

There was high variability in flight performance of females of *Ibalia leucospoides* (Fig. 1). Flight parameters studied were neither affected by feeding (*total distance flown*: $F_{(1,61)}=0.03$, $P=0.856$; *V30min*: $F_{(1,62)}=2.10$, $P=0.152$; *V60s*: $F_{(1,60)}=0.62$, $P=0.432$) nor by mass housing (conspecifics; *total distance flown*: $F_{(1,60)}=0.004$, $P=0.946$; *V30min*: $F_{(1,60)}=0.05$, $P=0.823$; *V60s*: $F_{(1,61)}=0.82$, $P=0.367$).

The variability in total distance flown by female wasps was mostly accounted for by morphological variables (wing loading and tibia length) (Table 1). Larger females flew farther than smaller females (TL: $F_{(1,62)}=6.11$, $P=0.016$) and, females with high wing loading flew longer total distances than females with low wing loading (WL: $F_{(1,62)}=7.32$, $P=0.008$). Wing loading had a significant effect on the maximum running mean speeds, both *V30min* and *V60s* increasing with wing loading ($F_{(1,63)}=7.73$, $P=0.007$ and $F_{(1,63)}=17.66$, $P<0.0001$, respectively).

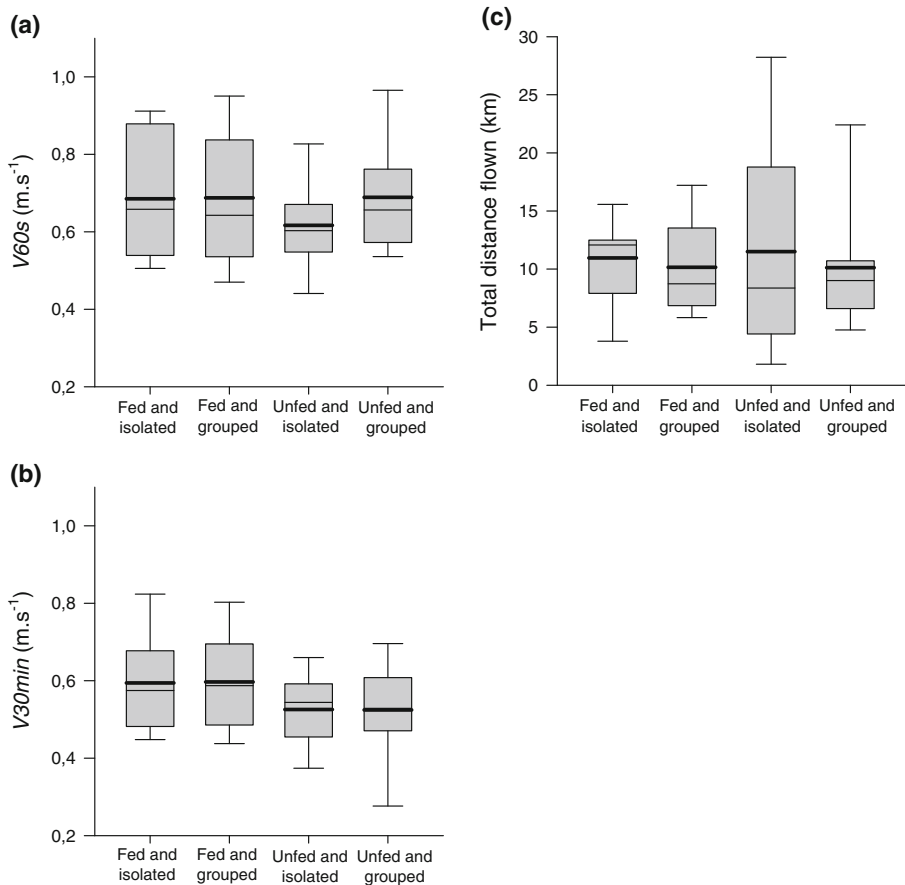
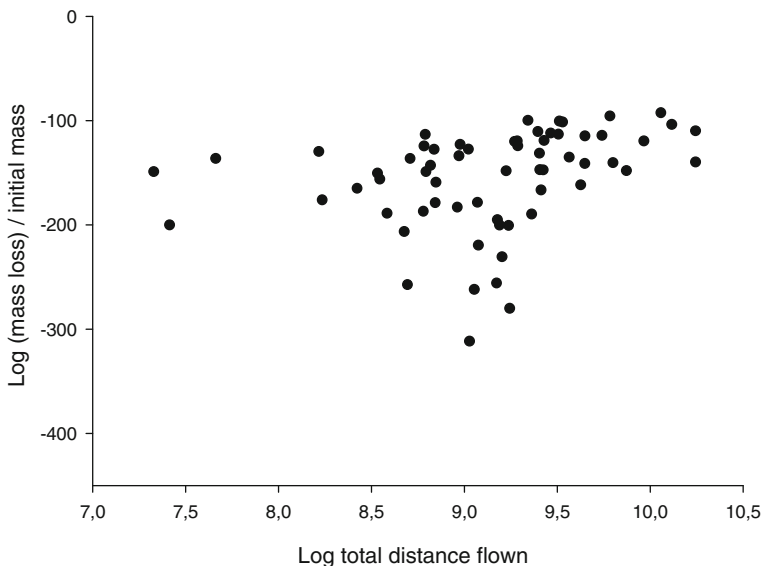


