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Synchronous Crepuscular Flight of Female Asian Gypsy Moths: Relationships of Light Intensity and Ambient and Body Temperatures

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Female gypsy moths (Lymantria dispar) *of Asian heritage studied in central Siberia and Germany exhibit a highly synchronous flight at dusk, after light intensity falls to about 2 lux. This critical light intensity sets the timing of flight behaviors independent of ambient temperature. Flight follows several minutes of preflight wing fanning during which females in Germany and those from a laboratory colony (derived from Siberian stock) raised their thoracic temperatures to 32–33°C at ambient temperatures of 19–22°C. Thoracic temperature of females in free flight exceeded the air temperature (19–22°C) by approximately 11–13°C. The duration of wing fanning was strongly dependent on ambient temperature. In Germany, where ambient temperatures at dusk ranged between 21 and 25°C, females wing fanned for only 2.1 ± 0.2 (SE) min; in the much colder temperatures prevalent at dusk in Bellyk, central Siberia (11–13°C), females spent 11.2 ± 0.6 min in preflight wing fanning. The majority (≤80%) of mated and even virgin females initiated flight during the evening of the day they eclosed. However, in Bellyk, a small proportion (12%) of females wing fanned for an extended time but then stopped, whereas others (8%) never wing fanned and, therefore, did not take flight. Females also were capable of flight when disturbed during the daylight hours in Germany where the maximal temperature was high (27–30°C), but not in Siberia, where temperatures peaked at only 17–19°C. However, Siberian females were able to propel themselves off the tree on which they were perched by executing several vigorous wing flicks when approached by the predaceous tettigoniid,* Tettigonia caudata.

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INTRODUCTION

The gypsy moth, *Lymantria dispar*, exhibits a broad variation of female flight capability. Females of the European strain as well as their descendents in North America do not fly, even though they have well-developed wings. The few reports of flight by North American females (Sandquist *et al.*, 1973) almost always refer to undersized or spent females that had already oviposited. In contrast, females native to parts of eastern Europe, all of Russia, and Japan are capable of sustained, long-distance flight (Ferguson, 1978). In general, flight capability is strongest in females from Japan and the Russian Far East and progressively diminishes westward.

Several characteristics of female Asian gypsy moth (AGM) flight have been identified. Migration can be a long distance phenomenon, with a few reliable reports of females flying upwards of 10 km, although 3 to 5 km is a more usual maximum distance (Baranchikov, 1988). Typical flight distances may be considerably shorter than this, but definitive data are lacking. At night, females are readily attracted to lights, particularly those that emit wavelengths less than 450 nm (Wallner *et al.*, 1995). Once attracted, females often settle nearby where they deposit their egg mass. Curiously, however, the females do not seek out larval host plants during flight. Suitable hosts instead must be found by the first-instar larvae which balloon on silk threads and are carried passively by wind currents until they land on or near a host plant (Mason and McManus, 1981).

The characteristics and function of female gypsy moth flight and the environmental cues that trigger it are poorly understood. In this report, we describe the preflight and flight behaviors of AGM females and the environmental signals that influence the onset of activity. We also determined the relationship between ambient temperature (T_a and body temperatures (T_{th}) of flying females in the field and under laboratory conditions.

MATERIALS AND METHODS

Flight behavior was studied from late July to early August at two sites: one near Bellyk, a small village in south–central Siberia, Russia (53.0N, 91.18E), where only the Asian strain occurs and the other near Lampertheim (State of Hessen), Germany (49.36N, 8.28E), an area that until recently harbored only the European race but has been invaded by Asian moths (and/or Asian-European crosses) during the last few years (Gossenauer-Mahron, 1995). Bellyk is situated

in a hilly region of upland steppes with forests in sheltered valleys composed mostly of birch (*Betula pendula*) with scattered larch (*Larix* spp.) and poplar (*Populus* spp.). The Lampertheim site is in a forested area dominated by beech (*Fagus sylvatica*) and oak (*Quercus* spp.) with some pine (*Pinus sylvestris*).

