Female Flight Propensity and Capability in *Lymantria dispar* (Lepidoptera: Lymantriidae) from Russia, North America, and Their Reciprocal F_1 Hybrids

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Environ. Entomol. 30(2): 380–387 (2001)

ABSTRACT In the laboratory, the timing of both preflight and flight behaviors of the Asian strain of female gypsy moths, *Lymantria dispar* L., was regulated primarily by light intensity. The shortest times to initiation of wing fanning and flight occurred at 0.1 lux, the lowest light intensity evaluated. A gradual decrease in light intensity, compared with an instantaneous decrease, prolonged time to flight. The highest percentage of female flight was observed at 0.1 lux. A higher percentage of females initiated flight when exposed to lower light intensities after the onset of normal scotophase rather than before scotophase. Virgin females were less likely to fly than mated females. Females fanned their wings longer at lower temperatures and when they were capable of only a gliding flight. Females that were flight-tested the same day they emerged tended to take longer to initiate flight than those 1–2 d old. At 0.1 lux, the majority of the Asian females, less than 2% of the F_1 hybrid females, and none of the North American females exhibited strong, directed flight. Over half of the F_1 hybrids glided for a few meters while flapping their wings, whereas none of the North American females exhibited even this level of flight. Thus, female flight capability will be reduced when flighted and nonflighted forms initially hybridize.

KEY WORDS *Lymantria dispar*, gypsy moth, female flight propensity, hybrids, migration, rhythm

THE RECENT INTRODUCTION into North America of strains of gypsy moth, *Lymantria dispar* L., with the capacity of females to fly (Bogdanowicz et al. 1993) prompted eradication programs in 1992 and 1994. Females of the European race of gypsy moth introduced into Massachusetts in 1869 do not fly (Forbush and Fernald 1896), whereas Asian females are reported to fly up to 100 km (Rozkhov and Vasilyeva 1982). Strains from Asia also possess other traits that make them more threatening to North American forests than the established strain, including a broader host range (Baranchikov 1988), shortened egg chill requirements (Keena 1996), and female attractancy to lights that results in egg deposition on vehicles or cargo (Wallner et al. 1995). In addition, the capacity for flight in females increases the potential rate of spread and may invalidate procedures developed for detection and delimitation of the European strain. Another concern is the extent to which flight capability would be maintained in hybrids of Asian and European strains.

Insect flight is controlled by polygenic factors (Harrison 1980; Dingle 1984, 1994; Han and Gatehouse 1989). Gypsy moth female vagility diminishes from East Asia to Europe (Baranchikov 1988) and flight capability is reduced in F_1 hybrids (Keena 1994, Reineke and Zebitz 1998), but the mode of inheritance has not fully been determined. There are detectable molecular differences among populations from Europe, Asia, and North America (Garner and Slavicek 1996), but their relationship to behavioral traits is unknown. Asian, Siberian, and European strains readily hybridize in the laboratory with gypsy moth collected from North America (Keena 1994).

Predicting the flight propensity of such hybrids is critical to designing and implementing management programs for this pest. Our objectives were to characterize propensity (proportion initiating flight) and capability (quality of flight) of female flight in Asian gypsy moth and reciprocal F_1 hybrids between Asian and North American strains, and discuss the implications of our findings on management programs.

Materials and Methods

Gypsy Moth Strains. The sources and letter designations of the Russian and North American gypsy moth strains used in our studies are given in Table 1. Voucher specimens for each strain were deposited at the Entomology Division, Yale Peabody Museum of Natural History, New Haven, CT. The 20 individual egg masses used in experiment 1 were from Mineralni, Russia (RM). This strain had not been reared previously in the laboratory before its evaluation. In experiment 2, >30 mixed Bellyk, Russia (RB), egg masses were used. Seventy individual egg masses from each of the Vancouver, BC (A), and Wrentham, MA (W), strains were used in experiment 3; each strain

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Table 1. Sources and designations for strains of gypsy moth evaluated for capacity of female flight

