

Competition between relatives and the evolution of dispersal in a parasitoid wasp

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Abstract

Evolutionary theory predicts that levels of dispersal vary in response to the extent of local competition for resources and the relatedness between potential competitors. Here, we test these predictions by making use of a female dispersal dimorphism in the parasitoid wasp *Melittobia australica*. We show that there are two distinct female morphs, which differ in morphology, pattern of egg production, and dispersal behaviour. As predicted by theory, we found that greater competition for resources resulted in increased production of dispersing females. In contrast, we did not find support for the prediction that high relatedness between competitors increases the production of dispersing females in *Melittobia*. Finally, we exploit the close links between the evolutionary processes leading to selection for dispersal and for biased sex ratios to examine whether the pattern of dispersal can help distinguish between competing hypotheses for the lack of sex ratio adjustment in *Melittobia*.

Introduction

Dispersal is a ubiquitous feature of natural populations, with important consequences for individual fitness and population dynamics (Roff & Fairbairn, 1991; Bowler & Benton, 2005; Ronce, 2007). By enabling the movement of individuals within their environment, dispersal allows organisms to exploit new resources and habitats, but doing so can be costly and involves high risk. For instance, the capacity for flight is energetically costly, dispersal increases the mortality risk because of predation, and there is a risk of not finding a suitable habitat. Across species, there is considerable variation in patterns of dispersal, which can encompass movement across a range of distances, the use of different dispersal mechanisms, and which can take place at various life history stages (Bowler & Benton, 2005; Ronce, 2007). Moreover, individuals vary in their ability to disperse, and likelihood

of doing so – even within the same species – which may be reflected in (adaptive) morphological differences between them. For example, in the cricket *Gryllus firmus*, long-winged, larger-bodied females disperse, whereas smaller, short-winged females do not (Roff & Fairbairn, 1991).

A wealth of evolutionary theory has highlighted three factors that can favour the evolution of dispersal: habitat quality, inbreeding, and competition between relatives. Spatiotemporal variation in habitat quality can select for dispersal because it creates uncertainty in resource availability – and in this instance, the direct benefits of dispersal can outweigh the costs (Roff, 1986; Greenwood-Lee & Taylor, 2001; Leturque & Rousset, 2002). If inbreeding depression is high and/or inbreeding is avoided, then this can select for sex-specific dispersal to find unrelated mates (Motro, 1991; Gandon, 1999; Roze & Rousset, 2005). When nondispersing individuals must compete for resources with relatives, Hamilton & May (1977) showed that dispersal can be favoured to reduce competition between relatives. In this case, dispersal is favoured because of its indirect fitness benefits to social partners, despite any direct costs incurred by the

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dispersing individual, and can be thought of as a cooperative, potentially altruistic trait (West *et al.*, 2007).

Here, we are concerned with how competition between relatives influences selection for dispersal. There have been numerous extensions of Hamilton & May's (1977) original model examining more detailed realistic scenarios to predict the consequences of factors such as dispersal rate, dispersal distance, population size, population dynamics, and age structure (Bulmer & Taylor, 1980; Comins *et al.*, 1980; Comins, 1982; Motro, 1982a,b, 1991; Frank, 1986b; Frank, 1998; Taylor, 1988, 1994; Crespi & Taylor, 1990; Taylor & Frank, 1996; Gandon, 1999; Gandon & Michalakis, 1999; Gandon & Rousset, 1999; Irwin & Taylor, 2000; Ronce *et al.*, 2000; Rousset & Billiard, 2000; Leturque & Rousset, 2002, 2003, 2004; Rousset & Gandon, 2002; Wild & Taylor, 2004; Roze & Rousset, 2005; Wild *et al.*, 2006). In contrast, there is a much smaller amount of experimental work directed at testing these theoretical predictions, with most empirical work having focused on the direct costs and benefits of dispersal, rather than predictions regarding the importance of social context (Crespi & Taylor, 1990; Roff & Fairbairn, 1991, 2007; Zera & Denno, 1997).

Our main aim is to test empirically a number of assumptions and predictions arising from theoretical models of dispersal evolution, with a particular focus on how dispersal can be favoured because of competition between relatives. The parasitoid wasp *Melittobia australica* exhibits both sex-specific dispersal and a within-sex dispersal dimorphism: only female offspring disperse, and amongst females, there is a pronounced dimorphism between dispersing (long wing) and nondispersing (short wing) females (Consoli & Vinson, 2002a; Matthews *et al.*, 2009). Previously, the relationship between sex allocation and male dispersal dimorphism has been considered in fig wasp species, but few studies have considered female dispersal (Greeff, 1997, 2002; Moore *et al.*, 2006; Nelson & Greeff, 2009). Dimorphic species generally provide excellent systems for studying the evolution of dispersal because the easily identified visible morphological differences correspond to different patterns of resource investment into key life history traits (Roff & Fairbairn, 1991; Zera & Denno, 1997). Moreover, comparing dispersing and nondispersing individuals within the same species, controls for any difference because of phylogeny. We first examine the nature of the dispersal dimorphism in *M. australica* by comparing the morphology, dispersal behaviour, and life history traits of the two female morphs. This allows us to test whether morphological differences between females are indeed associated with differences in dispersal propensity and trade-offs between the life history traits of dispersing and nondispersing individuals.

Second, we test theoretical predictions for how competition between relatives selects for dispersal by examining whether the production of non and dispersing morphs is adjusted in response to local conditions.

Theory predicts that selection for dispersal is increased when larger numbers of offspring are competing for a given resource, and when these offspring are related (i.e. produced by a lower number of mothers; Hamilton & May, 1977). We manipulated local resource competition and relatedness by varying the time female foundresses are given for oviposition (egg laying), and the number simultaneously ovipositing on a host. Finally, we examined the correlation between the proportion of dispersing females and the offspring sex ratio (proportion male offspring) to test several hypotheses suggested to explain the unusual lack of facultative sex ratio adjustment in response to local mate competition (LMC) observed in *Melittobia* species (see Discussion).

Methods

Natural history

Melittobia australica (Hymenoptera: Eulophidae) is a gregarious ectoparasitoid wasp and shares common natural history with other species in the *Melittobia* genus (Van den Assem *et al.*, 1980; Gonzalez *et al.*, 2004a,b; Matthews *et al.*, 2009). *Melittobia* species are known to have an unusually wide host range, although most commonly parasitize other Hymenoptera (Balfour Browne, 1922; Freeman & Parnell, 1973; Freeman, 1977; Van den Assem *et al.*, 1980; Dahms, 1984; Cooperband & Vinson, 2000; Gonzalez *et al.*, 2004b; Matthews *et al.*, 2009). Pronounced sexual dimorphism is found across the genus. Males are blind and flightless, remaining on the natal patch to compete for local mating opportunities (Buckell, 1928; Dahms, 1984; Gonzalez *et al.*, 2004b; Matthews *et al.*, 2009). Mating competition is fierce: males eclose earlier than females and will fight to the death, employing their highly modified mandibles in attack to remove limbs and decapitate opponents (Balfour Browne, 1922; Buckell, 1928; Dahms, 1984; Abe *et al.*, 2003b, 2005; Hartley & Matthews, 2003; Innocent *et al.*, 2007; Reece *et al.*, 2007; see also Hamilton, 1979). The males remaining alive at female eclosion will mate within the natal host. By contrast, females have fully functioning eyes and wings, and can disperse, or may stay to superparasitize the natal host. Females are able to lay large clutch sizes (200–1000+ depending on the type of host) (e.g. Balfour Browne, 1922; Abe *et al.*, 2005; Innocent *et al.*, 2007; Matthews *et al.*, 2009) and can adjust their offspring sex ratio through haplodiploid sex determination – daughters are produced from fertilized eggs, sons from unfertilized eggs. Highly female-biased sex ratios have been reported for a number of species in the *Melittobia* genus, in the order of 85–95% female offspring for both natural populations and in the laboratory (Schmieder, 1938; Van den Assem *et al.*, 1980; Abe *et al.*, 2003b, 2005; Cooperband *et al.*, 2003; Gonzalez *et al.*, 2004b; Innocent *et al.*, 2007). Moreover, a lack of sex ratio shift has been shown for

