Insect
science

Insect Science (2021) 0, 1–10, DOI 10.1111/1744-7917.12950

ORIGINAL ARTICLE

Size-dependent flight capacity and propensity in a range-expanding invasive insect

Chelsea Jahant-Miller[1,3], Russell Miller[2] and Dylan Parry[3]

[1]*Forest Health Protection, U.S. Forest Service, Coeur d'Alene, ID, 83815, USA;* [2]*School for Environment and Sustainability, Cooperative Institute for Great Lakes Research, University of Michigan, Ann Arbor, MI, 48106, USA and* [3]*Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, Syracuse, NY, 13210, USA*

Abstract For capital-breeding insects, all resources available for adult metabolic needs are accumulated during larval feeding. Therefore, body size at adult eclosion represents the total energetic capacity of the individual. For female capital breeders, body size is strongly correlated with lifetime fecundity, while in males, body size, which correlates with fitness, is less understood. In capital-breeding species with wingless, flightless, or dispersal-limited females, flight potential for male Lepidoptera has important implications for mate-finding and may be correlated with body size. At low population densities, failure to mate has been identified as an important Allee effect and can drive the success or failure of invasive species at range edges and in species of conservation concern. Th capital-breeding European subspecies of *Lymantria dispar* (L.), was introduced to North America in 1869 and now ranges across much of eastern North America. In *L. dispar*, females are flightless and mate-finding is entirely performed by males. We quantified male *L. dispar* flight capacity and propensity relative to morphological and physiological characteristics using fixed-arm flight mills. A range of male body sizes was produced by varying the protein content of standard artificial diets while holding other dietary components constant. Wing length, a proxy for body size, relative thorax mass, and forewing aspect were all important predictors of total flight distance and maximum speed. These results have important implications for mate-finding and invasion dynamics in *L. dispar* and may apply broadly to other capital-breeding insects.

Key words flight mill; Lymantria dispar; life-history; invasion dynamics; selective pressure

Introduction

Variation in resources and their allocation affect the quantity and fitness of offspring that individuals produce in a given environment (Boggs & Freeman, 2005; Boggs, 2009). For holometabolous insects, including Lepidoptera, energy and nutrients acquired in the larval stage are later redistributed to fuel the formation of adult body structures during the pupal stage and meet adult metabolic and reproductive needs (Boggs, 2009). While income breeding species feed as adults and use accumulated resources to supplement reproduction, capital breeders depend entirely on resources accrued as larvae for all adult functions (Tammaru & Haukioja, 1996; Davis *et al*., 2016). Thus, in capital breeders, body size is indicative of the total energy and material reserve available for adult dispersal, mate-finding, and reproduction.

Estimating fitness for female capital-breeding insects is done relatively easily by counting the number of eggs a female produces (Hough & Pimentel, 1978; Tammaru *et al*., 1996a; Tisdale & Sappington, 2001, Parry *et al*.,

Correspondence: Chelsea Jahant-Miller, Forest Health Protection, U.S. Forest Service; Coeur d'Alene, ID 83815, USA. Tel: (734) 972–6292; Email: chelsea.jahantmiller@usda.gov

2001). On the other hand, determining correlates of male fitness by quantifying the number of eggs fertilized following a controlled mating event or by measuring male flight capacity is more difficult and is done less frequently (e.g., Boggs & Gilbert, 1979; Svärd & Wiklund, 1989; Tammaru *et al*., 1996b; Tobin *et al*., 2014). Male flight may be particularly important for capital-breeding species where males do most or all of the mate-finding (Berec *et al*., 2018; Javoiš *et al*., 2019). Mate location is critical for overcoming mate-finding Allee effects in small isolated populations or those at low density near range edges (Contarini *et al*., 2009; Yamanaka & Liebhold, 2009; Rhainds, 2010). Therefore, factors that influence male flight capacity and mate-finding ability in capital-breeding species (e.g., resource acquisition and body size) may impact persistence of small populations and establishment in range-expanding populations.

The European strain of *Lymantria dispar* was introduced to North America in 1869 and now ranges from northern Minnesota to the Outer Banks of North Carolina (Grayson & Johnson, 2018). Adults are sexually dimorphic and, in North America, have flight-capable males and winged but flightless females (Doane & McManus, 1981). Thus, energy expended by adult females is allocated primarily to the production and emission of pheromone and the manufacturing and provisioning of eggs, whereas males allocate their resources to flight. While the strong linear relationship between female pupal mass and fecundity is well established (e.g., Hough & Pimentel, 1978; Faske *et al*., 2019), no studies to our knowledge have assessed the relationship between body size and flight capacity for male *L. dispar*. Given that insect body size is often correlated with metrics of flight capacity (e.g., Davis *et al*., 2012; Evenden *et al*., 2014; Jones *et al*., 2016), and flight-related morphology such as wing load and forewing aspect ratio affect flight capability in other Lepidoptera (Le Roy *et al*., 2019), male *L. dispar* flight capacity may also be affected by body size and flight-related morphology.

Fixed-arm flight mills provide a valuable avenue for investigating effects of physiological, morphological, and environmental variation on flight capacity and dispersal under controlled conditions (Minter *et al*., 2018; Naranjo, 2019). Although tethered flight mills have been used to determine the effect of morphological and physiological characteristics on females of the Asian subspecies of *L. dispar*, a strain with strong female flight ability (Shi *et al*., 2015, Yang *et al*., 2017), to our knowledge, none have done so for any strain of male *L. dispar*. Our study assessed the relationship between resource acquisition and allocation and male flight capacity for the European *L. dispar*, an economically and ecologically important invasive capital breeder. Specifically, we used flight mills to assess the direction and influence of several morphological and physiological characteristics on male *L. dispar* flight performance. We predicted that: (i) due to greater stored energetic resource availability with increasing male body size, increasing body size would correspond to greater flight distance, speed, and flight propensity; and (ii) variation in wing and thoracic morphology would affect male flight distance and speed.

