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Research article

Behavior

Evaluation of the Effects of Light Intensity and Time Interval After the Start of Scotophase on the Female Flight Propensity of Asian Gypsy Moth (Lepidoptera: Erebidae)

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Abstract

Asian gypsy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae), females are capable of flight, but little is known about what causes the variation in flight propensity that has been observed. The female flight propensity and capability of Asian gypsy moth from seven geographic populations (three from China, two from Russia, one from Japan, and one from Korea) were compared under all combinations of three light intensities (0.05, 0.10, and 0.40 lux) and during three time intervals after the start of scotophase. A total of 567 females were flight tested. Female flight propensity, time to initiate walking, fanning, and flying, and duration of fanning differed significantly among geographic populations. Females were less likely to voluntarily fly during the 0–1-h time interval after the start of scotophase than during the later time intervals (1–2 and 2–3 h), suggesting that the light intensity cue has to occur at the correct time after the expected start of scotophase for flight initiation. Light intensity did not significantly affect the proportion of females that voluntarily flew, but did impact the timing of the walking and fanning preflight behaviors. The interaction between light intensity and time interval after the start of scotophase had a significant effect on the proportion of females that fanned. The proportion of females with sustained flight capability varied among the populations evaluated. These results may aid in determining the risk of Asian gypsy moth dispersal, but further work is needed to assess other factors that play a role in flight propensity.

Key words: Asian gypsy moth, female flight, light intensity, scotophase

Flight capability can accelerate invasive species migration to and dispersal in new habitats, making their impacts harder to forecast and eradication more difficult. Broad variation in female flight capability (from full sustained flight to gliding downward while flapping their wings to completely incapable of flying) of gypsy moths has been documented. Generally, Asian females are reported to be strong fliers capable of ascending and long-distance flight (Rozkhov and Vasilyeva 1982); the flight capability diminishes westward in Europe (Keena et al. 2008) and disappears in Western Europe and North America (Sandquist et al. 1973, Ferguson 1978). In Asia, gypsy moth is indigenous east of the Ural Mountains in Russia, China, Japan, and Korea. Based on distinguishing morphological and genetic characters, the gypsy moths from some parts of Japan are *Lymantria dispar japonica* Motschulsky (Schintlmeister 2004), while the gypsy moths in other Asian areas are *L. dispar asiatica* Vnukovskij (Pogue and Schaefer 2007). For regulatory reasons, despite the new nomenclature, all gypsy moths having females that can fly are referred to as Asian gypsy moth (U.S. Department of Agriculture–Animal and Plant Health Inspection Service–Plant Protection and Quarantine [USDA-APHIS-PPQ] 2014). In addition to the females' capacity for flight (Keena et al. 2008), Asian gypsy moth larvae can feed on >600 host trees including conifers (USDA-APHIS-PPQ 2014), and eggs from some populations require a shorter time period at low temperatures to fulfill diapause requirements (Keena 1996, Wei et al. 2014). These three characters make Asian gypsy moth a pest of more concern than the European

gypsy moth, currently distributed widely in Europe and North America.

Several characteristics of female Asian gypsy moth flight have been previously evaluated. Females are readily attracted to lights, particularly those that emit wavelengths less than 450 nm (Wallner et al. 1995). The time of both preflight and flight behaviors of gypsy moth was found to be regulated primarily by light intensity, and the final light intensity, rather than a gradual reduction in light, was the trigger for the onset of flight and associated behaviors in this and many other nocturnal moths (Dreisig 1980, Keena et al. 2001). Environmental temperature had a great influence on the duration of wing fanning, and the highest proportion of females flew when the temperature was 19–22°C (Cardé and Hagaman 1983, Charlton et al. 1999). In a forest setting, Asian gypsy moth females commence synchronous flight after light intensity falls below 2 lux, independent of the ambient temperature (Charlton et al. 1999). In laboratory flight tests of Russian populations, flight latency was the shortest at the lowest intensity evaluated (0.1 lux), and females tended to fly after the start of scotophase rather than before (Keena et al. 2001). However, little is known about what causes the observed variation in flight propensity (proportion of females that initiate flight).