laboratory populations of several species (Abe *et al.*, 2003b, 2005; Cooperband *et al.*, 2003; Innocent *et al.*, 2007), despite evidence from the limited studies of natural populations that foundress number varies, and thus that there is variation in LMC in natural populations (Schmieder, 1933; Freeman & Ittyeipe, 1976, 1993; Van den Assem *et al.*, 1982; Dahms, 1984; Cooperband *et al.*, 2003; Matthews *et al.*, 2009). Previous studies have identified two distinct female morphs (Schmieder, 1933; Freeman & Ittyeipe, 1976, 1982; Dahms, 1984; Gonzalez & Matthews, 2008) and have suggested that morphological differences correlate with different patterns of dispersal and the associated life history strategies (Schmieder, 1933; Freeman & Ittyeipe, 1976, 1982; Dahms, 1984; Cooperband *et al.*, 2003; Consoli & Vinson, 2002a,b, 2004; Gonzalez *et al.*, 2004a). However, data accurately describing the morphological differences between females are scarce, and the associated differences in life history strategies have not been formally tested (Consoli & Vinson, 2002a; Matthews *et al.*, 2009).

General methods

Our stock population of *M. australica* – from which we took all experimental wasps – was established from field collections made in Shiga, Japan (2000). We cultured all wasps on *Bombus terrestris* pupae (Koppert, The Netherlands) and reared them at 25 °C with a 16 : 8 light : dark photoperiod. Development time is in the region of 14 days for males and nondispersing females, and 14–21 days for dispersing females, under these conditions. To establish each new generation, we placed groups of approximately 50 adult females with an unparasitized, early-stage *B. terrestris* pupa in 25 × 70 mm glass vials, stoppered with cotton wool.

Experimental methods – general

We carried out all experiments in two stages: the initial stage of experimental set up involved the manipulation of foundress females and used a fully factorial design common to all experiments (Table 1); we then randomly allocated replicates to experiments to answer specific questions for the later stages (involving manipulation of offspring). A replicate consisted of the offspring generation produced by a single female foundress or group of foundresses with a single host for oviposition. In this initial experimental design, we manipulated the number

of foundress females able to oviposit on a host, and simultaneously manipulated the length of time females were given for oviposition. This created variation in offspring relatedness across a range of clutch sizes (Table 1), and thus generated variation in both LMC and local competition for host resources between offspring, while allowing us to control for both clutch size and oviposition period when examining the effect of foundress number (and *vice versa*). Specifically, we set up 40 replicates of each of three foundress treatment levels: groups of 1, 5, or 15 females (a total sample size of 120) and allowed females to oviposit on their host for 3 or 6 days. Overall, this resulted in six treatment combinations: single females with 3- or 6-day oviposition, groups of five females with 3- or 6-day oviposition, and groups of 15 females with 3- or 6-day oviposition (Table 1). We used mated adult females for all six treatment combinations, chosen at random from stock populations approximately 48 h after emergence (to ensure mating had occurred), and randomly assigned each female to one of the six treatment levels. We placed all replicates in stoppered glass vials with early-stage *B. terrestris* pupae of known mass and age, and incubated them at 30 °C until offspring emergence. We then randomly assigned each replicate to one of the following experiments to investigate: (i) morphology; (ii) life history and dispersal behaviour; and (iii) patterns of morph-ratio and sex ratio. Specific methods for each of these investigations are detailed in the following sections. We ensured that all foundress by oviposition time treatment combinations, and therefore a range of clutch sizes, were represented within each of the subsequent experiments. We did not include replicates that failed to produce offspring, giving a total experimental sample size of 111 replicates.

Morph characterization

We first wanted to establish whether short wing (SW), long wing (LW), and intermediate (IM) female morphs existed in *M. australica* and characterize them. We sampled between 2 and 4 individuals of each morph class at random from each of 24 replicates, which spanned the full range of clutch size/foundress number combinations (see General methods). For each female sampled, we (i) scored the morph by eye (within 24 h of emergence); (ii) photographed using an Olympus SZX10 microscope (with DP20 camera) – with measurements of abdomen and wing length taken from these pictures; (iii) removed

Table 1 Summary of mean clutch sizes (\pm standard errors; range in brackets) for experimental treatment combinations (foundress \times oviposition duration).

Oviposition time (days)	Foundress number		
	1	5	15
3	106 \pm 29 (17–334)	258 \pm 28 (67–429)	536 \pm 64 (130–805)
6	206 \pm 43 (11–496)	640 \pm 53 (260–1063)	791 \pm 70 (147–1265)

the hind-left tibia – later photographed and measured to control for body size (microscope as above; Godfray, 1994); and (iv) dissected the abdomen on a glass slide and counted the number of fully developed eggs present (egg load). We found distinct SW and LW groups, so we tested for differences between them in key life history traits – longevity and fecundity – along with differences in dispersal behaviour.

Longevity

To assess longevity, we randomly chose a single female of each morph (SW, LW) from each of 45 replicates, which were spread across initial treatment combinations. We isolated females in glass vials (10 × 75 mm) 24 h after emergence (to allow for mating to occur, representative of natural conditions), and incubated them at 30 °C. We gave females sugar solution every 3 days via small discs of filter paper to allow more accurate discrimination of individual variation in longevity (Rivero & West, 2002). In addition, we repeated this treatment at 25 and 30 °C without sugar solution to confirm the overall pattern of longevity. We checked all vials daily and recorded the date of death of each female, then we removed, photographed and measured the rear-left tibia to control for body size. We recorded natal host mass for all replicates.

Fecundity

To determine fecundity, we chose 10 SW females and 10 LW females at random, each from a different replicate vial and we provided them each with an excess of host resources for oviposition. We placed each female in a stoppered glass vial with a single *B. terrestris* pupa of known age and mass, for eight days; eggs laid on this host were considered to be the 1st clutch. After 8 days, we removed all female foundresses that remained alive and provided each with a fresh host to lay their 2nd clutch; after the second 8-day period, we again moved foundresses to new hosts (3rd clutch). This successfully provided each female with a surplus of host resources, as only 39% of experimental foundresses laid any eggs on their 3rd host, laying an average of only 10 eggs (unpublished data). We collected females after their 3rd period of oviposition and removed and measured their rear-left tibias. We incubated all hosts at 30 °C, and at offspring emergence, we counted, sexed, removed, and (for females) scored morph of all individuals in each clutch. We found no significant correlation between host mass and total clutch size.

Dispersal behaviour

To estimate dispersal propensity, we fitted 20 replicates – sampling the full range of treatment combinations – with a one-way dispersal hat, which enables individuals to

leave the host vial, but prevents their return. This measure is used to indicate the likelihood of individuals to leave their natal patch. We collected individuals who ‘dispersed’ daily, counted and sexed them, and scored their morph. We removed all individuals remaining on the natal host at 4-day intervals – rather than daily – to allow time for more natural dispersal behaviour of recently emerged offspring; counted and sexed them, and scored their morph.

