



Research

Cite this article: Steyn VM, Mitchell KA, Terblanche JS. 2016 Dispersal propensity, but not flight performance, explains variation in dispersal ability. *Proc. R. Soc. B* **283**: 20160905.
<http://dx.doi.org/10.1098/rspb.2016.0905>

Received: 22 April 2016
 Accepted: 11 July 2016

Subject Areas:
 physiology, ecology

Keywords:
 behavioural syndromes, invasion, plasticity

Author for correspondence:
 John S. Terblanche
 e-mail: jst@sun.ac.za

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2016.0905> or via <http://rspb.royalsocietypublishing.org>.

Dispersal propensity, but not flight performance, explains variation in dispersal ability

Vernon M. Steyn, Katherine A. Mitchell and John S. Terblanche

Centre for Invasion Biology, Department of Conservation Ecology and Entomology, Stellenbosch University, Stellenbosch, South Africa

JST, 0000-0001-9665-9405

Enhanced dispersal ability may lead to accelerated range expansion and increased rates of population establishment, thereby affecting population genetic structure and evolutionary potential. Morphological, behavioural and physiological traits that characterize dispersive individuals from residents are poorly understood for many invertebrate systems, especially in non-polymorphic pterygote species. Here we examined phenotypic differences between dispersal-prone and philopatric individuals from repeated mark-release-recapture (MRR) experiments using an invasive agricultural pest, *Ceratitis capitata*. Comprehensive morphometric assessment and subsequent minimal adequate modelling using an information theoretic approach identified thorax mass:body mass ratio as a key predictor of disperser flies under semi-natural conditions. Performance differences in flight ability were then examined under controlled laboratory conditions to assess whether greater thorax mass:body mass ratio was associated with enhanced flight ability. The larger thorax:body mass ratio was associated with measurable differences in mean flight duration, most predominantly in males, and also by their willingness to disperse, scored as the number and duration of voluntary flights. No other measures of whole-animal flight performance (e.g. mean and peak vertical force, total or maximum flight duration) differed. Variation in voluntary behaviour may result in significant alterations of movement behaviour and realized dispersal in nature. This phenomenon may help explain intraspecific variation in the dispersal ability of insects.

1. Introduction

Dispersal, the movement of individuals from a natal patch to a novel environment [1], affects species' evolution and ecology [2], allowing the colonization of novel habitats [3], facilitating gene flow between populations [4,5] and contributing to evolutionary adaptation to novel environments [6]. The probability that an individual will move a particular distance from their natal habitat within their lifetime is depicted by the 'dispersal kernel' [1] and generally follows a specific right-skewed frequency distribution [7]. Consequently, only a small proportion of individuals in a population disperse over longer distances, with the majority remaining in closer proximity to their natal patch [8,9]. This has been well documented in several invertebrate species [9–11]. The dispersal kernel does not, however, provide information regarding trait variation between individuals.

Individuals within a population exhibit variation in their ability to disperse over large distances [12], with phenotypic differentiation between philopatric and dispersal-prone individuals well documented in traits such as wing size in insects [13] and birds [14], and leg length in vertebrates [15,16]. Variation in flight performance or dispersal ability between individuals is often related to differences in individual phenotypes such as thoracic muscle mass, wing size [17] or life-history trade-offs [18,19] and can impact endurance or power parameters via biophysical mechanisms. For example, wing size, via its influence on wing loading (body mass/wing area), is thought to have a pronounced effect on flight performance [20,21], with larger

winged individuals showing reductions in the power required to offset their mass but possibly at the cost of reduced manoeuvrability. Therefore, relatively larger wings generate more lift for the same power output [22] and should be favoured for dispersal (e.g. small- and large-winged morphs, [23]). Individuals with a larger thorax relative to body mass may also have an advantage owing to a higher flight muscle ratio which may result in more power available for flight [24].

The decision to disperse may be influenced by either context- or condition-dependent stimuli [2]. A context-dependent stimulus for dispersal can include a change in environmental conditions (e.g. density, resource availability or predation) [4,25,26]. However, condition-dependent dispersal occurs in response to changes in intrinsic physical state or physiological status within the organisms' body such as lipid reserves, muscle mass, hormones and stress [27,28]. These internal and external stimuli may also change over time, further complicating the identification of predictive traits of dispersal ability, especially in continuous (unimodal) phenotypic traits (but see, e.g. [13,29]). Behavioural drivers are, therefore, vital components of realized dispersal and have received increasing recent attention [4,9,30–33].

Here we simultaneously examine the influence of morphology, physiology and behaviour on flight performance in the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), an agricultural pest that significantly impacts food security [34,35], using an information theoretic approach, and a combination of semi-field and laboratory trials. We first determine the dispersal kernel of *C. capitata* and use this to identify traits characteristic of philopatric or dispersive individuals. In *C. capitata*, movement is limited to favourable conditions, and their performance and evolutionary fitness is influenced by environmental factors such as temperature [36,37]. Furthermore, *C. capitata* have marked variation in dispersal abilities among individuals from the same population [10], making them an ideal subject to examine the effects of phenotype, physiology and behaviour on dispersal in a non-polymorphic pterygote system. We then aimed to determine which aspects of flight performance are potentially associated with dispersal traits identified previously from other flying insects. As larger wings decrease the power requirements for flight, we hypothesized that the individuals with larger wings should have enhanced endurance or greater vertical force production. Furthermore, we predicted that a larger thorax mass : body mass ratio will lead to increased flight performance owing to the higher power-to-weight relationship and that this would perhaps be coupled with increased flight endurance.

2. Material and methods

(a) Study species

Ceratitis capitata pupae were procured from a large outbred population maintained at Citrus Research International (CRI) in Nelspruit, South Africa. In Stellenbosch, the pupae were placed in net cages at low density of 25°C with a 12:12 photoperiod in a climate chamber (LE-509, MRC, Holon, Israel). Protein supplementation can improve reproductive output in the laboratory [38]; however, no studies have shown that flies have access to, or frequently use, protein in the wild. Therefore, flies in our experiments were supplied with water and sugar crystals and allowed to feed ad libitum upon eclosion. No flies were used for more than one experiment.