Fig. 1 Flight parameters of *I. leucospoides* females according to the factorial design; **a** *V60s*, **b** *V30min* and **c** total distance flown. Flight parameters studied were neither affected by feeding nor by conspecifics (backward linear model: $P<0.005$). The thin horizontal line of each box plot marks the median of the sample and the thick horizontal line marks the mean of the sample

Table 1 Mean (\pm SE) morphological variables and weights of *I. leucospoides* females according to the factorial design

	Wing loading (g/cm ²) Mean \pm SE	Tibia length (cm) Mean \pm SE	Weight before flight (g) Mean \pm SE	Percentage body mass loss Mean \pm SE	n
Fed and isolated	0.0869 \pm 0.0015	0.4739 \pm 0.0075	0.0419 \pm 0.0016	9.48 \pm 1.10	19
Fed and grouped	0.0833 \pm 0.0026	0.4563 \pm 0.0071	0.0381 \pm 0.0022	11.86 \pm 1.47	17
Unfed and isolated	0.0730 \pm 0.0040	0.4492 \pm 0.0125	0.0326 \pm 0.0026	9.56 \pm 1.43	13
Unfed and grouped	0.0792 \pm 0.0030	0.4581 \pm 0.0089	0.0377 \pm 0.0022	8.14 \pm 1.33	16

Variations in weight before flight were analyzed in order to test whether some interference between wasps might have occurred while they were fed under the grouped housing conditions. Weight was significantly affected by feeding; fed females were heavier than unfed ones (mean \pm SE: 0.0401 \pm 0.0014 g and 0.0354 \pm 0.0017 g, respectively; $F_{(1, 62)}=14.205$, $P<0.001$), but this effect was independent of the presence of conspecifics. No interaction between feeding and conspecifics affected weight before flight ($F_{(1, 59)}=1.52$, $P=0.22$). In addition, the variability in wasp' weight was also explained by tibia length ($F_{(1,62)}=135.16$, $P<0.0001$). Finally, the body mass loss during the flight trial was affected by total distance flown ($F_{(1,61)}=5.89$, $P=0.018$) (Fig. 2), but was neither affected by feeding ($F_{(1,60)}=1.68$, $P=0.198$) nor by interaction between the two explanatory factors ($F_{(1,59)}=0.91$, $P=0.342$).

**Fig. 2** Female body mass loss during flight trials plotted against total distance flown (m, log-transformed). The total body mass change was estimated as $\log(\text{initial mass} - \text{final mass}) / \text{initial mass}$

Discussion

This study is the first one to quantify the flight capacity of *Ibalia leucospoides*, a biocontrol agent of *Sirex noctilio*, which is one of the most economically significant pests of softwood forestation. The present study assessed whether flight performance of *I. leucospoides* was affected by unlimited access to sugar-rich food and the presence of conspecifics (data controlled for body size). Our findings show in general, a high variability in the flight performance of females of *I. leucospoides*. Two morphological variables (tibia length and wing loading), which are surrogate variables of body size, affected flight potential. The total distance that could be flown by wasps increased with tibia length and wing loading, and speed increased with wing loading. Conversely, feeding and presence of conspecifics did not affect flight parameters. According to the results obtained, access to food and body size (TL) increased female weight before flights, regardless of the presence of (and contact with) con-specifics. Finally, body mass loss of females during flight trials depended only on the total distance flown.

