The relationship between pre-oviposition flight behaviour and reproductive timing in whitefly parasitoids


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Abstract. Although the timing of oogenesis appears to be a major life-history organizer in the parasitoid Hymenoptera, relatively little is known about how this trait correlates with population dispersal by flight in these wasps. Pre-oviposition flight behaviours of 1-day-old female wasps in a vertical flight chamber are measured to test correlations between these traits and with reproductive timing. The focus of the present study is on two genera of whitefly parasitoids (Encarsia and Eretmocerus) that differ in reproductive timing when feeding on a shared host (Bemisia tabaci). The two Eretmocerus species engage in vertical flight within 3 min of release far more frequently than the three Encarsia species. Because the former typically possess a more time-limited reproductive strategy than the latter, this lends support for a positive interspecific association between early-life reproduction and early-life flight incidence. Within species, however, egg load does not correlate with flight propensity for any of the tested species. Furthermore, in Eretmocerus eremicus, the relationship between effective flight distance (i.e. the product of vertical climb rate and flight duration) and egg load appears to be labile rather than fixed because different trials show evidence for either negative or positive correlations between these variables. The source of this context dependence may be variation in either biotic (e.g. longevity) or abiotic (e.g. temperature and relative humidity) factors.

Key words. Aphelinidae, Chalcidoidea, dispersal, egg load, vertical flight chamber.

Introduction

The parasitoid Hymenoptera (i.e. wasps that complete development on, and eventually kill, a single host insect) have long been considered to be a model for studying insect behavioural ecology and life-history evolution (Blackburn, 1991; Godfray, 1994; Mayhew & Blackburn, 1999; Wajnberg, 2006). Recent studies implicate the timing of female reproduction as a major life-history organizer for these insects (Jervis & Ferns, 2004; Jervis et al., 2008). The degree to which parasitoid wasps allocate larval resources to oogenesis is estimated using the ovigeny index (OI) (i.e. the ratio of egg load at adult eclosion to the lifetime potential egg production). Wasps with an OI approaching zero emerge with few mature eggs, whereas an OI of one describes a wasp that emerges with her entire lifetime egg complement matured. The OI correlates strongly with many life-history traits in parasitoid wasps, including adult lifespan, body size, nutritional investment per egg, and capacity for nutrient re-allocation (i.e. egg and thoracic muscle resorption) (Jervis et al., 2001; Jervis et al., 2003; Thorne et al., 2006).

Despite these findings, much remains to be determined about dispersal by flight and its relationship to reproductive timing in parasitoid wasps. In many insects, females tend to undertake migratory flights prior to completing egg development. The oogenesis–flight syndrome (Johnson, 1969) was developed as an explanation, stating that the same physiological mechanisms that stimulate flight behaviour inhibit oogenesis, and vice versa. Although many believe this direct physiological linkage to be unlikely (Sappington & Showers, 1992), there is still a general understanding that these two processes are antagonistic (Wheeler, 1996). More recent proponents of a negative relationship between reproductive timing and pre-oviposition...
dispersal by flight in holometabolous insects (Jervis & Ferns, 2004; Jervis et al., 2005, 2008) present support of this view, namely (i) evidence of competition between the thorax and abdomen for resources (Karlsson & Wickman, 1989; Stevens et al., 2000) and (ii) the idea that high initial egg loads can result in less favourable wing loading values as a result of increased mass (Labine, 1968; Chew & Robbins, 1984). In addition, a hypothesized trend towards wider host ranges with increased OI/decreased adult lifespan (Jervis et al., 2007) could relax selection for flight capacity. Although direct tests of a negative OI-flight relationship are problematic for any given insect taxon, the current data for Lepidoptera appear to be in general agreement with this hypothesis (Jervis et al., 2005).

