Sex-biased response in activity to light sources with different spectral composition in geometrid moths with flightless females (Lepidoptera: Geometridae)

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Abstract

Geometrid moths occurring in late autumn and early spring in temperate forest habitats are often harmful defoliators of deciduous stands. Their populations can cause locally cyclic outbreaks and thus preventive monitoring actions have been developed, mainly based on pheromone attraction of males. Females are mostly flightless with reduced or lost wings and reduced senses associated with flying. Males are standard flyers with well-developed eyes and must be able to deal with rapidly changing light conditions during their activity. Although such differences indicate sex-biased differences in reactions to light, this has been insufficiently tested. In conditions of an experimental arena and using light-emitting diodes, we tested the different reactions of the sexes for nine species to precisely defined short segments of the electromagnetic spectrum in the range 360–660 nm. Across all species, males preferred shorter wavelengths up to 500 nm, while females were nonselective and generally less active. The sexes differed by eye size and body mass, with males having significantly larger eyes and lower body mass. Between brachypterous and apterous females, the former had larger eye size, while body mass differences were statistically insignificant. There were differences between the sexes in move-to-light reactions and changes in eye size and body mass in line with wing reduction. While males preferred a relatively distinct range of shorter wavelengths, a method of attraction to lights with distinct narrow spectra could be used markedly to enhance the established methods of forest pest monitoring, either alone or in combination with chemical male attraction.

Keywords: light attraction, electromagnetic radiation, forest-pests ecology, biological control, LED, Lepidoptera

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Introduction

Nocturnal insect attraction to light sources is a phenomenon that has long been studied and so there is a large body of literature regarding this behaviour (e.g. Taylor & French, 1974; Southwood & Henderson, 2000; Fayle *et al.*, 2007). The available data are useful for detecting and monitoring pests and disease vectors (Hendricks *et al.*, 1975; Raimondo *et al.*,

2004; Cowan & Gries, 2009; Baker *et al.*, 2011), for practical nature conservation via short- or long-term studies (Conrad *et al.*, 2006; Kadlec *et al.*, 2009), and for making recommendations to eliminate light pollution (Eisenbeis & Hänel, 2009).

Numerous types of light sources – differing both in intensity of emitted light and in spectral composition – have been used during field research (Eguchi *et al.*, 1982; Kelber *et al.*, 2002). Based on these differences, it can be stated that insects are attracted to specific parts of the electromagnetic spectrum, and mainly to the ultraviolet (UV) range (Barghini & de Medeiros, 2012). For this reason, those light sources emitting a higher proportion within the UV spectrum both attract greater numbers of individuals (Rydell, 1992) and are attractive to more taxa (Van Langevelde *et al.*, 2011). Moreover, previous studies using light within precisely defined spectral ranges have demonstrated there to be sex-related differences in attraction to light. Females react much less to emitted lights (Altermatt *et al.*, 2009; Cowan & Gries, 2009; Baker *et al.*, 2011; Van Geffen *et al.*, 2015). In species wherein both sexes are fully winged, such differences could be explained by behavioural response in different parts of the reproduction cycle (Cowan & Gries, 2009).

Lepidoptera is an order with a high incidence of species having flightless females (Hackman, 1966; Heppner, 1991). Such females are typified by abdominal expansion and with continuous loss of wings and senses responsible for orientation in space during flight (Lau *et al.*, 2007; Meyer-Rochow & Lau, 2008). Hackman (1966) divided flightless females into two groups according to their mobility: the 'heavy egg-filled type' with very restricted movement and the 'mobile type' with well-developed legs. While 'heavy' females often remain in their cocoons, attract males by pheromones and lay eggs in the nearest surroundings, 'mobile' females are able to crawl short distances and lay eggs away from the place of their hatching (Hackman, 1966). Mobile females, despite the eyes reduction, must be able to orient in space. Their eyes retain some degree of visual sensitivity, even though they are smaller, with lower numbers of facets, and with slower adaptation to light changes relative to males (Meyer-Rochow & Lau, 2008). A research with lights of different spectral composition points to the fact that such females are still able to detect the moment of sunset when experimentally increased presence of light with shorter wavelengths inhibits their activity (Van Geffen *et al.*, 2015).

Among geometrids, and especially in the subfamilies Ennominae and Larentiinae (Leraut, 2009; Wahlberg *et al.*, 2010), there occurs a group of species with 'mobile type' females. Broadly polyphagous, these moths species colonize temperate woodlands in stable conditions, finding there sufficient food plant sources for larval development (Hackman, 1966), and frequently they occur also as defoliator pests in cyclical outbreaks (e.g. Alford, 2000; Raymond *et al.*, 2002; Tenow *et al.*, 2007). For this reason, changes in their population development are carefully monitored, primarily using diverse methods based on pheromone attraction of males (Hand *et al.*, 1987; Szöcs *et al.*, 1993; Alford, 2000). In the present study, by means of experiments in a simulator arena, we investigated (i) possible differences in visual ability within a selection of discrete ranges of precisely defined short vectors of the electromagnetic spectrum by males (as ordinary flying insects) and flightless females of nine geometrid species, mostly forest defoliators, (ii) whether or not possible differences vary among species and sexes, and (iii) if such differences in visual perceptions could be explained by the rate of eyes reduction in

contrast to continual wing loss. Thus, in a case of selectivity of specific narrow part of light spectrum by studied species, we could supplement the knowledge about their eco-physiology and discuss possible improvements of the existing monitoring system.

