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Author for correspondence:

Myles H. M. Menz

e-mail: myles.menz@iee.unibe.ch

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Higher flight activity in the offspring of migrants compared to residents in a migratory insect

Laura J. Dällenbach¹, Alexandra Glauser¹, Ka S. Lim², Jason W. Chapman^{3,4} and Myles H. M. Menz^{1,5}

¹Institute of Ecology and Evolution, University of Bern, Bern 3012, Switzerland

²Computational and Analytical Science, Rothamsted Research, Harpenden AL5 2JQ, UK

³Centre for Ecology and Conservation, and Environment and Sustainability Institute, University of Exeter, Penryn TR10 9EZ, UK

⁴College of Plant Protection, Nanjing Agricultural University, Nanjing, People's Republic of China

⁵School of Biological Sciences, The University of Western Australia, Crawley 6009, Western Australia, Australia

MHMM, 0000-0002-3347-5411

Migration has evolved among many animal taxa and migratory species are found across all major lineages. Insects are the most abundant and diverse terrestrial migrants, with trillions of animals migrating annually. Partial migration, where populations consist of resident and migratory individuals, is ubiquitous among many taxa. However, the underlying mechanisms are relatively poorly understood and may be driven by physiological, behavioural or genetic variation within populations. We investigated the differences in migratory tendency between migratory and resident phenotypes of the hoverfly, *Episyrphus balteatus*, using tethered flight mills. Further, to test whether migratory flight behaviour is heritable and to disentangle the effects of environment during development, we compared the flight behaviour of laboratory-reared offspring of migrating, overwintering and summer animals. Offspring of migrants initiated more flights than those of resident individuals. Interestingly, there were no differences among wild-caught phenotypes with regard to number of flights or total flight duration. Low activity in field-collected migrants might be explained by an energy-conserving state that migrants enter into when under laboratory conditions, or a lack of suitable environmental cues for triggering migration. Our results strongly suggest that flight behaviour is heritable and that genetic factors influence migratory tendency in *E. balteatus*. These findings support the growing evidence that genetic factors play a role in partial migration and warrant careful further investigation.

1. Introduction

Migration has evolved independently among many animal taxa, and migrating animals comprise a large proportion of all major lineages [1–4], with insects being the most abundant and speciose terrestrial migrants [5–7]. The most common type of migration is partial migration, which is defined by variation in migratory tendency within species [8–10]. Hence, partially migratory populations are composed of a mixture of resident and migratory individuals simultaneously [8,9]. Many examples of partially migratory species have been reported in mammals, birds, fish and invertebrates [8].

As natural selection acts upon individuals, it is important to determine the underlying mechanisms driving differences in individual migratory tendency [8]. Individual differences in migratory tendency between animals of the same population may underpin the extent of partial migration observed within species [8,11]. Possible drivers of differences in migratory tendency can be heterogeneity within populations, such as physiological, morphological,

behavioural or genetic variation [8]. For example, in birds, morphological variation has been shown to correlate with migratory tendency, with a smaller body size usually associated with migratory behaviour [12]. Furthermore, behavioural differences linked to migratory tendency have been found in the fish *Rutilus rutilus*, where bold individuals are more likely to migrate [11], and in insects [13]. This provides evidence for a strong behavioural component influencing partial migration, and suggests that differences in activity between individuals correlate with migratory tendency or variation in dispersal ability in insects [14].

Migratory behaviour has been shown to be heritable in a number of animal taxa. The blackcap, *Sylvia atricapilla*, is a particularly well-studied example, where migratory activity and the behaviour associated with it, known as migratory restlessness, is strongly heritable (e.g. [15,16]). The heritability of flight behaviour is also known in insects (reviewed by [2]). For example, migratory tendency has been shown to be heritable in the moths *Spodoptera exempta*, *Mythimna separata*, *Helicoverpa armigera* and *Cydia pomonella*, and the grasshopper *Melanoplus sanguinipes* [17–21]. However, in other species such as *Locusta migratoria* and *Schistocerca gregaria*, migratory behaviour is strongly influenced by environmental factors [19]. Therefore, we suggest that behavioural plasticity in response to environmental factors, and the heritability of behavioural traits, will both play an important role in determining levels of partial migration within populations.