Expectations regarding the relationship between early-life reproduction and pre-oviposition flight behaviour in parasitoid wasps must take into account hypothesized selective pressures leading to variation in OI and its life-history correlates. The models of Ellers & Jervis (2003, 2004) predict the evolution of high OIs when habitats are rich (i.e. high host abundance and low stochasticity in host encounter rates) or highly stochastic in host availability. In the first scenario, a negative relationship between OI and pre-oviposition flight capacity might be expected because high OI individuals, with their comparatively shorter lifespans (both intra- and interspecifically; Jervis et al., 2001; Thorne et al., 2006), should gain less benefit from leaving their likely richer natal patches in search of alternatives. Alternatively, if high OIs have evolved in the presence of high variability in host availability, then selection may favour more rapid initial patch assessment and rejection for high OI individuals because these have a comparatively shorter lifespan during which to deposit their relatively larger initial egg loads (Jervis & Ferns, 2004). This scenario could potentially lead to a positive relationship between OI and pre-oviposition flight capacity (note that lifetime dispersal capacity in low OI species could still certainly exceed that of high OI species, given the larger body size and longer lifespan of the former; Jervis & Ferns, 2004).

Other considerations may also lead to an expected deviation from a negative relationship between early reproductive investment and pre-oviposition flight in parasitoid wasps. Wing loading constraints in parasitoids with high early egg loads may be less pronounced in small (<25 μg) species, such as many members of Chalcidoidea. This may occur for several reasons, including the utilization of flight mechanisms that generate additional lift per wing stroke (Miller & Peskin, 2005) and a lowered settling velocity at such low Reynolds numbers (Byrne et al., 1988). It is noteworthy that costs associated with increased wing loading, even in larger insects, may not substantially impact flight capacity in nature (Kingsolver, 1999). Furthermore, at the interspecific level, parasitoid wasps exhibit wide variance in egg size. Because egg investment appears to be negatively correlated with OI (Jervis et al., 2001), it is conceivable that parasitoid species with higher OIs, despite their higher initial egg loads, actually invest equivalent (or even lower in the case of extremely yolk-poor eggs) amounts of nutrients in reproduction at a given time than those with lower OIs (Jervis et al., 2001; Jervis & Ferns, 2004).

The use of a vertical flight chamber (Kennedy & Booth, 1963; Blackmer & Byrne, 1993) provides an opportunity to empirically test oogenesis-flight relationships in small parasitoids. This apparatus provides both an estimate of the maximum potential self-directed distance that an individual insect is capable of moving, as well as a measurement of the effort of the sustained vertical climbs toward a skylight cue that is critical to an insect’s success in leaving the flight boundary layer. The free-flight behaviour of the small (~1 mm long) aphelinid parasitoid Eretmocerus eremicus Rose and Zolnerowich has been examined previously in the vertical flight chamber (Bellamy & Byrne, 2001; Blackmer & Cross, 2001), demonstrating that this technique can be adopted in additional studies of parasitoid flight behaviour. Finally, support for the generality of trends observed in vertical flight chamber studies is provided by dispersal studies of populations of the whitefly Bemisia tabaci (Gennadius) conducted in the field (Byrne et al., 1996).

In the present study, data are presented from vertical flight chamber studies of 1-day-old, naïve (with respect to host encounters) female whitefly parasitoids (Chalcidoidea: Aphelinidae) of five different species in two genera (Encarsia and Eretmocerus). Despite sharing a common host, B. tabaci, these species differ widely in a variety of life-history variables, including reproductive timing. Egg load data are gathered and correlations to several flight characteristics both within and across species are tested. Because all the experimental wasps are of the same age, egg load could be used as an accurate measure of intraspecific variation in reproductive timing.