Materials and methods

Insect rearing

In natural environments, the mass of male *L. dispar* pupae and adults varies greatly as a function of diet quality, population density, and temperature experienced as a larva (Carter *et al*., 1991; Lindroth *et al*., 1997; Lazarevic *et al*., 2004; Jahant-Miller *et al*., 2020). To investigate the effects of male size on flight capacity required methodology to produce a range of sizes while minimizing the effects of other confounding factors on flight metrics. To produce a range of male sizes for experimentation, we used an agar-based artificial *L. dispar* diet (Leonard & Doane, 1966) and manipulated protein content while holding all other nutrients constant. Males were reared on four diet formulations (high protein, medium-high protein, medium-low protein, low protein; Table S1). To compensate for reduced protein content, the equivalent amount by weight of food grade cellulose powder was added to keep the weight ratio of other ingredients equal across all diet mixes. Fresh diet was poured in 0.47 L plastic-lined paper soup containers and provided to larvae *ad libitum*. Larvae were reared in a growth chamber at 25°C and a photoperiod of 15 : 9 (L : D). Upon pupation, individuals were weighed to the nearest 0.000 1 g and returned to the growth chamber in individual 59.15 mL plastic containers until adult emergence.

Flight mill design

Flight mills were assembled using the design described by Jones *et al*. (2010; Appendix 1). During each assay, a moth was attached distally to a rotating arm (18.34 cm diameter) and a magnetic sensor detected a small magnet below the flight mill arm at each full rotation as the moth powered the mill (Fig. 1A). The magnetic sensor was connected to a microcontroller (Fig. S1) that read up to eight sensors and converted rotation and time information to a USB signal for logging by a terminal program (TeraTerm) on a personal computer. Opposite-facing

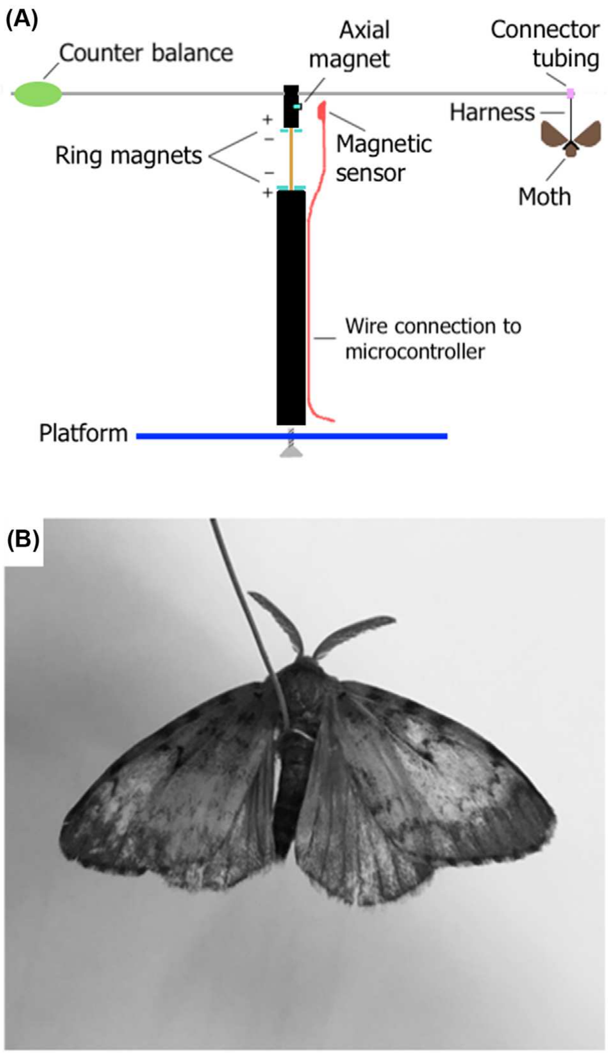

Fig. 1 (A) Schematic of fixed-arm flight mill with tethered moth. Rotating arm is held above mill using opposite-facing magnets to reduce rotational friction. A magnetic sensor detected magnetic impulse at each full rotation and a computer program linked to flight mill recorded each rotation with a timestamp. (B) Male *L. dispar* with inverted y shaped harness glued to descaled first abdominal segment. Image was taken following 24 h flight assay.

magnets reduced rotational friction by levitating the flight mill arm above the axle.

Flight assay

Pupae were checked at least twice daily for adult emergence. Moths that emerged and were not flown right away were held individually in small plastic containers at 4 ˚C until ready to be flown. All flight assays were initiated within 24 hours of emergence. Prior to harness placement, moths were cold anesthetized at approximately −18 °C for up to 2 min, then weighed to the nearest 0.000 1 g. Inverted y-shaped wire harnesses (Fig. 1B) were glued dorsally to the descaled first abdominal segment using cyanoacrylate gel super glue. Moths were reweighed with the harness and attached to the distal end of the flight mill arm using thin plastic tubing. A piece of soft polymer clay equal to the weight of the moth and harness was attached to the opposite end as a counterbalance.