Strain	Country	Closest city and region	Location[a]	Collection date	Stage collected
RM	Russia	Mineralni, Primorski region	44.10° N 133.15° E	Aug 1992	20 individual egg masses
RB	Russia	Bellyk, Krasnoyarsk region	54.30° N 91.18° E	Dec 1992	>30 mixed egg masses
A	Canada	Vancouver, British Columbia[b]	49.30° N 123.10° W	Sept 1991	>100 mixed egg masses
W	United States	Wrentham, Norfolk County, MA	42.05° N 71.20° W	Feb 1992	>200 individual egg masses

[a] Approximate latitude and longitude of collection site.
[b] Egg masses were scraped from the superstructure of the Russian grain ship, Allalinhorn, which had just arrived from the Far East Russian port of Nakhodka (42.50° N, 132.50° E).

had been reared in the laboratory for two generations before use. Also included in experiment 3 were 70 egg masses resulting from each reciprocal cross between the A and W strains in the previous generation. The reciprocal crosses are referred to as A × W and W × A, where the strain of the female parent is listed first.

Rearing Methods. All rearings to produce the adults used in these experiments were conducted in walk-in environmental chambers maintained at 25 ± 1°C, 60 ± 5% RH, and a photoperiod of 16:8 (L:D) h. In all three experiments, larvae were reared in groups of 10 in 237-ml clear plastic cups with unwaxed paper lids for 35 to 40 d. Each cup contained 90 ml of high wheat germ diet (Bell et al. 1981). In experiments 1 and 3 some larvae were reared until pupation individually in 118-ml clear plastic cups (Sweetheart, Owings Mill, MD) with unwaxed paper lids until pupation. Each 118-ml cup contained 40 ml of diet.

Group-reared pupae were harvested, sexed, and stored by sex, egg mass (family), and strain in 473- or 237-ml unwaxed squat paper cups with clear plastic lids until adult eclosion. Individually reared pupae were harvested, sexed, and stored individually in the 237-ml (males) or 473-ml (females) paper cups until eclosion. To facilitate conducting bioassays from 1100 to 1600 hours, all pupae were held (a minimum of 2 d) in a chamber where the timing of scotophase initiation corresponded to noon; this was 10 h earlier than in the chamber where the larvae were held. Adults were removed daily and held in paper cups until paired individually in 473-ml paper cups for mating. Matings were random within strain or cross, except that sibling matings were avoided. Virgins not used for flight tests were returned to the chamber where the pupae were held until tested or mated on subsequent days. Both mated and virgin females to be flight tested that day were held in constant light.

Flight Evaluation. In the field, female flight is initiated at dusk when incident light is <3 lux and continues for 2–3 h (Wallner et al. 1995, Charlton et al. 1999). Light intensity within the USDA. Forest Service primary quarantine facility located in Ansonia, CT, was regulated to simulate field conditions. Flight assessments were conducted in a white room (8 by 7 m) with a 2.5 m high ceiling, where the temperature was maintained at 18–21°C. Along one wall, a long shelf (40 cm wide by 7 m), 1 m from the mottled white floor, held 12 pignut hickory (*Carya glabra* K. Koch) sapling stem sections (60 cm high by 10 cm diameter) with bark, each mounted on 20-cm^3 pieces of plywood (2 cm thick). Each of the 12 females to be flight-tested was given a unique number on its forewing with an indelible black felt tipped pen. Marked females were placed 10 cm from the bottom of each bolt using a twig. The light was reduced as required by the experiment, using a 150-W incandescent floodlight controlled by a rheostat. The light, located near the center of the room and 3 m from the bolts with females, was mounted vertically in an open wooden box (1 by 1 by 1 m) painted black and set on the floor. This lighting system created a relatively even light throughout the room with a faint corona on the white ceiling. Light intensity was measured with a Gossen Luna-Pro meter (Li-Cor Company, Lincoln, NE) at moth eye level.

Each replicate consisted of 12 females. Because of the difficulty observing moth behavior under dim light and documenting the exact timing of their activities, 3–4 persons (2–3 observers and one recorder) were needed. The following behavioral responses and their duration were recorded over a 45-min observation period: initiation of wing fanning, walking, and flight from the bolts. Females were rated as either strong fliers (directed flight in which the female circled the room), weak fliers (flight of >1 m lacking upward displacement), or incapable of flight (launched themselves from the bolts, but either could not or did not attempt to fly, or remained stationary, wing fanned, or walked). Flight bioassays were conducted from 1 h before to 4 h after the start of scotophase (1100 to 1600 hours) and averaged three sessions per day. During the period of December 1992 to December 1993 we evaluated ≈2,200 females.