Materials and methods

Parasitoids

Five aphelinid species that parasitize B. tabaci were examined during the course of the present study. Encarsia formosa (Gahan) is a parthenogenetic endoparasitoid with OI = 0.1 (Jervis et al., 2001) and is notable for its large, anhydropic (high yolk content) oocytes (Donnell & Hunter, 2002). Encarsia pergandiella Howard is also a parthenogenetic endoparasitoid with a low OI but, unlike En. formosa, it possesses small, hydropic (low yolk content) oocytes (Donnell & Hunter, 2002). Encarsia sophia (Girault & Dodd) is a sexually reproducing parasitoid with a low OI in which females develop on primary whitefly hosts and males develop as ectoparasitic hyperparasitoids (Hunter & Kelly, 1999). Eggs in this species are anhydropic, and at least as large as those of En. formosa. Two Eretmocerus species were also examined: Eretmocerus eremicus and Eretmocerus nr emiratus Zolnerowich and Rose. Eretmocerus spp. are endo-ectoparasitoids (i.e. they initially develop outside of the host and later penetrate whitefly nymphs to complete development; Gerling et al., 2001). Although eggs in this genus are anhydropic, they are considerably smaller than the eggs of anhydropic Encarsia spp. (M. K. Asplen, personal observation). Although Eretmocerus spp. appear to be syn-ovigenic (OI < 1.0), the combination of their relatively short life-spans, high initial egg loads, and oviposition behaviours
often leads to a failure of realized fecundity to match potential fecundity (akin to the ‘functional pro-ovigeny’ concept; Jervis et al., 2001) in both the laboratory and field (Asplen & Byrne, 2006).

All parasitoids used in the present study were from laboratory cultures housed in the M. S. Hunter laboratory on the University of Arizona main campus (Tucson, Arizona). The whitefly/plant host combination used there is B. tabaci and Vigna unguiculata (L.) Walpers (cowpea), c.v., ‘California Blackeye #46’. Encarsia formosa was originally collected in 2004 from B. tabaci on the University of Arizona main campus. Encarsia pergandiella was originally collected from B. tabaci in Brazil in 1994. The En. sophia colony was initiated from parasitized B. tabaci nymphs collected from Maricopa County, Arizona, in 2005. Males of this autoparasitic species were reared from Er. eremicus on B. tabaci/V. unguiculata. Eretmocerus nr emiratus parasitizing B. tabaci were originally collected in 2003 from greenhouses on the University of Arizona main campus. Eretmocerus eremicus was originally purchased from Koppert Biological Systems, Inc. (Romulus, Michigan) in 1997 and 1998. This colony was later infused with Er. eremicus from Novartis Beneficials for Crop Management (Oxnard, California) in 2000.

Vertical flight chamber procedures

Parasitized fourth-instar whitefly nymphs from each of the above parasitoid colonies were removed from cowpea leaves and placed individually into honey-provisioned, capped polystyrene tubes (12 × 75 mm). These were then held in a Nor-Lake DP36-78 growth chamber (Nor-Lake Scientific, Hudson, Wisconsin) (27 ± 2°C, LD 16:8 h) and monitored daily between 06.00 h and 12.00 h for adult parasitoid emergence. Newly-eclosed (<5 h old) female parasitoids were either held alone (parthenogenetic species) or with a conspecific male (biparental species) for 24 ± 2 h. This period was considered sufficient to ensure mating in biparental species (Bellamy & Byrne, 2001). Mating status has been previously shown to influence parasitoid dispersal behaviour (Bellamy & Byrne, 2001). At least 30 min prior to flight chamber evaluation, either male parasitoids were removed or females were gently transferred to a clean polystyrene tube, again provisioned with honey.

The behaviours of 420 female parasitoids were measured in a vertical flight chamber (Fig. 1). All observations took place between 10.00 h and 14.00 h, which was 3–7 h after the growth chamber lights were turned on. Tubes containing individual female wasps were placed in the chamber, where they underwent a 10-min acclimation period. Each tube was then placed individually in a rack in the centre of the chamber and the wasp given 3 min to engage in flight toward the skylight cue. Jumps or trivial flights that did not reach the top of the wind tunnel (a vertical distance of ∼69 cm) were scored as no flight because such movements in nature would likely not lead to emigration from the current patch. If flight was initiated within 3 min, vertical airflow was introduced into the chamber at a velocity necessary to maintain the parasitoid in a stable flight plane (Blackmer & Byrne, 1993). After the parasitoid landed, with no further flight initiated within 1 min, the wasp was re-captured and stored at −80°C. From these data, the proportion of wasps that flew divided by the total number of wasps examined over a given trial (see below) was calculated as the flight propensity for that trial (Table 1).