Pupae were collected from areas near the study sites as described by Cardé *et al.* (1996) and held outdoors in an emergence box exposed to natural light and temperature. Immediately following eclosion, females were coaxed gently onto typical calling (pheromone-releasing) sites, namely, tree trunks or leaves, 1–2 m above ground level. From this time on, females were not disturbed, so that they could expand their wings and display natural mating, preflight, and flight behaviors. Individual females were identified by a number affixed below them on the tree trunk or nearby foliage.

Female behaviors were observed by scan sampling at 30-min intervals during most of the day, then every 5 min starting 1 h before sunset, and at 1-min intervals beginning when the first moth started wing fanning until the last moth flew or stopped wing fanning. The following behaviors and events were noted at each sampling occasion: (1) initiation of wing fanning; (2) stationary wing fanning; (3) walking, whether or not wing fanning; and (4) taking flight.

Ambient temperature (T_a) was recorded continuously (in Russian) with a battery-operated, microprocessor-based, temperature recorder (White Box Inc. Model CT-485, Stamford, CT) or at each sampling point (in Germany) with a digital thermometer (Physitemp BAT-12 with MT-29/l probe; Clifton, NJ) positioned in the shade. In Germany, light intensity was recorded with a Gossen Ultra Pro by pointing the sensor straight up to the unobstructed sky overhead or horizontally and directly at the tree on which the females clung, from 2 m away. Measurements of light intensity and thoracic temperatures (T_{th}) could not be made in Siberia owing to the theft of most of our equipment. We instead estimated light intensity from standard tables (Beck, 1980), based on the date, latitude, and time of sunset; the actual illumination level on some nights was slightly less than the standard values becauase of cloud cover.

Thoracic temperatures of females in Germany were measured to the nearest 0.1°C with a Physitemp BAT-12 with MT-29/l probe. Females that we saw initiate flight, those in free flight, those that flew to artificial light (having flown for an unknown period of time), or those sitting on trees (30–60 min before the onset of the evening flight) were captured and within 4 s, the probe was inserted laterally into the thoracic flight muscle. Moths were held by the wing tips to minimize transfer of heat. T_a was recorded just prior to measuring T_{th}.

Additional T_{th} measurements on AGM females were made at a primary quarantine facility (USDA Forest Service, Ansonia, CT). These females were derived from feral stock collected in Black Lake in south–central Siberia, Russia (ca. 500 km W of Lake Baikal) and had been in culture for three generations at the time of testing. Flight assays were conducted in an 8 × 7 × 2.5-m-high room.

Photophase illumination was provided by fluorescent lights giving 600 lux. An incandescent floodlight (which remained lit throughout the photoperiod) was set by rheostat to produce a scotophase light intensity of ca. 2 lux (after the fluorescent lights were abruptly turned off), which stimulated preflight and flight activities. Mated females were placed, 30 min before lights-off, on 0.6 m long × 0.1 m diameter long sections oriented vertically. Within 30 min after lights-off, females began wing fanning, and then most took flight. T_{th} was measured as described above after the females had flown for at least 2 min (Wallner *et al.*, 1995). Wing loadings (body mass (mg)/cm^2 wing area) of a sample of 24 AGM females that included a representation of relatively small (800- to 1000-mg), medium (1100- to 1300-mg) and large (>1300-mg)-bodied moths were calculated. Fore- and hindwings were removed from one side, arranged in a natural, overlapping flight position, and photocopied. The wing outlines were cut out, and their surface areas were measured with a leaf area meter (LI-3000 meter/LI-3050A drive belt; Li-Cor, Lincoln, NE).