In experiment 1, to ascertain which light intensity elicited activity most rapidly and consistently, female response was evaluated at 0.1, 0.4, 0.9, 1.9, and 3.4 lux. To determine if it is the gradual decline in light that occurs in nature or simply reaching a threshold light intensity that is necessary for flight initiation, a second experiment was conducted. In experiment 2, the 0.1-, 0.4-, and 0.9-lux intensities were tested for female response by an instantaneous drop from 475 lux to these light intensities versus a stepped reduction in luminescence every 3 min, ending at one of these light intensities. The sequence of light intensities in the

stepped reductions were 12.8, 9.0, 6.0, 3.4, 1.9, 0.9, 0.4, and 0.1 lux, and the test began when the room lights were turned off. The effects of mating status on female flight also were assessed. In experiment 3, the flight capability of an Asian strain intercepted on a Russian ship, a North American strain, and reciprocal F_1 hybrids between two strains were assessed. Bioassays using mated females were started after the entrained scotophase (1200 hours), following an instantaneous drop to 0.1 lux.

Statistical Analyses. Analysis of variance (ANOVA) (PROC GLM, SAS Institute 1990b) was used for time measurements and categorical ANOVA (PROC CATMOD, SAS Institute 1990a) was used for the ratings of female flight. Time data for individuals that did not fly and/or wing fan were coded as missing values in the analyses. In each case, we first used a full model that included all first-order interactions. All time measurements were analyzed in seconds but rounded to minutes in the figures and tables. In experiment 1, the ANOVAs evaluated the following effects: light intensity (five levels), hours after the start of scotophase the bioassay was run (−1.0–0.0, 0.1–2.0, 2.1–4.0), female age (0–3 d posteclosion), temperature during the bioassay (19, 20, 21°C), and bolt (1–12). In experiment 2, the ANOVAs evaluated the following effects: final light intensity (three levels), hours after the start of scotophase (−1.0–0.0, 0.1–1.0, 1.1–2.0, 2.1–3.0), female age (0 or 1), temperature (18–21°C), light treatments (instantaneous, gradual), and mating status (virgin, mated). In experiment 3, the ANOVAs evaluated the following effects: genetic cross (A × A, W × W, A × W, W × A), hours after the start of scotophase (same as experiment 2), female age (0–2), and rating of female flight (strong flight, gliding flight, no flight). All main effects and all interaction terms, except those containing female age in experiment 2, could be estimated. Generally, the results for factors with no significant effect were not presented. In the CATMOD analysis only the effects of time of day, light intensity, mating status (experiment 2 only), and light treatments (experiment 2 only) were evaluated due to the small sizes of some groups.

Bonferroni *t*-tests (SAS Institute 1990b) were used to compare treatment means within each significant factor in the ANOVA. Analysis of weighted-least-squares and specific contrasts were used to compare treatments within each significant factor in the CATMOD analysis. Chi-square tests were used to compare percentages in flight rating categories between treatments.

Results

Experiment 1: Response to Light Intensity. RM females generally remained motionless for several minutes before initiating wing fanning. They fanned for a few minutes, remaining where they were placed on the bolt, and then walked to the top of the bolt while wing fanning and initiated flight. The duration of preflight wing fanning by RM females was not affected by light intensity ($F = 0.35$; df = 4, 306; $P = 0.8421$), hours after the start of scotophase the bioassay was conducted ($F = 1.40$; df = 2, 306; $P = 0.2483$; Fig. 1), female age ($F = 2.09$; df = 3, 306; $P = 0.1022$), temperature during the bioassay ($F = 0.71$; df = 3, 306; $P = 0.5473$), or interactions among these factors. However, flight latency was significantly affected by the number of hours after the start of scotophase the bioassay was conducted ($F = 6.14$; df = 2, 306; $P = 0.0024$), female age ($F = 5.23$; df = 3, 306; $P = 0.0015$), temperature during the bioassay ($F = 3.27$; df = 3, 306; $P = 0.0216$), and the interaction between number of hours after the start of scotophase and female age ($F = 3.60$; df = 4, 306; $P = 0.0070$). In addition, females flew significantly sooner when exposed to 0.1 or 0.4 lux light than 0.9 lux light (Bonferroni *t*-test, $\alpha = 0.05$, critical value of $t = 2.828$). The fewer hours after the start of scotophase the flight bioassay occurred, the longer the time until flight was initiated (Fig. 1). Zero- to 2-d-old females initiated flight significantly sooner than 3-d-old females (Bonferroni *t*-test, $\alpha = 0.05$, critical value of $t = 2.656$). In general, females initiated flight sooner at temperatures ≥20°C than temperatures <20°C. There was no clear pattern for the interaction between the number of hours after the start of scotophase and female age. This interaction may have been biased due to lower numbers of 2- to 3-d-old females compared with the 0–1-d olds.