Dispersal, sex ratio, and competition between relatives

In this experiment, we investigated the production of offspring morph-ratio (proportion of long-wing females) and offspring sex ratio (proportion of males) simultaneously, varying both the number of foundresses and the extent of local competition. Females are predicted to alter the proportion of LW daughters in response to foundress number, which determines relatedness between competing offspring (Comins *et al.*, 1980; Comins, 1982). This is analogous to the extensive sex ratio literature where it has been shown comprehensively, across numerous species – in particular amongst parasitoids – that females adjust their sex ratio in response to an indirect cue of relatedness, foundress number (West *et al.*, 2005; West, 2009); and do not use kin recognition or other direct cues of relatedness (Shuker *et al.*, 2004; Reece *et al.*, 2004). Relatedness can influence selection in one of two ways: a conditional or facultative response may occur in response to natural variation in relatedness; or a fixed response may evolve over evolutionary time, in response to the average level of relatedness. Here, we are testing to see whether females adjust the offspring sex ratio or ratio of dispersal morphs facultatively, in response to the level of relatedness they experience on a patch (Herre, 1985, 1987). We used 12–15 replicates from each initial foundress × time combination (81 replicates in total; treatments described previously). These treatment combinations created variation in relatedness across a gradient of clutch sizes and therefore variation in level of LMC; this allowed us to distinguish between – and control for – the effects of increasing clutch size alone, and any additional effects of high foundress number in the analysis. All foundress females we used were of LW morph, mimicking the likely pattern of LW females to disperse to new hosts in natural populations. We randomly assigned hosts across treatment levels and measured their mass. We collected foundresses after the given period of oviposition and removed, photographed and measured their rear-left tibia. We then incubated hosts at 30 °C until offspring emergence. Once offspring began to emerge, we inspected hosts daily and removed, counted, sexed, and scored the morph of any emerging offspring. We calculated total clutch size, female offspring morph-ratio, and offspring sex ratio for each replicate. We found no

significant correlation between host mass and total clutch size (see Table 1: summary of clutch sizes per treatment combination).

Statistical analysis

We carried out principal component analysis (PCA) on morphological measurements, including tibia length, wing length, abdomen length, and egg load as y -variables. PCA combines these morphological variables to generate a series of linear variables (principal components), which best summarize the overall variation in the data set (Quinn & Keough, 2002). To test the validity of our morph groupings made by eye, we then performed discriminant function (DF) analysis upon the resulting principal component scores, with morph classification (as assigned by eye) as the x -variable. DF analysis defines significantly different groups within the dataset and determines how accurately individuals are assigned to the original groups by comparison between DF and original scores (Quinn & Keough, 2002).

We used linear models to test for differences between morph groups in principal components 1 and 2 (PC1 & PC2), egg load and body size. We also tested for differences in the life history traits fecundity and longevity, and for order effects in the timing of egg laying in this way. We calculated mean ovigeny index (OI) for SW and LW females: OI is defined as the proportion of a females' lifetime egg complement present as mature eggs at emergence, and so we calculated the ratio of average initial egg load to average lifetime fecundity using data from both the morph description experiment (for egg load) and from the life history experiment (for fecundity) (Godfray, 1994; Jervis *et al.*, 2001; Jervis & Ferns, 2004; Rivero & West, 2002).

We used linear models to test for the effects of foundress number, oviposition duration, and clutch size on the offspring morph-ratio females produced, transforming the morph-ratio data using the arcsin-squareroot transformation. To analyse sex ratio data, which could not be suitably transformed to analyse with linear models, we used generalized linear models (GLMs) to test for variation in sex ratio in response to variation in foundress number and oviposition duration; we included clutch size, host mass, and age in the maximal model as covariates. We used GLMs to analyse untransformed proportion data, which assume a binomial error distribution and use a logit link function for maximum power (Hardy & Field, 1998; Wilson & Hardy, 2002). Model simplification was based upon analysis of deviance, where changes in deviance are compared to a chi-squared distribution. We calculated the heterogeneity factor (HF) to test for overdispersion of data (leading to possible overestimation of significance); in cases where $HF < 4$, we scaled data and tested for significance using F -tests to correct for overdispersion (Crawley, 1993, 2002, 2007). In all cases, interactions are presented only

where significant at the level of $P < 0.01$ (Crawley, 1993, 2002, 2007).

We compared the dispersal behaviour of LW and SW females using linear mixed-effect models, where the probability of dispersal was used as the response variable; morph, clutch size, foundress number and oviposition time were then included as possible explanatory variables (and each factor controlled for when assessing significance of other variables), and host was included as a random effect in the model. All multivariate analyses were carried out using the JMP statistics package (JMP version 5.0.1.2, Copyright © 1989–2003 sas Institute Inc., Cary, NC, USA), linear mixed-effect models were run in Genstat (version 8.1, VSN International, Hemel Hempstead, UK), and we carried out all further analyses in R (R version 2.3.1, Copyright © 2006, The R Foundation for Statistical Computing).

Results

Morph description

We found two distinct female morphs, short wing (SW) and long wing (LW), which we could accurately identify with both morphological measurements and by eye. SW females had relatively short wings and an enlarged abdomen, whilst LW females had wings longer than their body and a relatively reduced abdomen size, for a given body size (Fig. 1). The majority of the variation in the morphological measurements we took (90%) was explained by principal components (PCs) 1 and 2 (which contributed equally; Table 2). Specifically, an increase in

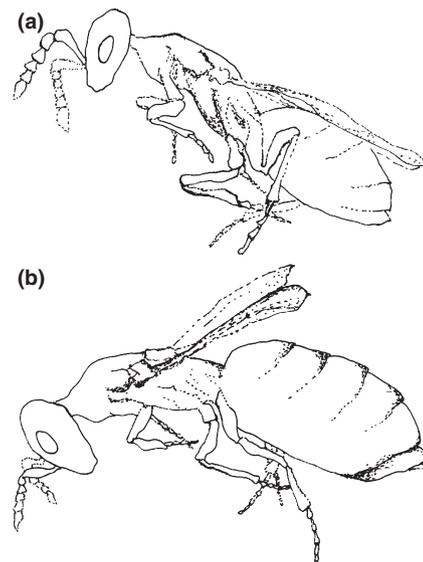


Fig. 1 The two female morphs of *Melittobia australica*: (a) a long-wing (LW) female and (b) a short-wing (SW) female (actual size approximately 1–2 mm).

Table 2 Results of principal component analysis, showing the amount of variation explained by principal components 1–4 (eigenvalues); and the contribution ('loading') of each y variable to each principal component (PC 1–4; eigenvectors).

	PC 1	PC 2	PC 3	PC 4
Eigenvalue				
Percent	1.8439	1.7130	0.2793	0.1638
Cumulative	46.0977	42.8261	6.9813	4.0949
Percent	46.0977	88.9238	95.9051	100.0000
Eigenvectors				
Tibia length	0.07682	0.70671	-0.67456	0.19908
Abdomen length	0.65078	0.28006	0.16501	-0.68617
Wing length	-0.28451	0.64529	0.69077	0.15966
Egg number	0.69974	-0.07568	0.20146	0.68121

wing length for a given body size was associated with a decrease in both abdomen length and egg load, described by the negative correlation between the contribution of wing length, and abdomen length and egg load, to PC 1 (see Table 2). Overall, this suggests that there is a shape difference between the two morphs, and in addition, we found a significant difference in this shape parameter (PC1) between the SW and LW groups (PC1: $F_{1,137} = 153$, $P < 0.001$; Fig. 2). For both morphs, increasing body size was associated with a proportional increase in the size of other morphological traits measured (positive/near-zero loading for PC2 for all traits; see Table 2), with no significant difference in body size (PC2 scores) between SW and LW females (PC2: $F_{1,137} = 3.42$, $P = 0.067$; Fig. 2). We found the SW and LW morph groupings were significantly different (with individuals scored as IM falling in the SW group), illustrated by the clear difference in SW and LW group means from DF analysis, based on individuals' scores for PC1 and 2. A number of IM individuals were identified when scored by eye, and approximately 12% of individ-