(b) Semi-field releases

Four separate greenhouse releases were conducted in the summer ($26.1 \pm 4.1^\circ\text{C}$). To assess whether thermal history influenced recapture rates and disperser trait determination (e.g. [39,40]), approximately 1000 one- or two-day-old flies were acclimated at one of three thermal conditions (20°C, 25°C or 30°C) for 2 days prior to release. Flies from each treatment group were marked with one of the three fluorescent powders (pink, blue and yellow) that were randomly assigned prior to each release. A three-component protein pheromone attractant (ammonium acetate, trimethylamine hydrochloride and 1,4-diaminobutane; Biolure®, Chempac, Paarl, South Africa) that attracts both sexes of *C. capitata* [41] was opened for 10 min at one end of a 15×3 m rectangular greenhouse before being sealed into an airtight container to create a pheromone gradient. Flies were then released from ground level at the opposite end of the empty greenhouse and allowed to move without human interference. By creating distance classes (1.5, 4.5, 7.5, 10.5 and 13.5 m ± 1.5 m) and counting how many individuals were in each class (except the first class) every 30 min, we determined the proportion and distance flies had moved at each time point. The census took less than 5 min per class, allowing a snapshot image of the distribution to be achieved. The time taken for the first individuals to reach the lure end of the greenhouse was recorded. The first 55 individuals to reach the pheromone lure (typically <20 min) were considered as 'dispersers' and those who did not leave the release point after 3 h were 'philopatric'. Dispersers and philopatric individuals were placed singly into labelled Eppendorf tubes, into a cooler with crushed ice and transported to the laboratory where they were frozen at -80°C . Subsequently, they were dissected and their wings removed for phenotypic measurements.

(c) Morphological and physiological traits

The extracted wings were mounted on microscope slides and imaged using a Leica (MZ16A, Leica, Wetzlar, Germany) microscope fitted with a digital camera. Wing morphometric analysis was conducted using 14 landmarks per wing (electronic supplementary material, figure S1a). Wing size and shape were determined by comparing the location of these landmarks on the wings of the recaptured individuals in MORPHOJ (v. 1.06b) [42]. After the entire fly was weighed, it was carefully dissected to allow the thorax and abdomen to be weighed separately, using an ultramicrobalance (UMX-2, Mettler Toledo Inc., Columbus, OH, USA; to ± 1 μg). All traits (relative wing size, thorax mass, abdomen mass and entire body mass) measured that were not highly correlated ($R \geq 0.8$) were included in a minimal adequate model (MAM) (following [43]), along with acclimation treatment and sex, to determine whether any of these phenotypic traits were associated with dispersal ability. This MAM analysis highlighted that a larger thorax mass : body mass ratio is an important identifier of dispersers relative to philopatric individuals. There is, however, an inherent difference in the thorax mass : body mass ratio between males and females ($n = 358$, $F = 19.77$, $p < 0.001$, electronic supplementary material, figure S2). Therefore, the criteria for assigning dispersers and philopatric individuals from thorax mass : body mass ratio were assigned on a sex-specific basis (male dispersers thorax to body ratio > 0.47 (47%) of total body mass and in females' > 0.43 (43%)). Once flies were categorized into either dispersers or philopatric flies, and when the sex ratios were equal, further analyses were conducted independent of sex.

(d) Laboratory flight experiments

One- or 2-day-old flies were reared at 25°C for 2 days prior to the flight test. The flies were attached to a FORT10 force transducer (World Precision Instruments, Sarasota, FL, USA) by gluing a