RESULTS

Description of Preflight and Flight Behaviors

Most females eclosed from midmorning to midafternoon (Cardé *et al.*, 1996) and, depending on temperature, began calling 30 to 120 min later, followed soon after by mating. The females almost always remained in the same spot until nightfall, whether or not the copulating males disengaged. The onset of the flying phase was indicated by a slow, partial elevation of the wings accompanied by a few side-to-side rocking movements and often by voiding of the meconium. Some females walked for a short distance (5–25 cm) before elevating their wings. Wing fanning started shortly thereafter (<60 s). The wing vibrations were at first low in amplitude but progressed within ca. 10 s to a sustained, very high-amplitude (60–90°), wing fanning. After stationary wing fanning for a variable, temperature-dependent time, females rapidly ascended the trunk, walking while wing fanning. Some females walked only a few cm, but most climbed 1–2 m and a few as much as 10 m high before taking flight. Females situated on leafy branches walked while wing fanning to the terminal leaves and then took flight. Observing subsequent behaviors was difficult, but several females in Bellyk flew upward ca. 25–100 m, then made one to several large (ca. 50- to 200-m-diameter) horizontal loops before heading off in a generally westerly direction, until they were lost from sight.

Females even flew or attempted to fly while the male was still *in copula*. Such females dragged the male behind them as they began walking while wing fanning up the tree trunk, at which point the male usually would release his hold prior to takeoff. A few females actually took flight with the male still in tow.

To determine whether virgin females also would fly at dusk, 12 Lampertheim females were held, from the time they eclosed, in a 1.5-m-high × 2 × 2-m screen enclosure to exclude males. All of these females flew within 10 min after their mated counterparts. After about 15–30 min of flight and walking while wing fanning on the screen, they again settled, and all resumed calling.

At dusk on one unusually warm (14°C) evening in Bellyk, we witnessed hundreds of females flying individually or in small clusters of 2–10 about 3–10 m above and aligned with a straight dirt road. The road was oriented almost directly east–west and crossed a large clearing surrounded by forest. Over 90% of the females flew westward toward the last fading light, but occasional females flew in the opposite direction. The females appeared to be using the road as a landmark, because almost all flew directly above it, whereas only a few flew parallel and none at an angle to it. In the forest west of the clearing, we discovered that hundreds of females were laying egg masses under the narrow overhang of an approximately 0.5-m-high bank that bordered the road.

We also sporadically observed females during late afternoon in Bellyk flying slowly in large ascending and descending circles, usually around landmarks such as an isolated tree in a field or a fence post. Closer examination of the area near some gate posts revealed that many females had crawled ca. 20 cm below ground into crevices surrounding the base of the posts and were ovipositing there. Despite the much higher population density in Germany, we rarely saw females flying before dark, although we did see one female rise in flight from a clump of grass at 2010, nearly 2 hours before nightfall.

Onset of Wing Fanning and Flight in Relation to Light Intensity

The onset of wing fanning and flight activity in relation to time of day and natural light intensity in Lampertheim is shown in Fig. 1. The first moth began wing fanning at 2155, and the last at 2211, a span of just 16 min. Wing fanning started only when light intensity dipped below about 3 lux. In Bellyk, the wing fanning phase was much more protracted (Fig. 2); the first moth began wing fanning at 2205, and the last at 2232, an interval of 27 min. Activity peaked between 2215 and 2225, during which interval the majority of the females started to wing fan. Based on standard tables, we estimated the light intensity in Bellyk to be 3–5 lux at the time when wing fanning began.

Initiating flight followed the same trend. In Lampertheim, all females commenced flight during a short 20-min interval after light intensity dipped below 2 lux (Fig. 1). In Bellyk, moths began taking flight later and over a longer interval; the flight onset period lasted from 2217 to 2256 (Fig. 2). Peak flight onset occurred from 2225 to 2230, during which most of the females took off.