Global transport of cargo is the pathway along which Asian gypsy moth has made incursions to North America, because females are attracted to lights at shipping terminals and oviposit egg masses on ship superstructures and departing cargo. Larvae may also crawl onto cargo, and pupate if it is stored out of doors near infested forests. The pupae may then move around the world, and adults may fly out of cargo containers or holds when they are opened. This research intends to further clarify how female moths from across the geographic range in Asia react to different light intensities, including the onset and duration of preflight behaviors and timing of flight behaviors, when presented at different time intervals after the start of scotophase. Understanding the variation in flight propensities (proportion of females that initiate flight) and capabilities (flight level of the females: sustained flight or glide) of different geographic populations will aid managers in predicting when and where females will fly so they can apply appropriate management options.

Materials and Methods

Seven Asian gypsy moth populations from across the geographic range were collected and the details for each population are given in Table 1. Moths were reared in the USDA Forest Service quarantine facility in Ansonia, CT. Voucher specimens were deposited at the Entomology Division, Yale Peabody Museum of Natural History, New Haven, CT. Hatch from 100 mixed egg masses, for all but the SK and JI populations (15 and 16 egg masses, respectively), were reared to adults at 25 ± 1°C, 60% relative humidity, and a photoperiod of 16:8 (L:D) h. The artificial diet and larval rearing methods can be found in Keena et al. (2001). Pupae were harvested and held in groups by population and sex in 1.6-liter paper containers (Solo Cup Company, Lake Forest, IL), with a piece of clear plastic secured over the top with a rubber band. Pupae were checked daily for emergence. To facilitate flight testing in the afternoons, the light in the chamber where the pupae and the adults were held went off at noon (scotophase was initiated). Previous work had shown that the percentage of females that exhibited strong directed flight was reduced if tested before or soon after the set scotophase (Keena et al. 2001).

On the day of emergence, under full ambient lighting adults were individually moved to 236-ml paper cups (Solo Cup Company) covered with a 15.2- by 15.2-cm plastic bag secured with a rubber band. Each female was mated in her container to a 0–2-d-old male no more than 3 h before the flight test to prevent egg laying before flight (although most Asian females will not initiate egg laying until after flight which occurs after the beginning of scotophase [Charlton et al 1999]). Females were held in constant light until tested. In the field, female flight is initiated at dusk (<3 lux) and continues for 2–3 h and very few females will initiate flight during the daylight unless disturbed (Charlton et al. 1999). Also, in laboratory experiments it was found that females would not initiate flight behaviors when the light level was slowly decreased until the light level was ≤ 0.4 lux (Keena et al. 2001). Female behavior was observed in all combinations of three constant light intensities (0.05 lux, 0.10 lux, and 0.40 lux) and three time intervals after the start of scotophase (sessions initiated between 0–1 h after, 1–2 h after, and 2–3 h after the set start of scotophase in the chamber where the pupae and adults were held). A 150-W incandescent floodlight was set to the desired light intensity using a rheostat before the room lights were turned off at the beginning of each test. The light was held in a wooden box (1 by 1 by 1 m) so that a faint corona would be projected on the ceiling and the light intensity was measured with a Li-Cor Model li-189 photometer (Li-Cor Co., Lincoln, NE) at moth eye level. Posts (60 cm high by 10-cm-diameter sections of dry tree branches) mounted on plywood bases were located on shelves 1 m from the floor at both ends of the room, 3 m from the light box, and 60 cm apart. This spacing of posts was sufficient to prevent adjacent moths from disturbing each other. The space used for flight testing was a 4- by 7-m screened mesh enclosure and the temperature in the room was maintained at 20–25°C. Marked female moths (a unique number was written with sharpie marker on one wing) were individually

Table 1. Approximate location (latitude and longitude) of source populations and designations for populations of gypsy moth evaluated in this study, arranged by latitude from north to south