I. leucospoides females are capable of long-distance flights but exhibit about half of the flight potential of their host *S. noctilio* (the latter ranged between a minimum of 1 to a maximum of nearly 50 km per day in similar experimental conditions [Bruzzone et al. 2009]). However, recent field studies suggest that *S. noctilio* dispersal within a forest is very limited -less than 150 m- exhibiting a highly clumped spatial pattern of tree attacks during the endemic phase of host population growth (Corley et al. 2007). It is worth mentioning that even displaying half of host flight capacity, the flight potential of *I. leucospoides* may allow them to fly from tree to tree searching for hosts. Therefore, the flight potential displayed by *I. leucospoides* females could allow a thorough exploitation of host patches within and between aggregates of pest-attacked trees within pine plantations (see also Corley et al. 2010). However, whether *I. leucospoides* is able to follow its host during a regional spread process remains as an open question.

Flight capacity in insects is affected by their morphological traits. For example, Shirai (1995) showed that the larger moths of *Plutella xylostella* display greater flight abilities than smaller ones. Another example is *Sirex noctilio*; large females are capable of longer and faster flights than smaller ones (Bruzzone et al. 2009). Furthermore, Dudley and Srygley (1994) and Berwaerts et al. (2002) in their studies on the relationship between morphological variation and variation in flight performance have found a positive correlation between speed or acceleration capacity, and both size indicators and wing loading. According with this, in the present study, wasps with greater body sizes and wing loading ratios are able to fly longer distances than smaller ones. This fact may be due to a greater level of body general reserves. In addition, a high wing loading ratio increases flight speed. Therefore, the wing loading per se had an effect on flight performance in *I. leucospoides*, independently of adult feeding treatment. In this sense, this study provides additional evidence that morphological traits are crucial aspects of flight capability in insects.

Adult feeding with sugar is known to increase longevity and fecundity in many parasitoid species (Schmale et al. 2001; Siekmann et al. 2001), and to modify the propensity to search for hosts (Takasu and Lewis 1995; Stapel et al. 1997). Adult

food consumption, namely by providing additional resources, may increase flight performance. For instance, Wanner et al. (2006) showed for the synovigenic parasitoid species *Cotesia glomerata*, that fed adult female wasps are able to increase flight capacity. They also showed that nectar with different nutritional values has different effects on flight activity in this species. In contrast to these findings, in this study flight parameters in *I. leucospoides* were not affected by prior access to food. It is possible that such an effect may manifest itself on subsequent days of flight. For instance, it is possible that carbohydrate energy reserves in unfed wasps are sufficient to fuel 1 day of flight at a similar level as fed wasps, but that flight on later days would be reduced or not feasible.

An alternative explanation for this lack of effect of food provisioning on flight capacity of *I. leucospoides* females may be related to the life-history traits and nutritional strategies of this species. Parasitoid wasps differ in their egg maturation strategies (Flanders 1950; Jervis et al. 2001). Some parasitoids emerge with their entire or near entire, complement of eggs (the so-called pro-ovigenic parasitoids) and some others continue to mature eggs throughout their reproductive life (the so-called synovigenic parasitoids). While the synovigenic parasitoids need to feed (from hosts or sugar sources) to fuel both somatic functions and reproduction, pro-ovigenic species may rely on sugar sources for maintenance and locomotion only (Rivero and Casas 1999; Jervis et al. 2001; Rivero et al. 2001; Pelosse 2008). As a consequence, females of pro-ovigenic species should, in theory, have lower need for supplementary food (Jervis and Heimpel 2007). Given that *I. leucospoides* is a nearly pro-ovigenic parasitoid, it is possible that the effects of food obtained as an adult on flight performance is minimal. In this species, females could carry a nutrient storage (obtained during their larval development) sufficient to meet all their maintenance and locomotion needs.