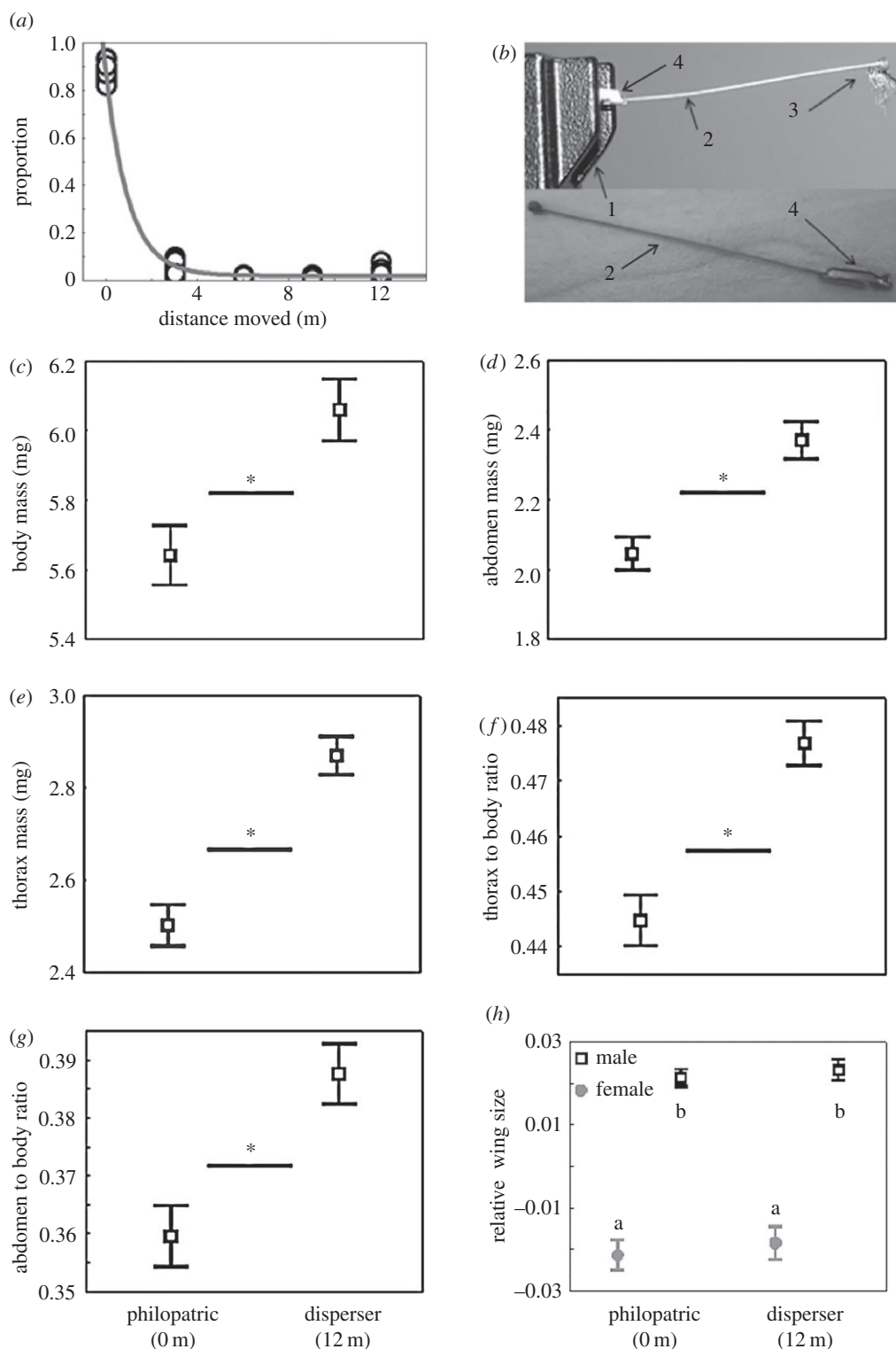


Figure 1. (a) The proportion of *Ceratitis capitata* individuals found at a given distance 30 min after release (at 0 m) and allowed to move unobstructed to a lure attractant at the opposite end (12 m) of the greenhouse (semi-field). The scatterplot shows data from four releases and is best described by a decaying exponential curve (electronic supplementary material, table S3). (b) The force transducer (1), the number 2 insect pin (2), a *C. capitata* individual (3) attached to the thorax in a slightly inclined position and the custom-designed mount (4). The bottom of (b) shows the pin and mount separated from the force transducer. (c–h) Comparison of phenotypic traits between philopatric (0 m) and disperser flies (12 m). Body mass (c), abdomen mass (d), thorax mass (e), thorax mass to body mass ratio (f), abdomen mass to body mass ratio (g), and relative wing size from geometric morphometrics principle components analysis scores (h). Asterisks indicate significant differences for (b–f). Lowercase letters in (h) show statistically homogeneous groups (error bars: \pm s.e.).

number 2 insect pin from the top to the middle of the pro-thorax with hand-warmed leg wax (Mandy's[®], LEE-CHEM Laboratories, Durban, South Africa). The wax is viscous, ensuring it remains only where it is placed and the position of attachment allowed the wings full range of motion while not interfering with the click mechanism. The pin was snugly inserted into a custom-designed mount that was then slid firmly onto the leaf

of the force transducer (figure 1b). The flies used in the force transducer experiment ($n = 54$) were divided into either dispersers or philopatric individuals (large versus smaller thorax mass to body mass ratio, respectively) retroactively, using the same criterion identified from the semi-field releases. Force measurements were performed in a temperature-controlled room ($25 \pm 1^\circ\text{C}$). In the few cases where an individual did not

fly on its own, the insect was stimulated by gently blowing air over the head. If flight was not achieved or if the flight was shorter than 5 s, it was regarded as a failed attempt. To obtain estimates of repeatability, seven replicate flight force trials were conducted on each fly, and individuals were allowed at least 2 min of rest between replicates.

The vertical force produced by an individual fly was recorded every 0.01 s in Newtons (converted from voltage using a calibration equation) using EXPEDATA v. 1.8.0.2 (Sable Systems, Las Vegas, NV, USA). Peak forces were determined by calculating the difference between the highest (or strongest) consecutive 5 s of force output within a flight window and a 30 s steady state when the insect was at rest. Mean force was determined by calculating the difference between the force output of the entire flight window and the 30 s resting force produced. A repeated-measures analysis was conducted to assess the repeatability of these parameters. Only the number of successful flights increased with trial number, but none of the other flight performance variables changed significantly across trials (electronic supplementary material, tables S1 and S2).

Several flight parameters were measured using the high-precision force transducer set-up: flight success ratio, flight class, total flight duration, maximum flight duration, mean flight duration, peak force and mean force. Flight success ratio was scored as the number of successful flights (greater than 5 s) divided by the number of attempts. Flight class, whether an individual flew or not, was also compared between philopatric and dispersive individuals.

(e) Statistical analyses

(i) Dispersal kernel

TABLECURVE 2D v. 5.01.02 (SYSTAT Inc., San Jose, CA, USA) was used to fit multiple equations to the dispersal kernel data (electronic supplementary material, table S3). To determine whether the dispersal kernel was purely a result of density or if other factors may be playing a role, a simple correlation was performed testing whether releases with higher release densities caused a larger proportion of the flies to move the maximum (13.5 ± 1.5 m) distance the test allowed.

(ii) Morphometric analysis

All further statistical analyses were undertaken in R v. 3.1.2 (R Inc., Boston, MA, USA). The data were tested for normality using Shapiro–Wilk's test. Body mass, mean and maximum flight duration were not normally distributed and log-transformed. A generalized linear model (GLM), with a Gaussian distribution and an identity link function, was used to determine the effect of sex and dispersal category (disperser versus philopatric) and their possible interaction on the morphological characters (including wing size, thorax mass, abdomen mass, body mass and ratios of these) in *C. capitata* individuals released in the greenhouse. To test the prediction that larger wing size is associated with greater flight endurance, linear regression analyses were conducted with total flight duration as the dependent variable and wing area or wing loading as the explanatory variable. To determine whether there was antagonistic selection between thorax mass and wing size (e.g. [29]), logistic regressions were conducted where the distance moved (0 or 12 m) was used as the dependent variable. To quantify the association of thorax mass and wing size on the distance the individuals moved, multiple logistic regressions were conducted.

(iii) Minimal adequate model

The MAM was used to determine the most important phenotypic traits explaining variation in dispersal in *C. capitata*. The data considered in the linear model were all the phenotypic trait data (thorax mass, abdomen mass, body mass, thorax-to-body

Table 1. Final linear model from the minimal adequate model (MAM) analysis determining the traits contributing to the phenotypic differences between dispersive and philopatric individuals as determined from the semi-field releases. (The full starting model was a general linear model including abdomen mass, body mass, thorax mass, wing size, sex, acclimation treatment and their interaction on dispersal category (philopatric or disperser). Model simplified by excluding non-significant terms (following [43]). Factors in italics indicate significance at $p = 0.05$.)

coefficients	estimate	s.e.m.	t-value	p-value
intercept	−0.427	0.509	−0.837	0.405
<i>abdomen mass</i>	<i>0.535</i>	<i>0.239</i>	<i>2.233</i>	<i>0.028</i>
body mass	0.162	0.212	0.764	0.446
thorax mass	−0.267	0.441	−0.607	0.545
<i>abdomen mass</i> × <i>thorax mass</i>	<i>0.449</i>	<i>0.211</i>	<i>2.133</i>	<i>0.035</i>
<i>abdomen mass</i> × <i>body mass</i>	<i>−0.241</i>	<i>0.095</i>	<i>−2.534</i>	<i>0.013</i>

mass ratio, wing size) and several categorical variables (e.g. sex and acclimation treatment). The model was simplified (following [43]), non-significant terms with the highest order interactions were removed from the model sequentially and the model fits were compared after removal via ANOVA. If the models were significantly improved, the term was left out of the model. This process was repeated until the removal of a factor did not improve the model or if the highest order interaction had a significant interaction effect.