Population	Country	Collecting location	Latitude	Longitude	Laboratory generation	Female sample size
RB	Russia	Shira, Khakassi	54.41° N	90.00° E	30	81
CR	China	Harbin, Heilongjiang	45.78° N	126.61° E	3	81
RM	Russia	Mineralni, Primorski	44.10° N	133.15° E	30	81
CL	China	Sandeli, Liaoning	41.51° N	122.37° E	4	81
CB	China	Yanzikou, Beijng	40.32° N	116.15° E	4	81
JI	Japan	Takizawa, Morika, Nishine Hachimantai City, Northern Iwate District, Honshu	39.73° N	141.08° E	15	81
SK	South Korea	Samhwa-Dong, Gangovon-Do	37.49° N	129.06° E	9	81

The JI population was started using a combination of egg masses from three locations.

placed 10 cm up from the bottom of each post (5 on each end of the room) gingerly using a soft forceps to reduce induction of escaping behaviors.

Nine females from each population were flight tested at each light intensity and time interval combination. No more than four females from each population were flown per day to ensure replication over days. A total of 81 females from each population were tested. The flight protocols described by Keena et al. (2001) were used and are briefly provided here. Up to 10 females (maximum number of posts) chosen randomly from different populations were tested in each session, a maximum of three sessions per day. The initiation times of the following behaviors were recorded over a 45-min observation period: wing fanning, walking, and flight. All females that did not initiate fanning in the 45-min period or those that fanned but did not initiate flight within 15 min were involuntarily tested. An involuntary test involved inducing them to fan to warm up their wing muscles while sitting on a wooden ruler or an observer's hand, then recording their subsequent flight behavior.

The females were assigned to one of the following two categories based on the flight capability exhibited: sustained flight or glide (unsustained flight gliding > 2 feet). Immediately after each flight session, females were placed on their back on the smooth work surface in a laminar flow hood and observed to determine if they could right themselves by flapping their wings against the surface (Keena et al. 2008). The females were then weighed on an electronic balance (Ohaus, Parsippany, NJ) accurate to 0.0001 g.

Both discrete and continuous variables were analyzed using PROC GLIMMIX (SAS Institute 1999). The following behaviors were scored as present or absent: walking, fanning, and flying. For each of these discrete behavioral variables, a binary distribution with a logit link was used. Population, light intensity, time interval after the start of scotophase and all possible two- and three-way combinations were treated as fixed effects for each model. A model using post number, population, light intensity, and the interaction between population and light intensity was run using just the data for the 2–3 time frame only (time with most flight activity) to determine if the proportion of females that flew varied by the post the moth was placed on. Combinations that were found to be statistically insignificant were dropped from the final model. Least-square mean comparisons with the Tukey–Kramer significance test at $\alpha = 0.05$ were used (SAS Institute 1999).

The continuous variables evaluated were time from beginning of the session to initiation of walking, fanning, and flying; duration of fanning; and female body weight. PROC UNIVARIATE (SAS Institute 1999, Cary, NC) was used to evaluate the fit of the data to various distributions. The Shapiro–Wilk and the Anderson–Darling indices were used to test normality. The best distribution was chosen based on the Kolmogorov–Smirnov test. The gamma distribution with a log link function was used for all the continuous variables except for duration of fanning for which the lognormal distribution with an identity link was used. These distributions were necessary because the data had long right tails due to overdispersion. Population, light intensity, time interval after the start of scotophase, and all possible two- and three-way combinations were treated as fixed effects for each model. The only exception was that when female weight was evaluated, only population was included in the model. Combinations that were found to be statistically insignificant were dropped from the final model. The models for time to initiate walking and flight used female age as a random effect. The model for duration of fanning treated room temperature as random effect. The model for time to initiate fanning included both female age and room temperature as random effects. Differences among means were determined by the least-squares means test with $\alpha = 0.05$ and a conservative Tukey–Kramer grouping. For each model, the homogeneity of variance was assessed using Levene's test and residuals were evaluated for normality.

Results

The seven Asian gypsy moth populations differed significantly in female body weight ($F = 20.65$; df = 6, 560; $P < 0.0001$), ranging from 1.222 to 1.641 g. Females from the CB population were significantly heavier than females from all other populations. Females from the CL, SK, and RM populations were significantly heavier than those from the RBI and JI populations.