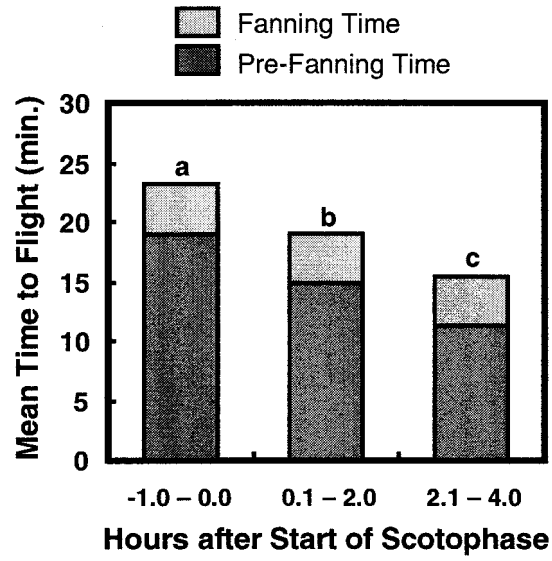

Fig. 1. Mean time to flight for gypsy moth females from Mineralni, Russia, tested at different times before and after the start of scotophase. Different letters indicate significant differences in total time to flight based on Bonferroni *t*-tests with a critical value of $t = 2.407$ for $\alpha = 0.05$ (SAS Institute 1990b).

The percentage of RM females that exhibited strong directed flight was significantly higher for bioassays conducted after the start of scotophase than before (Fig. 2). Significantly more females exhibited strong directed flight at 0.1 lux than at any of the higher light intensities (Fig. 3). Individuals that did not exhibit strong directed flight, either because the bioassay was

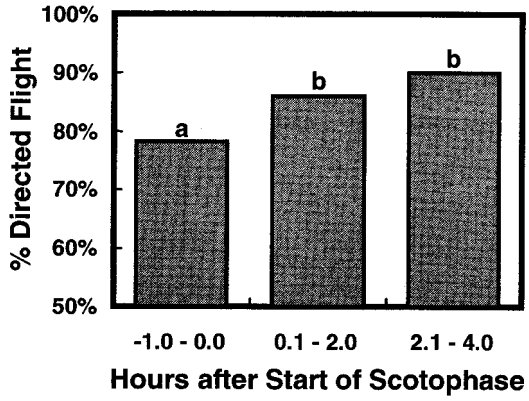

Fig. 2. Percentage of strong directed flight for gypsy moth females from Mineralni, Russia, tested at different times before and after the start of scotophase. Different letters indicate significant differences based on chi-square tests (SAS Institute 1990a).

conducted before or just after the start of scotophase or the light intensity was high, generally did not attempt flight at all. The interaction between hours after the start of scotophase and light intensity was significant ($\chi^2 = 17.40$, df = 7, $P = 0.0150$); but when the three time periods were compared within each light intensity, there were no significant differences in the percentage of females that exhibited strong directed flight.