Although the age-dependent variation in flight capacity can be a recurrent pattern attributed to species-specific temporal changes in physiological status (Johnson and Rowley 1972; Schumacher et al. 1997; Elliott and Evenden 2009; Lukáš et al. 2010) this is not a rule for all parasitoids. For example, flight duration of *Nasonovia vitripennis* does not differ between young and old individuals (King 1993). In the present study, female wasps of a given age -7 days old- were used. This age lies in the middle range of the estimated female lifespan. Additional studies should be performed to discern if flight behavior at different ages retains the same characteristics.

No effects of housing in groups of 4 were noted on flight parameters. Females do not interfere with each other when feeding in groups and have a similar body mass increase compared with females housed alone with a food source. This observation, coupled with the results noted for the feeding treatment, can have important applied implications. The results indicate that mass rearing, even in the absence of food provisioning, is unlikely to negatively affect the subsequent flight performance of released parasitoids and so success in the biological control of *S. noctilio* populations in pine plantations. These results were obtained by analyzing tethered flight; the next step is to confirm these findings in free flight experiments. This study is a first attempt to evaluate conditions of food provisioning and grouping in the setting of laboratory mass rearing of this species. Additional efforts have to be made to understand how to manipulate the fitness of this parasitoid prior to release in order to maximize their efficiency in pest control.

The lack of effect of food intake on a highly energy-demanding activity as flight may reflect a particular property of pro-ovigenic parasitoids. However, further research is required to provide empirical evidence of the dynamics of nutrient utilization during flight and of the potential role that food could have on other life history traits (longevity and fecundity) of *I. leucospoides*.

Acknowledgments We acknowledge financial support from ANPCyT, Argentina (PICT 0-1200/06), CNRS, France (PICS 4144) and INTA, Argentina. We thank C. Lazzari, P. Pelosse and D. Giron for their valuable comments on an earlier version of the manuscript. We thank Enzo Sauro (Centro Atómico Bariloche) for helping us design the computer interface board.

References

- Beenackers AMT (1969) Carbohydrate and fat as a fuel for insect flight, A comparative study. *J Insect Physiol* 15:353–361
- Bernstein C, Jervis MA (2008) Food-searching in parasitoids: the dilemma of choosing between ‘immediate’ or future fitness gains. In: Wajnberg E, Bernstein C, Van Alphen JJM (eds) Behavioral ecology of insect parasitoids: from theoretical approaches to field applications. Blackwell, Oxford, pp 129–171
- Berwaerts K, Van Dyck H, Aerts P (2002) Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*. *Functional Ecol* 16:484–491
- Bianchi FJJA, Booij CHJ, Tschamkete T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc R Soc Lond B Biol Sci* 273:1715–1727
- Blackmer JL, Naranjo SE, Williams LH (2004) Tethered and untethered flight by *lygus hesperus* and *lygus lineolaris* (Heteroptera: Miridae). *Environ Entomol* 33:1389–1400
- Bruzzone OA, Villacide JM, Bernstein C, Corley JC (2009) Flight variability in the woodwasp *Sirex noctilio* (Hymenoptera: Siricidae): an analysis of flight data using wavelets. *J Exp Biol* 212:731–737
- Byrne DN, Buchmann SL, Spangler HG (1988) Relationship between wing loading, wingbeat frequency and body mass in homeopterous insects. *J Exp Biol* 135:9–23
- Chapman RF (1998) The insects: structure and function. Cambridge University Press, Cambridge
- Chrystal RN (1930) Studies of the *Sirex* parasites. Oxford Forestry Memories No 11. Oxford University Press, London, U.K
- Cockbain AJ (1961) Fuel utilization and duration of tethered flight in *Aphis fabae* Scop. *J Exp Biol* 38:163–174
- Corley JC, Capurro AF, Bernstein C (2004) Prolonged diapause and the stability of host-parasitoid interaction. *Theor Popul Biol* 65:193–203
- Corley JC, Villacide JM, Bruzzone OA (2007) Spatial dynamics of a *Sirex noctilio* woodwasp population within a pine plantation in Patagonia. *Entomol Exp Appl* 125:231–236
- Corley JC, Villacide JM, van Nouhuys S (2010) Patch time allocation by the parasitoid *Ibalia leucospoides* (Hymenoptera: Ibalidae): the influence of con-specifics, host abundance and distance to the patch. *J Insect Behav* 23:431–440
- Crawley MJ (2007) The R book. Wiley, Chichester
- Cronin JT, Reeve JD, Wilkens R, Turchin P (2000) The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. *Oikos* 90:127–138
- Desouhant E, Driessen G, Lapchin L, Wielgaard S, Bernstein C (2003) Dispersal between host populations in field conditions: navigation rules in the parasitoid *Venturia canescens*. *Ecol Entomol* 28:257–267
- Dudley R, Srygley RB (1994) Flight physiology of neotropical butterflies: allometry of airspeeds during natural free flight. *J Exp Biol* 191:125–139
- Elliott CG, Evenden ML (2009) Factors influencing flight potential of *Choristoneura conflictana*. *Physiol Entomol* 34:71–78
- Fernández-Arhex V, Corley JC (2005) The functional response of *Ibalia leucospoides* (Hymenoptera: Ibalidae), a parasitoid of *Sirex noctilio* (Hymenoptera: Siricidae). *Biocontrol Sci Tech* 15:207–212
- Fernández-Arhex V, Corley JC (2010) The effects of patch richness on con-specific interference in the parasitoid *Ibalia leucospoides* (Hymenoptera, Ibalidae). *Insect Sci* 17:379–385

