

# Experimental evidence for male biased flight-to-light behavior in two moth species

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## Abstract

Many studies report a greater abundance of male than female moths in light trap catches. The finding was interpreted as evidence for male-biased attraction to light, but alternatives could not be ruled out. For example, it is not known, how much the sex ratio in the catches deviates from the natural sex ratio. To overcome these limitations, we experimentally tested the flight-to-light behavior of two moth species, *Yponomeuta cagnagella* (Hübner) (Lepidoptera: Yponomeutidae) and *Ligdia adustata* (Denis and Schiffmüller) (Lepidoptera: Geometridae), under standardized conditions in an enclosed environment. In our test, we controlled the sex ratio, age, and population size. We recorded the moths caught in the trap and those that remained outside. Depending on the species, between 27 and 72% of all moths were caught in the light trap. We found that male moths were significantly and about 1.6 times more frequently attracted to the light than female moths. Our results were consistent for both species and hold good on the level of populations. We experimentally supported the general observation of a sexual dimorphism in the flight-to-light behavior of moths. Possible functional explanations include different flight activities of males and females or differences in the perception of light between males and females. Our experimental demonstration of a sexual dimorphism in the flight-to-light behavior of moths together with the common observation of an overrepresentation of males in light traps and other artificial light sources has implications for population and conservation biology.

## Introduction

Over the last decades, artificial night lighting has increased globally (Cinzano et al., 2001). Artificial night lighting – or ecological light pollution as it is also called (Longcore & Rich, 2004; Rich & Longcore, 2006) – is assumed to negatively affect animal and plant species, for example, because it changes the behavior of many nocturnal species (Beier, 2006; Gauthreaux & Belser, 2006; Salmon, 2006), including that of moths (Frank, 1988, 2006; Kolligs, 2000; Nowinszky, 2004). Light sources that exhibit such attraction range from fires and candles to streetlights and illuminated advertising (Frank, 1988; Nowinszky, 2004). At the light source, attracted moths are often killed by direct burning

(Nowinszky, 2003), experience a higher risk of predation by bats and other predators (Warren, 1990; Svensson & Rydell, 1998; Rydell, 2006), and exhibit reduced fitness because of distraction from normal mating or feeding behaviors (Frank, 1988). Therefore, outdoor lighting is blamed for declines in populations of many moth species (Frank, 1988, 2006). Besides the unintended effect of artificial night lighting on nocturnal insects, ecologists and taxonomists have for years been using light traps to study the biology and biogeography of moths (Nowinszky, 2003) and to monitor occurrence and abundance of pest species in order to reduce their populations (Weissling & Knight, 1994; Nowinszky, 2003).

Even though artificial night lighting affects thousands of species and light traps are widely used, relatively little is known about the mechanisms and consequences of moths flying to artificial light. The two most plausible adaptive theories for the flight-to-light behavior are the light compass theory (Buddenbrook, 1937; Sothibandhu & Baker,

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1979; Baker, 1987) and the open space theory (Mazochin-Porshnyakov, 1960, 1965). The light compass theory states that nocturnal insects use celestial light sources, such as the moon, for orientation. The moths adjust their flight direction in fixed angles relative to the moon in order to fly in a straight line. Because of the moon's large distance from earth, the emitted light rays are about parallel. In contrast, light rays emitted from an artificial light source close to the observer are divergent. Approaching insects erroneously take them as parallel and orient their flight direction constantly in the same angle to the light rays. Thereby they circle spirally around the artificial light source and approach it. The open space theory assumes that nocturnal insects fly to open space, which is suitable for their activities. Open space such as clearings in or borders of a forest is brighter at night due to moon or starlight. The theory states that insects fly straight to artificial light sources and erroneously take it as open space. In both cases, the artificial light interacts with the moth's natural orientation.