Experiment 2: Gradual Versus Instantaneous Reduction of Light Intensity. The length of time RB females wing-fanned before they flew was significantly affected by mating status ($F = 4.36$; df = 1, 201; $P = 0.0381$) and light treatment (direct verses stepped; $F = 5.40$; df = 1, 201; $P = 0.0232$). In addition, RB females wing fanned longer at lower temperatures (18–19°C) than at higher temperatures (20–21°C), based on Bonferroni *t*-tests ($\alpha = 0.05$, critical value of

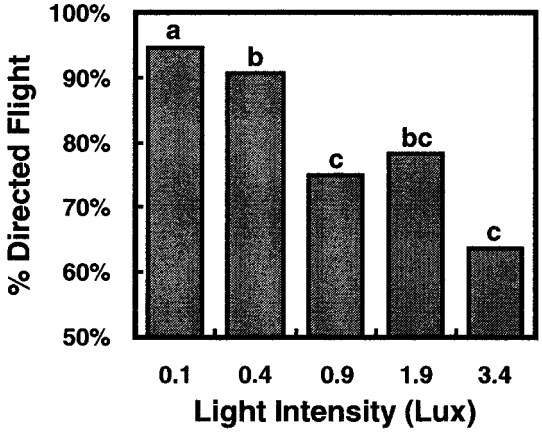

Fig. 3. Percentage strong directed flight for gypsy moth females from Mineralni, Russia, tested at different light intensities. Different letters indicate significant differences based on chi-square tests (SAS Institute 1990a).

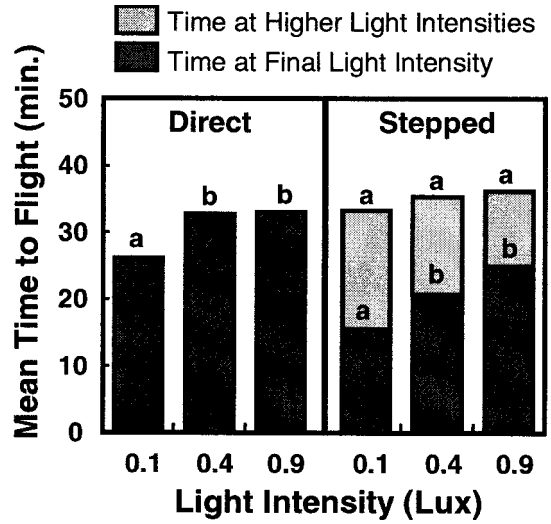

Fig. 4. Mean time to flight for gypsy moth females from Bellyk, Russia, tested at three light intensities that were reached either instantaneously (direct) or through a gradual reduction in light intensity (stepped). Different letters within each light treatment for total time to flight and time spent at the final light intensity for gradual reduction treatments indicate significant differences based on Bonferroni *t*-tests with a critical value of $t = 2.968$ for $\alpha = 0.05$ (SAS Institute 1990b).

$t = 2.66462$). Mated RB females fanned longer than virgin RB females. Females exposed to higher final light intensities fanned longer when the light was instantaneously dropped than when the light was decreased gradually.

Time to flight initiation in RB females was significantly affected by temperature ($F = 6.29$; df = 3, 199; $P = 0.0262$), light treatment ($F = 13.76$; df = 1, 199; $P = 0.0005$), the interaction between hours after the start of scotophase and light treatment ($F = 6.03$, df = 1, 199; $P = 0.0149$), and the interaction between final light intensity and mating status ($F = 3.74$, df = 2, 199; $P = 0.0255$). Flight latency was shortest for females exposed to 0.1 lux directly (Fig. 4). In females experiencing a stepped regime of light reduction, only two females flew before the final light intensity was reached; two scheduled to go to 0.1 lux flew at 0.4 lux. Final light intensity attained had no significant effect on total time to flight initiation when the light intensity was stepped down, but did have a significant effect on time spent at final light intensity before flight was initiated (Fig. 4). In addition, the time females spent before flight at each final light intensity in the gradual reduction treatments was less than the total time females in the instantaneous reduction treatments spent at the same light intensity ($F = 10.40$, df = 199, $P = 0.0015$). RB females took longer to initiate flight at lower temperatures than at higher temperatures, as did RM females. The time to initiation of flight was shortest for 1.1–2.0 h after the start of scotophase for direct light reduction and for 2.1–3.0 h after the start of scotophase for gradual light reduction. Virgin fe-