(iv) Flight physiology

GLMs were used to determine the effect of dispersal category and sex on flight parameters measured. A GLM with a Gaussian distribution and an identity link function was used to determine the effect of category on flight success ratio for all the tested individuals. Separate GLMs, with a binomial distribution and a logit link function, were used to determine the effect of dispersal category on flight class and sex for all variables for all the tested individuals. All further analyses were conducted on only the individuals who achieved flight; therefore, GLMs (Gaussian distribution, identity link function) were used to determine the effect of dispersal category and sex on peak force, mean force, total flight duration, maximum and mean flight duration.

3. Results

(a) Semi-field releases

Of the $n = 812 \pm 131$ individuals released over four releases, $3.6 \pm 0.5\%$ (mean \pm s.e.) reached the pheromone side of the greenhouse in 30 min, with the majority of individuals moving less than 3 m (figure 1a). Less than $2.2 \pm 0.5\%$ of the flies were found in the middle of the greenhouse; therefore, if the individual moved, it typically found its way to the other end of the greenhouse. The dispersal kernel for *C. capitata* is best described by a decaying exponential curve (detailed curve fitting comparisons shown in the electronic supplementary material, table S3) and was consistent between releases. Furthermore, the dispersal kernel was not a result of fly density, as there was no correlation ($R = -0.18$; $p = 0.72$) between the release density and the proportion of flies that

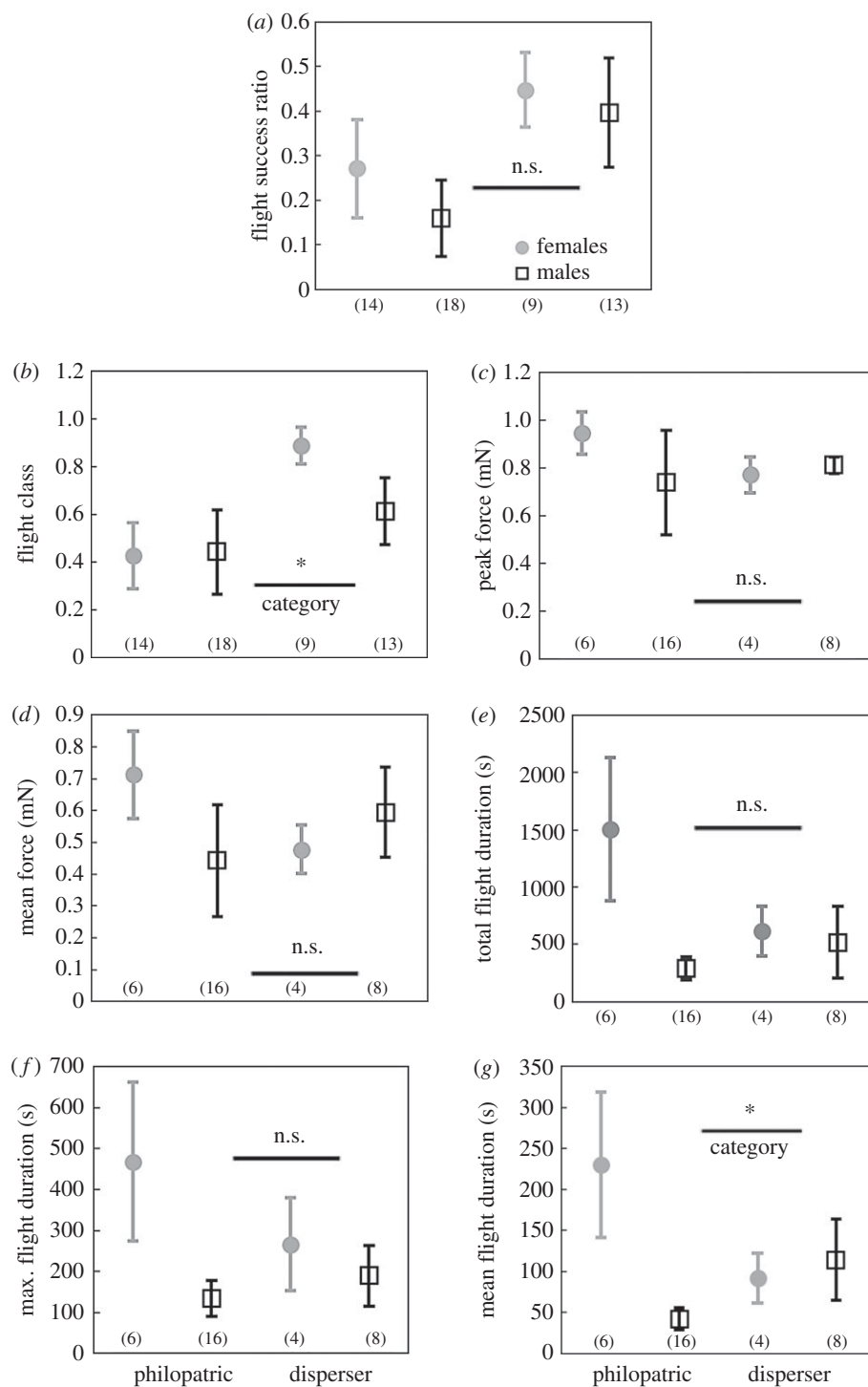


Figure 2. Summary results (mean \pm s.e.) for the flight parameters measured using the force transducer compared between philopatric and dispersive individuals. (a) Flight success ratio, (b) flight class, (c) peak vertical flight force, (d) mean vertical flight force, (e) total flight duration, (f) maximum (max.) flight duration and (g) mean flight duration of *Ceratitis capitata* individuals (see table 2 for full results). Values in brackets indicate the number of flies examined; asterisks in (b,g) indicate significance at $p = 0.05$.

moved the maximum distance in 3 h ($17.5 \pm 1.9\%$). In all, 358 flies were collected for analysis: 220 females and 138 males. Of these, 53% of females were categorized as dispersers compared with 34% in males. However, this variation between sexes was not significantly different (GLM Wald's $\chi^2 = -0.067 \pm 0.034$, $p = 0.224$).