The duration of preflight wing fanning was strongly dependent on ambient temperature. In Lampertheim, where the ambient temperature at dusk was com-

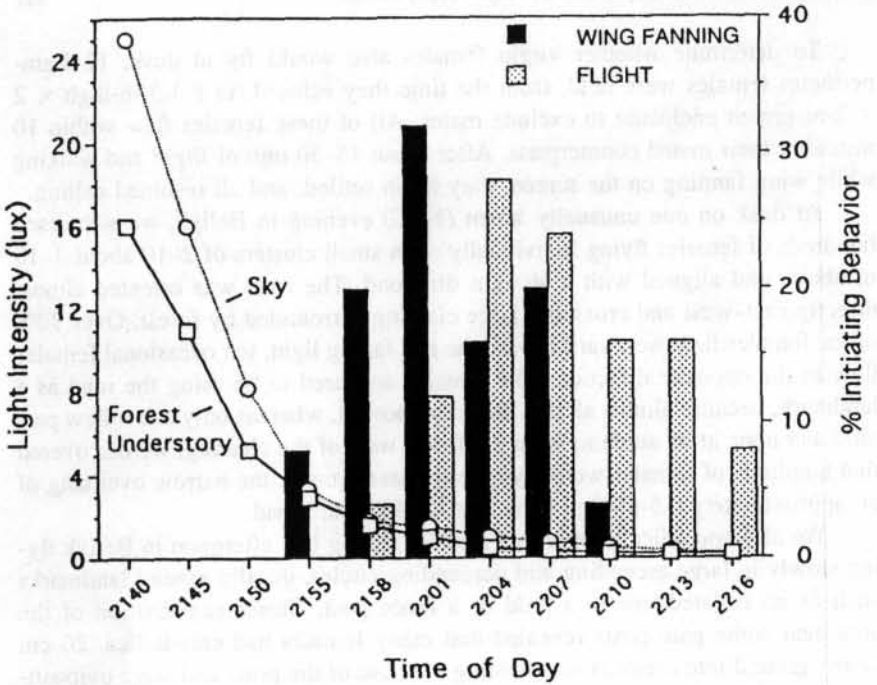

Fig. 1. Temporal pattern of AGM wing fanning and flight initiation in relation to light intensity in Lampertheim, Germany (July 15, 1994; temperature, 22–23°C). $n = 34$.

paratively high (21–23°C), females wing fanned for only 2.1 ± 0.2 min before taking flight (Fig. 1), and all took flight on their first night as adults. Temperatures at nightfall in Bellyk were much lower (12.5–13.5°C), and females wing fanned, on average, for 11.1 ± 0.63 min before taking flight (Fig. 2). Most (42 of 59) of the females flew on their first night after eclosion, but a few ($n = 5$) never wing fanned that first night or else were still mating at dusk ($n = 5$). The remaining seven females wing fanned for 17.1 ± 2.4 min (range, 10–22 min) but then abruptly stopped. These females spent more time wing fanning than did females that flew (*t* test; $t = -3.03$, df = 64, $P = 0.003$); they remained in the same spot for the next 24 h, scarcely moved, and never called or remated. The following evening, they underwent another preflight warmup before flying away.

Thoracic Temperature/Flight Relationships

The T_{th} of resting females in Lampertheim was elevated only slightly over T_a (Table I). Females maintained a mean T_{th} of 32–33°C during free flight in