Many ecological studies document differences in species' tendency to fly to light (Kolligs, 2000; Nowinszky, 2003). Some moth species are highly attracted to light sources, whereas others almost never come to light sources, even though they occur in direct vicinity (Kolligs, 2000). A further common observation of many field studies is a higher proportion of males than females caught in light traps (Malicky, 1974; Frank, 1988; Acharya, 1995; Kiss et al., 2003). For example, the sex ratio of 45 out of 51 Noctuidae species caught in light traps was male biased, it was equal for three species, and female biased for another three (Williams, 1939). Based on this, it is generally hypothesized that male moths are more readily attracted to light sources than female moths. However, all these studies only examined the trapped individuals but not the base population (Kiss et al., 2003). The studies were done under outdoor conditions and the reports are often anecdotal and not based on controlled experiments. It is not known which proportion of the whole population is attracted and caught at all, and how much the sex ratio in the catches deviates from the natural sex ratio or from the sex ratio of the currently active population. Without this information, the extent of a sexual dimorphism in the flight-to-light behavior remains speculative. Information on sex-biased flight-to-light behavior is required to extrapolate the sex ratio and size of the natural population from the individuals found at the light sources. The sex ratio and proportion of attracted individuals are also important for population genetics. Sexual dimorphism in the moth's flight-to-light behavior and an increased mortality of one sex influence population structure. When one sex becomes rare, effective population size will be reduced relative to the actual population size (Hartl & Clark, 1997). A male-biased

attraction may be especially harmful when it superimposes existing sex ratio deviations caused by sex-biased predation (Acharya, 1995) or sex ratio distorting parasites such as *Wolbachia* (Fujii et al., 2001; Charlat et al., 2003).

The limitations of correlative observations have been recognized by several authors (Geier, 1960; Weissling & Knight, 1994; Kolligs, 2000). Some authors partially diminish the limitation by using several trapping methods. They compare the sex ratio between population samples caught with bait or light traps and find differences in the sex ratio of moths caught in different types of traps. Light traps seem to be more attractive for male moths. Bait traps seem to be more attractive for female moths, probably because female moths often depend on energy-rich food sources for egg maturation (Scoble, 1995). However, the question whether and how much males and females differ quantitatively in their attractability by light sources can only be answered experimentally. We experimentally studied the flight-to-light behavior of two moth species – the small ermine moth, *Yponomeuta cagnagella* (Hübner) (Lepidoptera: Yponomeutidae), and the scorched carpet moth, *Ligdia adustata* (Denis and Schiffermüller) (Lepidoptera: Geometridae) – that were bred and reared in the laboratory. Both species are known to be attracted to light sources (Menken et al., 1992; Ebert et al., 2003). We were especially interested in the population's overall and sex-specific proportions of individuals that were attracted towards a standard light trap. We performed all our experiments under standardized laboratory conditions. The enclosed environment of a flight chamber allowed us to count both the individuals caught in the light trap and those that remained outside. We standardized the environmental conditions such as temperature and humidity, and excluded night sky views of the moon or stars. We also excluded structures within the habitat such as trees or conspicuous skylines that are used by moths as landmarks for orientation. All of these factors are known to influence the flight-to-light behavior of moths (Frank, 1988; Nowinszky, 2003).

## Materials and methods

### Collection and breeding of *Yponomeuta cagnagella*

*Yponomeuta cagnagella* is univoltine and adults fly in late spring. The eggs are laid in clusters of 50–100 on the twigs of the host plant, European spindle [*Euonymus europaeus* L. (Celastraceae)] (Menken et al., 1992). The larvae are gregarious and tie leaves together in loose webs, feeding within these communal webs and continuously extending them; they pupate inside the webs and hatch within 10–20 days. Upon eclosion, *Y. cagnagella* is not yet sexually mature. Females start calling for males only at the age of about 10 days (Hendrikse, 1979). The average age at first mating

**Table 1** Exact location of the 10 places where we collected caterpillars of *Yponomeuta cagnagella*

Name of the location	Region	Country	Latitude (N)	Longitude (E)
Bachgraben	Basel	Switzerland	47°33′	7°33′
Kannenfeldpark	Basel	Switzerland	47°34′	7°34′
Reinacher Heide	Basel	Switzerland	47°29′	7°36′
Spalentor	Basel	Switzerland	47°33′	7°34′
Röschenz Müli	Jura mountains	Switzerland	47°25′	7°28′
Chlösterli	Jura mountains	Switzerland	47°25′	7°22′
Blochmont	Alsace	France	47°26′	7°20′
Fuchswiese	Alsace	France	47°26′	7°20′
Hegenheim	Alsace	France	47°33′	7°33′
Doucier	Burgundy	France	46°39′	5°46′

is 14.6 days, and females may mate with several males (Bakker et al., 2008). Individuals rarely disperse further than 100 m from their place of eclosion (Menken et al., 1992) and gene flow between populations is low (Menken et al., 1980).