Flight assays began at the start of the photophase (light period) and ran for 24 h with photoperiod of 15 : 9 (L : D). Photophase and scotophase temperatures were 25 °C and 15 °C, respectively, which are similar to ambient temperatures *L. dispar* encounter in their invasive range. During flight assays, total distance and duration of each individual flight was recorded, along with morphological (pupal mass, moth mass, wing length, width, and area, thorax width, height and shape, relative thorax mass, relative abdominal mass, and forewing aspect) and physiological (mass lost during flight, relative mass lost during flight) moth characteristics. Moths that had stopped flying were encouraged to fly every 15 min using gentle tactile stimulation (i.e., paintbrush touches to the legs, posterior edge of the wings, or antennae) for the first 8 h of each flight assay. Moths that became detached from the flight mill during the flight assay or that did not fly at all due to injury during preflight procedures were excluded from analyses. Following the 24-h flight assay, moths were removed from flight mills, frozen, and reweighed to quantify mass lost during flight. The right forewing of each male was removed and scanned, and the digital image of each wing was analyzed using ImageJ software to determine wing length, wing width, and wing area. Thorax mass and abdominal mass were measured by carefully separating each tagma using a scalpel and weighing them individually on a digital balance to the nearest 0.000 1 g. Wing load was calculated as initial moth mass divided by two times the wing area (g/cm^2). Forewing aspect ratio was calculated as four times the squared length of the forewing divided by forewing area (mm/cm^2). Relative thorax mass was calculated as the mass of the thorax divided by the preflight moth mass, and relative abdominal mass was calculated as the mass of the abdomen divided by the preflight moth mass. Thorax width and height were measured to the nearest 0.01 mm using a digital caliper. Thorax shape was calculated as the width of the thorax divided by the height. Mass lost during flight was measured as the initial mass of the moth minus the mass of the moth measured immediately after the flight assay, and ratio of mass lost was

Table 1 Summary statistics for dependent (total distance, maximum speed attained) variables and wing length.

Flight capacity metric	Mean ± SD	Median	Minimum	Maximum
Total distance (km)	19.96 ± 16.74	15.98	1.24	68.22
Maximum speed (m/s)	1.21 ± 0.37	1.21	0.32	1.93
Wing length (mm)	2.06 ± 0.21	2.03	1.64	2.53

calculated as mass lost during flight divided by initial moth mass.

Flight propensity was measured as the number of flights consisting of more than 100 full rotations initiated upon tactile stimulation divided by the total number of touches for each individual moth. One hundred rotations was equal to approximately 58 m of linear flight.

Variable selection

Total distance flown and maximum speed were used as dependent variables. Based on biological significance, wing length, which correlates strongly with pupal mass (Tobin *et al*., 2016; Jahant-Miller *et al*., 2020), was chosen to represent body size, and proportionate mass lost during flight (RatioMD), forewing aspect ratio (FWa), and relative thorax mass (RTM) were also included in the model and each represented a different physiological or morphological component. Variables selected for the full models were not strongly correlated ($P < 0.4$). Flight mill identity was included in both models as a random effect to capture any variation in measured flight capacity metrics caused by any physical differences in flight mill design. Since insects do not need to produce lift during tethered flight, wing load was not included in flight capacity analyses.

Statistical analysis

All data analyses were performed in R (version 3.6.1, R Core Development Team, 2019). Significance level for all analyses was $\alpha = 0.05$. Effects of morphological and physiological characteristics on metrics of male flight capacity were analyzed using mixed effects linear regression analysis. Fixed effects and pairwise interaction effects were tested using stepwise model selection (package *lmerTest*; Kuznetsova *et al*., 2017). For each dependent variable, full and reduced models were compared using Akaike information criterion and analysis of variance (ANOVA) hypothesis testing. Model normality and homoscedasticity were checked using residual plots. Total distance flown was square root transformed to improve normality. Effect of wing length on flight propensity was compared using one-way ANOVA.

Results

A total of 96 male *L. dispar* were flown. Mean pupal mass of flown moths was 0.41 ± 0.013 g (mean ± SE) and ranged 0.19–0.73 g, values that encompass much of the variation seen in males from natural populations (Jahant-Miller *et al*., 2020). Mean wing length was 2.06 ± 0.021 cm and ranged 1.64–2.53 cm (Table 1). High protein diet produced the greatest mean pupal mass (0.4362 ± 0.014 g), followed by medium-high (0.4002 ± 0.048 g), medium-low (0.3409 ± 0.027 g), and low (0.1823 ± 0.014 g). High, medium-high, and medium-low protein diets supported relatively high survival rates, while low protein diet did not. As a result, no moths reared on low protein diet were used in flight assays. In total, high protein, medium-high, and medium-low diets produced 70, 11, and 15 moths flown in flight assays, respectively.

Flight capacity

Wing length was the strongest predictor for both flight capacity metrics (total distance and maximum speed) in the mixed regression models (Tables 2, 3). Total distance flown ($F_{1,99} = 98.47, P < 0.0001$; Fig. 2A) and maximum speed ($F_{1,93} = 80.17, P < 0.0001$; Fig. 3A) were significantly impacted by wing length. Large moths in the upper quartile for wing length ($n = 27$, $X_{\mathrm{WL}} = 2.33$ cm [2.22–2.53 cm]) flew on average 31.6 km (11.6–68.2 km), or 282% more than small moths in the lower quartile ($n = 24$, $X_{\mathrm{WL}} = 1.80$ cm [1.64–1.89 cm]) which flew on average 11.2 km (0.12–44.9 km). Forewing aspect ratio had a significant negative effect on total distance ($F_{1,91} = 30.32, P < 0.0001$; Fig. 2D) and maximum speed ($F_{1,93} = 17.70, P < 0.0001$; Fig. 3B). Reduced forewing aspect was associated with greater flight speed and greater total distance flown. Relative thorax mass had a significant positive effect on total flight distance ($F_{1,91} = 28.17, P < 0.001$; Fig. 2B).

Table 2 Intercept and slope coefficients for total distance (m) mixed linear regression. Total distance was square root transformed to improve residual normality.

Explanatory variable	Estimate	SE	Lower CI (5%)	Upper CI (95%)	t (df = 91)	P	Est. model R^2
Intercept	75.77	110.41	−137.95	46.41	0.69	0.49	0.59
Wing length	204.78	20.63	161.58	239.59	9.92	<0.001	
Relative mass lost	−14.16	24.58	−120.40	−6.67	−0.58	0.57	
Forewing aspect ratio	−50.94	9.25	−67.40	−32.53	−5.51	<0.001	
Relative thorax mass	507.00	95.52	289.33	651.88	5.31	<0.001	

Table 3 Intercept and slope coefficients for maximum speed (m/s) mixed linear regression.