An individual parasitoid’s rate of climb was measured on a per second basis using an AS-201 hotwire anemometer (Gray-Wolf Sensing Solutions®, Trumbull, Connecticut) connected to a laptop computer. The summed rates over the total flight duration(s) were recorded as the effective flight distance (EFD; Table 1) for that individual. In addition, temperature and relative humidity (RH) measurements from inside the flight chamber were taken at the start of an experimental series using a portable weather station.

Eight vertical flight chamber trials were performed. Two trials each were conducted using En. formosa [EF1 (March 2005 to April 2005; n = 61) and EF2 (October 2005 to December 2005; n = 56)]; En. pergandiella [EP1 (July 2005 to August 2005; n = 63) and EP2 (May 2006 to June 2006; n = 44)]; and Er. eremicus [EE1 (April 2005 to July 2005; n = 54) and EE2 (January 2006 to May 2006; n = 57)]. Owing to their more erratic flight behaviour and difficulty in recapture, only one trial each was performed using En. sophia (July 2006 to August 2006; n = 55) and Er. nr emiratus (June 2006 to October 2006; n = 30).

Egg load assessment

Previously frozen parasitoids recaptured from the flight studies were dissected in insect Ringer’s solution. The whole-body tissues were then stained with methyl green (Asplen &
netic pseudoreplication, with the validity of pooling congeners tests. Genus-level comparisons were used to avoid phyloge-informed statistical tests (Harvey & Pagel, 1989; Jervis et al.

The alternative approach of conducting phylogenetically-trial comparisons for EFD were performed using two-tailed relatively small number of taxa studied. Interspecific and inter-

and unequal variances were assumed for $t$ values, see Table 1; $t_{14}$ = 42, $P < 0.001$); and (ii) flight chamber temperature was higher in EE2 than in EE1 (back-transformed means of 29.6 and 25.7°C, respectively; $t_{44} = 10.40, P < 0.001$); and (iii) adult longevity for female members of the Er. eremicus colony at the end of EE2 was sig-

ificantly longer than that of similarly measured females after EE1 (back-transformed means of 10.5 and 6.6 days, respectively; $t_{42} = 5.10, P < 0.001$).

Intergeneric comparisons

Heterogeneity chi-square tests revealed that congener pool-

ing was valid for Encarsia spp. ($\chi^2 = 0.69$, d.f. = 2, $P = 0.71$), but not for Eretmocerus spp. ($\chi^2 = 6.19$, d.f. = 1, $P = 0.01$). Significantly fewer incidences of vertical flight within 3 min were observed between Encarsia females (13 out of 179; 7.3%) and those of both Er. eremicus (22 out of 57; 38.6%; $\chi^2 = 28.8$, d.f. = 1, $P < 0.001, n = 236$) and

Byrne, 2006) and the mature eggs counted under a compound microscope. In addition, the hind tibia length, forewing length, and forewing width of each parasitoid were measured using an ocular micrometer.

Statistical analysis

Differences in flight propensity (yes or no) between Encarsia spp. and Eretmocerus spp. were compared using chi-square tests. Genus-level comparisons were used to avoid phyloge-

netic pseudoreplication, with the validity of pooling congeners assessed through heterogeneity chi-square tests (Zar, 1984). The alternative approach of conducting phylogenetically-informed statistical tests (Harvey & Pagel, 1989; Jervis et al., 2001) was an inviable option in the present study because of the relatively small number of taxa studied. Interspecific and inter-

trials did not differ significantly in EFD (for values, see Table 1; $t_{55} = 1.91, P = 0.07$), egg load (back-transformed means of 43.6 and 46.6 eggs, respectively; $t_{77} = 1.36, P = 0.18$), hind tibia length (back-transformed mean of 0.25 mm in each trial; $t_{77} = 0.24, P = 0.81$), or forewing area (back-transformed mean of 0.18 mm² in each trial; $t_{65} = 1.14, P = 0.26$). Three variables, however, did differ significantly between the EE1 and EE2 trials: (i) flight chamber RH was higher in EE1 than in EE2 (back-transformed means of 30.1% and 20.8%, respectively; $t_{44} = 8.37, P < 0.001$); (ii) flight chamber temperature was higher in EE2 than in EE1 (back-transformed means of 29.6 and 25.7°C, respectively; $t_{44} = 10.40, P < 0.001$); and (iii) adult longevity for female members of the Er. eremicus colony at the end of EE2 was sig-

ificantly longer than that of similarly measured females after EE1 (back-transformed means of 10.5 and 6.6 days, respectively; $t_{42} = 5.10, P < 0.001$).