Philopatric individuals (flies that moved less than 3 m) and dispersers (flies that moved the maximum distance greater than 12 m) differed according to thorax mass, abdomen mass, body mass, thorax mass : body mass ratio and abdomen mass : body mass ratio (electronic supplementary material, table S4; figure 1). These traits also showed significant sex dimorphism; however, there was no sex \times dispersal category

interaction. Therefore, the phenotypic traits differed in the same manner between the sexes and do not influence whether or not individuals will disperse. Rather, there is an inherent difference in body and wing size between the sexes. The mean body mass (pooled sexes) of dispersers (6.1 ± 1.2 mg, mean \pm s.e.) was significantly greater than that of philopatric individuals (5.6 ± 1.2 mg; electronic supplementary material, table S4; figure 1b), with thorax and abdomen mass being significantly larger in dispersers than that in philopatric individuals (disperser abdomen 2.4 ± 0.7 mg, thorax 2.9 ± 0.6 mg versus philopatric abdomen 2.1 ± 0.6 mg, thorax 2.5 ± 0.6 mg; figure 1c,d). Furthermore, body mass : thorax mass ratio was significantly different between dispersers and

Table 2. Results of generalized linear models dispersal category (i.e. disperser versus philopatric) on various flight parameters scored using the force transducer in the laboratory for *Ceratitis capitata*. (The flight success ratio and flight class of all individuals tested and peak force (mN), mean force (mN), total flight duration, maximum (max.) flight duration and mean flight duration of individuals that achieved flight in *C. capitata* measured in a temperature-controlled room with a force transducer. Factors in italics indicate significance at $p = 0.05$. AIC, Akaike information criterion; s.e.m., standard error of the mean.)

trait	AIC	factor	Wald's χ^2	s.e.m.	t-value	p-value
flight success ratio	54.26	intercept	0.448	0.089	5.071	7.020
		sex	-0.051	0.138	-0.368	0.715
		category	-0.177	0.135	-1.308	0.197
		sex \times category	-0.061	0.213	-0.288	0.774
flight class	69.37	<i>intercept</i>	<i>2.079</i>	<i>0.750</i>	<i>2.773</i>	<i>0.006</i>
		sex	-1.609	0.942	-1.708	0.088
		<i>category</i>	<i>-2.367</i>	<i>0.924</i>	<i>-2.561</i>	<i>0.010</i>
		sex \times category	1.674	1.276	1.312	0.190
peak force (mN)	57.13	<i>intercept</i>	<i>-0.389</i>	<i>0.129</i>	<i>-3.017</i>	<i>0.005</i>
		sex	0.174	0.223	0.780	0.442
		category	0.308	0.247	1.250	0.221
		sex \times category	-0.573	0.400	-1.431	0.163
mean force (mN)	62.05	<i>intercept</i>	<i>-0.882</i>	<i>0.138</i>	<i>-6.370</i>	<i><0.001</i>
		sex	0.336	0.240	1.400	0.172
		category	0.498	0.265	1.877	0.070
		sex \times category	-1.007	0.431	-2.341	0.026
total flight duration(s)	69.68	<i>intercept</i>	<i>2.363</i>	<i>0.159</i>	<i>14.823</i>	<i><0.001</i>
		sex	-0.046	0.276	-0.166	0.869
		category	0.564	0.305	1.849	0.074
		sex \times category	-0.512	0.496	-1.033	0.310
max. flight duration(s)	79.58	<i>intercept</i>	<i>1.778</i>	<i>0.185</i>	<i>9.618</i>	<i><0.001</i>
		sex	0.211	0.320	0.659	0.515
		category	0.643	0.354	1.818	0.079
		sex \times category	-0.751	0.575	-1.308	0.201
mean flight duration(s)	78.17	<i>intercept</i>	<i>1.391</i>	<i>0.179</i>	<i>7.761</i>	<i><0.001</i>
		sex	0.092	0.310	0.297	0.768
		<i>category</i>	<i>0.709</i>	<i>0.343</i>	<i>2.064</i>	<i>0.048</i>
		sex \times category	-0.787	0.557	-1.412	0.168

philopatric individuals (figure 1e). The thorax mass of the dispersers accounted for $47.7 \pm 0.4\%$ of the total body mass, whereas the thorax of the philopatric individuals accounted for a significantly lower proportion ($44.5 \pm 0.5\%$) of the total body mass (figure 1e). Wing size did not differ between dispersers and philopatric individuals (figure 1g). Total flight duration was not associated with wing area ($n = 34$; $R^2 = 0.02$; $F = 0.54$; $p = 0.47$), even after adjusting for body size (i.e. wing loading) ($n = 34$; $R^2 = 0.04$; $F = 1.30$; $p = 0.26$). There was no evidence of antagonistic selection between thorax mass and wing size ($n = 120$; $\chi^2 = 2.29$; $p = 0.13$). There was a difference in wing shape between the sexes, but no differences in wing shape between philopatric and dispersive individuals for either of the sexes (electronic supplementary material, figure S1).

The variables retained in the final MAM model to explain variation in dispersal ability included a significant interaction between the abdomen and thorax mass as well as abdomen and body mass. The main effects included only abdomen

mass, thorax mass and body mass as explanatory factors. Wing size, acclimation treatment and sex were excluded as potential explanatory factors from the final model. All further statistical tests reported here include only the variables retained in the MAM (table 1).