In Europe, some hoverfly species (Diptera, Syrphidae) are partially migratory, where part of the population overwinters in the breeding grounds as adults, while others travel large distances in search of a milder climate [13,22–25]. *Episyrphus balteatus* is the most common migrant hoverfly in Europe and during winter a part of the population remains in the habitat and overwinters as larvae, pupae or adults [26–29], whereas other individuals of the population migrate south to the Mediterranean in autumn, where they breed throughout the winter [30,31]. *Episyrphus balteatus* is an important pollinator and the larvae are efficient aphid predators, playing a significant role in the biocontrol of agricultural crop pests [31–33]. Adult overwintering hoverflies are almost exclusively females that are in a facultative reproductive diapause, whereas males of *E. balteatus* are thought to be unable to increase their fat bodies, and therefore are more susceptible to cold temperatures and are not expected to overwinter [34,35]. Most studies so far have focused on the southward flights to the Mediterranean in autumn [24,29,35]. Females migrate with an undeveloped reproductive system, but with sperm storage organs already full of sperm [35]. Currently, there is no description of the northward flight back to central and northern Europe in spring [30,36]. The short lifespan of this species indicates that the migration system of *E. balteatus* is multi-generational, with a single generation moving south in the autumn and successive generations moving north in the spring [13,30,36], as is typical of many latitudinal insect migrations [5]. Interestingly, no genetic differentiation has yet been found between different overwintering strategies of *E. balteatus* [37], with very low genetic distances between populations and a lack of population subdivision [38]. Therefore, it is thought all individuals may have the genetic material for the expression of the different overwintering phenotypes and that their decision for one of the strategies may depend on

environmental and individual factors [37]. To date it is unclear whether environmental or genetic factors are responsible for the decision of individuals to migrate, or whether it is a combination of both.

Behavioural traits, such as the propensity to engage in long-distance flight and flight tendency, are crucial proxies for migratory potential or individual migratory tendency, and can be quantified using tethered flight mills under controlled conditions [14]. Tethered flight trials are a good way to measure flight behaviour and have been used to investigate flight potential in a number of insect species (e.g. [14,18,21,39–41]). In this study, we investigated the migratory tendency between different migratory phenotypes of *E. balteatus* using tethered flight mills. In order to disentangle environmental effects that possibly trigger migration, such as weather and food resources, we investigated differences in the flight behaviour of first generation hoverflies deriving from overwintering, migrating and summer populations. Furthermore, to investigate the importance of environmental effects, wild-caught hoverflies from both migrating and overwintering populations were also tested. Specifically, we aimed to answer the following questions. (i) Do first generation offspring of adults taken from summer populations, migrating groups, or overwintering populations differ in their number and total duration of flights? (ii) Are there gender differences in these flight behaviours among hoverflies descended from different phenotypes? (iii) Are there gender differences in flight behaviour among hoverflies captured during migration?

We expect individuals deriving from migrating populations to attempt more flights and spend more time flying on the tethered flight mills than individuals deriving from overwintering or summer populations. Moreover, we expect migrating and overwintering individuals collected in the field to differ in their flight behaviour; with migrating animals showing a stronger tendency to fly and a longer duration of flight. Since females have been observed in significantly larger numbers while migrating, they are expected to attempt more flights and spend more time flying on the mill than males.

2. Methods

(a) Study animals

Hoverflies for flight mill experiments were divided into three phenotypes: resident overwintering, resident summer and migratory. Resident overwintering and summer hoverflies were caught in the surroundings of Bern, Switzerland (46°56'38" N, 7°26'49" E), from April to November 2016 on sunny and warm days (electronic supplementary material, figure S1). Individuals caught in April were assigned to the overwintering phenotype, since only females were found during this period of time ($n = 10$). Males would indicate the possible return of migrants, as they do not normally overwinter [35]. Additional overwintering flies were caught in November ($n = 25$). Because of harsh conditions in the beginning of November, migrants are believed to have started migrating south already. Flies designated as summer individuals were caught in June and July, in the same locations as overwintering flies. Migrating flies ($n = 88$) were captured at Col de Bretolet (46°08'34.1" N, 6°47'45.2" E), an alpine pass at 1923 m a.s.l. on the border between Switzerland and France, in September and October 2016 (electronic supplementary material, figure S1). Migrating flies were caught during active migration, heading southwest over the pass in large numbers.