Explanatory variable	Estimate	SE	Lower CI (95%)	Upper CI (95%)	t (df = 91)	P	Est. model R^2
Intercept	1.53	0.68	0.20	2.86	2.25	0.03	0.48
Wing length	1.21	0.13	0.94	1.47	8.95	< 0.001	
Forewing aspect ratio	−0.26	0.06	−0.37	−0.14	−4.21	< 0.001	

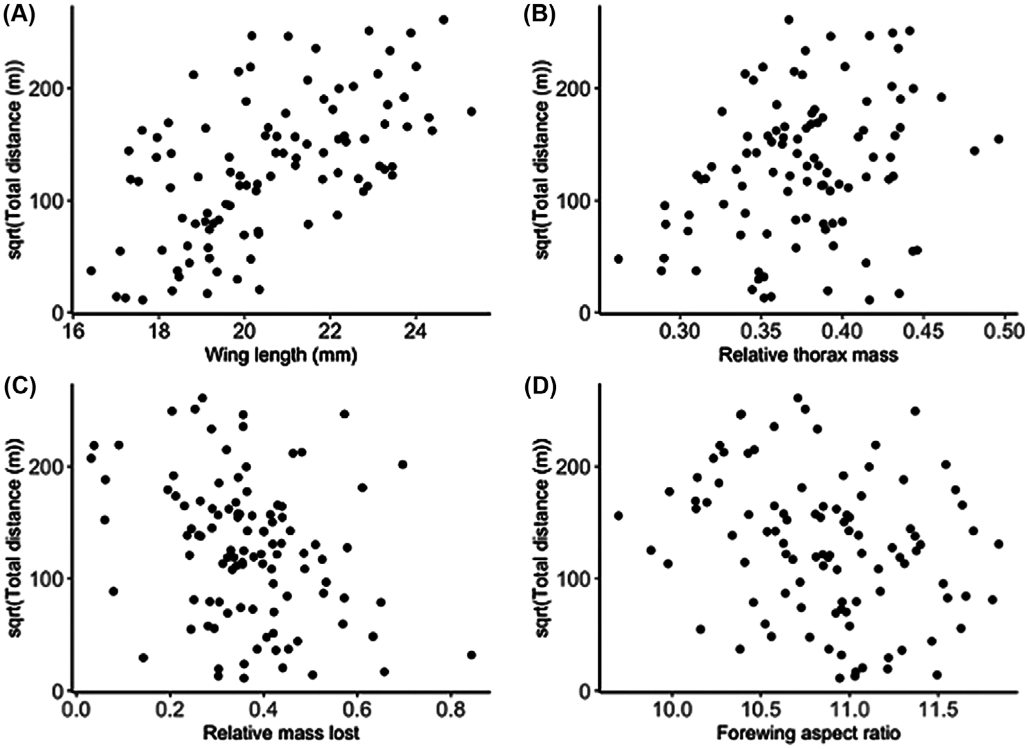

Fig. 2 Scatter plots for the effect of wing length, forewing aspect ratio, relative thorax mass, and relative mass lost during flight on distance flown.

Flight propensity

All but five moths recorded at least one response flight consisting of more than 100 full rotations; wing lengths of those that did not were 17.0, 17.22, 17.62, 19.13, and 20.34 mm. Wing length had a significant effect on proportion of sustained flights initiated ($F_{4,91} = 9.43$, $P < 0.001$; Fig. 3C); males with greater wing length were

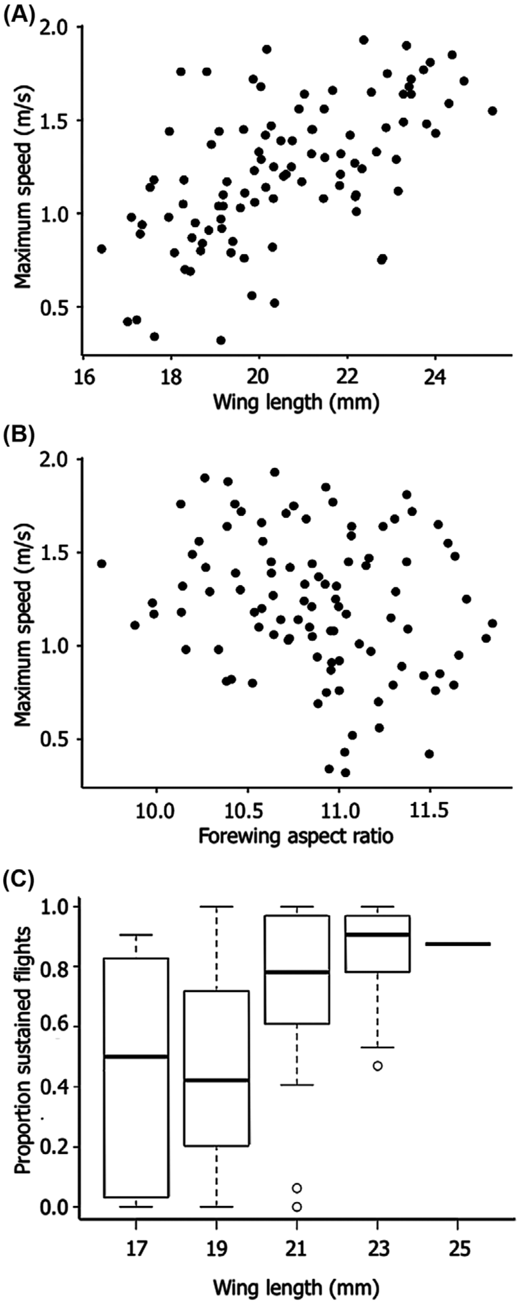

Fig. 3 Scatter plots for significant factors impacting maximum speed attained by male *L. dispar*, including (A) wing length and (B) forewing aspect ratio. Raw data are plotted to visualize effects of wing length and forewing aspect ratio on maximum speed. (C) Boxplot depicting relationship between mean proportion of sustained flights initiated and wing length.

more likely to initiate sustained flight than males with smaller wings.