Results

Summary statistics for flight parameters over all species and tri-

als are given in Table 1. Considerable inter-trial variation was

The numbers of individual flights used to determine effective flight distance (EFD) descriptive statistics are in parentheses (note that Encarsia spp. exhibit a much lower flight propensity compared with Eretmocerus spp.). NA, not available.
Eretmocerus nr (EE2)* 34/34 0.47/0.01 1/1 0.49/0.92

Eretmocerus eremicus

Eretmocerus eremicus (EE1)* 26/26 1.11/0.68 1/1 0.29/0.41

a covariate (EL + HTL). The two Encarsia sophia observed are denoted by an asterisk (*).

The two Eretmocerus eremicus trials (EE1 and EE2) were analysed separately. Egg load effects were modelled either alone (EL) or with hind tibia length as a covariate (EL + HTL) (except for Encarsia sophia; see text). Species (or trials) for which positive correlations between egg load and hind tibia length are observed are denoted by an asterisk (*).

Interspecific comparisons within Eretmocerus

Vertical flight propensity significantly differed between the two Eretmocerus species (\(\chi^2 = 6.28, \text{d.f.} = 1, P = 0.01, n = 87\)), with Er. nr eremicus females showing a greater propensity than Er. eremicus (66.7–38.6%). No significant differences in EFD were observed between Er. eremicus and Er. nr eremicus individuals using either data from the EE1 

(\(t_{17} = 0.12, P = 0.90\)) or EE2 

(\(t_{19} = 1.77, P = 0.09\)) trials.

Egg load and flight propensity within species

In all four species tested, egg load did not significantly correlate with the propensity to fly (Table 2). This finding holds regardless of whether egg load is modelled either alone or after correction for body size for three species, although it should be noted that egg load and hind tibia length are positively correlated for the three Eretmocerus trials (denoted by asterisk in Table 2; EE1: \(r = 0.52, P = 0.006\); EE2: \(r = 0.59, P < 0.001\); Er. nr eremicus: \(r = 0.91, P < 0.001\)). The multiple logistic regression model for En. sophia yielded a significant effect of hind tibia length on flight propensity, yet the parameter values were unstable, suggesting that this statistical method was not valid for this species (results not reported).

Egg load and effective flight distance in E. eremicus

Female parasitoids from the EE1 trial failed to show a significant relationship between egg load and EFD (Fig. 2A and Table 3: EL alone). Hind tibia length (Fig. 2B) as the sole explanatory variable did not correlate well with EFD in females from the EE1 trial (Table 3: HTL alone). When these two variables were modelled together in a multiple regression model (\(F_{2.7} = 8.11, P = 0.02, R^2 = 0.70\)), however, a significant positive relationship existed between egg load and EFD (Table 3: EL with HTL); whereas hind tibia length correlated negatively with this flight variable (Table 3: HTL with EL). This translates into an estimated 14.6% increase in median EFD [95% confidence interval (CI) = 5.8 – 24.2%] for each egg carried, whereas a 0.01-mm increase in hind tibia length relates to an estimated 34.4% reduction in median EFD (95% CI = 5.5 – 54.6%).