We collected L2- and L3-stage larvae of *Y. cagnagella* between 22 April 2007 and 8 May 2007 by beating branches of the larval food plant. Thereby, we sampled animals independent of the subsequent experimental test method (light trapping). We collected larvae in 10 locations (Table 1): four in or near Basel (Switzerland), two in the Jura mountains (Switzerland), three in the Alsace (France), and one in the Burgundy (France). The various locations supposedly held different population of *Y. cagnagella*. Per location, we collected larvae from two to eight (mean 4.9) communal webs. Larvae within one web are usually full-sibs from the same clutch (Hendrikse, 1979; Menken et al., 1992). Each web contained at least 20–30 larvae, up to 100.

We reared the larvae under standardized conditions in the laboratory. All larvae of a web were placed in a 500-ml plastic box, with a paper tissue at the bottom and small holes for aeration in the lid, together with fresh spindle leaves ad libitum. We cleaned the boxes every 2nd or 3rd day, removed old leaves, and replaced the paper tissue. All boxes were kept in a climate chamber at 80% r.h. and L16:D8, corresponding to summer conditions. During the light phase, temperature was 23 °C, during the dark phase it was lowered to 19 °C. To avoid abrupt changes from light to dark (and vice versa), the light phase included a continuous 1-h dawn and dusk phase. Larvae of a clutch synchronously stop eating about 4–5 days before pupation (Menken et al., 1992). Thenceforward, we stopped refreshing food and did not remove the lid anymore. The larvae pupated and moths hatched about 10 days later. We used these moths for the flight-to-light experiment.

#### Collection and breeding of *Ligdia adustata*

*Ligdia adustata* is bivoltine and nocturnally active. The species is widely distributed in Europe and western Asia,

along with its only larval food plant, *E. europaeus*. The adults fly moderately well. They do not disperse very far and fly especially in the understorey of forests, but also occur in settlement areas (Ebert et al., 2003).

*Ligdia adustata* flies in two overlapping generations from mid-April to beginning of September (Ebert et al., 2003; Altermatt et al., 2006). The females lay their eggs singly on leaves or twigs of the food plant. Larvae can be found from May to September. The first pupae, occurring from May onwards, eclose the same summer to form the second generation. Later pupae overwinter and eclose in the next spring to make up the first generation of the next year. The larvae pupate in a loose cocoon in the leaf litter. It is unknown whether pupae of the first generation can also overwinter instead of eclosing within the same summer.

We sampled a *L. adustata* population between Muttentz and Pratteln, east of Basel (47°31′N, 7°39′E). We collected larvae with the scooping method between 12 and 20 July 2006. Thereby, we got a population sample independent of the subsequent experimental test method (light trapping). We collected 47 L2- to L4-stage larvae. We kept the larvae in a climate chamber at 70% r.h., L16:D8, with 25 °C during the light phase and 20 °C during the dark phase; the first and last hour of the light phase mimicked dusk and dawn, respectively. The caterpillars were kept in 160-ml plastic vials in groups of 1–10 animals and fed fresh European spindle leaves ad libitum. Leaves were refreshed every 3 days and regularly sprayed with water. Within 20 days, the larvae pupated in a loosely woven cocoon between leaves or on the ground of the vial. We sprayed the pupae only once a week with water.

Out of the pupae, six female and three male moths eclosed. We put them together in a 1.5-l glass jar in the climate chamber and provided diluted sugar-water to feed on. The moths readily copulated and females started laying eggs. Larvae emerged 4–5 days later. We transferred 355 larvae in groups of 5–10 into plastic vials and kept them as described above. In total 335 caterpillars pupated. A small

proportion of moths hatched without diapausing. Because of the low hatching success, we placed the remaining pupae into a 1–2-months winter diapause (1 °C, 90% r.h., and complete darkness). Thereafter, hatching success was larger. We used all adult moths from this F1 generation for the flight-to-light experiment.