Discussion

Insect body size is often correlated with greater flight distance and speed (e.g., Dingle *et al.*, 1980; Shirai, 1991; Bruzzone *et al.*, 2009; Evenden *et al.*, 2014; Fahrner *et al.*, 2014; Jones *et al.*, 2016). This study is the first to assess the impact of body size and flight morphometrics on measures of flight capacity for male *L. dispar*. Wing length, a proxy for body size, was the most important predictor for both metrics of flight capacity; large moths were more likely than small moths to initiate sustained flight, and once initiated, larger moths tended toward longer, faster sustained flights than smaller moths. The greatest distance flown in the present study was more than 68 km and was accomplished by one of the largest moths (24.6 mm wing length). However, many midsize moths (19–21 mm wing length) in our study also flew total distances greater than 30 km. Moths with wing lengths between 19 mm and 21 mm are common in both endemic and high-density populations (Tobin *et al.*, 2016; Jahant-Miller *et al.*, 2020). Due to altered physical properties of tethered flight relative to free flight, such as a forced flight path, lack of natural flight stimuli, and the fact that tethered insects do not need to produce lift, extrapolation of tethered flight distances to flight potential in natural settings should be done with caution (Minter *et al.*, 2018).

Other significant predictors for metrics of flight capacity included forewing aspect ratio for speed and distance, and relative thorax mass for distance, and relative mass lost during flight for distance. Aspect ratio describes the shape of a wing where higher values indicate a longer, narrower wing and lower values indicate a shorter, broader wing. For aircraft and some flying animals including insects, aspect ratio is negatively correlated with flight speed and positively correlated with flight efficiency during gliding flight because longer, narrower wings produce less drag (Saville, 1957; Dudley & Srygley, 1994; Davis *et al.*, 2012). Energy storage for insect flight and flight musculature are thoracic components and flight metrics such as distance and speed are often correlated with increased relative thorax mass (Dudley & Srygley, 1994; Marden, 2000; David *et al.*, 2015). Relative mass lost during flight had a negative relationship with total distance flown, indicating that larger moths may use a smaller proportion of their stored resources than smaller moths and may have the capacity to continue flying longer than our flight assay allowed.

Most female *L. dispar* mate only once and appear non-selective, thus, the first male to reach the female has a reproductive advantage (Doane & McManus, 1981). This suggests that being the fastest flier with the greatest endurance would be ideal; however, large body size can generally only be attained at the cost of longer larval development. All else being equal (i.e., foliar quality, temperature, etc.), genetically larger individuals take more time to develop than smaller conspecifics (Hough & Pimentel, 1978; Teder *et al*., 2014, but see Thompson *et al*., 2020 for latitudinal differences among populations). Adaptation towards greater flight capacity may ultimately put larger males at a mating disadvantage unless environmental conditions require mate-finding flights that cover greater distances, such as in low-density populations. Conversely, as a protandrous species, larger male *L. dispar* could gain a mating advantage over smaller males if delaying emergence improves synchrony with female emergence (Robinet *et al*., 2007), especially in low-density populations. While body size is the greatest factor impacting flight capacity, changes to wing or thorax morphology can also alter *L. dispar* flight ability and could do so without affecting development time.

Density-dependent shifts in mating or mate-finding morphology occur in other arthropods. In the amphipod *Gammarus roeselii*, individuals exhibit differential allocation to mating morphology in response to population density (Lipkowski *et al*., 2019). In high-density *G. roeselii* populations where mating competition is relatively intense, individuals express larger antennae to increase mate selectivity and larger grasping legs to reduce the likelihood of having a mate stolen. In a wing-dimorphic planthopper *Prokelisia dolus* Wilson, flight-capable males in low-density populations with fully developed wings had greater mate-finding ability compared to wingless morphs, but at the cost of reduced fecundity (Langellotto & Denno, 2001).

Morphological and physiological adaptation that facilitates dispersal has been documented for several plant and animal phyla at invasion fronts, as well as areas in which species frequently undergo extinction and colonization events (Phillips *et al*., 2006; Darling *et al*., 2008; Forsman *et al*., 2010; Schäfer *et al*., 2018). In cane toads, *Rhinella marina* (Linneaus), for example, dispersal ability increases with leg length and more recently established populations (e.g., those at the invasion front) in Australia have longer legs than populations behind the invasion front (Phillips *et al*., 2006). Similar intraspecific variation in dispersal-related morphology and physiology has been reported for the butterfly *Melitaea cinxia* (Linneaus) and for invasive starlings, *Sturnus vulgaris* Linneaus, in Australia (Haag *et al*., 2005).

In low-density populations, emigration can exacerbate inverse density-dependent Allee effects such as mate-finding success and cooperative feeding behaviors, and ultimately lead to range retraction (Taylor & Hastings, 2005; Tobin *et al*., 2009). However, in *L. dispar*, male dispersal from established populations in the range interior to the range margin could improve mating success by alleviating Allee effects caused by mate-finding failure typical of very low-density populations (Sharov *et al*., 1995; Liebhold & Bascompte, 2003; Contarini *et al*., 2009; Tobin *et al*., 2009). Increased dispersal ability of male *L. dispar* from just behind the invasion front to nascent satellite populations ahead of it has the potential to increase establishment success and the rate of range expansion.