Analysis of data from the EE2 trial illustrates a different relationship between egg load and EFD. In these wasps, egg load and EFD showed a strong negative correlation (Fig. 2C and Table 3: EL alone), such that carrying one additional egg leads to a 13.8% decrease in median EFD (95% CI = 5.4 – 21.4%). As with the EE1 data set, hind tibia length alone did not correlate significantly with EFD (Fig. 2D and Table 3: HTL alone). When the effects of egg load and hind tibia length on EFD were modelled together (\(F_{2.12} = 5.92, P = 0.02, R^2 = 0.50\)), a significant decrease in median EFD was observed with increasing egg load [Table 3: EL with HTL; estimate: 12.5% per one-egg increase (95% CI = 2.6 – 21.3%)], but no significant correlation exists between EFD and hind tibia length (Table 3: HTL with EL).

It should be noted that the positive egg load-EFD correlation detected using EE1 data is heavily influenced by data from a single female (egg load = 70; EFD = 280.47 m). If this individual is excluded from the analyses, then no significant relationship between egg load and EFD is found (simple linear regression, \(t_7 = -0.52, P = 0.62\) and the multiple regression model is no longer significant (\(F_{2.6} = 1.00, P = 0.42\)). In addition, exclusion of this outlier renders the previously non-significant difference in EFD between the two trials significant (\(t_{20} = 2.72, P = 0.01\)), such that EE2 females had an estimated 4.1-fold longer median EFD than EE1 females (95% CI = 1.1- to 15.4-fold). No other relationships qualitatively changed after outlier exclusion.

Discussion

Whether or not a female parasitoid will fly depends on several factors (Wajnberg, 2006), including host patch quality, oviposition experience, age, mating status, and weather conditions. In addition, relative reproductive effort may exert an influence on both flight incidence and distance, especially in young females prior to host location. The present studies of female whitefly parasitoids attempt to test two competing hypotheses regarding the association between reproductive timing and pre-oviposition flight: the commonly-held view of an antagonistic relationship (akin to the oogenesis-flight syndrome) and
a positive relationship related to potential differences in the relative benefits and costs of flight in small parasitoid wasps. The results with respect to interspecific variation in readiness to fly are consistent with the latter hypothesis, whereas intraspecific comparisons show no (in the case of flight propensity and egg load) or mixed (in the case of EFD and egg load in the two *Er. eremicus* trials) support for either of the two hypotheses.

**Comparisons between Encarsia and Eretmocerus**

Despite sharing a common host, *Encarsia* and *Eretmocerus* possess very different reproductive life histories. In a study of *Bemisia* parasitoids, Qiu et al. (2004) show that female *Er. eremicus* and *Eretmocerus mundus* exhibit rapid reproduction during the first day of adult life followed by a much lower oviposition rate thereafter. This contrasts with the results for *En. formosa*, which maintains a relatively lower oviposition rate throughout adult life. These divergent strategies could, in part, explain the variation in flight propensity observed between the two genera in the present study. The naïve females used here are studied at an age likely more closely aligned to peak reproduction for *Eretmocerus* spp. than for *Encarsia* spp. This could lead to a higher relative risk of time limitation for the two *Eretmocerus* spp., in turn leading to a relatively quicker rejection time on the depauperate ‘patch’ (in this case, the empty tube) than for the three *Encarsia* species. Note that the life-history divergences described above are most likely pronounced for *Encarsia* species carrying relatively small numbers of anhydropic eggs (e.g. *En. formosa* and *En.*
ation, field studies of strongly synovigenic Aphelinus α statistically significant at parasitoids, flight is a large component of foraging behaviour among aphidiine braconids (OI ∼ parasitoid Hymenoptera. Among aphids parasitoids, flight is a large component of foraging behaviour among aphidiine braconids (OI ∼; Jervis et al. 2001; see also Powell et al., 1998; Guerrieri et al., 2002), whereas strongly synovigenic Aphelinus spp. tend to search for hosts predominantly by walking (Mason & Hopper, 1997). In addition, field studies of Anagrus epos (Chalcidoidea: Mymaridae) indicate strong downwind movement and a female bias in new patch colonization (Corbett & Rosenberg, 1996), suggesting that small, pro-ovigenic parasitoid species are capable of substantial emigratory flights under natural conditions. Finally, although having evolved away from the parasitoid life-history, short-lived female fig wasps (Chalcidoidea: Agaonidae) frequently engage in long distance, wind-aided flights (Compton et al., 2000). Given the biological diversity within the parasitoid Hymenoptera, however, adequate testing of the aforementioned hypothesis is possible only through analyses of large data sets that correct for phylogenetic relatedness and other confounding factors. Unfortunately, such data sets are not currently available.