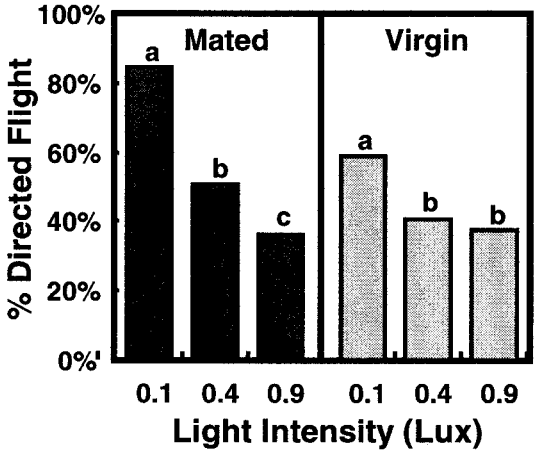

Fig. 5. Percentage strong directed flight for virgin and mated gypsy moth females from Bellyk, Russia, tested at different light intensities. Different letters within a mating status indicate significant differences based on chi-square tests (SAS Institute 1990a).

males took longer to initiate flight at 0.1 lux than at 0.4 or 0.9 lux, whereas the reverse was true for mated females.

The propensity of RB female flight (number of females initiating flight) was significantly greater for individuals bioassayed after the start of scotophase than before at 0.9 lux ($\chi^2 = 6.64$, df = 1, $P = 0.0100$), but not at 0.1 or 0.4 lux. Final light intensity had a significant effect on RB female flight propensity ($\chi^2 = 35.17$, df = 2, $P < 0.0001$). Significantly more females, both mated and virgin, exhibited strong directed flight at 0.1 lux than at either of the higher light intensities (Fig. 5). In addition, significantly more mated females exhibited strong directed flight at 0.1 lux than virgin females ($\chi^2 = 12.74$, df < 1, $P = 0.0001$). The light treatments had no significant effect on flight propensity ($\chi^2 = 0.41$, df = 1, $P = 0.5211$) and interactions between factors were not significant.

Experiment 3: Flight Propensity and Capability of Hybrids. The majority of the A females exhibited strong directed flight and no W females flew (Table 2). Most females of both reciprocal F_1 hybrids were capable of only gliding flight or did not fly (Table 2). Significantly more W × A females exhibited flight than A × W females ($\chi^2 = 4.60$, df = 1, $P < 0.05$). Also, 1.7% of the W × A hybrid females were capable of directed flight, whereas none of the A × W females exhibited more than gliding flight (Table 2). The prefanning time was shortest for A females and longest for W females, with hybrids being intermediate (Table 2). Cross had a significant effect on wing fanning duration ($F = 2.87$, df = 3.467, $P = 0.0363$). The A females fanned for a significantly shorter time than any of the other females (Table 2). Females capable of strong directed flight or gliding flight had shorter fanning times than those that could not fly (Bonferroni *t*-test, $\alpha = 0.05$, critical value of $t = 2.40516$). Female age had a significant effect on both fanning time ($F = 9.66$; df = 2, 467; $P = 0.0001$) and time to flight ($F = 3.48$; df = 2, 335; $P = 0.0318$); females that had eclosed more recently fanned longer and flew later than those that were 1 or 2 d old. The number of hours after the start of scotophase ($F = 4.33$; df = 3, 467; $P = 0.0051$) and interaction between number of hours after the start of scotophase and cross ($F = 240$; df = 9, 467; $P = 0.0116$) both had significant effects on wing fanning duration. The shortest fanning times were recorded for the A × A, A × W, and W × A females that were bioassayed 1.1–2.0 h after the start of scotophase, whereas the shortest times for the W × W cross were 2.1–3.0 h after the start of scotophase.

The W and A females each exhibited unique behaviors. More than 60% of the W females perched on the bolt and laid eggs without ever fanning, whereas >90% of the A females fanned in place then walked up the bolt and took flight (Fig. 6). The hybrids exhibited a mixture of behaviors, but >90% fanned (often followed by walking and sometimes flight, Fig. 6). Several of the hybrid females fanned in place, and then walked to the top of the bolt without taking flight; instead, they continued to walk up and down the bolt while wing fanning. When this continued uninterrupted for 15 min without a flight attempt, the female was removed and allowed to launch from a person's finger. In almost every case, the female either glided or dropped off, unable to fly.