Size-dependent effects of flight ability on mate-finding may be relevant to other capital-breeding Lepidoptera, especially populations experiencing Allee effects and those in which females are non-dispersing prior to mating. A body size effect on mate-finding success has been shown in some other capital-breeding Lepidoptera. For example, male autumnal moth *Epirrita autumnata* Borkhausen mating in low-density field populations were larger than mean population size, indicating that there may be a size-dependent advantage, although it is unclear whether it is from mate-finding or mating competition (Tammaru *et al*., 1996b). Evenden *et al*. (2015a) identified a mate-finding Allee effect in a capital-breeding spring defoliator, *Malacosoma disstria* Hübner; caged females were mated more frequently in high-density populations than low. Although large males originating from endemic populations were more likely to initiate mate-searching flight behavior than small males from outbreak populations, there was no apparent mate-finding advantage for larger body size (Evenden *et al*., 2015a, Evenden *et al*., 2015b). Mated males of the saturniid *Rothschildia lebeau* Guerin-Meneville tended to be larger on average than non-mated males in a field study that used caged females to attract endemic males (Agosta, 2010).

Adaptive shifts in wing morphology facilitating dispersal ability at the invasion front are unknown in *L. dispar*. Counterselection favoring small male body size may be driven by short growing seasons and cool climates encountered by range-expanding populations in northern regions. In addition, a significant component of *L. dispar* range expansion is driven by human-vectored movement of life stages (Sharov & Liebhold, 1998; Bigsby *et al*., 2011; Tobin & Blackburn, 2014). Movement of propagules from established areas to range front populations may swamp any adaptive change. Despite known barriers to adaptation, recent studies indicate that rapid adaptation is occurring in *L. dispar* populations in response to environmental conditions at range margins (e.g., Thompson *et al.*, 2017, 2020; Faske *et al.*, 2019). Future studies should take advantage of common garden studies, which disentangle genetic and environmental effects on body size, to detect potential shifts in *L. dispar* body size or flight morphology in this and other range-expanding invasive insects.

Acknowledgments

Many thanks to Melody Keena (USFS), Ann Hajek and Tonya Bittner (Cornell University) for their advice on improving larval rearing procedures. We thank Toomas Tammaru (University of Tartu) for graciously reviewing and providing substantive comments on an earlier version of the manuscript. Kristine Grayson (Richmond University), David Althoff (Syracuse University) and Melissa Fierke and Colin Beier (SUNY-ESF) provided helpful comments on earlier versions of the manuscript. Thanks to Kiyoto Tanemura (Michigan State University) for help with writing R code and to Dr. Lianjun Zhang (SUNY-ESF) for input on statistical analyses. Our lab technician Marina Wittman provided valuable assistance weighing and mixing diet ingredients. Funding was provided by Macrosystems Biology (Grant 1702701 to Kristine Grayson, Sal Agosta, and Dylan Parry) and Gypsy Moth Slow-the-Spread Foundation, Inc (Grant 19-01-13 to DP).

Author contributions

CJM and DP conceived and designed the experiments. RM designed the flight mill apparatus and provided technical assistance. CJM performed the experiments and analyzed the data. CJM and DP wrote the manuscript.

Disclosure

The authors declare no competing or financial interests.

References

Agosta, S.J. (2010) Male body size and mating success and their relation to larval host plant history in the moth *Rothschildia lebeau* in Costa Rican dry forest. *Biotropica*, 42, 201–207.

Berec, L., Kramer, A.M., Bernhauerová, V. and Drake, J.M. (2018) Density-dependent selection on mate search and evolution of Allee effects. *Journal of Animal Ecology*, 87, 24–35.

Bigsby, K.M., Tobin, P.C. and Sills, E.O. (2011) Anthropogenic drivers of gypsy moth spread. *Biological Invasions*, 13, 2077–2090.

Boggs, C.L. and Gilbert, L.E. (1979) Male contribution to egg production in butterflies: Evidence for transfer of nutrients at mating. *Science*, 206, 83–84.

Boggs, C.L. (2009) Understanding insect life histories and senescence through a resource allocation lens. *Functional Ecology*, 23, 27–37.

Boggs, C.L. and Freeman, K.D. (2005) Larval food limitation in butterflies: Effects on adult resource allocation and fitness. *Oecologia*, 144, 353–361.

Bruzzone, O.A., Villacide, J.M., Bernstein, C. and Corley, J.C. (2009) Flight variability in the woodwasp *Sirex noctilio* (Hymenoptera: Siricidae): An analysis of flight data using wavelets. *Journal of Experimental Biology*, 212, 731–737.

Carter, M.R., Ravlin, F.W. and McManus, M.L. (1991) Changes in gypsy moth (Lepidoptera: Lymantriidae) fecundity and male wing length resulting from defoliation. *Environmental Entomology*, 20, 1042–1047.

Contarini, M., Onufrieva, K.S., Thorpe, K.W., Raffa, K.F. and Tobin, P.C. (2009) Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. *Entomologia Experimentalis et Applicata*, 133, 307–314.

Darling, E., Samis, K.E. and Eckert, C.G. (2008) Increased seed dispersal potential towards geographic range limits in a Pacific coast dune plant. *New Phytology*, 178, 424–435.

David, G., Giffard, B., Van Halder, I., Piou, D. and Jactel, H. (2015) Energy allocation during the maturation of adults in a long-lived insect: Implications for dispersal and reproduction. *Bulletin of Entomological Research*, 105, 629–636.

Davis, A.K., Chi, J., Bradley, C. and Altizer, S. (2012) The redder the better: Wing color predicts flight performance in monarch butterflies. *PLoS ONE*, 7, e41323.

Davis, R.B., Javoiš, J., Kaasik, A., Õunap, E. and Tammaru, T. (2016) An ordination of life histories using morphological proxies: Capital vs. income breeding in insects. *Ecology*, 97, 2112–2124.