It is important to note that, in the present study, females of examined species are collected from laboratory cultures of different ages. Longer colony ages could increase the likelihood of laboratory selection against dispersal (Visser et al., 1992). In addition, not all trials are conducted concurrently, and thus different conditions across trials may contribute to the interspecific variation observed. Finally, it is possible that the five species have different diurnal activity peaks. In light of these concerns, several lines of evidence are offered to support the robustness of the present findings: (i) significant differences in flight propensity between the two genera are observed even if analyses are restricted to concurrent studies of the two youngest colonies [i.e. En. sophia colony (~1 year old) versus Er. nr emiratus colony (~3 years old); χ² = 28.5, d.f. = 1, P < 0.0011, n = 85]; (ii) mass-reared Er. eremicus females disperse effectively in the field (Bellamy & Byrne, 2001); and (iii) bias towards afternoon dispersal in En. formosa disappears under the ‘long day’ (LD 16:8 h) conditions used in the present study (Ekbom, 1982).

Reproduction and dispersal capacity within species

For all species examined in the present study, egg load does not appear to correlate with vertical flight propensity. Egg load also has no effect on patch residence time in the braconid Asobara tabida (Thiel & Hoffmeister, 2004), suggesting that this may be a general trend in parasitoid wasps.

When comparing data from the two Er. eremicus trials, a marked difference is found in the correlations between EFD and egg load. Females from the EE2 trial show an antagonistic oogenesis–flight relationship, suggesting that flight-related costs exist for females with high reproductive investment. In the EE1 trial, however, it appears that factors may have led to relatively increased benefits for, and/or relaxed constraints upon, high flight capability with increased reproductive effort. This appears to result in either a breakdown in antagonism between these traits, or a positive relationship between them, depending on the inclusion of a statistical outlier. These results suggest both lability and context dependence in the relationship between pre-oviposition dispersal distance and early-life egg maturation in Er. eremicus.

Three measured variables differ unambiguously between the two Er. eremicus trials: adult longevity, flight chamber temperature, and flight chamber relative humidity. The present study was not designed to measure the independent effects of these variables, however, the aforementioned differences suggest that explanations for the observed inter-trial variance could include that increased longevity correlates with higher dispersal costliness per egg carried, and/or that environmentally-induced phenotypic plasticity exists in the oogenesis-flight relationship. A third possibility is that costs associated with flight only manifest themselves during prolonged flights. Although the lack of a negative association between EFD and egg load in the EE1 trial could be viewed as support for this latter hypothesis, the direction of the outlying value is inconsistent with this conclusion. Regardless of the cause, however, the results obtained in the present study strongly suggest that an immutable relationship between reproduction and dispersal need not be expected among conspecific parasitoid wasps.

Conclusions

The present study represents an important step in understanding how flight may fit within the broader context of parasitoid life-history evolution. Additional studies are needed to

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The explanatory variables of egg load (EL) and hind tibia length (HTL) were examined both in separate simple linear regression models (= alone) and together in a single multiple regression model (= with the other variable). For whole model results and relationship estimates, see text. P-values shown in bold are statistically significant at α = 0.05.
determine whether the observed disparity in flight propensity between Encarsia and Eretmocerus is largely a function of host absence in the natal patch. It is possible, and indeed hypothesized, that increased host availability and oviposition experience will substantially decrease the incidence of emigratory behaviour in Eretmocerus. In addition, studies of larger parasitoid taxa (i.e. ichneumonoids) would indicate whether the small size of aphelinids may impact oøogenesis–flight relationships. Finally, flight trials after laboratory selection on female longevity and under strictly controlled environmental conditions could demonstrate the causes of context-dependence in the E. eremicus egg load–flight relationship.

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