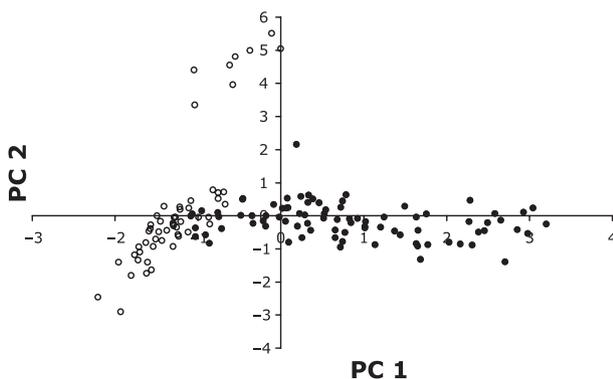


Fig. 2 Score for principal component 1 (PC1) plotted against score for principal component 2 (PC2), taken from the principal component analysis based upon morphological measurements, for sampled individuals of SW (closed circles) and LW (open circles) morph.

uals (17 of 139) were placed in the alternative group based upon their morphological measurements, from that which they were assigned to when scored by eye, by DF analysis; in nearly all cases, these were IM individuals, which were the most likely to lie on the classification boundary between groups. We used these groups, SW (females scored SW or IM by eye) and LW (females scored LW by eye) to classify individuals for all further analyses.

Differences in life history and behaviour

We examined several key life history traits and dispersal behaviour to test whether morphologically different females adopt alternative strategies. SW and LW morphs differed in dispersal behaviour, but not overall body size or longevity. LW individuals showed a significantly higher propensity for dispersal from their natal patch than SW individuals ($F_{1,31} = 550.18$, $P < 0.001$; Fig. 3a). Although SW females dispersed less than LW females, the dispersal of SW females – when compared across replicates of varying clutch size – increased with clutch size ($F_{1,31} = 85.81$, $P < 0.001$). In contrast, there was no significant difference in body size ($F_{1,137} = 3.1$, $P = 0.08$) or longevity (with sugar: $F_{1,104} = 0.092$, $P = 0.7625$; no sugar: $F_{1,69} = 2.32$, $P = 0.13$; Fig. 3b) between the two morphological groups. The length of the hind-left tibia, our measurement of body size, was an average of 0.30 mm (SE \pm 0.0009) for SW females, and 0.30 mm (SE \pm 0.005) for LW females. The mean longevity was 6.7 days (SE \pm 0.2) for SW females and 6.6 days (SE \pm 0.2) for LW females, at 30 °C (with sugar; Fig. 3b).

Although SW and LW females did not differ in their overall fecundity, they did differ in when they produced eggs. SW females laid a mean total of 316 eggs (SE \pm 65), whilst LW females laid a mean total of 478 eggs (SE \pm 104) ($F_{1,20} = 1.12$, $P = 0.30$). In contrast, there was a difference between SW and LW females in both when they produced and when they laid eggs. Specifically: (i) SW females had a larger number of eggs developed at emergence than LW females – SW females carrying an average of 8.3 eggs (SE \pm 0.6), and LW females carrying an average of 0.7 (SE \pm 0.2) eggs at emergence ($F_{1,136} = 278$, $P < 0.001$; Fig. 3c); and (ii) SW females laid a higher proportion of eggs in the 1st clutch than LW females, and this pattern was reversed for the 2nd clutch (1st clutch, SW 10% more eggs: $\chi^2_1 = 232.7$, $P < 0.001$; 2nd clutch, LW 9% more eggs: $\chi^2_1 = 183.3$, $P < 0.001$; Fig. 3d). This pattern was also reflected in the OI of the two morphs. The OI measure shows where individuals lie on the continuum between synovigeny and proovigeny, and is equal to the proportion of a female's lifetime eggs produced present at emergence, which varies from 0 to 1, where 0 represents no eggs mature at emergence (synovigeny) and 1 represents all eggs fully developed at emergence (proovigeny) (Jervis *et al.*, 2001, 2003; Jervis & Ferns, 2004). Whilst all

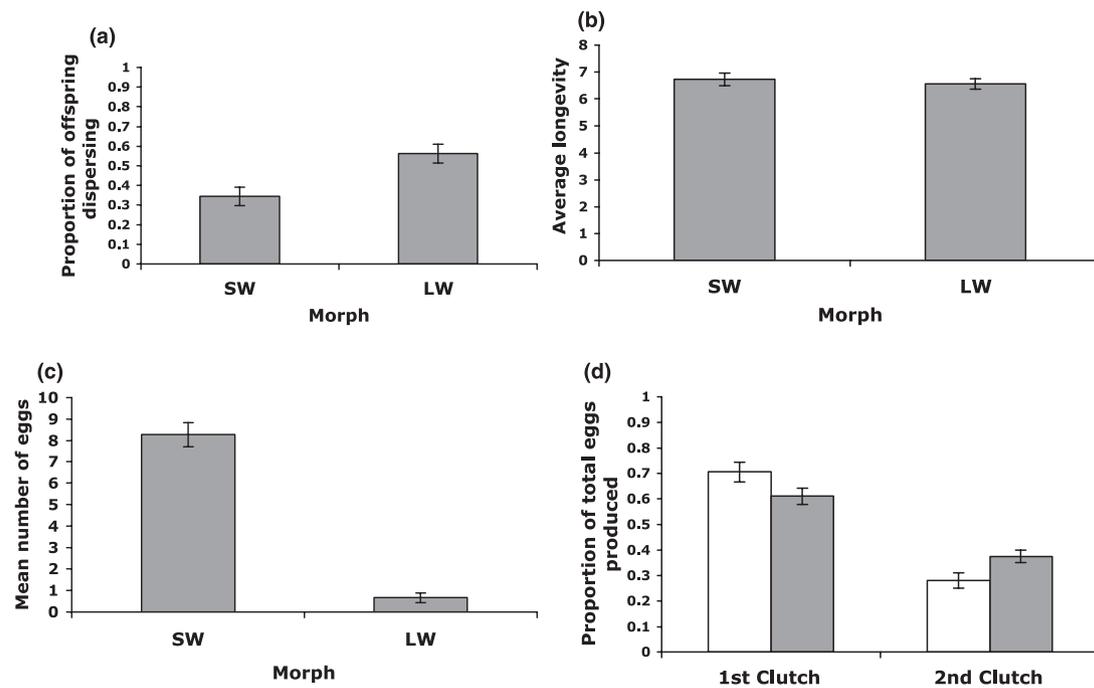


Fig. 3 (a) Mean proportion of female offspring within a brood that dispersed, from the total number of short-wing (SW) and the total number of long-wing (LW) females within a brood; (b) mean longevity for short-wing (SW) and long-wing (LW) females; (c) mean initial egg-load (IEL; number of eggs fully matured at emergence) for short-wing (SW) and long-wing (LW) morphs; (d) proportion of total eggs laid in first and second clutches by SW females (white bars) and LW females (shaded bars). In all cases error bars indicate standard errors.

females were relatively synovigenic (the majority of eggs are matured after emergence), the OI indicates that SW females were relatively more proovigenic than LW females ($OI_{SW} = 0.026$, $OI_{LW} = 0.001$).