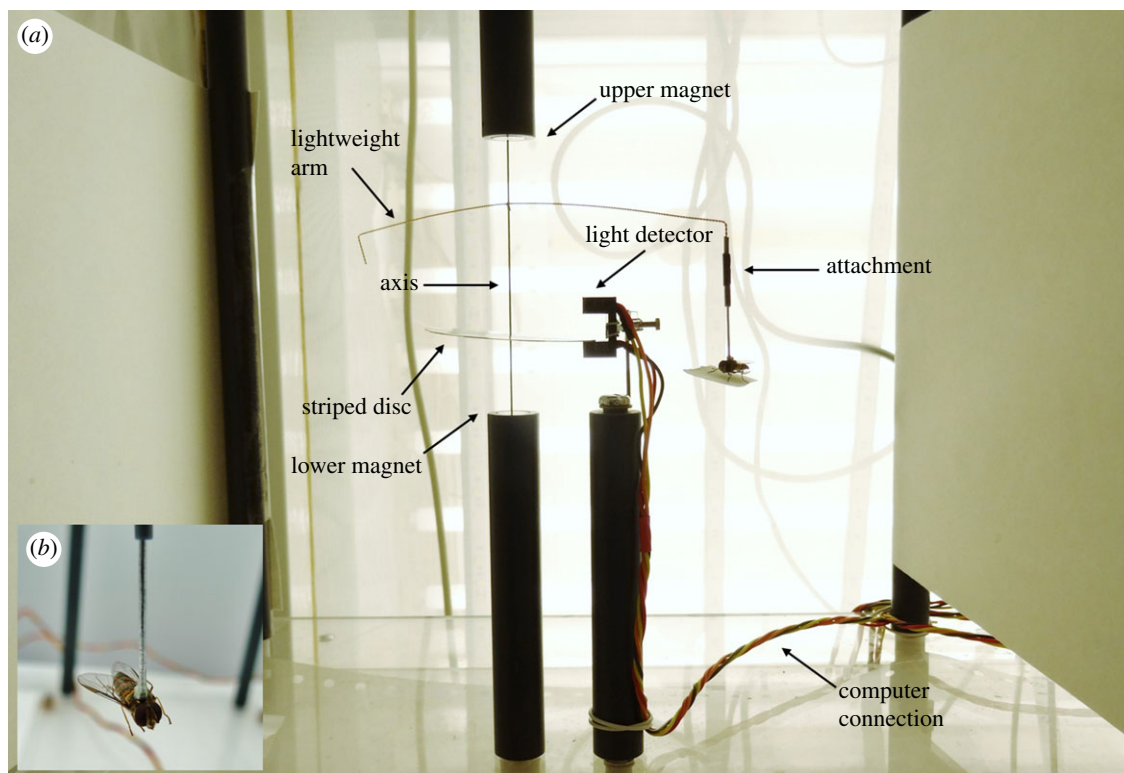


Figure 1. Tethered flight mill. (a) Labeled photograph of an individual flight mill and (b) a close-up of *Episyrphus balteatus* attached to the flight mill. (Online version in colour.)

Hoverflies were put into flight cages ($45 \times 45 \times 90$ cm) that consisted of a white plastic frame covered by nylon gauze in a climate chamber at 20°C , with a day–night cycle of 16:8 h light:dark. Flies were kept in groups of up to 20 individuals per cage. Each cage had a layer of kitchen paper on the bottom. One Petri dish with moist cotton wool served as water supply and an additional Petri dish contained cotton wool with sugar water (10% sugar) and some mashed pollen. Additionally, flies were provided with a small ball of pollen, powdered sugar and honey (60% pollen, 30% powder sugar and 10% honey). All Petri dishes were checked and refilled daily.