Eighty-one percent of the 567 tested females walked during the study and although there was significant variation among populations for this behavior ($F = 3.03$; df = 6, 556; $P < 0.0064$), correcting for multiple tests indicated the differences among the populations were not separable. Light intensity ($F = 8.25$; df = 2, 556; $P = 0.0003$) and time interval after the start of scotophase ($F = 5.81$; df = 2, 556; $P < 0.0032$) had a significant effect on whether females initiated walking or not during the session. Significantly fewer females walked under the 0.40 than the 0.10 or the 0.05 lux and during the 0–1 than the 1–2 or 2–3 time intervals after the start of scotophase.

The proportion of females that fanned during the study differed significantly among populations ($F = 8.23$; df = 6, 552; $P < 0.0001$). For example, the proportion of RM females that fanned was significantly higher than the proportion of females from the CL, SK, and JI populations (Fig. 1). Interactions between light intensity and time interval after the start of scotophase had a significant impact on the proportion of females that fanned ($F = 4.16$; df = 4, 552; $P = 0.0025$). The lowest proportion of females fanned during the 0–1-h time interval after the start of scotophase when the light intensity was 0.40 lux (Fig. 2).

The proportion of females that voluntarily flew was significantly different among populations ($F = 15.31$; df = 6, 556; $P < 0.0001$). A significantly higher proportion of RM females flew voluntarily than did females from all other populations. Significantly higher proportions of females from the CR, CB, RB, and CL populations flew voluntarily than did those from the SK and JI populations (Fig. 3). Time interval after the start of scotophase had a significant influence on the proportion of females that flew ($F = 4.07$; df = 2, 556; $P = 0.00177$); significantly fewer females voluntarily flew during the 0–1-h time interval after the start of scotophase than during either

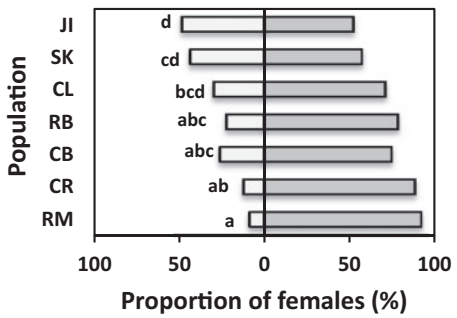

Fig. 1. Comparison of the proportion of females that fanned among seven gypsy moth populations. Filled bars represent the proportion of females that fanned during the test; blank bars represent those that did not. Population bars followed by different letters were significantly different based on Tukey–Kramer's multiple comparison tests at a 5% significance level.

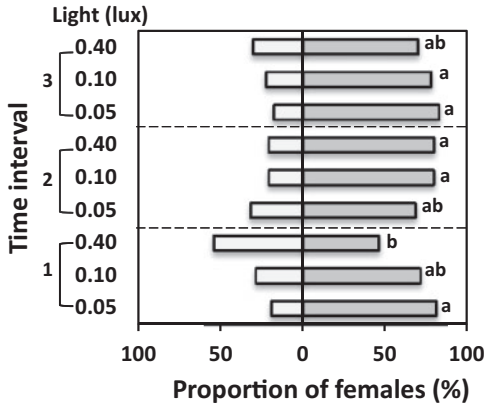

Fig. 2. Comparison of the proportion of females that fanned under nine different combinations of time interval after the start of scotophase (trail start times 1 = 0–1 h, 2 = 1–2 h, and 3 = 2–3 h) and light intensity. Filled bars represent the proportion of females that fanned during the test; blank bars represent those that did not. Population bars followed by different letters were significantly different based on Tukey–Kramer's multiple comparison tests at a 5% significance level.