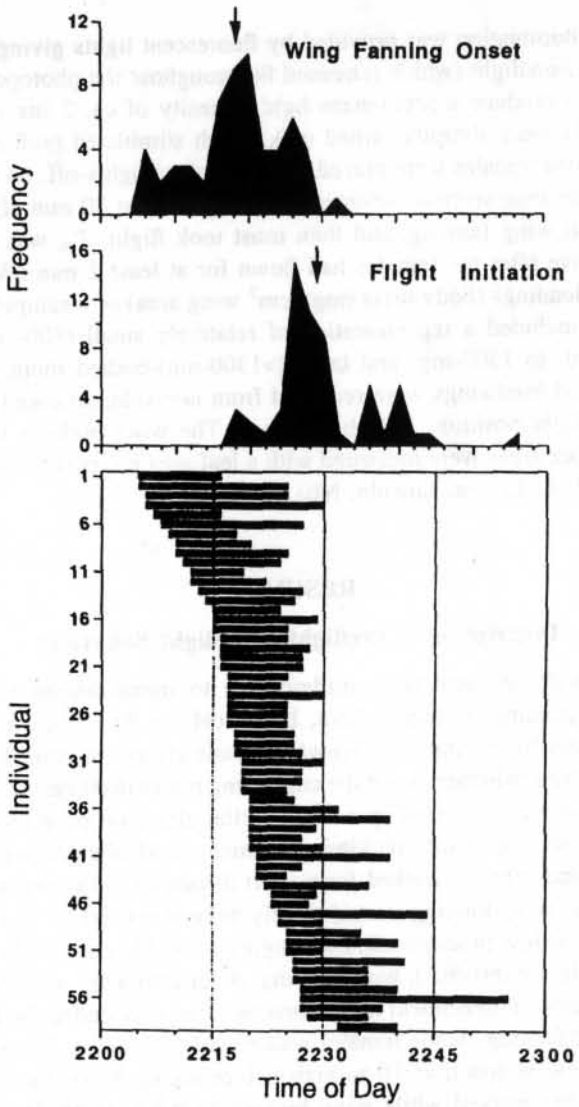

Fig. 2. Temporal distribution of onset and duration of preflight wing fanning and onset of flight of individual AGM females in Bellyk, Siberia (August 2 and 3, 1993) arranged chronologically. $n = 59$. Horizontal bars represent the duration of wing fanning. Arrows indicate the mean onset of behaviors. The ambient temperature during this interval was 12.5–13°C. Females that never wing fanned or that wing fanned but then stopped and, thus, did not fly are not shown.

Table I. Mean ± SE (Range) Pre- and Postflight Body Temperatures of Female Asian Gypsy Moths in Relation to Ambient Temperature[a]

			In-flight	
	T_a	Preflight T_{th}	T_{th}	$T_{th} - T_a$
Wild	21.4 ± 0.1 (20.4–22.2)	—[b]	32.1 ± 0.3 (28.5–34.2)	10.7 ± 0.3 (7.7–12.5)
Laboratory	19.5 ± 0.1 (19.0–21.0)	20.4 ± 0.1 (19.2–21.5)	32.7 ± 0.5 (29.0–36.2)	13.1 ± 0.4 (10.0–16.6)

[a]Wild moths were from Lampertheim, Germany. Laboratory moths were derived from insects collected in the Black Lake region of south-central Siberia.
[b]Not measured; n = 25 for laboratory and 19 for wild moths.

T_a's ranging between 19 and 22°C. We also captured three females just after they flew to and were still fluttering on a sheet near a light (between 2237 and 2248); their T_{th}'s were 32.7, 33.6, and 34.8°C, similar to the values obtained for females captured in free flight.

On an unusually warm (28–29°C) evening in Lampertheim, we attempted to get perched females to fly prematurely. Most (8 of 13) females could be induced to fly by gently prodding them or touching their wings even though they had not wing fanned. Three females flew even when we merely approached (<2 m) them. The T_{th} of these females already exceeded 30°C, which was close to their threshold for flight and just 2–3°C less than the mean T_{th} of flying females. The mean T_{th} of resting laboratory females held at a T_a and 19–20°C was 20.5°C (SD, 0.13°C; range, 19.2–21.5°C), again just slightly elevated (0.93 ± 0.10°C) over T_a. After flying for at least 2 min, their mean T_{th} rose to 32.7°C (SD, 0.46°C; range, 29–36.2°C).

Females had a mean body mass (SE) of 1161 ± 43 mg and mean total wing area of 15.5 ± 0.4 cm^2, giving a mean wing loading of 74.5 ± 1.5 mg/cm^2. However, wing loading was not a static value (Fig. 3), because a significant ($P < 0.001$) increase in wing loading occurred as female body mass increased ($y = 18.493x - 216.158$; $r^2 = 0.421$); i.e., wing area did not scale linearly with body mass.