(b) Laboratory flight assays

The tested individuals were divided into groups according to their thorax-to-body ratio as this ratio incorporates both changes in abdomen mass and its interactions with body mass or thorax mass. Furthermore, it allows testing of the prediction that flight muscle mass is positively associated with flight performance. Therefore, flight parameters were measured and compared between dispersers (larger thorax mass : body mass ratio) and philopatric (smaller thorax mass : body mass ratio) individuals assigned according to the thorax mass : body mass ratio seen in the semi-field release results (figure 2). Flight class (figure 2c), but not success ratio (figure 2b), differed significantly

Table 3. Generalized linear model results for the effect of mass distribution between body segments (abdomen to thorax (A : T) mass ratio) and sex effects on key flight performance parameters. (The flight success ratio and flight class of all individuals tested and mean force (mN) of individuals that achieved flight in *Ceratitis capitata* measured in a temperature-controlled room with a force transducer. Factors in italics indicate significance at $p = 0.05$. AIC, Akaike information criterion; s.e.m., standard error of the mean.)

trait	AIC	factor	Wald's χ^2	s.e.m.	t-value	p-value
flight success ratio	51.66	<i>intercept</i>	1.008	0.272	3.709	< 0.001
		<i>A : T mass ratio</i>	-0.733	0.303	-2.416	0.019
		<i>sex</i>	-0.459	0.424	-1.084	0.284
		<i>A : T ratio \times sex</i>	0.382	0.539	0.709	0.482
flight class	74.15	<i>intercept</i>	1.633	0.335	4.880	< 0.001
		<i>A : T mass ratio</i>	-1.087	0.374	-2.910	0.006
		<i>sex</i>	-0.705	0.522	-1.351	0.183
		<i>A : T ratio \times sex</i>	0.547	0.663	0.825	0.413
mean force (mN)	3.79	<i>intercept</i>	0.670	0.251	2.671	0.012
		<i>A : T mass ratio</i>	-0.161	0.309	-0.521	0.606
		<i>sex</i>	-0.043	0.365	-0.118	0.907
		<i>A : T ratio \times sex</i>	0.038	0.488	0.079	0.938

between dispersers and philopatric individuals who flew (table 2). The dispersers successfully achieved and maintained flight $42.7 \pm 7.0\%$ of the time, whereas only $22.7 \pm 7.4\%$ of the philopatric individual's flight attempts were successful. The peak force (figure 2*d*) and mean force (figure 2*e*) did not differ significantly between dispersers and philopatric individuals. The total, maximum flight duration did not differ between dispersers and philopatric individuals (table 2, figure 2*f,g*); however, mean flight duration was significantly different between the dispersal categories (table 2, figure 2*h*). The mean force was also not associated with abdomen mass:thorax mass ratio when sex and the interaction were included in the model, indicating that the mass distribution of the flies was not associated with flight performance (table 3). However, there was an effect of mass distribution on flight success and flight class with a negative association between abdomen:thorax mass ratio and these traits (table 3). The interaction between sex and the mass distribution was not significant for any traits examined (table 3).

4. Discussion

Individual variation in dispersal-related traits is rarely identified in species with unimodal variation in phenotypes. Understanding the variation in these phenotypic traits is paramount to understanding whether adaptive variation is a prerequisite or acquired trait in, e.g. geographically range-restricted species or rapidly spreading species [44]. In this study, considering all phenotypes previously identified for dispersive individuals in flying organisms, a heavier thorax mass:body mass ratio showed the closest association with dispersal in *C. capitata*. While abdomen mass may also have contributed to this ratio difference, individuals with a larger abdomen relative to thorax mass did not perform better, suggesting that a shift in the flies' centre of gravity was not associated with the ratio differences seen in dispersers and philopatric individuals. However, the phenotypic differences in thorax:body mass between dispersers and philopatric individuals were associated with only one difference in flight performance, (mean flight

duration, table 2) in contrast to previous studies [13]. Instead, dispersing individuals showed greater willingness to move, seen in the significant difference in flight class (table 2, figure 2*c*). Moreover, the flight performance parameters measured on the force transducer did not differ between philopatric and dispersive individuals for those who achieved flight, with the exception of mean flight duration (table 2, figure 2*h*). Thus, the physiology of the philopatric individuals was generally not compromised and they are as flight capable as dispersive individuals; however, male dispersers did appear to fly for longer, on average, compared with philopatric males. Consequently, it appears that morphology may still be a predictor of willingness to move. This is particularly evident in the significant negative association between the mass of abdomen and thorax and flight success and flight class (table 3).

The main phenotypic difference between philopatric and dispersive individuals is associated with condition-dependent behaviour (e.g. relative muscle mass and dispersal propensity); however, this is in contrast to field observations linking dispersal to context-dependent behaviour (e.g. food searching) in introduced populations elsewhere (California, [45]). While several studies have examined the effect of landscape and environmental conditions on dispersal ability of diverse species (e.g. [25,30,46]), few have focused on condition-dependent behaviour affecting dispersal. This is not altogether surprising, as there are larger costs in overcoming drag in flight, rather than in producing lift in *Drosophila melanogaster* [47]. Furthermore, as dispersal is more likely to be achieved by several, smaller inter-patch movements as opposed to one sustained flight (e.g. [4]), the increased mean flight duration most evident in the male flies may not have significant ecological consequences for this species.

Another factor worthy of further consideration is the use of a protein-based lure (i.e. food attractant) for encouraging movement in the semi-field environment. When trapping for *C. capitata*, Biolure[®] has been shown to have the greatest recapture rate of both sexes compared with sex pheromone-based lures [41]. This is because Tephritids in general have limited access to protein in their natural diet despite this being essential for reaching sexual maturity, e.g. [48]. By not providing access

to a protein source while in the laboratory, the attractiveness of the lure should have been heightened for all flies released; however, it was only a small proportion of flies that made it to the lure within the timeframe of the semi-field experiments. Consequently, we believe the lure-based dispersal method worked adequately to assess the dispersal ability of these flies.

This study contributes novel empirical evidence to our understanding of dispersal propensity [2,4,9,32] and highlights the importance of including intraspecific phenotypic variation. However, few studies consider plastic changes to phenotypic traits that may, in turn, influence key behaviours such as boldness, exploration and activity. Behavioural characteristics associated with activity have long been known to be both heritable and adaptive (e.g. [49,50]). A greater inclination to move is likely to be a critical aspect to dispersal behaviour and inter-individual variation. The fact that variation in dispersal propensity has persisted in an outbred laboratory-reared colony of *C. capitata* suggests an evolutionary advantage exists to maintaining these traits and that a genetic basis is likely. If selection for more willing dispersers proves possible in *C. capitata*, this may lead to the improvement of quality

control measures for dispersal ability for laboratory- or mass-rearing techniques (with applications to pest management). If flies with greater propensity and ability to disperse could be selected for in cultures used for sterile insect release methods, the efficacy of control could perhaps be increased. The knowledge gained on the dispersal ability of this species will also result in improved understanding of invasion potential and geographical range dynamics.