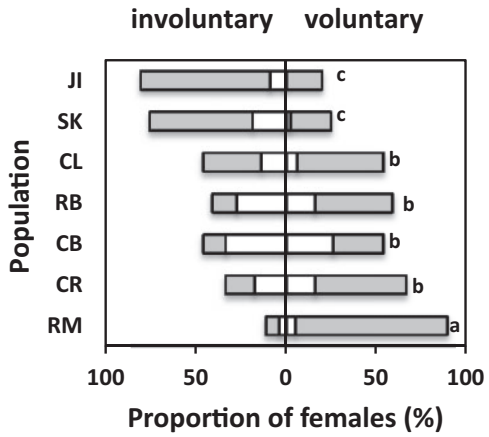

Fig. 3. Comparison of proportion of females that voluntarily flew (right side of center line), which is a measure of their flight propensity, and those that had to be involuntarily flown (left side) to determine their flight capability among seven gypsy moth populations. The type of voluntary and involuntary flight observed is shown; the filled part of the bars on each side represents the proportion of females that were capable of sustained flight and the blank bars represent the proportion that could only glide. Population bars followed by different letters indicate significant differences in the proportion of females that voluntarily flew based on Tukey–Kramer's multiple comparison tests at a 5% significance level.

of the other two time intervals. The proportion of females that voluntarily flew did not differ significantly with light intensity ($F = 2.30$; df = 2, 556; $P = 0.1011$). The proportion of females that flew during the 2–3 time frame did not differ significantly with the post on which they were flight tested ($F = 1.01$; df = 9, 537; $P = 0.4318$).

The distribution of flight capabilities for all populations is also shown in Fig. 3. RM and JI populations had the largest proportion of females capable of sustained flight—91% and 92%, respectively, while the CB population had the least at 40%. There were several females from each population that had the capability for sustained flight but did not voluntarily take flight under the experimental conditions. Ninety-nine percent of all the females flight tested were able

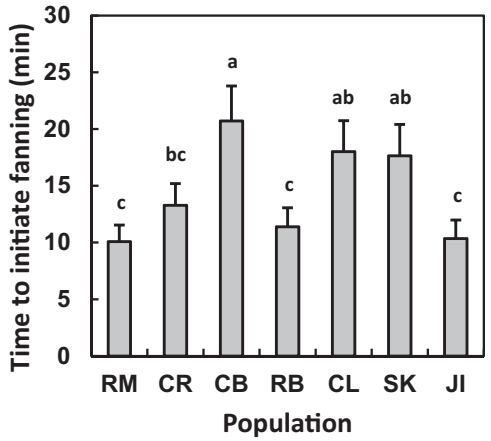

Fig. 4. Comparison of time for females to initiate fanning among seven gypsy moth populations (mean ± SE). Population bars followed by different letters indicate significant differences in the time to initiate fanning among populations based on Tukey–Kramer's multiple comparison tests at a 5% significance level.

to right themselves, with the exception of the RB population in which only 94% of the could right themselves.

Time to the initiation of walking (time between when the test started and the female commenced walking) differed significantly by populations ($F = 12.93$; df = 6, 507; $P < 0.0001$), time interval after the start of scotophase ($F = 6.30$; df = 2, 507; $P = 0.0020$), and light intensity ($F = 5.87$; df = 2, 507; $P = 0.0030$). Females from the CB (17 ± 2 min) and SK (16 ± 2 min) populations started walking significantly later than other populations (averaged 6 to 11 min). It took females significantly longer to start walking during the 0–1-h time interval after the start of scotophase (13 ± 1 min) than during the other intervals (averaged 10 ± 1 min) and at the 0.40 lux light intensity (13 ± 1 min) than at the other light intensities (averaged 10 ± 1 min).

Time to the initiation of fanning (time between when the test started and the female started fanning) varied significantly by populations ($F = 14.66$; df = 6, 363; $P < 0.0001$), time interval after the start of scotophase ($F = 7.53$; df = 2, 363; $P = 0.0006$), and light intensity ($F = 5.06$; df = 2, 363; $P = 0.0068$). RM, RB, and JI populations started fanning significantly earlier than CB, CL, and SK populations (Fig. 4). Females took significantly longer time to commence fanning during the 0–1-h time interval after the start of scotophase (16 ± 2 min) than the other two time intervals (13 ± 2 min). At the lowest light intensity (0.05 lux, 13 ± 2 min) time to the initiation of fanning was significantly shorter than at the brighter light intensity (0.40 lux, 16 ± 2 min) and the time to the initiation of fanning for females in the middle light intensity (0.10 lux, 14 ± 2 min) was intermediate.