Patterns of sex ratio and morph-ratio

The proportion of LW females varied significantly with total clutch size and oviposition period, but not with the number of females laying eggs (foundress number). We found no statistically significant variation in the proportion of LW females with increasing foundress number when controlling for clutch size and oviposition period ($F_{2,76} = 0.14$, $P = 0.9$; Fig. 4). A higher proportion of long-wing females (larger morph-ratio) were produced with both increasing clutch size ($F_{2,78} = 58.9$, $P < 0.001$; Fig. 4) and also with longer oviposition period ($F_{2,78} = 41.2$, $P < 0.001$; Fig. 4). Considering the sex ratio, there was a significant increase in sex ratio with increasing foundress number ($F_{2,78} = 3.9$, $P = 0.02$; Fig. 5). However, this represents a very slight shift in sex ratio of 1.7% males (from 2.4% to 4.1%), as the number of foundresses was increased from 1 to 15 – in comparison with the expected 46% shift under LMC theory (Hamilton, 1967). There was no significant effect of the duration of oviposition upon offspring sex ratio

($F_{2,78} = 0.46$, $P = 0.5$; Fig. 5) nor were there any significant interactions.

Discussion

We have shown that *M. australica* females have two morphologically distinct dispersal morphs – long wing (LW) and short wing (SW) (Figs 1 and 2). SW females had relatively shorter wings and larger abdomens, whereas LW females had reduced abdomen size and wings longer than body length (Fig. 1). Considering their life history strategies, SW females exhibit a lower propensity to disperse than LW females, emerge with a higher proportion of eggs fully developed, and lay a higher proportion of eggs in their first clutch (Fig. 3). In contrast, the morphs did not differ in their body size, longevity, or overall fecundity (Fig. 3). We then considered whether the ratio of the different female morphs was adjusted in response to local competition and relatedness (measured in terms of variation in foundress number), as predicted by theory. We found that a higher proportion of long-wing morphs was produced with both increasing clutch size and longer oviposition period, but that the proportion of long-wing female offspring did not vary with the number of foundresses laying eggs on a patch – which influences the relatedness of competing

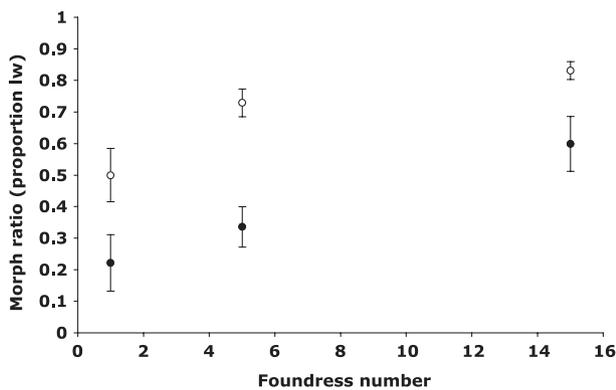


Fig. 4 Variation in mean brood morph ratio (proportion long-wing females) across a range of foundress number treatments (1, 5 or 15 females); females were given an oviposition period of either 3 days (closed symbols) or 6 days (open symbols). Increasing foundress number corresponds to higher intensity of local mate competition. Error bars indicate standard errors.

females that do not disperse (Fig. 4). Our results suggest that resource competition is the major influence upon variation in the dispersal rate in *Melittobia* species.

Dispersal

How does the dispersal polymorphism in *Melittobia* compare with our understanding of dispersal polymorphism more generally? Across a range of polymorphic insect species, a trade-off between dispersal and other fitness-related life history traits has often been found, which most commonly manifests as increased fecundity coupled with decreased age of first reproduction for the nondispersing morph (Roff, 1984; Roff & Fairbairn, 1991; Zera & Denno, 1997). In contrast, we found no difference in absolute fecundity between LW and SW females. However, SW females did have greater initial investment in egg production (higher OI), and laid a higher proportion of eggs earlier, suggesting that SW females have an earlier age of first reproduction – previous work suggests that SW *Melittobia* females start to lay eggs soon after locating hosts, whereas LW females must develop eggs before laying (Matthews *et al.*, 2009). The majority of studies have found no difference in longevity between morphs, as we have now shown is also the case for *M. australica* (Roff, 1984; Roff & Fairbairn, 1991). One possible explanation for the discrepancy between predicted life history trade-offs and experimental data is that – particularly in the case of parasitoids – differences in life history traits such as fecundity and longevity are unlikely to manifest fully under laboratory conditions (Jervis *et al.*, 2001, 2003; Jervis & Ferns, 2004; Godfray, 1994). Nonetheless, physiological differences between morphs have been shown in other species, where nutrients were allocated differentially to different life history traits (Zera

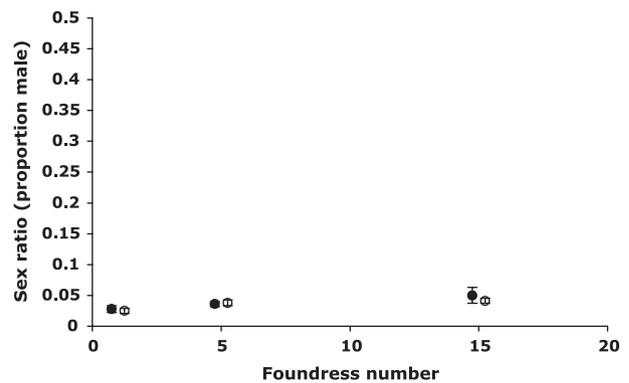


Fig. 5 Mean brood sex ratios (proportion male offspring) across treatments of varying foundress number (1, 5 or 15 females), when females were given either 3 days (closed symbols) or 6 days (open symbols) for oviposition. Increasing foundress number corresponds to increasing intensity of local mate competition. The error bars indicate standard errors.

& Denno, 1997). Furthermore, a number of studies have shown that dispersal itself – and in particular, the capacity for flight – is energetically costly, largely because the wing muscles of dispersing individuals are costly to develop and maintain, which may result in a compensatory decrease in metabolic rate (Roff *et al.*, 2003; Roff & Gelinas, 2003; Roff & Fairbairn, 2007; Nespolo *et al.*, 2008). In addition, differences between morphs in longevity and fecundity may be more complex than predicted under experimental conditions, and testing these traits simultaneously may better reflect competition between morphs under natural conditions.

Morphological differences between dispersal morphs have previously been shown to correspond to dispersal ability, usually higher in the winged morph (Roff & Fairbairn, 1991; Socha & Zemek, 2003). At the population level, a higher proportion of winged individuals has been found to correlate with both the increasing presence of wing muscles and an increasing behavioural propensity of long-wing individuals to disperse (Roff & Fairbairn, 1991). We have shown that LW females have a higher propensity to disperse, and that dispersal propensity increases along with the proportion of long-wing morphs – associated with increasing clutch size (Figs 3 and 4). However, the rate of long-wing dispersal is less than 100%, and an interesting extension of these experiments could consider the variation in dispersal probability within morph groups. The process of morph determination is less well understood, with evidence that genetic, hormonal, and environmental influences may be important (Roff, 1984; Zera & Denno, 1997; Roff & Gelinas, 2003). Previous work on *Melittobia* species suggests that morph determination is neither solely genetically or hormonally controlled (Consoli & Vinson, 2002a,b, 2004; Consoli *et al.*, 2004), and our experimental results provide indirect evidence that environmental

conditions are important, as the proportion of long-wing morphs was most strongly influenced by clutch size – which correlates with resource availability. Further work is needed to consider the potential for maternal or offspring control of morph determination, and further studies of natural populations are required to assess dispersal patterns, the extent of overlapping generations, and foundress number variation.