(b) Rearing of *E. balteatus* in the laboratory

Hoverflies were reared in a climate chamber at 20°C with a day–night cycle of 16:8 h light:dark. A bean plant (*Vicia faba*) infested with aphids (*Acyrtosiphon pisum*) was placed into the cage on the same day the hoverflies were caught, to stimulate egg laying. Bean plants were checked for eggs and larvae daily. Larvae were placed individually in vials with a bean leaf for shelter. Larvae were fed between 20 and 30 aphids daily. When pupated, the leaf and the leftover aphids were taken out of the vial to increase the chance of a smooth emergence [27,42]. Once emerged, the flies were put into a flight cage ($45 \times 45 \times 90$ cm) for between 12 and 24 h, where they were given the possibility to feed and fly before the start of the experiments.

(c) Tethered flight mill experiments

Tethered flight mills were used to investigate the flight behaviour of individual *E. balteatus* (figure 1). Flight mills were designed at Rothamsted Research (patent: [43]) and consist of a lightweight wire arm suspended between two magnets, which results in almost no resistance against the turning of the arm. This means that even weak fliers are able to turn the mill and fly rotationally in a horizontal plane (see also [14]). The hoverfly was glued to a pin, attached to one end of the arm of the mill, using a contact adhesive. A striped disc attached to the axis turns with the

arm (figure 1). A light sensor detects the movement of the disc and records the distance flown (m), time spent flying (s) and flight speed (m s^{-1}). These data are used to calculate measurements of distance, duration and speed of specific flights (e.g. the furthest flight or the first flight). The system used had five channels, allowing five individual insects to be flown simultaneously. Data for each individual was processed using a custom-written script (K.S.L.) in Matlab (MathWorks; see also [14,41] for further details on the flight mills).

Flight experiments were conducted between May and November 2016. Flight trials were conducted throughout the day during 09.00–22.00. Care was taken to spread the trials of the different phenotypes throughout the day. All experiments were carried out in a sealed climate chamber at 20°C with a day–night cycle of 16:8 h light:dark. Flies with damaged wings, or that were no longer able to fly were not used for the experiments. Before attachment to the pin, a flight test was conducted by using a vial and releasing the fly in to the air. If a hoverfly was not able to fly, it was excluded from any further experiments. All individuals were randomly assigned to one of the five flight mills. Hoverflies were flown in a clockwise rotation. Immediately after putting the flies on the flight mills, they were given a piece of paper (approx. 1×1 cm) as a platform. At the start of the experiments, the piece of paper was removed as simultaneously as possible from all flies. Hoverflies that did not start flying were stimulated to fly once by putting a finger under their body and then removing it. During the experiments, the flies were able to see each other, therefore, experiments were only conducted when at least two individuals were present. All individuals were left on the flight mill for 4 h. Any hoverfly that looked damaged, unhealthy or that died during the experiment was excluded from further analysis (5 of 232 animals tested). Observational experiments were also carried out to distinguish flight from hovering: hovers never resulted in the striped disc of the flight mill moving for more than 10 s, and thus flights of less than 10 s were excluded. Immediately after the flight mill experiments, hoverflies were stored separately in a freezer (-20°C).

To investigate differences in flight ability and behaviour between wild-caught individuals, a subset of migratory individuals

Table 1. Results of linear mixed-effects models comparing the number of flights and total flight duration between phenotypes and sexes of *Episyrphus balteatus*. Laboratory-reared animals include offspring of migrants (males $n = 13$, females $n = 13$), overwintering (males $n = 23$, females $n = 23$) and summer animals (males $n = 26$, females $n = 20$). Wild-caught adults included migrating (males $n = 6$, females $n = 22$) and overwintering flies (males $n = 14$, females $n = 8$). Significance values ($p < 0.05$, indicated by italic type) for fixed effects were determined using likelihood-ratio tests (χ^2 , see Methods for further details of the analysis).

	d.f.	χ^2	<i>p</i> -value
laboratory reared			
number of flights (log)			
phenotype	2	7.723	0.021
sex	1	3.231	0.072
time of day	1	0.422	0.517
phenotype \times sex	2	0.136	0.934
total flight duration (log)			
phenotype	2	3.947	0.139
sex	1	0.374	0.541
time of day	1	1.190	0.275
phenotype \times sex	2	0.675	0.714
wild caught			
number of flights (log)			
phenotype	1	0.008	0.930
sex	1	1.623	0.203
time of day	1	0.000	0.985
phenotype \times sex	1	1.291	0.256
total flight duration (log)			
phenotype	1	0.238	0.626
sex	1	1.327	0.249
time of day	1	0.438	0.508
phenotype \times sex	1	3.748	0.053