#### Flight-to-light experiment

We experimentally tested the flight-to-light behavior of both male and female *Y. cagnagella* and *L. adustata* moths in a flight chamber under constant climatic conditions. We built the flight chamber in a room without windows. The flight chamber was frustum-shaped, measuring 2.5 × 5.7 m at the bottom, 1.8 × 5.7 m at the top, and 3 m high. In the flight chamber, moths were supposedly attracted from every spot, as the effective range of light traps is about 3–5 m (Baker & Sadovy, 1978). The chamber was made out of beamless, black cotton fabric (poplin black). Also the ceiling and the floor were covered with the fabric. At the joints of the frustum, the cotton fabric was either sewed or folded and fixed with safety pins. The flight chamber was accessible from one side. Temperature in the flight chamber ranged between 20 and 22 °C. Before each experimental test, a humidifier raised the r.h. to 80%. Subsequently during the overnight tests, r.h. dropped to about 60%.

At one long side of the flight chamber, we placed a standard Heath trap (Heath, 1970) equipped with a fluorescent tube (TL 6W/05; Philips, Eindhoven, The Netherlands). The lamp was connected to a time switch. Prior to the test, all moths were kept at L16:D8 in the climate chamber (see above). Thereby, moths could adapt physiologically to the day-to-night change. The flight-to-light tests started in the evening (the tests started at about 20:00 hours and lasted until 08:00 hours). They were done synchronously to the night conditions in the climate chamber. We released moths in the dark at the long side of the flight-chamber opposite to the light trap. We turned on the light either immediately after release of the moths (*Y. cagnagella*) or 1 h after release (*L. adustata*). The light trap worked for 12 h. The next morning, we checked the trap immediately after the light turned off (*Y. cagnagella*) or within 1 h after the light turned off (*L. adustata*). We collected all animals that were in the trap (attracted to the light source) and outside the trap (not attracted to the light source) separately. Animals that died during the night were excluded from the analysis.

Because of the asynchronous hatching of *Y. cagnagella* moths from different populations, we tested the flight-to-light behavior of *Y. cagnagella* in 9 nights over a period of 3 weeks. For the flight-to-light test, we always used 2- to 3-day-old *Y. cagnagella* moths. At that age, their wings are completely hardened, but moths are not yet sexually

mature and have not yet started calling (Hendrikse, 1979). We marked the moths individually with felt-tip pens (Ehrlich & Hanski, 2004) to recognize their population of origin. We tested moths from different *Y. cagnagella* populations simultaneously. We sexed the moths only after the flight-to-light test.

Likewise, we did flight-to-light tests with *L. adustata* on 12 nights. We tested all *L. adustata* moths at the age of 1–3 days (young) and the surviving moths again at the age of 10–13 days (old). Between the two flight trials (young and old), we kept the *L. adustata* moths together in 1.5-l glass jars, containing a wet cloth as a water source and cotton wool drenched in diluted sugar water as a food source.

#### Statistical analysis

We tested for a difference in male and female flight-to-light behavior. For *Y. cagnagella*, we did the comparison on the level of populations and used a paired t-test. For *L. adustata*, we had moths from only one population, and thus did the comparison within this population with a Fisher's exact test. Fisher's test was used for the flight-to-light experiment with young (1–3 days) and old (10–13 days) *L. adustata* separately. For the statistical analysis we used the program R (R Development Core Team, 2007).