Fanning duration (total time fanning before the female voluntarily left the post) differed significantly by populations ($F = 5.07$; df = 6, 252; $P < 0.0001$), but not by light intensity ($F = 0.50$; df = 2, 252; $P = 0.6056$) or time interval after the start of scotophase ($F = 0.51$; df = 2, 252; $P = 0.6029$). Females from RM, CB, and JI fanned a significantly shorter time than RB and CL females (Fig. 5).

Time to the initiation of flight (time between when the test started and the female took off from the post voluntarily) differed significantly by populations ($F = 14.52$; df = 6, 284; $P < 0.0001$), and time interval after the start of scotophase ($F = 5.99$; df = 2, 284; $P = 0.0028$), but not by light intensity ($F = 2.65$; df = 2, 284; $P = 0.0724$). Females from the JI population took flight significantly

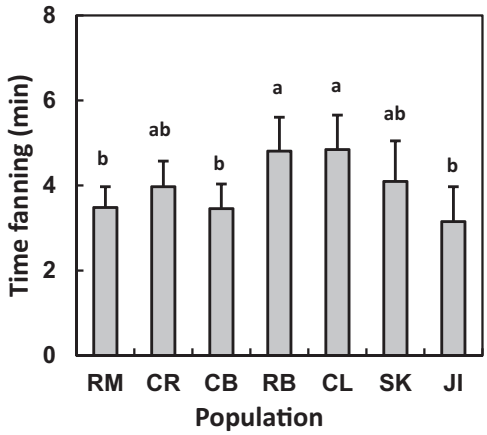

Fig. 5. Comparison of time fanning prior to voluntary flight for the females among seven gypsy moth populations (geometric mean ± SE). Population bars followed by different letters indicate significant differences in the time that females fanned among populations based on Tukey–Kramer's multiple comparison tests at a 5% significance level.

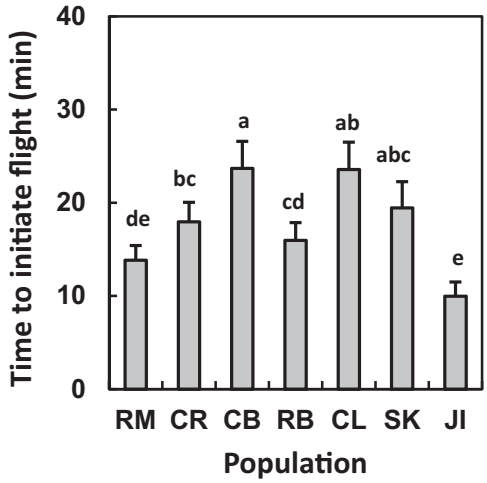

Fig. 6. Comparison of time to initiate flight for females among seven gypsy moth populations (mean ± SE). Population bars followed by different letters indicate significant differences in the time it took females to initiate flight among populations based on Tukey–Kramer's multiple comparison tests at a 5% significance level.

earlier than females from the other populations except for RM (Fig. 6). Females initiated flight significantly later during the 0–1-h time interval after the start of scotophase (19 ± 2 min) than during the other two time intervals (1–2 h, 17 ± 2 min; 2–3 h, 16 ± 2 min).

Discussion

Female flight propensity varied among Asian gypsy moths that originated from China, Japan, Korea, and Russia. There were females in each population that did not initiate flight voluntarily but were capable of sustained flight; SK and JI populations had the highest proportion of females that did not fly voluntarily and the RM population had the lowest. It is unclear whether this would occur in nature, or, if they just did not receive the proper cues to initiate flight under the conditions evaluated in this study. The time interval after the start of scotophase during which the flight test was started had a significant effect on female flight propensity; fewer females flew during the 0–1-h time interval while more flew at the latter two time intervals. This suggests that even when the critical light level to trigger the onset of flight behaviors is given, flight may not be initiated unless that cue is received during the correct time frame, and that this timing varies among individuals or populations. The range of light intensities evaluated in this study did not have a significant effect on female flight propensity, indicating the upper and lower light intensity thresholds for female flight initiation are somewhere outside this range. This agrees with earlier work that found that gypsy moth females fly when the ambient light intensity drops below 2 lux (Charlton et al. 1999).