($n = 40$, table 1) and all overwintering individuals captured in November ($n = 25$, table 1) were used for tethered flight mill experiments directly. In this case, flies were given a minimum of 12 h to acclimate to the conditions in the climate chambers before the start of the experiments. The experiment was started within the first 72 h after capture. All laboratory-reared individuals were flown within the first day after eclosion to ensure that they did not already show reproductive behaviour [17].

(d) Statistical analysis

All statistical analyses were conducted using R version 3.3.2 [44]. Initially, a generalized linear mixed-effects model with a binomial error distribution was used to compare flight ability between the first generation offspring of the different overwintering phenotypes, using the 'lme4' package for R [45]. Sex, phenotype, the interaction between sex and phenotype, and the time of day each trial was started were incorporated as fixed effects in the model. Date of the trials was included as a random factor in the model. Time at which the trials were started and date of the trials were included to account for the possible confounding effects of diel periodicity and atmospheric factors beyond our control, on flight behaviour (see electronic supplementary material, table S1). The significance of the fixed

factors was analysed using likelihood-ratio tests (chi-squared), comparing the full model to a model without the focal explanatory variable. If a variable was not significant ($p > 0.05$), it was removed from the model, until only significant terms remained. The same procedure was not applied to compare flight ability between wild caught overwintering and migrating flies, as only three flies from 65 tested did not react.

For further analysis, only data from flies that had flown at least two flights over 1 m s^{-1} were included to ensure that we only analysed individuals that were able to fly on the mill (table 1; electronic supplementary material, table S1). A correlation test was performed to determine the relationship between the variables recorded with the flight mills (electronic supplementary material, figure S2). Three parameters considered important for migration were initially chosen: total duration of flights, total distance flown and number of flights. As total distance and total duration were correlated (electronic supplementary material, figure S2), further analyses were conducted using total duration and number of flights.

Total flight duration and number of flights were compared between first generation offspring from the different phenotypes (summer, migrating and overwintering), using linear mixed-effects models, with a Gaussian distribution, using 'lme4'. We fitted the same model structures as in the initial models for flight ability, including sex, phenotype, the interaction between sex and phenotype, and time of the trials as explanatory factors. Date of the trials was included as a random factor in the models. The same procedure was done for the comparison of the different wild caught phenotypes. The significance of the fixed factors was analysed using likelihood-ratio tests, comparing the full model to a model without the focal explanatory variable. The response variables flight duration and number of flights were log-transformed, so that the residuals of the models visually indicated a normal distribution. We calculated the marginal and conditional coefficient of determination (R^2) for each of our models, using the `r.squaredGLMM` function of the R package 'MuMIn' [46]. The marginal R_m^2 represents the proportion of variance explained by the fixed factors, while the conditional R_c^2 represents the proportion of variance explained by the fixed and random factors [47].

3. Results

Overall, 72% of all individuals (168 of 231) were able to fly on the flight mills. There were no differences in flight ability between phenotypes or sexes for either wild-caught or laboratory-reared flies (electronic supplementary material, table S1). The confounding variable, time of day at which the trials were started, was not significant in any of the models (table 1; electronic supplementary material, table S1).

There was no significant interaction between sex and phenotype for the laboratory-reared flies (table 1). However, there was a significant difference between the phenotypes ($R_m^2 = 0.083$, $R_c^2 = 0.174$; table 1). The offspring of migrants initiated significantly more flights than the offspring of overwintering animals (d.f. = 114, $p = 0.046$) and the offspring of summer animals (d.f. = 114, $p = 0.008$; table 1 and figure 2*a*). By contrast, the number of flights did not differ between offspring of overwintering and summer females (d.f. = 114, $p = 0.421$).