Dispersal theory suggests that competition between relatives can be important in the evolution of dispersal (Hamilton & May, 1977; Comins *et al.*, 1980; Comins, 1982). Theory predicts that higher levels of dispersal will be favoured if fewer foundresses lay eggs on each patch, because this leads to a greater mean relatedness between the competing nondispersers in the local population (Comins *et al.*, 1980; 1982). Our data provide no support for this prediction in relation to *Melittobia* (Fig. 4), suggesting that variation in relatedness has little influence on selection for facultative adjustment of dispersal by females. However, relatedness could still be important in this species if a fixed response has evolved in response to average relatedness over evolutionary time (which cannot be addressed with this data). A possible explanation for this lack of conditional response to variation in relatedness could be that there is no selection on females to respond to variation in foundress number (the cue commonly used by female insects to assess relatedness), if most females are solitary; in this case, we would expect a fixed rate of offspring dispersal (Herre, 1987). This is unlikely as data from natural populations of *Melittobia* suggest that foundress number does vary (Freeman & Ittyeipe, 1976; Freeman, 1977; Gonzalez *et al.*, 2004b; Matthews *et al.*, 2009). Alternatively, if the females on natural patches are all highly related, then variation in foundress number does not equate to substantial variation in offspring relatedness; in this case, we would also expect no variation in dispersal strategy (Frank, 1998).

Theory also predicts that the number of competitors can influence dispersal decisions, where an increase in the number of competitors for resources on a patch will favour an increased rate of dispersal (Hamilton & May, 1977; Ronce *et al.*, 2000; Consoli & Vinson, 2002a). We found support for this prediction, with an increasing proportion of long-wing females produced with increasing clutch size (Fig. 4). Increasing foundress number has two potential effects, lowering average relatedness, but also influencing the number of competitors; in this case, the effect of increased competition appears to be much more important. Previous studies on *Melittobia* species have also shown that SW females develop from the first eggs laid, and all later eggs develop into LW females (Consoli & Vinson, 2002b, 2004; Abe *et al.*, 2005; Matthews *et al.*, 2009); here, we found indirect support for this pattern, as the proportion of LW females emerging increased throughout the oviposition period. Increasing competition for resources is expected to result in the production of more LW female offspring because

the amount of resources available for oviposition decreases, and females must therefore disperse to find new hosts. Similarly, the pattern of producing SW females earlier in oviposition may be as a result of the low value of producing late-developing SW females: once the early-developing SW have laid eggs on the natal host, few resources remain for further oviposition by later SW.

Dispersal and sex allocation

The sex ratio behaviour of *Melittobia* poses a significant problem for sex allocation theory, as an exceptional case in a field that otherwise has extremely strong empirical support, and therefore needs to be explained (West *et al.*, 2005; West, 2009). When offspring of one sex disperse less, related members of the nondispersing sex experience a greater degree of competition, and so selection favours a sex ratio biased towards the dispersing sex (Hamilton, 1967; Bulmer & Taylor, 1980; Taylor, 1981). Hamilton (1967) showed that when mating occurs before only the females disperse, a female-biased sex ratio is favoured, which becomes less biased as more females lay eggs per patch. However, *Melittobia* females do not adjust their offspring sex ratios in response to the number of foundresses laying eggs per patch (Fig. 5; Abe *et al.*, 2003a,b, 2005; Cooperband *et al.*, 2003; Innocent *et al.*, 2007), widely observed to be the cue for facultative sex ratio adjustment across insect species (West, 2009). Several hypotheses have been proposed for the lack of sex ratio shift in these species: that foundress number does not vary in natural populations, high relatedness between foundress females, and fatal fighting between males (Herre, 1987; Frank, 1998; Abe *et al.*, 2003a, 2007). Lack of variation in foundress number in natural populations would result in no selection for adjustment of sex ratio (Herre, 1987). Alternatively, if co-founding females are highly related, a female-biased sex ratio is predicted irrespective of foundress number, as there is little variation in relatedness between competing males in this case (Frank, 1998). Finally, fatal fighting between male *Melittobia* could select against the production of sons and favour a lack of sex ratio shift in response to LMC (Abe *et al.*, 2003a, 2007; see also Shuker *et al.*, 2005). Although evidence supports the occurrence of multiple foundress scenarios (Schmieder, 1933; Freeman & Ittyeipe, 1976, 1993; Van den Assem *et al.*, 1982; Cooperband *et al.*, 2003; Matthews *et al.*, 2009), empirical data give mixed support to the idea that selection because of male fighting can fully explain the sex ratio (Freeman & Ittyeipe, 1976; Abe *et al.*, 2003a,b, 2005, 2007; Innocent *et al.*, 2007), and there is no conclusive explanation for this unusual pattern of sex allocation at present.

Given that the same selective forces influence both sex ratios and dispersal (Bulmer & Taylor, 1980; Motro, 1991; Taylor, 1994; Frank, 1998; Perrin & Mazalov, 2000; Rousset & Billiard, 2000; Leturque & Rousset, 2003, 2004; Wild & Taylor, 2004), can the pattern of dispersal

in *Melittobia* help us explain its unusual sex ratio behaviour? The various possible explanations of a lack of sex ratio adjustment in *Melittobia* wasps have different consequences for the evolution of dispersal. Theory predicts that just as an increasing number of foundresses laying eggs per patch selects for less female-biased sex ratios (Hamilton, 1967), it also selects for lower rates of dispersal (Comins *et al.*, 1980; Comins, 1982), which, in this case, translates into a higher proportion of the short-wing morph. The male fighting hypothesis does predict variation in dispersal under LMC: in this case, male fighting selects against sex ratio adjustment with variable foundress number, but does not select against variation in female dispersal rate (Abe *et al.*, 2003a, 2007). In contrast, if the lack of sex ratio adjustment is because of foundress number (N) not normally varying (Herre, 1987), or high relatedness between foundresses (Frank, 1985, 1986a,b; Abe *et al.*, 2005), then, as supported by our data, we would not expect the proportion of long-wing females to be varied with the number of foundress females. However, the lack of influence of foundress number on both sex ratio adjustment and variation in the proportion of long-wing morphs should not be seen as definitive evidence against the male fighting hypothesis, because there are other possible reasons why the proportion of long-wing morphs is not varied (see previous section). Extensions of existing theoretical models that more closely describe key aspects of the biology of *Melittobia* species may allow more specific predictions for dispersal to be made, considering for instance the allocation of resources to LW and SW daughters, and the dispersal probabilities of each morph. Moreover, data on natural variation in foundress number, the potential for overlapping generations of females, and patterns of sex ratio and morph production are limited. Therefore, the key next step is to obtain a greater amount of information about the population structure of natural populations of *Melittobia*.