Predator Avoidance Flight

On several occasions in Bellyk we observed females that had mated or were still *in copula* propel themselves off the tree where they clung after being approached or contacted by the large (~60 mm in length) predaceous tettigoniid, *Tettigonia caudata*. These katydids were common in Bellyk; during midafternoon, they slowly walked upward on tree boles (apparently searching for food) before flying to another tree and repeating the process. Twice we watched a tettigoniid slowly and deliberately approach a mating pair of gypsy moths, then pounce on and capture the male and devour its body. Two other observed predatory attempts were unsuccessful; one involved a mating pair and the other a lone mated female. Females were able to evade the predator by abruptly catapulting from the tree trunk on which they perched, downward to the ground at a ca. 45° angle. This maneuver apparently was accomplished by a sudden, vigorous wing movement followed by several rapid wing beats. Evasive action always was initiated by the female rather than by her male mating partner.

It is noteworthy that when we confined individual katydids in 1-L cups with female gypsy moths, the normally quiet females immediately became agitated, fanned their wings vigorously, and attempted to escape. The katydid quickly pounced on the back of the moth and proceeded to consume its thorax and upper abdomen.

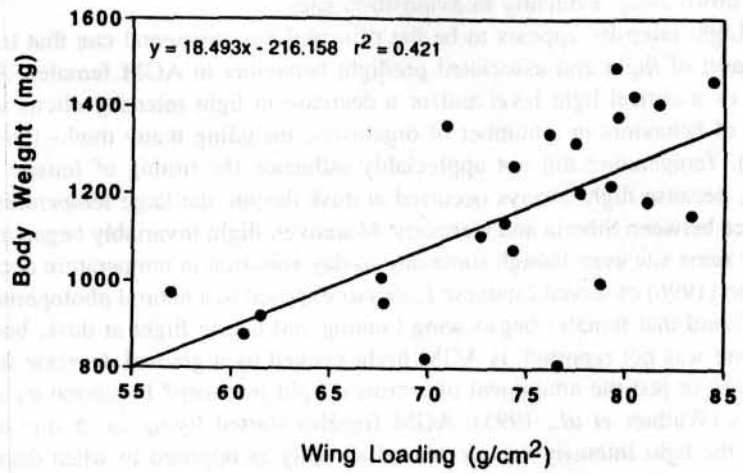

Fig. 3. Relationship between wing loading and body mass of 24 laboratory-reared AGM females descended from Siberian (Black Lake) stock.

DISCUSSION

Unmated AGM females were normally sedentary, as are their North American counterparts. They sit quietly all day long, with the only discernible movements being the slow, rhythmic exposure and retraction of their pheromone glands (Tang *et al.*, 1992); the gradual elevation of their wings by some individuals during calling; and a few minimal movements when they mate (Charlton and Cardé, 1990). But at dusk, mated AGM females throughout the forest abruptly and almost simultaneously begin fanning their wings and, just minutes later,

embark on a synchronous, mass flight. Within 15 min, all but a few stragglers have flown away, evidently to oviposition sites.

Light intensity appears to be the principal environmental cue that triggers the onset of flight and associated preflight behaviors in AGM females. Attainment of a critical light level and/or a decrease in light intensity elicits a wide array of behaviors in a number of organisms, including many moths (Dreissig, 1980). Temperature did not appreciably influence the timing of female AGM flight, because flight always occurred at dusk despite the large temperature difference between Siberia and Germany. Moreover, flight invariably began at dusk in the same site even though some day-to-day variation in temperature occurred. Koshio (1996) observed Japanese *L. dispar* exposed to a natural photoperiod and also found that females began wing fanning and taking flight at dusk, but temperature was not reported. Is AGM flight evoked by a gradual decrease in light intensity or just the attainment of a critical light intensity? In laboratory experiments (Wallner *et al.*, 1995), AGM females started flying ca. 5 min sooner when the light intensity was decreased abruptly as opposed to when decreased gradually, a phenomenon also seen in other moths (Dreisig, 1980). Whether photoperiod plays a role in flight initiation and the possibility that this behavior has a circadian basis has not been investigated.