Data accessibility. Data from this publication are archived with Dryad: <http://dx.doi.org/10.5061/dryad.g1228>.

Authors' contributions. V.M.S. conducted the work, ran statistical analyses and drafted the manuscript. K.A.M. and J.S.T. conceived and designed the study, interpreted results and co-wrote the manuscript. All authors approved the final manuscript.

Competing interests. We have no competing interests.

Funding. V.M.S. and J.S.T. are supported by the National Research Foundation (NRF) and the Centre for Invasion Biology. K.A.M. was supported by the Claude Leon Foundation.

Acknowledgements. Welgevallen Experimental Farm and Citrus Research International provided logistic support. We thank the anonymous referees for constructive comments that helped improve the work.

References

- Ronce O. 2007 How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Syst.* **38**, 231–253. (doi:10.1146/annurev.ecolsys.38.091206.095611)
- Pennekamp F, Mitchell KA, Chaine A, Schtickzelle N. 2014 Dispersal propensity in *Tetrahymena thermophila* ciliates: a reaction norm perspective. *Evolution* **68**, 2319–2330.
- Le Galliard J-F, Massot M, Clobert J. 2012 Dispersal and range dynamics in changing climates: a review. In *Dispersal and spatial evolutionary dynamics* (eds J Clobert, M Baguette, TG Benton, JM Bullock), pp. 317–336. Oxford, UK: Oxford University Press.
- Bowler DE, Benton TG. 2005 Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* **80**, 205–225. (doi:10.1017/S1464793104006645)
- Alleaume-Benharira M, Pen IR, Ronce O. 2006 Geographical patterns of adaptation within a species' range: interactions between drift and gene flow. *J. Evol. Biol.* **19**, 203–215. (doi:10.1111/j.1420-9101.2005.00976.x)
- Hoffmann A, Griffin P, Dillon S, Catullo R, Rane R, Byrne M, Rebecca J, Sgrò C. 2015 A framework for incorporating evolutionary genomics into biodiversity conservation and management. *Climate Change Resp.* **2**, 1–24. (doi:10.1186/s40665-014-0009-x)
- Murrell DJ, Travis JM, Dytham C. 2002 The evolution of dispersal distance in spatially-structured populations. *Oikos* **97**, 229–236. (doi:10.1034/j.1600-0706.2002.970209.x)
- Harris EJ, Olalquiaga G. 1991 Occurrence and distribution patterns of the Mediterranean fruit fly in desert areas in Chile and Peru. *Environ. Entomol.* **20**, 174–178. (doi:10.1093/ee/20.1.174)
- Bitume EV, Bonte D, Ronce O, Bach F, Flaven E, Olivieri I, Nieberding CM. 2013 Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecol. Lett.* **16**, 430–437. (doi:10.1111/ele.12057)
- Meats A, Smallridge CJ. 2007 Short- and long-range dispersal of medfly, *Ceratitis capitata* (Diptera: Tephritidae), and its invasive potential. *J. Appl. Entomol.* **131**, 518–523. (doi:10.1111/j.1439-0418.2007.01168.x)
- Makino SI, Yamane S, Sunose T, Aoki S. 1987 Dispersion distance of queens from natal sites in the two haplometrotic paper wasps *Polistes riparius* and *P. snelleni* (Hymenoptera: Vespidae). *Res. Popul. Ecol.* **29**, 111–117. (doi:10.1007/BF02515429)
- Kokko H, Lopez-Sepulcre A. 2006 From individual dispersal to species ranges: perspectives for a changing world. *Science* **313**, 789–791. (doi:10.1126/science.1128566)
- Berwaerts K, Van Dyck H, Aerts P. 2002 Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*. *Funct. Ecol.* **16**, 484–491. (doi:10.1046/j.1365-2435.2002.00650.x)
- Nilsson JA. 1989 Causes and consequences of natal dispersal in the marsh tit, *Parus palustris*. *J. Anim. Ecol.* **58**, 619–636. (doi:10.2307/4852)
- Phillips BL, Brown GP, Webb JK, Shine R. 2006 Invasion and the evolution of speed in toads. *Nature* **439**, 803–803. (doi:10.1038/439803a)
- Perkins AT, Phillips BL, Baskett ML, Hastings A. 2013 Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecol. Lett.* **16**, 1079–1087. (doi:10.1111/ele.12136)
- Dudley R. 2000 *Biomechanics of insect flight: form, function, evolution*. Princeton, NJ: Princeton University Press.
- Zera AJ, Harshman LG. 2001 The physiology of life history trade-offs in animals. *Annu. Rev. Ecol. Syst.* **32**, 95–126. (doi:10.1146/annurev.ecolsys.32.081501.114006)
- Hanski I, Saastamoinen M, Ovaskainen O. 2006 Dispersal-related life-history trade-offs in a butterfly metapopulation. *J. Anim. Ecol.* **75**, 91–100. (doi:10.1111/j.1365-2656.2005.01024.x)
- Rayner JMV. 1979 A new approach to animal flight mechanics. *J. Exp. Biol.* **80**, 17–54.
- Ellington CP. 1984 The aerodynamics of hovering insect flight. *Phil. Trans. R. Soc. Lond. B* **305**, 1–181. (doi:10.1098/rstb.1984.0049)
- Marden JH. 1987 Maximum lift production during take-off in flying animals. *J. Exp. Biol.* **130**, 235–258.
- Steenman A, Lehmann AW, Lehmann GUC. 2015 Life-history trade-off between macroptery and reproduction in the wing-dimorphic pygmy grasshopper *Tetrix subulata* (Orthoptera: Tetrigidae). *Ethol. Ecol. Evol.* **27**, 93–100. (doi:10.1080/03949370.2014.885466)
- Thomas CD, Hill JK, Lewis OT. 1998 Evolutionary consequences of habitat fragmentation in a localized butterfly. *J. Anim. Ecol.* **67**, 485–497. (doi:10.1046/j.1365-2656.1998.00213.x)
- Clobert J, Galliard L, Cote J, Meylan S, Massot M. 2009 Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**, 197–209. (doi:10.1111/j.1461-0248.2008.01267.x)
- Bitume EV, Bonte D, Ronce O, Olivieri I, Nieberding CM. 2014 Dispersal distance is influenced by parental and grand-parental density. *Proc. R. Soc. B* **281**, 20141061. (doi:10.1098/rspb.2014.1061)