## Results

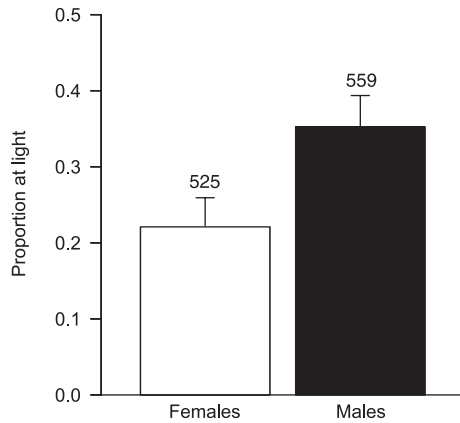
#### *Yponomeuta cagnagella*

All moths hatched after about 2 weeks in the pupal stage. The overall population sex ratio (females relative to males) was  $0.99 \pm 0.097$  (standard error). For the flight-to-light experiment we released 1 102 *Y. cagnagella* moths from 10 populations. Eighteen individuals died or were lost during the experiment (< 2% of total). We thus had data on 1 084 individuals. Per population we had 50–210 individuals. Overall, 313 of all individuals were caught in the light trap (197 males and 116 females). Males were about 1.6 times more frequently attracted to the light trap than females and the difference is highly significant, using the population as unit of replication (paired t-test:  $t = 3.3$ , d.f. = 9,  $P = 0.01$ ; Figure 1).

#### *Ligdia adustata*

Minimal pupal dormancy lasted about 12 days. Afterwards, 21 moths of the F1 generation hatched. Another 82 moths hatched after the mimicked winter diapause. The rest of the pupae either died or moths were crippled because of problems while hatching. Thus, in total we had 103 healthy adult moths (33 males, 70 females).

For the test of the young moths, 103 *L. adustata* moths were released 1–3 days post-eclosion. Twelve individuals (= 12%) were lost or died during the experimental procedures



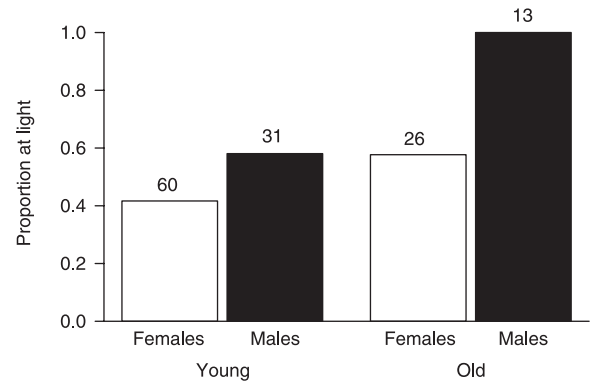
**Figure 1** Mean proportion (+ standard error) of females and males of the small ermine moth, *Yponomeuta cagnagella*, caught in the light trap. In total, 1 084 moths of 10 populations were included in the experiment. Over all populations, males are significantly more attracted to the light than females. Numbers above the bars indicate the total number of male and female moths used in the experiment.

and were excluded from the analysis. Forty-four individuals survived until the test of the old moths (aged 10–13 days). Of those, five individuals were lost or died during the experiment. Light trap catch was 47% of the young and 72% of the old moths. Young and old males were attracted 1.4 and 1.7 times more by the light trap than respective females. This difference is not significant for the moths tested when young (Fisher's exact test:  $P = 0.08$ ) but highly significant for the older moths ( $P = 0.007$ ; Figure 2). As the old moths were not an independent sample of the young moths, we explicitly refrained from comparing the two age classes.

## Discussion

We experimentally tested the flight-to-light behavior of *Y. cagnagella* and *L. adustata* under standardized conditions in an enclosed environment. We explicitly used animals that were reared from larvae or raised in the laboratory to exclude confounding effects of the environment. To our knowledge, it is the first experimental study that investigated the flight-to-light behavior of moths under fully controlled conditions.

In both species we found a significantly stronger flight-to-light behavior of male moths compared with females. This experimentally supported the correlative observation of a sexual dimorphism in the flight-to-light behavior of moths. Contrary to field observations (Malicky, 1974; Frank, 1988; Acharya, 1995; Kiss et al., 2003), we controlled the total population size and compared the sex ratio of



**Figure 2** Proportion of females and males of scorched carpet moth, *Ligdia adustata*, caught in the light trap. In total, 91 moths of one population were included in the experiment and tested at two ages. First, all moths were tested 1–3 days post-hatching (young). Second, all surviving moths were tested again at the age of 10–13 days post-hatching (old). Males were more attracted to the light than females, but the difference is only significant for old moths. Numbers above the bars indicate the total number of male and female moths used in the experiment.

moths caught in the trap with that of moths that were not caught. Our results were consistent across the two species, belonging to different moth families. The results are robust because they hold good on the level of populations in *Y. cagnagella* (Figure 1).