Preflight wing fanning or wing tremulation is a widespread phenomenon in moths and other insects that functions to raise thoracic temperatures to levels sufficient to allow flight (Casey, 1980; Heinrich, 1981, 1993). Gypsy moth females also wing fan to elevate their body temperatures in preparation for flight. The duration of this phase is dependent on ambient temperature as it is for many other moths (Krogh and Zeuthen, 1941; Dorsett, 1962; McCrea and Heath, 1971; Cardé and Hagaman, 1983), being much more protracted in cold temperatures than in warm.

Some of the female gypsy moths we observed in Bellyk apparently did not attain a critical thoracic temperature, for they never flew despite wing fanning for upward of 20 min in the cold temperatures typically recorded there at dusk. In Lampertheim, on the other hand, where evening temperatures were high, all females flew after wing fanning for only a couple of minutes. The inverse relationship between ambient temperature and time needed for warmup is consistent with observations of other moths (Heinrich, 1993). Females in Lampertheim that were disturbed during late afternoon were also capable of flight, even though their thoracic temperatures were 5–6°C below their normal values at takeoff. Most of these females flew less than 10 m, but one flew about 50 m in ascending flight before landing, probably achieving warm-up "on the fly" (Heinrich, 1981). Conversely, pheromone-stimulated male gypsy moths often wing fan before taking flight, even when their thoracic temperatures already exceed the threshold for flight (Cardé and Hagaman, 1983). This suggests that other factors such as mobilization of energy stores by both sexes or perhaps wing fanning-aided sampling of airborne semiochemicals by males may contribute to the duration of the wing fanning phase in Lepidoptera and the timing of flight initiation relative to it.

Gypsy moth females are large-bodied moths with body masses that typically range from 0.8 to 1.5 g. For their body mass, they have a relatively high average wing loading of about 75 mg/cm^2. Their wing loading exceeds those recorded for all but a few arctiids and is at the low end of values typical of sphingids (Bartholomew and Heinrich, 1973). Wing loading of female AGM is also approximately fourfold higher than that of the slim-bodied North American gypsy moth males (Casey, 1980), whose physique is similar to that of AGM males.

Thoracic temperatures of flying females stabilized between 32 and 35°C, which were 11–13°C higher than the ambient temperatures of 19–22°C. These T_{th} values are lower than might be expected for moths of this body mass and wing loading. Bartholomew and Heinrich (1973) recorded the body temperatures of free flying moths from a number of different families (but not Lymantriidae) and found that, in general, the larger the moth, the higher its flight temperature. In their study, moths weighing more than 800 mg (all Sphingidae) had thoracic temperatures approaching 45°C. To our knowledge, no one has examined body temperature/flight relationships of female lymantriids which tend either to be much larger than conspecific males or else lack wings. Thoracic flight temperatures also tend to increase directly with wing loading, both for species within a family and between families (Bartholomew and Heinrich, 1973; Heinrich, 1981). Moreover, gypsy moth females are insulated heavily with a dense covering of long scales on their thorax and abdomen, a feature usually associated with maintenance of higher thoracic temperatures (Heinrich, 1981). On the other hand, factors such as wing beat frequency and metabolic rates also correlate positively with thoracic flight temperatures (Heinrich, 1981). We did not measure the wing beat frequency of female AGM, but it is almost certainly lower than that of sphingids.