Table 2. Results of flight bioassay using an Asian strain intercepted in North America (A), a North American Strain (W), and F_1 reciprocal hybrids between the two strains (W × A and A × W)

Cross[a]	Individuals, %			Time ± SE (min)[b]		*n*
	Directed flight	Gliding flight	No flight	Pre-fanning	Fanning	
A × A	87.6	10.6	1.8	9.9 ± 6.1a	4.0 ± 2.1a	113
A × W	0.0	50.8	49.2	13.2 ± 7.9b	7.1 ± 4.8b	187
W × A	1.7	64.7	33.6	11.7 ± 7.8ab	6.4 ± 4.1b	235
W × W	0.0	0.0	100.0	25.4 ± 16.1c	7.5 ± 10.1b	50

[a] The strain of the female parent is listed first.

[b] Times followed by the same letter within a column are not significantly different based on a Bonferroni *t*-test with a critical value of $t = 2.65342$ for $\alpha = 0.05$ (SAS Institute 1990b).

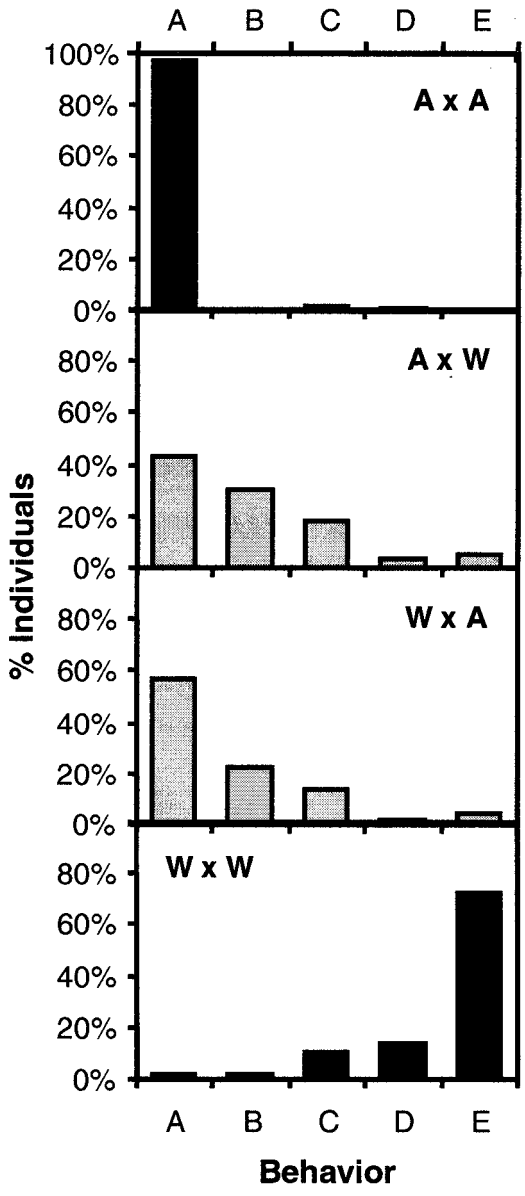

Fig. 6. Characterization of the preflight behaviors of an Asian strain (A), a North American strain (W), and F_1 hybrids between the two. The strain of the female parent is listed first. The mutually exclusive behavioral categories (listed from strong flight to no flight) are (A) stationary wing fanning, walking while fanning to the top of the bolt and launching; (B) stationary wing fanning, walking up, down and all around while fanning and may launch; (C) stationary fanning that may be discontinuous; (D) sitting in place or walking <10 cm; and (E) same as D plus laid eggs.

Discussion

The timing of both preflight and flight behaviors was regulated primarily by light intensity; a drop in light intensity was required for these behaviors to be initiated. This is consistent with the finding that diminished light is the primary cue that triggers the onset of flight and associated behaviors in many other nocturnal moths (Dreisig 1980). A gradual decrease in light intensity prolonged the time to flight, rather than decreasing the time to flight as Dreisig (1980) predicted. The longer time to flight when the light intensity was gradually decreased was due both to the time spent at higher light intensities under which few females would naturally initiate flight and to longer wing fanning periods. This further supports light intensity rather than a gradual decrease in light, per se, as the cue for flight in gypsy moth females.