Dingle, H., Blakley, N.R. and Miller, E.R. (1980) Variation in body size and flight performance in milkweed bugs (*Oncopeltus*). *Evolution; Internation Journal of Organic Evolution*, 34, 371–385.

Doane, C.C. and McManus, M.E. (1981) *The gypsy moth: research toward integrated pest management*. U.S. Department of Agriculture.

Dudley, R. and Srygley, R. (1994) Flight physiology of neotropical butterflies: Allometry of airspeeds during natural free flight. *Journal of Experimental Biology*, 191, 125–139.

Evenden, M.L., Whitehouse, C.M. and Sykes, J. (2014) Factors influencing flight capacity of the mountain pine beetle

(Coleoptera: Curculionidae: Scolytinae). *Environmental Entomology*, 43, 187–196.

Evenden, M.L., Whitehouse, C.M. and Jones, B.C. (2015a) Resource allocation to flight in an outbreaking forest defoliator *Malacosoma disstria*. *Environmental Entomology*, 44, 835–845.

Evenden, M.L., Mori, B.A., Sjostrom, D. and Roland, J. (2015b) Forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae), mate-finding behavior is greatest at intermediate population densities: Implications for interpretation of moth capture in pheromone-baited traps. *Frontiers in Ecology and Evolution*, 3, 78.

Fahrner, S.J., Lelito, J.P., Blaedow, K., Heimpel, G.E. and Aukema, B.H. (2014) Factors affecting the flight capacity of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae), a classical biological control agent of *Agrilus planipennis* (Coleoptera: Buprestidae). *Environmental Entomology*, 43, 1603–1612.

Faske, T.M., Thompson, L.M., Banahene, N., Levorse, A., Herrera, M.Q., Sherman, K. *et al*. (2019) Can gypsy moth stand the heat? A reciprocal transplant experiment with an invasive forest pest across its southern range margin. *Biological Invasions*, 21, 1365–1378.

Forsman, A., Merilä, J. and Ebenhard, T. (2010) Phenotypic evolution of dispersal-enhancing traits in insular voles. *Proceedings of the Royal Society B: Biological Sciences*, 278, 225–232.

Grayson, K.L. and Johnson, D.M. (2018) Novel insights on population and range edge dynamics using an unparalleled spatiotemporal record of species invasion. *Journal of Animal Ecology*, 87, 581–593.

Haag, C.R., Saastamoinen, M., Marden, J.H. and Hanski, I. (2005) A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2449–2456.

Hough, J.A. and Pimentel, D. (1978) Influence of host foliage on development, survival, and fecundity of the gypsy moth. *Environmental Entomology*, 7, 97–102.

Jahant-Miller, C., Tobin, P.C. and Parry, D., (2020) Spatial and temporal changes in male gypsy moth wing morphology reflect host tree phenology and habitat quality. *Agricultural and Forest Entomology*, 22, 390–400.

Javoiš, J., Davis, R.B. and Tammaru, T. (2019) A comparative morphometric study of sensory capacity in geometrid moths. *Journal of Evolutionary Biology*, 32, 380–389.

Jones, H.B., Lim, K.S., Bell, J.R., Hill, J.K. and Chapman, J.W. (2016) Quantifying interspecific variation in dispersal ability of noctuid moths using an advanced tethered flight technique. *Ecology and Evolution*, 6, 181–190.

Kuznetsova, A., Brockhoff, P.B. and Christensen, R.H.B. (2017) lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, DOI: 10.18637/JSS.V082.I13.

Langellotto, G.A. and Denno, R.F. (2001) Benefits of dispersal in patchy environments: Mate location by males of a wing-dimorphic insect. *Ecology*, 82, 1870–1878.

Lazarevic, J., Peric-Mataruga, V., Vlahovic, M., Mrdakovic, M. and Cvetanovic, D. (2004) Effects of rearing density on larval growth and activity of digestive enzymes in *Lymantria dispar* L. (Lepidoptera: Lymantriidae). *Folia Biologica (Krakow)*, 52, 105–112.

Le Roy, C., Debat, V. and Llaurens, V. (2019) Adaptive evolution of butterfly wing shape: From morphology to behaviour. *Biological Reviews*, 94, 1261–1281.

Leonard, D.E. and Doane, C.C. (1966) An artificial diet for the gypsy moth, *Porthetria dispar* (Lepidoptera: Lymantriidae). *Annals of the Entomological Society of America*, 59, 462–464.

Liebhold, A. and Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, 6, 133–140.

Lindroth, R.L., Klein, K.A., Hemming, J.D. and Feuker, A.M. (1997) Variation in temperature and dietary nitrogen affect performance of the gypsy moth (*Lymantria dispar* L.). *Physiological Entomology*, 22, 55–64.

Lipkowski, K., Plath, M., Klaus, S. and Sommer-Trembo, C. (2019) Population density affects male mate choosiness and morphology in the mate-guarding amphipod *Gammarus roeselii* (Crustacea: Amphipoda). *Biological Journal of the Linnean Society*, 126, 899–911.

Marden, J.H. (2000) Variability in the size, composition, and function of insect flight muscles. *Annual Review of Physiology*, 62, 157–178.

Minter, M., Pearson, A., Lim, K.S., Wilson, K., Chapman, J.W. and Jones, C.M. (2018) The tethered flight technique as a tool for studying life-history strategies associated with migration in insects. *Ecological Entomology*, 43, 397–411.

Naranjo, S.E. (2019) Assessing insect flight behavior in the laboratory: A primer on flight mill methodology and what can be learned. *Annals of the Entomological Society of America*, 112, 182–199.

Parry, D., Goyer, R.A. and Lenhard, G.J. (2001) Macrogeographic clines in fecundity, reproductive allocation, and offspring size of the forest tent caterpillar *Malacosoma disstria*. *Ecological Entomology*, 26, 281–291.