- Flanders SE (1950) Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Can Entomol* 82:134–140
- Hassell MP, May RM (1973) Stability in insect host–parasite models. *J Anim Ecol* 42:693–736
- Hoebeke ER, Haugen DA, Haack RA (2005) *Sirex noctilio*: discovery of a Palearctic siricid woodwasp in New York. *Newsletter of the Michigan Entomological Society* 50:24–25
- Hurley BP, Slippers B, Wingfield MJ (2007) A comparison of control results for the alien invasive woodwasp, *Sirex noctilio*, in the southern hemisphere. *Agric Forest Entomol* 9:159–171
- Jervis MA, Kidd NAC, Walton M (1992) A review of methods for determining dietary range in adult parasitoids. *Entomophaga* 37:565–574
- Jervis MA, Kidd NAC (1996) Parasitoid adult feeding behaviour and biocontrol: a review. *Biocontrol News and Information* 17:11–26
- Jervis MA, Heimpel GE, Ferns PN, Harvey JA, Kidd NAC (2001) Life-history strategies in parasitoid wasps: a comparative analysis of ‘ovigeny’. *J Anim Ecol* 70:442–458
- Jervis MA, Heimpel GE (2007) Phytophagy. In: Jervis MA (ed) *Insects as natural enemies: a practical perspective*. Springer, The Netherlands, p 543
- Johnson CG (1969) Migration and dispersal of insects by flight. Methuen, UK
- Johnson BGJ, Rowley WA (1972) Age-related ultra-structural changes in the flight muscle of the mosquito, *Culex tarsalis*. *J Insect Physiol* 18:2375–2389
- Kidd NAC, Jervis MA (2007) Population dynamics. In: Jervis MA (ed) *Insects as natural enemies: a practical perspective*. Springer, The Netherlands, p 515
- King B (1993) Flight activity in the parasitoid wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae). *J Insect Behav* 6:313–321
- Lewis WJ, Stapel JO, Cortesero AM, Takasu K (1998) Understanding how parasitoids balance food and host needs: importance to biological control. *Biol Control* 11:175–183
- Lukáš J, Bernstein C, Gu H, Dorn S (2010) Could different environmental conditions select for different flight characteristics in sexual and asexual parasitoid *Venturia canescens*? *Entomol Exp Appl* 136:80–88
- Madden JL (1968) Behavioural responses of parasites to the symbiotic Fungus associated with *Sirex noctilio* F. *Nature* 218:189–190
- Madden JL (1981) Egg and larval development in the woodwasp *Sirex noctilio*. *Australian J Zool* 29:493–506
- Madden JL (1988) *Sirex* in Australasia. In: Berryman AA (ed) *Dynamics of forest insect populations: patterns, causes and implications*. Plenum Press, pp 407–427
- Martínez A, Fernández-Arhex V, Corley JC (2006) Chemical information from the fungus *Amylostereum aerolatum* and host foraging behaviour in the parasitoid *Ibalia leucospoides*. *Physiol Entomol* 31:1–5
- Pelosse P (2008) Rôle des compromis évolutifs dans la spécialisation et la coexistence d’espèces compétitrices. *Développements théoriques et expérimentaux chez les insectes parasitoïdes*. PhD thesis, Lyon 1 University, France
- Rivero A, Casas J (1999) Incorporating physiology into parasitoid behavioural ecology: the allocation of nutritional resources. *Res Popul Ecol* 41:39–45
- Rivero A, Giron D, Casas J (2001) Lifetime allocation of juvenile and adult nutritional resources to egg production in a holometabolous insect. *Proc R Soc Lond Biol Sci* 268:1231–1238
- R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Roff DA (1977) Dispersal in dipterans: its costs and consequences. *J Anim Ecol* 46:443–456
- Roland J, Taylor PD (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386:710–713
- Sappington TW, Fescemyer HW, Showers WB (1995) Lipid and carbohydrate utilization during flight of the migratory moth, *Agrotis ipsilon* (Lepidoptera: Noctuidae). *Arch Insect Biochem Physiol* 29:397–414
- Schmale I, Wäckers FL, Cardona C, Dorn S (2001) Control potential of three hymenopteran parasitoid species against the bean weevil in stored beans: the effect of adult parasitoid nutrition on longevity and progeny production. *Biol Control* 21:134–139
- Schumacher P, Weyeneth A, Weber DC, Dorn S (1997) Long flights in *Cydia pomonella* L. (Lepidoptera: Tortricidae) measured by a flight mill: influence of sex, mated status and age. *Physiol Entomol* 22:149–160
- Senger SE, Roitberg BD, Thistlewood HMA (2007) Relative flight responses of *Rhagoletis indifferens* as influenced by crowding, sex, and resources. *Entomol Exp Appl* 123:91–100