Light intensity, the number of hours after the start of scotophase the bioassays were conducted, and mating status affected flight propensity (proportion of females initiating flight). The percentage of individuals that fly at a given light intensity depended on how many of the individuals' thresholds have been met or exceeded. However, low light intensities that occurred before scotophase resulted in fewer individuals initiating flight than the same light intensity if it occurred after the start of scotophase. Other insects also demonstrate a decrease in reactivity as the time gets further away from the normal transition time (Dreisig 1980). Finally, under the same light intensities, virgin females were less likely to fly than mated females. Virgin females often called (protruded their abdominal tip, exposing their pheromone gland) for a period of time sometimes followed by flight. The time of flight also was extended for virgin females due to this calling period, but there was no effect on flight capability.

Temperature and individual flight capability (flight rating a female exhibited) had the largest effect on duration of wing fanning. Wing fanning is required to raise the thoracic temperature to the level necessary for flight, and at lower ambient temperatures this takes a longer time than at higher temperatures (Cardé and Hagaman, 1983, for males; Charlton et al. 1999, for females). Individuals not capable of strong directed flight (especially A × W, W × A, and some W) fanned longer than those capable of strong directed flight (RM, RB, and A). It is possible that females "test" for lift the first time they walk to the top and, if the necessary cues are not present, they continue wing fanning and retesting for lift. Many of the females that follow this pattern ultimately launch themselves from the bolt and glide for a short distance.

Female age had an impact on both fanning time (RM) and time to flight (RB, A, and hybrids). Females (RB, RM, and A) that were flight tested the same day they eclosed tended to take longer to initiate flight, even though fanning time was the same as for those 1–2 d old. We suspect that this delay was due to the need for wing hardening after eclosion and before flight. Some Siberian females observed in the field were found to wait until the day after eclosion before initiating flight (Cardé 1994). RM females that were 3 d old had longer fanning durations than those 0–2 d old. This could have been due to lower energy reserves, resulting in lower wing beat frequencies, or to muscle degradation over time.

Flight capability of female gypsy moths appears to be genetically determined, although a genetic basis for

the differences seen within populations with no known hybridization has not been established. For example, a few individuals in the RM, RB and W populations have a different flight capability from the majority. Some RM and RB females are only capable of gliding whereas most are strong fliers. A few W females, after wing fanning and walking to the top, launched themselves off the bolts, only to glide <0.5 m to a soft landing, rather than the usual plummet and hard landing when W females fell off the bolt. This is consistent with observations that a very small proportion of North American female gypsy moths glide in the forest (Sandquist et al. 1973), and early reports that some European female gypsy moths could fly a short distance (Forbush and Fernald 1896, Bergmann 1953). In our tests, about half of the hybrids were capable of gliding varying distances, an intermediate level between strong flight (Asian parent) and no flight (North American parent). This is consistent with a multiple gene mode of inheritance that is common for flight in other insects (Harrison 1980, Dingle 1984, Han and Gatehouse 1989) and with the results obtained by Reineke and Zebitz (1998) from crosses between Asian and European moths. This suggests that if flighted females are introduced into areas where the nonflighted form already is established, full flight capability will not be present in the initial hybrid. However, the gliding ability of hybrids could still result in greater dispersal of the population in a single year than occurs for the nonflying form. Further research on the inheritance of flight in gypsy moths is required to determine if full flight capability would be exhibited in later hybrid generations.

It is not understood why gypsy moth females from some areas fly and others do not fly. It has been theorized that females in Russia and the Far East fly to find thermally favorable oviposition sites (Baranchikov 1988), to escape predators (Charlton et al. 1999), or to escape deteriorating habitats and colonize new ones (Reineke and Zebitz 1998). The presence of a selective advantage, possibly one already theorized, seems the most likely explanation because even North American gypsy moths, which do not fly, still exhibit some remnants of flight behavior (e.g., wing fanning at dusk and launching from their perches). The lack of flight in the North American and European gypsy moth females could then be explained by a relaxing of the selection pressure, possibly coupled with founder effects. Further examination of the geographic distribution of flight and the genetic basis for flight in gypsy moths is necessary to understanding its dispersal and managing introductions of flighted females.

Acknowledgments

We thank A. Liebhold and J. Podgwaite for their critical review of the manuscript, and D. Randall for statistical review. J. Bell and G. Turova assisted in obtaining egg masses from Canada and Russia, respectively, and M. Greenberg, P. Moore, L. Murphy, C. ODell, D. Roberts-Paschall, and S. Taylor provided technical assistance.

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Received for publication 14 August 2000; accepted 6 November 2000.