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References

- Abe, J., Kamimura, Y., Ito, H., Matsuda, H. & Shimada, M. 2003a. Local mate competition with lethal male combat: effects of competitive asymmetry and information availability on a sex ratio game. *J. Evol. Biol.* **16**: 607–613.
- Abe, J., Kamimura, Y., Kondo, N. & Shimada, M. 2003b. Extremely female-biased sex ratio and lethal male-male combat in a parasitoid wasp, *Melittobia australica* (Eulophidae). *Behav. Ecol.* **14**: 34–39.
- Abe, J., Kamimura, Y. & Shimada, M. 2005. Individual sex ratios and offspring emergence patterns in a parasitoid wasp, *Melittobia australica* (Eulophidae), with superparasitism and lethal combat among sons. *Behav. Ecol. Sociobiol.* **57**: 366–373.
- Abe, J., Kamimura, Y. & Shimada, M. 2007. Sex ratio schedules in a dynamic game: the effect of competitive asymmetry by male emergence order. *Behav. Ecol.* **18**: 1106–1115.
- Balfour Browne, F. 1922. On the life history of *Melittobia acasta*, Walker; a chalcid parasite of bees and wasps. *Parasitology* **14**: 349–370.
- Bowler, D.E. & Benton, T.G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* **80**: 205–225.
- Buckell, E.R. 1928. Notes on the life history and habits of *Melittobia chalybii* ashmead (Chalcidoidea: Elachertidae). *Pan-Pac Entomol.* **5**: 14–22.
- Bulmer, M.G. & Taylor, P.D. 1980. Dispersal and the sex-ratio. *Nature* **284**: 448–450.
- Comins, H.N. 1982. Evolutionarily stable strategies for localized dispersal in 2 dimensions. *J. Theor. Biol.* **94**: 579–606.
- Comins, H.N., Hamilton, W.D. & May, R.M. 1980. Evolutionarily stable dispersal strategies. *J. Theor. Biol.* **82**: 205–230.
- Consoli, F.L. & Vinson, S.B. 2002a. Clutch size, development and wing morph differentiation of *Melittobia digitata*. *Entomol. Exp. App.* **102**: 135–143.
- Consoli, F.L. & Vinson, S.B. 2002b. Larval development and feeding behaviour of the wing dimorphics of *Melittobia digitata* Dahms (Hymenoptera: Eulophidae). *J. Hymenopt. Res.* **11**: 188–196.
- Consoli, F.L. & Vinson, S.B. 2004. Wing morph development and reproduction of the ectoparasitoid *Melittobia digitata*: nutritional and hormonal effects. *Entomol. Exp. App.* **112**: 47–55.
- Consoli, F.L., Tian, H.S., Vinson, S.B. & Coates, C.J. 2004. Differential gene expression during wing morph differentiation of the ectoparasitoid *Melittobia digitata* (Hym., Eulophidae). *Comp. Biochem. Physiol. A* **138**: 229–239.
- Cooperband, M.F. & Vinson, S.B. 2000. Host-acceptance requirements of *Melittobia digitata* (Hymenoptera: Eulophidae), a parasitoid of mud dauber wasps. *Biol. Control* **17**: 23–28.
- Cooperband, M.F., Matthews, R.W. & Vinson, S.B. 2003. Factors affecting the reproductive biology of *Melittobia digitata* and failure to meet the sex ratio predictions of Hamilton's local mate competition theory. *Entomol. Exp. App.* **109**: 1–12.
- Crawley, M. 1993. *GLIM for Ecologists*. Blackwell Scientific, Oxford.
- Crawley, M. 2002. *Statistical Computing*. Wiley (UK), Chichester.
- Crawley, M. 2007. *The R Book*. Wiley (UK), Chichester.
- Crespi, B.J. & Taylor, P.D. 1990. Dispersal rates under variable patch density. *Am. Nat.* **135**: 48–62.
- Dahms, E.C. 1984. A review of the biology of species in the genus *Melittobia* (Hymenoptera: Eulophidae) with interpretations and additions using observations on *Melittobia australica*. *Mem. Queensl. Mus.* **21**: 337–360.
- Frank, S.A. 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution* **39**: 949–964.
- Frank, S.A. 1986a. The genetic value of sons and daughters. *Hereditas* **56**: 351–354.

- Frank, S.A. 1986b. Dispersal polymorphisms in subdivided populations. *J. Theor. Biol.* **122**: 303–309.
- Frank, S.A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ.
- Freeman, B.E. 1977. Aspects of regulation of size of Jamaican population of *Sceliphron-assimile* Dahlbom (Hymenoptera: Sphecidae). *J. Anim. Ecol.* **46**: 231–247.
- Freeman, B.E. & Ittyeipe, K. 1976. Field studies on cumulative response of *Melittobia* sp (Hawaiiensis complex) (Eulophidae) to varying host densities. *J. Anim. Ecol.* **45**: 415–423.
- Freeman, B.E. & Ittyeipe, K. 1982. Morph determination in *Melittobia*, a Eulophid wasp. *Ecol. Entomol.* **7**: 355–363.
- Freeman, B.E. & Ittyeipe, K. 1993. The natural dynamics of the eulophid parasitoid *Melittobia-Australica*. *Ecol. Entomol.* **18**: 129–140.
- Freeman, E. & Parnell, J.R. 1973. Mortality of *Sceliphron-assimile*-Dahlbom (Sphecidae) caused by eulophid *Melittobia-chalybii*-Ashmead. *J. Anim. Ecol.* **42**: 779–784.
- Gandon, S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* **200**: 345–364.
- Gandon, S. & Michalakis, Y. 1999. Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. *J. Theor. Biol.* **199**: 275–290.
- Gandon, S. & Rousset, F. 1999. Evolution of stepping-stone dispersal rates. *Proc. R. Soc. Lond. B Biol. Sci.* **266**: 2507–2513.
- Godfray, H. 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton University Press, Princeton, NJ.
- Gonzalez, J.M. & Matthews, R.W. 2008. Female and male polymorphism in two species of *Melittobia* parasitoid wasps (Hymenoptera: Eulophidae). *Flor. Entomol.* **91**: 162–169.
- Gonzalez, J.M., Abe, J. & Matthews, R.W. 2004a. Offspring production and development in the parasitoid wasp *Melittobia clavicornis* (Cameron) (Hymenoptera: Eulophidae) from Japan. *Entomol. Sci.* **7**: 15–19.
- Gonzalez, J.M., Teran, J.B. & Matthews, R.W. 2004b. Review of the biology of *Melittobia acasta* (Walker) (Hymenoptera: Eulophidae) and additions on development and sex ratio of the species. *Caribb. J. Sci.* **40**: 52–61.
- Greeff, J.M. 1997. Offspring allocation in an externally ovipositing fig wasp with varying clutch size and sex ratio. *Behav. Ecol.* **8**: 500–505.
- Greeff, J.M. 2002. Mating system and sex ratios of a pollinating fig wasp with dispersing males. *Proc. R. Soc. Lond. B Biol. Sci.* **269**: 2317–2323.
- Greenwood-Lee, J.M. & Taylor, P.D. 2001. The evolution of dispersal in spatially varying environments. *Evol. Ecol. Res.* **3**: 649–665.
- Hamilton, W.D. 1967. Extraordinary sex ratios. *Science* **156**: 477–488.
- Hamilton, W.D. 1979. Wingless and fighting males in fig wasps and other insects. In: *Sexual Selection and Reproductive Competition in Insects* (M.S. Blum & N.A. Blum, eds), pp. 167–220. Academic Press, New York.
- Hamilton, W.D. & May, R.M. 1977. Dispersal in stable habitats. *Nature* **269**: 578–581.
- Hardy, I.C.W. & Field, S.A. 1998. Logistic analysis of animal contests. *Anim. Behav.* **56**: 787–792.
- Hartley, C.S. & Matthews, R.W. 2003. The effect of body size on male-male combat in the parasitoid wasp *Melittobia digitata* (Hymenoptera: Eulophidae). *J. Hymenopt. Res.* **12**: 272–277.
- Herre, E.A. 1985. Sex-ratio adjustment in fig wasps. *Science* **228**: 896–898.
- Herre, E.A. 1987. Optimality, plasticity and selective regime in fig wasp sex-ratios. *Nature* **329**: 627–629.
- Innocent, T.M., Savage, J., West, S.A. & Reece, S.E. 2007. Lethal combat and sex ratio evolution in a parasitoid wasp. *Behav. Ecol.* **18**: 709–715.
- Irwin, A.J. & Taylor, P.D. 2000. Evolution of dispersal in a stepping-stone population with overlapping generations. *Theor. Popul. Biol.* **58**: 321–328.
- Jervis, M.A. & Ferns, P.N. 2004. The timing of egg maturation in insects: ovigeny index and initial egg load as measures of fitness and of resource allocation. *Oikos* **107**: 449–460.
- Jervis, M.A., Heimpel, G.E., Ferns, P.N., Harvey, J.A. & Kidd, N.A.C. 2001. Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *J. Anim. Ecol.* **70**: 442–458.
- Jervis, M.A., Ferns, P.N. & Heimpel, G.E. 2003. Body size and the timing of egg production in parasitoid wasps: a comparative analysis. *Funct. Ecol.* **17**: 375–383.
- Leturque, H. & Rousset, F. 2002. Dispersal, kin competition, and the ideal free distribution in a spatially heterogeneous population. *Theor. Popul. Biol.* **62**: 169–180.
- Leturque, H. & Rousset, F. 2003. Joint evolution of sex ratio and dispersal: conditions for higher dispersal rates from good habitats. *Evol. Ecol.* **17**: 67–84.
- Leturque, H. & Rousset, F. 2004. Intersexual competition as an explanation for sex-ratio and dispersal biases in polygynous species. *Evolution* **58**: 2398–2408.
- Matthews, R.W., Gonzalez, J.M., Matthews, J.R. & Deyrup, L.D. 2009. Biology of the parasitoid *Melittobia* (Hymenoptera: Eulophidae). *Ann. Rev. Ent.* **54**: 251–266.
- Moore, J.C., Loggenberg, A. & Greeff, J.M. 2006. Kin competition promotes dispersal in a male pollinating fig wasp. *Biol. Lett.* **2**: 17–19.
- Motro, U. 1982a. Optimal rates of dispersal. 1. Haploid populations. *Theor. Popul. Biol.* **21**: 394–411.
- Motro, U. 1982b. Optimal rates of dispersal. 2. Diploid populations. *Theor. Popul. Biol.* **21**: 412–429.
- Motro, U. 1991. Avoiding inbreeding and sibling competition – the evolution of sexual dimorphism for dispersal. *Am. Nat.* **137**: 108–115.
- Nelson, R.M. & Greeff, J.M. 2009. Evolution of the scale and manner of brother competition in pollinating fig wasps. *Anim. Behav.* **77**: 693–700.
- Nespolo, R.F., Roff, D.A. & Fairbairn, D.J. 2008. Energetic trade-off between maintenance costs and flight capacity in the sand cricket (*Gryllus firmus*). *Funct. Ecol.* **22**: 624–631.
- Perrin, N. & Mazalov, V. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am. Nat.* **155**: 116–127.
- Quinn, G.P. & Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Reece, S.E., Shuker, D.M., Pen, I., Duncan, A.B., Choudhary, A., Batchelor, C.M. & West, S.A. 2004. Kin discrimination and sex ratios in a parasitoid wasp. *J. Evol. Biol.* **17**: 208–216.
- Reece, S.E., Innocent, T.M. & West, S.A. 2007. Lethal male-male combat in the parasitoid *Melittobia acasta*: are size and competitive environment important? *Anim. Behav.* **74**: 1163–1169.
- Rivero, A. & West, S.A. 2002. The physiological costs of being small in a parasitic wasp. *Evol. Ecol. Res.* **4**: 407–420.