We see two hypotheses, not mutually exclusive, that may explain the sexual dimorphism in the flight-to-light behavior of the moths. First, the male bias in the light traps may be a correlated side product of some general sex-specific trait. Flying around in search of females, male moths often show a greater flight activity than females (Scoble, 1995). Females are less active and lure the males. In the most extreme case, females of some species have reduced wings and have lost their flight capacity. A higher mobility increases the likelihood to get in the vicinity of a light source. Eventually, the moths may be attracted to the light and, in our case, be caught in the trap. If the likelihood to fly to the light is correlated with the activity of an individual, it may explain the sexual dimorphism in the flight-to-light behavior.

The second class of hypotheses is based on a direct adaptive value, as with the light compass theory (Buddenbrook, 1937; Sotthibandhu & Baker, 1979; Baker, 1987) and the open space theory (Mazochin-Porshnyakov, 1960, 1965), which are both explained in the introduction. The sex-specific expression of an adaptive trait can be manifold, such as larger eyes, or bigger optical lobes, which could lead to a difference in the ability to perceive light. Several moth species possess sexually dimorphic eyes (Lau et al., 2007; Meyer-Rochow & Lau, 2008). In such species, the eyes of the males are larger and more sensitive to light. Males of

insect species other than moths also often possess better vision (Hornstein et al., 2000). By having larger and/or more sensitive eyes, male moths may experience stronger attraction by artificial light sources than female moths (Lau et al., 2007; Meyer-Rochow & Lau, 2008). As a consequence, males may be more frequently attracted to artificial night light sources than females. Because moths attracted to artificial lights suffer an increased mortality (Frank, 1988; Warren, 1990; Longcore & Rich, 2004), the trait will be under selection. However, this interpretation remains speculative, because light adaptation of moths' eyes and its adaptive value are still not satisfactorily investigated (reviewed by Nowinski, 2003).

Over the last decades, artificial night lighting has strongly increased (Cinzano et al., 2001; Longcore & Rich, 2004) and negatively affects many species (Frank, 1988; Longcore & Rich, 2004). Depending on the spectral composition, moths can be strongly attracted to light sources. Attracted individuals have a high mortality or reduction in reproductive success, because they suffer from an increased predation by bats or predators (Warren, 1990; Acharya, 1995), die of exhaustion after circling around the light for hours (Frank, 1988), or cease from mating and oviposition. Furthermore, individuals may leave their native habitat and end up in unsuitable areas (Frank, 1988; Longcore & Rich, 2004). To predict effects of artificial night lighting, it is important to know which animals from a population are attracted and possibly killed. Individuals of *L. adustata* were, when tested, most likely sexually mature, whereas all *Y. cagnagella* individuals were tested before they were sexually mature. The data suggest that *L. adustata* moths are less attracted when younger (possibly due to different flight activities). The individuals may still reproduce before being killed at a light source. However, these results should be carefully interpreted, as the dataset was rather small and another moth species, *Cydia pomonella* (L.), showed the reversed pattern (Geier, 1960).

Male biased flight-to-light behavior may also influence dispersal rates and connectivity of populations. Often, males disperse more than females and create gene flow between populations. When increased flight activity directly increases the likelihood to fly into a light source, selection will act against active and mobile individuals. The surviving individuals would disperse less widely and this could lead to increased isolation of populations, aggravating the already all-to-common habitat fragmentation. Especially those populations that are separated by areas densely covered with light sources (such as built-up city area, large illuminated buildings, roads, and bridges) may become genetically isolated. The consequences of sex-biased flight-to-light behavior may thus lead to a loss of genetic diversity similar to effects caused by habitat fragmentation and to selection

for less-mobile individuals. As the consequences of artificial night lighting on moths are poorly understood, it would seem timely and necessary to shed light on them!

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