- Shirai Y (1995) Longevity, flight ability and reproductive performance of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), related to adult body size. *Res Popul Ecol* 37:269–277
- Siekman G, Tenhumberg B, Keller MA (2001) Feeding and survival in parasitic wasps: sugar concentration and timing matter. *Oikos* 95:425–430
- Sirof E, Bernstein C (1996) Time sharing between host searching and food searching in solitary parasitoids: state dependent optimal strategies. *Behav Ecol* 7:189–94
- Spradbery JP (1970a) Host finding by *Rhyssa persuasoria*, an ichneumonid parasite of siricid woodwasps. *Anim Behav* 18:103–114
- Spradbery JP (1970b) The biology of *Ibalia drewseni* Borries, a parasite of siricid woodwasps. *Proc Entomol Soc London B* 45:104–113
- Spradbery JP (1977) The oviposition biology of siricid woodwasps in Europe. *Ecol Entomol* 2:225–230
- Stapel JO, Cortesero AM, De Moraes CM, Tumlinson JH, Lewis WJ (1997) Extrafloral nectar, honeydew and sucrose effects on searching behavior and efficiency of *Microplitis croceipes* (Hymenoptera: Braconidae) in cotton. *Environ Entomol* 26:617–623
- Suarez RK, Darveau CA, Welch KC, O'Brien DM, Roubik DW, Hochachka PW (2005) Energy metabolism in orchid bee flight muscles: carbohydrate fuels all. *J Exp Biol* 208:3573–3579
- Tenhumberg B, Siekman G, Keller MA (2006) Optimal time allocation in parasitic wasps searching for hosts and food. *Oikos* 113:121–131
- Takasu K, Lewis WJ (1995) Importance of adult food sources to host searching of the larval parasitoid *Microplitis croceipes*. *Biol Control* 5:25–30
- Vogt JT, Appel AG, West MS (2000) Flight energetics and dispersal capability of the fire ant. *Solenopsis invicta* Buren. *J Insect Physiol* 46:697–707
- Wanner H, Gu H, Dorn S (2006) Nutritional value of floral nectar sources for flight in the parasitoid wasp, *Cotesia glomerata*. *Physiol Entomol* 31:127–133
- Yu H, Zhang Y, Wu K, Wyckhuys KAG, Guo Y (2009) Flight potential of *Microplitis mediator*, a parasitoid of various lepidopteran pests. *BioControl* 54:183–193