27. Zera AJ. 2003 The endocrine regulation of wing polymorphism in insects: state of the art, recent surprises, and future directions. *Integr. Comp. Biol.* **43**, 607–616. (doi:10.1093/icb/43.5.607)
28. Guerra PA. 2011 Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. *Biol. Rev.* **86**, 813–835. (doi:10.1111/j.1469-185X.2010.00172.x)
29. Hoffmann AA, Ratna E, Sgro CM, Barton M, Blacket M, Hallas R, De Garis S, Weeks AR. 2007 Antagonistic selection between adult thorax and wing size in field released *Drosophila melanogaster* independent of thermal conditions. *J. Evol. Biol.* **20**, 2219–2227. (doi:10.1111/j.1420-9101.2007.01422.x)
30. Van Dyck H, Baguette M. 2005 Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic Appl. Ecol.* **6**, 535–545. (doi:10.1016/j.baae.2005.03.005)
31. Edelsparre AH, Vesterberg A, Lim JH, Anwari M, Fitzpatrick MJ. 2014 Alleles underlying larval foraging behaviour influence adult dispersal in nature. *Ecol. Lett.* **17**, 333–339. (doi:10.1111/ele.12234)
32. Palmer SCF, Coulon A, Travis JMJ. 2014 Inter-individual variability in dispersal behaviours impacts connectivity estimates. *Oikos* **123**, 923–932. (doi:10.1111/oik.01248)
33. Sindair ELE, Noronha de Souza CR, Ward AJW, Seebacher F. 2014 Exercise changes behaviour. *Funct. Ecol.* **28**, 652–659. (doi:10.1111/1365-2435.12198)
34. De Meyer M, Robertson MP, Peterson AT, Mansell MW. 2008 Ecological niches and potential geographical distributions of Mediterranean fruit fly (*Ceratitidis capitata*) and natal fruit fly (*Ceratitidis rosa*). *J. Biogeogr.* **35**, 270–281.
35. Malacrida AR, Gomulski LM, Bonizzoni M, Bertin S, Gasperi G. 2007 Globalization and fruit fly invasion and expansion: the medfly paradigm. *Genetica* **131**, 1–9. (doi:10.1007/s10709-006-9117-2)
36. Nyamukondiwa C, Weldon CW, Chown SL, le Roux PC, Terblanche JS. 2013 Thermal biology, population fluctuations and implications of temperature extremes for the management of two globally significant insect pests. *J. Insect Physiol.* **59**, 1199–1211. (doi:10.1016/j.jinsphys.2013.09.004)
37. Esterhuizen N, Clusella-Trullas S, van Daalen CE, Schoombie RE, Boardman L, Terblanche JS. 2014 Effects of within-generation thermal history on the flight performance of *Ceratitidis capitata*: colder is better. *J. Exp. Biol.* **217**, 3545–3556. (doi:10.1242/jeb.106526)
38. Blay S, Yuval B. 1997 Nutritional correlates of reproductive success of male Mediterranean fruit flies (Diptera: Tephritidae). *Anim. Behav.* **54**, 59–66. (doi:10.1006/anbe.1996.0445)
39. Kristensen TN, Hoffmann AA, Overgaard J, Sørensen JG, Hallas R, Loeschke V. 2008 Costs and benefits of cold acclimation in field-released *Drosophila*. *Proc. Natl Acad. Sci. USA* **105**, 216–221. (doi:10.1073/pnas.0708074105)
40. Chidawanyika F, Terblanche JS. 2011 Costs and benefits of thermal acclimation for codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae): implications for pest control and the sterile insect release programme. *Evol. Appl.* **4**, 534–544. (doi:10.1111/j.1752-4571.2010.00168.x)
41. Grout TG, Daneel JH, Ware AB, Beck RR. 2011 A comparison of monitoring systems used for *Ceratitidis* species (Diptera: Tephritidae) in South Africa. *Crop Prot.* **30**, 617–622. (doi:10.1016/j.cropro.2011.01.005)
42. Klingenberg CP. 2011 MorphoJ: an integrated software package for geometric morphometrics. *Mol. Ecol. Resour.* **11**, 353–357. (doi:10.1111/j.1755-0998.2010.02924.x)
43. Crawley MJ. 2007 *The R Book*. New York, NY: John Wiley & Sons Ltd.
44. Richardson JL, Urban MC, Bolnick DI, Skelly DK. 2014 Microgeographic adaptation and the spatial scale of evolution. *Trends Ecol. Evol.* **29**, 165–176. (doi:10.1016/j.tree.2014.01.002)
45. Pierre RY. 2007 Economic impact of a Mediterranean fruit fly outbreak in Florida. PhD thesis, University of Florida, Gainesville, FL, USA.
46. Vinatier F, Lescouret F, Duyck PF, Martin O, Senoussi R, Tixier P. 2011 Should I stay or should I go? A habitat-dependent dispersal kernel improves prediction of movement. *PLoS ONE* **6**, e21115. (doi:10.1371/journal.pone.0021115)
47. Lehmann F-O, Dickinson MH. 1997 The changes in power requirements and muscle efficiency during elevated force production in the fruit fly *Drosophila melanogaster*. *J. Exp. Biol.* **200**, 1133–1143.
48. Faria MJ, Pereira R, Delliger T, Teal PEA. 2008 Influence of methoprene and protein on survival, maturation and sexual performance of male *Ceratitidis capitata* (Diptera: Tephritidae). *J. Appl. Entomol.* **132**, 812–819. (doi:10.1111/j.1439-0418.2008.01360.x)
49. Swallow JG, Carter PA, Garland Jr T. 1998 Artificial selection for increased wheel-running behavior in house mice. *Behav. Genet.* **28**, 227–237. (doi:10.1023/A:1021479331779)
50. Garland Jr T. 2003 Selection experiments: an underutilized tool in biomechanics and organismal biology. In *Vertebrate biomechanics and evolution* (eds VL Bels, J-P Gasc, A Casinos), pp. 23–56. Oxford, UK: BIOS Scientific Publishers.