Preflight behaviors such as walking and fanning appeared to be regulated by light intensity and time interval after the start of scotophase. Females remained motionless on their posts longer when tested right after the start of scotophase than in the later time intervals. Likewise, females started walking and fanning later under the 0.40 lux than under 0.05. Both light intensity and timing of expected scotophase, therefore, appear to be vital cues in determining the onset of preflight behaviors, as has been observed in other insects (Wensler 1974, Dreisig 1980). An endogenous rhythm seemed to prepare the females for the onset of flight, while the ambient light intensity triggered the initiation of preflight behaviors. This is in line with previous work on both Asian gypsy moths (Keena et al. 2001) and *Onitis alexis* Klug (Coletoptera: Scarabaeidae, Houston and McIntyre 1985) which showed that if the light intensity at which they would normally fly occurs before the normal scotophase, the insects did not initiate flight.

Preflight wing fanning increases thoracic muscle temperature in preparation for flight (Casey 1980, Heinrich 1993), and the duration of fanning depends on ambient temperature for many moths, being much longer in colder environments than in warm (Krogh and Zeuthen 1941, Dorsett 1962, McCrea and Heath 1971). Even when female age and ambient temperature (which varied from 20.1 to 24.9°C) were factored out by treating them as random effects, fanning time for each population to attain a critical thoracic temperature varied in this study. Earlier work showed that Asian gypsy moths fan their wings longer both at lower temperatures and when they are not capable of sustained flight (Keena et al. 2001). However, the population differences in fanning time still remained when the proportion of females that only glided in this study were taken into account. For example, the RM population had few females that glided but the mean fanning time was comparable to that of the CB population in which about half of the females that voluntarily left their post only glided. This suggests that there are either innate differences between the populations in fanning time or that some other factor yet unidentified may affect the duration of fanning.

Asian gypsy moth females are reported to be strong fliers, but the proportion of females capable of strong flight varied among the populations evaluated in this study. Seventy-two percent of all the 567 tested females exhibited the capability of sustained flight (combined voluntary and involuntary flight), while the rest attempted to fly but only glided (while vigorously flapping their wings) to the ground several feet away from the site where they launched. This is consistent with previous work on gypsy moths that has shown that flight capability is not fixed in most populations (Keena et al. 2008) and that it is a polygenic trait (Keena et al. 2007). Further evidence of this variation in flight capability is demonstrated by the differences in the flight capability of two populations that have been previously evaluated. The RB and RM populations had 55% and 92%, respectively, of the females capable of sustained flight under 0.10 lux while in an earlier evaluation under the same conditions

100% and 68%, respectively, of the females were capable of sustained flight (Keena et al. 2008). Genetic changes over time in the flight ability of laboratory-reared colonies of other insects have been seen (Bush and Neck 1976) and may explain these differences since these two strains have been in the laboratory the longest of those tested. The higher percentage of gliding type flight in the CB population may be due to a higher wing load (body weight divided by wing area) for these females since they were heavier (1.64 g ± 0.04 SE) than the females from the same population reported previously and females incapable of sustained flight have higher wing loads (Shi et al. 2015). In addition, larval diet has been shown to affect female flight capability. Individuals reared on foliage are capable of stronger flight than those reared on artificial diet (Keena et al. 1997), so we are likely underestimating the flight capability of all these populations.

This study provides useful insights into the factors that affect female flight propensity and the variation in flight capability among Asian gypsy moth populations, which are needed for determining the dispersal risk of the Asian gypsy moth. Detailed work has been done in Siberian Russia, close to where the RB population originated, to assess the natural propensity of females to take flight (Charlton et al. 1999), but similar work has not been done for other Asian populations, so the applicability of these results for female flight propensity in a natural setting is unknown. If the differences between populations in female flight propensity and capability do exist in a natural setting then some Asian populations would pose a lower risk for being moved in international trade. Further work is needed to determine what other environmental stimulus might affect female flight propensity and if Asian populations do vary in flight propensity under more natural settings.

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