Although the offspring of migrants initiated more flights than the offspring of the other phenotypes, this increase did not translate into longer total flight duration (table 1 and figure 2*b*). Similarly, there was no significant interaction between sex and phenotype in relation to total flight duration (table 1 and figure 2*b*).

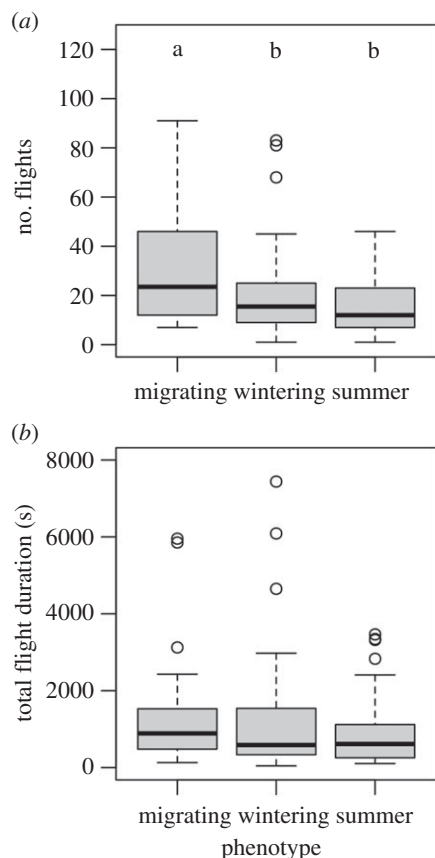


Figure 2. (a) Number of flights and (b) flight duration in seconds between first generation hoverflies reared in the laboratory from migrating, overwintering and summer animals. Significant contrasts ($p < 0.05$) are indicated by different lower case letters. One outlier from the number of flights of overwintering flies has been excluded from the plot for clarity.

The increased flight activity observed in the offspring of migrants compared with other phenotypes was not reflected in the comparison between wild-caught migrants and overwintering flies (table 1 and figure 3). There was no significant interaction between sex and phenotype for either number of flights, or total flight duration (table 1).

4. Discussion

We have demonstrated behavioural differences between the offspring of resident and migrating *E. balteatus*, with the offspring of migrants undertaking more flights than the offspring of summer or overwintering animals. Interestingly, we found no difference in flight behaviour between actively migrating and overwintering hoverflies collected from the field, under laboratory conditions. There were no differences observed in flight ability between sexes or phenotypes.

The observed behavioural differences between the offspring of hoverflies from different overwintering strategies suggest that the decision to migrate in hoverflies might be heritable. While Raymond *et al.* [37] did not detect any genetic differentiation between different overwintering strategies, using microsatellites, such differentiation might not be detected using neutral markers [48]. First generation migrants initiated more flights throughout the experiment than offspring of overwintering hoverflies. Heritability of migratory tendency has been found in several species of insects, such as the moths *Mythimna separata* [18] and *Spodoptera exempta* [20], and the grasshopper *Melanoplus sanguinipes* [19], but this is the first

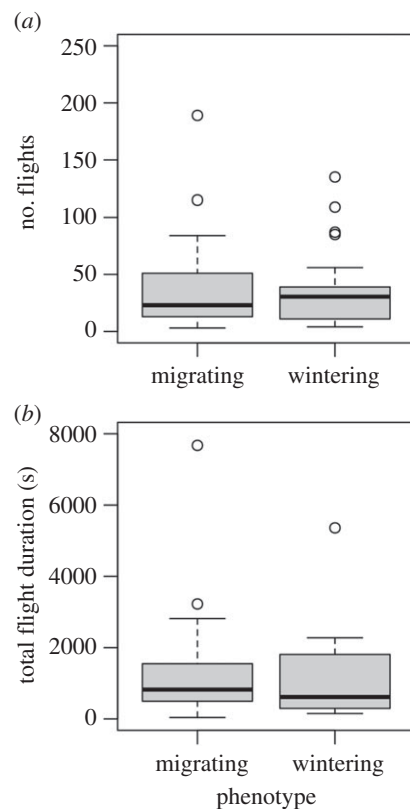


Figure 3. (a) Number of flights and (b) total flight duration in seconds between wild-caught migrating and overwintering hoverflies. There were no significant contrasts ($p < 0.05$).

investigation of this phenomenon in hoverflies. Furthermore, many previous studies that have investigated heritability in migratory traits in insects have often focused on wing-dimorphic insects, where migratory and non-migratory forms differ in wing morphology (see [2]).