- Roff, D.A. 1984. The cost of being able to fly – a study of wing polymorphism in 2 species of crickets. *Oecologia* **63**: 30–37.
- Roff, D.A. 1986. The evolution of wing dimorphism in insects. *Evolution* **40**: 1009–1020.
- Roff, D.A. & Fairbairn, D.J. 1991. Wing dimorphisms and the evolution of migratory polymorphisms among the insects. *Am. Zool.* **31**: 243–251.
- Roff, D.A. & Fairbairn, D.J. 2007. Laboratory evolution of the migratory polymorphism in the sand cricket: combining physiology with quantitative genetics. *Physiol. Biochem. Zool.* **80**: 358–369.
- Roff, D.A. & Gelinis, M.B. 2003. Phenotypic plasticity and the evolution of trade-offs: the quantitative genetics of resource allocation in the wing dimorphic cricket, *Gryllus firmus*. *J. Evol. Biol.* **16**: 55–63.
- Roff, D.A., Crnokrak, P. & Fairbairn, D.J. 2003. The evolution of trade-offs: geographic variation in call duration and flight ability in the sand cricket, *Gryllus firmus*. *J. Evol. Biol.* **16**: 744–753.
- Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution *Ann. Rev. Ecol. Evol. Syst.* **38**: 231–253.
- Ronce, O., Gandon, S. & Rousset, F. 2000. Kin selection and natal dispersal in an age-structured population. *Theor. Popul. Biol.* **58**: 143–159.
- Rousset, F. & Billiard, S. 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *J. Evol. Biol.* **13**: 814–825.
- Rousset, F. & Gandon, S. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *J. Evol. Biol.* **15**: 515–523.
- Roze, D. & Rousset, F. 2005. Inbreeding depression and the evolution of dispersal rates: a multilocus model. *Am. Nat.* **166**: 708–721.
- Schmieder, R.G. 1933. The polymorphic forms of *Melittobia chalybii* ashmead and the determining factors involved in their production (Hymenoptera chalcidoidea, Eulophidae). *Biol. Bull.* **65**: 338–354.
- Schmieder, R.G. 1938. The sex ratio in *Melittobia chalybii* ashmead, gametogenesis and cleavage in females and in haploid males (Hymenoptera Chalcidoidea). *Biol. Bull.* **74**: 256–266.
- Shuker, D.M., Reece, S.E., Taylor, J.A.L. & West, S.A. 2004. Wasp sex ratio behaviour when females on a patch are related. *Anim. Behav.* **68**: 331–336.
- Shuker, D.M., Pen, I., Duncan, A.B., Reece, S.E. & West, S.A. 2005. Sex ratios under asymmetrical local competition: theory and a test with parasitoid wasps. *Am. Nat.* **166**: 301–316.
- Socha, R. & Zemek, R. 2003. Wing morph-related differences in the walking pattern and dispersal in a flightless bug, *Pyrrhocoris apterus* (Heteroptera). *Oikos* **100**: 35–42.
- Taylor, P.D. 1981. Intra-sex and inter-sex sibling interactions as sex-ratio determinants. *Nature* **291**: 64–66.
- Taylor, P.D. 1988. An inclusive fitness model for dispersal of offspring. *J. Theor. Biol.* **130**: 363–378.
- Taylor, P.D. 1994. Sex-ratio in a stepping-stone population with sex-specific dispersal. *Theor. Popul. Biol.* **45**: 203–218.
- Taylor, P.D. & Frank, S.A. 1996. How to make a kin selection model. *J. Theor. Biol.* **180**: 27–37.
- Van den Assem, J., Gijswijt, M.J. & Nubel, B.K. 1980. Observation of courtship and mating strategies in a few species of parasitic wasps (Chalcidoidea). *Neth. J. Zool.* **30**: 208–221.
- Van den Assem, J., Denbosch, H. & Prooy, E. 1982. *Melittobia* courtship behavior – a comparative-study of the evolution of a display. *Neth. J. Zool.* **32**: 427.
- West, S.A. 2009. *Sex Allocation*. Princeton University Press, Princeton, NJ.
- West, S.A., Shuker, D.M. & Sheldon, B.C. 2005. Sex-ratio adjustment when relatives interact: a test of constraints on adaptation. *Evolution* **59**: 1211–1228.
- West, S.A., Griffin, A.S. & Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**: 415–432.
- Wild, G. & Taylor, P.D. 2004. Kin selection models for the co-evolution of the sex ratio and sex-specific dispersal. *Evol. Ecol. Res.* **6**: 481–502.
- Wild, G., Greenwood-Lee, J. & Taylor, P.D. 2006. Sex allocation and dispersal in a heterogeneous two-patch environment. *Theor. Popul. Biol.* **70**: 225–235.
- Wilson, K. & Hardy, I.C.W. 2002. Statistical analysis of sex ratio: an introduction. In: *Sex Ratios* (I.C.W. Hardy, ed.), pp. 48–92. Cambridge University Press, Cambridge.
- Zera, A.J. & Denno, R.F. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annu. Rev. Entomol.* **42**: 207–230.

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