Phillips, B.L., Brown, G.P., Webb, J.K. and Shine, R. (2006) Invasion and the evolution of speed in toads. *Nature*, 439, 803.

Rhainds, M. (2010) Female mating failures in insects. *Entomologia Experimentalis et Applicata*, 136, 211–226.

Robinet, C., Liebhold, A. and Gray, D. (2007) Variation in developmental time affects mating success and Allee effects. *Oikos*, 116, 1227–1237.

Saville, D.B.O. (1957) Adaptive evolution in the avian wing. *Evolution*, 11, 212–214.

Schäfer, M.A., Berger, D., Rohner, P.T., Kjaersgaard, A., Bauerfeind, S.S., Guillaume, F. *et al.* (2018) Geographic clines in wing morphology relate to colonization history in New World but not Old World populations of yellow dung flies. *Evolution; Internation Journal of Organic Evolution*, 72, 1629–1644.

Sharov, A.A. and Liebhold, A.M. (1998) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications*, 8, 1170–1179.

Sharov, A.A., Liebhold, A.M. and Ravlin, F.W. (1995) Prediction of gypsy moth (Lepidoptera: Lymantriidae) mating success from pheromone trap counts. *Environmental Entomology*, 24, 1239–1244.

Shi, J., Chen, F. and Keena, M.A. (2015) Differences in wing morphometrics of *Lymantria dispar* (Lepidoptera: Erebidae) between populations that vary in female flight capability. *Annals of the Entomological Society of America*, 108, 528–535.

Shirai, Y. (1991) Seasonal changes and effects of temperature on flight ability of the diamondback moth*, Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology*, 26, 107–115.

Svärd, L. and Wiklund, C. (1989) Mass and production rate of ejaculates in relation to monandry/polyandry in butterflies. *Behavioral Ecology and Sociobiology*, 26, 395–402.

Tammaru, T. and Haukioja, E. (1996) Capital breeders and income breeders among Lepidoptera: Consequences to population dynamics. *Oikos*, 73, 561–564.

Tammaru, T., Kaitaniemi, P. and Ruohomäki, K. (1996a) Realized fecundity in *Epirrita autumnata* (Lepidoptera: Geometridae): Relation to body size and consequences to population dynamics. *Oikos*, 77, 407–416.

Tammaru, T., Ruohomäki, K. and Saikkonen, K. (1996b) Components of male fitness in relation to body size in *Epirrita autumnata* (Lepidoptera, Geometridae). *Ecological Entomology*, 21, 185–192.

Tardif, R. and Secrest, J.P. (1970) Devices for cleaning and counting eggs of the gypsy moth. *Journal of Economic Entomology*, 63, 678–679.

Taylor, C.M. and Hastings, A. (2005) Allee effects in biological invasions. *Ecology Letters*, 8, 895–908.

Teder, T., Vellau, H. and Tammaru, T. (2014) Age and size at maturity: A quantitative review of diet-induced reaction norms in insects. *Evolution; Internation Journal of Organic Evolution*, 68, 3217–3228.

Thompson, L.M., Faske, T.M., Banahene, N., Grim, D., Agosta, S.J., Parry, D., Tobin, P.C., Johnson, D.M. and Grayson, K.L. (2017) Variation in growth and developmental responses to supraoptimal temperatures near latitudinal range limits of gypsy moth Lymantria dispar (L.), an expanding invasive species. *Physiological Entomology*, 42, 181–190.

Thompson, L.M., Powers, S.D., Appolon, A., Hafker, P., Milner, L., Parry, D. *et al.* (2020) Climate-related geographical variation in performance traits across the invasion front of a widespread non-native insect. *Journal of Biogrography*, DOI: https://doi.org/10.1111/jbi.14005.

Tisdale, R.A. and Sappington, T.W. (2001) Realized and potential fecundity, egg fertility, and longevity of laboratory-reared female beet armyworm (Lepidoptera: Noctuidae) under different adult diet regimes. *Annals of the Entomological Society of America*, 94, 415–419.

Tobin, P.C. and Blackburn, L.M. (2014) Long-distance dispersal of the gypsy moth (Lepidoptera: Lymantriidae) facilitated its initial invasion of Wisconsin. *Environmental Entomology*, 37, 87–93.

Tobin, P.C., Bolyard, J.L., Onufrieva, K.S. and Hickman, A.D. (2014) The effect of male and female age on *Lymantria dispar* (Lepidoptera: Lymantriidae) fecundity. *Journal of Economic Entomology*, 107, 1076–1083.

Tobin, P.C., Robinet, C., Johnson, D.M., Whitmire, S.L., Bjørnstad, O.N. and Liebhold, A.M. (2009) The role of Allee effects in gypsy moth, *Lymantria dispar* (L.), invasions. *Population Ecology*, 51, 373–384.

Tobin, P.C., Cremers, K.T., Hunt, L. and Parry, D. (2016) All quiet on the western front? Using phenological inference to detect the presence of a latent gypsy moth invasion in northern Minnesota. *Biological Invasions*, 18, 3561–3573.

Uller, T. and Leimu, R. (2011) Founder events predict changes in genetic diversity during human-mediated range expansions. *Global Change Biology*, 17, 3478–3485.

Yamanaka, T. and Liebhold, A.M. (2009) Mate-location failure, the Allee effect, and the establishment of invading populations. *Population Ecology*, 51, 337–334.

Yang, F., Luo, Y. and Shi, J. (2017) The influence of geographic population, age, and mating status on the flight activity of the Asian gypsy moth *Lymantria dispar* (Lepidoptera: Erebidae) in China. *Applied entomology and zoology*, 52, 265–270.

Manuscript received April 8, 2021
Final version received June 28, 2021
Accepted July 13, 2021

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix 1 Detailed flight mill design.

Fig. S1 Microcontroller schematic.

Table S1 Formulations for gypsy moth lab diet with varying quantities of protein.