Interestingly, no significant difference was detected in total flight duration between the offspring of migrating and resident flies. It is believed that environmental cues such as wind [49–51] or a change in temperature [52] are important for the departure or the continuation of migratory movement in insects [5]. Hoverflies did not receive these environmental cues in the laboratory, as temperature stayed constant throughout the experiment, and simulating wind in the laboratory was not possible, since flight mills record even the slightest movement. The absence of these environmental cues might be the reason why the short flights did not turn into longer migratory flights. However, the increased number of flights in the offspring of migrants suggests that they are more prone to flying than the offspring of other phenotypes. Heritability in the urge to fly, also called migratory restlessness, is relatively well explored in birds (e.g. [16,53–55]). Here, the number of attempted flights in *E. balteatus* could be considered as a comparable assay to migratory restlessness, and may prove useful for determining migratory propensity in hoverflies and other migratory insects.

No significant difference was detected between wild-caught migrants and overwintering individuals in number of flights or total flight duration. We believe that this relative lack of activity is due to an energy-conserving state these migrating animals fall into when caught during active migration and transported to the laboratory. Similar results were found by Odermatt *et al.* [13], who showed that migratory flies tended to be consistently less active

than summer individuals, when tested in the laboratory. Migratory flights have been shown to involve immense energy expenditures in birds [56] and this is also true for insects [57,58]. Thus, we may expect physiological differences between migratory and resident phenotypes, as shown by Attisano *et al.* [39] in milkweed bugs, *Oncopeltus fasciatus*. Another reason for the lack of difference in flight behaviour between wild caught migratory and overwintering hoverflies could be due to the absence of certain environmental cues in the laboratory. Similar to triggering migration, individuals collected from the field might depend on these environmental cues for the continuation of their migratory flight. Since, in the laboratory, they are not exposed to these cues, they may conserve their energy for when they are able to continue their migration [13]. While holding wild-caught flies under laboratory conditions prior to experiments could possibly have some influence on behaviour, we decided that the best way to reduce confounding variables to a minimum was to hold all experimental flies (briefly) under the same conditions. If we had kept them all under the different conditions reflecting their natural state, this would certainly have increased the potential for confounding variables. However, this is unlikely to have had any effect on our result that the offspring of migrants showed increased flight activity compared with the offspring of non-migrants.

Contrary to our predictions, we did not find any differences in the number of flights or the flight duration between sexes within phenotypes. While male and female hoverflies both migrate, males are often the less abundant sex during migration [59]. Male migrants do not have any reproductive constraints, whereas females migrate with an undeveloped reproductive system [35]. While no differences were shown in resting metabolic rate between male and female *E. balteatus* [60], this is yet to be investigated in migrating individuals. The lack of

difference in flight duration between male and female offspring of migrants might be explained by the offspring being freshly emerged and a maximum of 48 h old. Reproduction is not important in the first few days, and females only start laying eggs after 12 days [61]. However, they were not expected to differ in their propensity to fly, given the number of flights is less restricted by the difference in energy expenditure of the two sexes, since most of the energy is used during long flights.

In summary, we have shown that offspring of different phenotypes differ in their flight behaviour, strongly suggesting genetic factors influencing migratory tendency in *E. balteatus*. Moreover, we hypothesize that appropriate environmental cues are important for maintaining migration, as we found no difference in flight behaviour between the wild-caught phenotypes. Future investigations should include studies under field conditions that are close to conditions hoverflies experience during migration, allowing environmental factors to be incorporated into tethered flight experiments.

Data accessibility. Data are available from the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.44hc2>) [62].

Authors' contributions. L.J.D., A.G., K.S.L., J.W.C. and M.H.M.M designed the experiments. L.J.D. and A.G. carried out the experiments with assistance from K.S.L. and M.H.M.M. L.J.D. wrote the initial draft of the manuscript with assistance from M.H.M.M, and input and revisions from all authors.

Competing interests. We declare we have no competing interests.

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