The function or adaptive significance of flight by female AGM is still not clear. Baranchikov (1988) has theorized that females fly to find thermally favorable oviposition sites. Egg embryonation in this species begins soon after oviposition, and larvae are fully formed in about a month. Development then ceases, and the larvae spend the winter in diapause. According to Baranchikov (1988), females seek out situations such as rocky outcrops where the eggs will be exposed to higher temperatures, thus enabling the larvae to complete development before the onset of unsuitably cold temperatures in the harsh climate and short summers of Siberia. In Bellyk, we did indeed find egg masses in such rock crevices in high, south-facing outcrops, but we found many egg masses in other areas as well, such as in cracks or crevices under banks or at the base of trees or posts. The latter sites were most likely not subject to higher temperatures,

because they were usually in shaded forests and/or had northern exposures. An alternate is that egg masses so situated may be afforded greater survival value because they would be below the snow line and thus not subject to lethally low winter temperatures. In northern Michigan, NAGM egg masses closest to the ground and below the snowline had much higher egg hatch than did masses located 90 cm above ground (Smitley *et al.*, 1998). Other factors such as avoidance of predators and parasites also may influence selection of oviposition sites as has been shown to occur in Japanese gypsy moths (Higashiura, 1988, 1989). For instance, Higashiura (1988) found that egg masses deposited below the eventual snow line suffered lower avian predation than did egg masses situated above the snow.

North American gypsy moth females tend to oviposit very close to their calling site. Conversely, AGM females, as well as nun moth, *Lymantria monacha*, and rosy gypsy moth, *Lymantria mathura*, fly even when they are surrounded by suitable larval host plants or when they are already sitting on a host in locales with few and widely scattered trees, as was the case in the Siberian Far East (Wallner *et al.*, 1995). Migratory flight is a prelude but not a precondition to oviposition, because even virgins will fly, even though most females are mated by dusk except in all but the lowest population densities (Sharov *et al.*, 1995).

The possible evolutionary advantages of migration have been well documented (Johnson, 1969; Dingle, 1985). For AGM, flight may offer a means of "escaping" an area before parasite and pathogen loads rise and eventually cause high mortality. On the other hand, migratory flight may depress fecundity (Rankin and Burchsted, 1992). However, Keena (1995) found that AGM females that flew were no less fecund than females that were prevented from flying. This is not surprising, given that eggs in gypsy moths are fully developed prior to eclosion. Nor is flight triggered merely by high-population densities, as is the case for other moths such as the spruce budworm, *Choristoneura fumiferana* (Fisher and Greenbank, 1979). Cardé *et al.* (1996) studied low- to very high-density AGM populations across Eurasia and at every site, all females flew regardless of population density.

Even though North American gypsy moths do not fly, they still evidently exhibit some remnants of flight behavior. Virgin females will call from the same spot throughout the day and night, provided that the temperature is sufficiently high (Charlton and Cardé, 1982; Webster and Yin, 1997). At lights-off, however, they briefly become active, walking around for several minutes and, at times, fluttering their wings before they again settle down and resume calling (Charlton, personal observations). ODell and Mastro (1980) charted the activity rhythms of laboratory-reared female North American gypsy moths held outside in enclosures and observed similar behaviors. Females called and were stationary most of the day, but they did display two brief periods of activity, one at dusk and another

at dawn, at which time they wing fanned while walking up tree trunks (ODell and Mastro, 1980).

Although this behavior might not be considered flight, several females in Bellyk that had mated or were still *in copula* launched themselves off of trees when approached by the large, predaceous tettigoniid, *T. caudata*. This katydid or one having similar behaviors that frequents woodlands is not found in Western Europe or North America. Gypsy moth females, at least those in Europe and North America, are not often preyed upon and make little or no attempt to conceal themselves (Doane, 1968; Charlton and Cardé, 1992). In fact, North American females usually must be prodded repeatedly before they will walk even a short distance. Koshio (1996) noted, on the contrary, that Japanese gypsy moth females (which are capable of strong flight) perching on tree trunks often were preyed upon by birds. Could the relaxation of predation pressure have contributed to the evolution of flightlessness in Western European females and their descendants in North America? The comparative study of intraspecific populations adapted to different environments and subject to divergent selection pressures may provide useful insights into the selective forces behind such evolutionary changes.

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