Materials and methods

Study species

Experiments were carried out on nine species of geometrid moths with flightless females (table 1) belonging to the subfamilies Ennominae – *Agriopis aurantiaria* (Hübner, 1799), *A. leucophaearia* (Denis & Schiffermüller, 1775), *A. marginaria* (Fabricius, 1776), *Alsophila aceraria* (Denis & Schiffermüller, 1775), *A. aescularia* (Denis & Schiffermüller, 1775), *Erannis defoliaria* (Clerck, 1759), *Theria rupicapraria* (Denis & Schiffermüller, 1775) – and Larentiinae – *Operophtera brumata* (Linnaeus, 1758), *O. fagata* (Scharfenberg, 1805) (Leraut, 2009; Wahlberg *et al.*, 2010). These crepuscular and nocturnal species are commonly distributed in forest habitats throughout Central Europe, where they often constitute a majority of late autumn and early spring lepidopteran communities (Leraut, 2009). With the exception of *T. rupicapraria* (an oligophagous species feeding on shrubs of the family Rosaceae), all the species are widely polyphagous on deciduous trees and shrubs, and most of them are among the heavy defoliators of forest stands (Alford, 2000). Adults are active from late September to December (*A. aurantiaria, A. aceraria, E. defoliaria, O. brumata, O. fagata*) or from January to April (other species) (Leraut, 2009). Females are wholly apterous or with much-reduced wings (brachypterous). After hatching, they crawl to the nearest tree or shrub to wait for males with which to mate; they then crawl up into the tree or shrub, where they lay eggs (Hackman, 1966; Van Dongen *et al.*, 1998; Meyer-Rochow & Lau, 2008; Leraut, 2009).

Moths sampling

Individuals were collected always one night before an experiment during the time when adults are active (i.e. October–November 2013, March–April 2014) in an older deciduous forest stand dominated by oaks and beech near Kromeriz, Czech Republic (49°08′28″N, 17°15′32″ E, altitude: 550 m a.s.l.). Moths were searched by torchlight from twilight to midnight by walking through stands. Males were captured by insect net directly during flight or were found sitting on trees and shrubs; all observed females were captured during crawling or sitting on tree trunks and shrubs. Individuals were held separately by sex and species in plastic boxes under shady conditions and natural temperatures until the next night.

Experimental design and moth characteristics

The sensitivity of moths' eyes to various light spectra was tested in a cylindrical experimental arena (3 m in diameter, 2 m high). The walls were made from black light-impermeable polyester textile. The interior was thus protected against unwanted light penetration from the surrounding environment (Eisenbeis & Hänel, 2009). The arena was installed under shelter in outdoor conditions to avoid possible behavioural changes due to unnatural temperatures and the experiments were realized under temperatures when adults are active (up to −2°C; Lorentzen, 1974). In the centre of the arena there was installed a transparent box, in which the tested moths were

Table 1. Morphometric characteristics of studied species and total numbers of individuals and of individual measurements carried out in the experiment.

Species	No. indiv.		No. measur.		Female wings	Eye size (mm) Mean ± SD (range)		Dry body mass (mg) Mean ± SD (range)	
	M	F	M	F		M	F	M	F
Agriopis aurantiaria (Hübner, 1799)	13	7	52	15	BRA	0.9134 ± 0.0539 (0.8194–0.9904)	0.7369 ± 0.0453 (0.6742–0.7986)	7.1 ± 1.1 (5.6–9.5)	6.8 ± 1.2 (4.8–8.3)
Agriopis marginaria (Fabricius, 1776)	12	37	48	106	BRA	0.8441 ± 0.0608 (0.7346–0.9566)	0.6351 ± 0.0581 (0.5226–0.7972)	6.6 ± 1.3 (4.2–8.3)	11.4 ± 3.7 (4.6–19.2)
Agriopis leucophaearia (Denis & Schiff., 1775)	10	3	40	4	APT	0.8146 ± 0.0513 (0.7448–0.8868)	0.5656 ± 0.0504 (0.5150–0.6158)	5.1 ± 0.8 (3.9–6.3)	8.1 ± 3.4 (4.2–10.4)
Alsophila aceraria (Denis & Schiff., 1775)	17	13	68	25	APT	0.8000 ± 0.0397 (0.7460–0.8720)	0.5596 ± 0.0372 (0.4886–0.6192)	6.5 ± 1.2 (4.2–9.2)	9.2 ± 4.0 (2.0–13.6)
Alsophila aescularia (Denis & Schiff., 1775)	13	1	52	4	APT	0.8583 ± 0.0460 (0.7720–0.9168)	0.5896 (–)	6.3 ± 0.6 (4.9–7.6)	14.2 (–)
Erannis defoliaria (Clerck, 1759)	12	2	48	3	APT	1.0770 ± 0.0522 (0.9722–1.1910)	0.7637 ± 0.0389 (0.7362–0.7912)	13.2 ± 3.1 (6.1–17.9)	30.7 ± 10.0 (23.6–37.8)
Operophtera brumata (Linnaeus, 1758)	15	15	60	34	BRA	0.7082 ± 0.0386 (0.6306–0.7546)	0.5726 ± 0.0325 (0.5180–0.6396)	4.0 ± 0.8 (2.5–5.2)	6.8 ± 3.9 (2.0–13.5)
Operophtera fagata (Scharfenberg, 1805)	12	13	43	31	BRA	0.8068 ± 0.0812 (0.6842–0.9298)	0.6523 ± 0.0464 (0.5772–0.7320)	6.3 ± 1.5 (4.3–8.2)	5.9 ± 2.5 (2.8–11.4)
Theria rupicapraria (Denis & Schiff., 1775)	8	1	32	2	BRA	0.6948 ± 0.0312 (0.6542–0.7332)	0.5310 (–)	4.3 ± 0.7 (3.3–5.4)	7.6 (–)

No. indiv., number of individuals per sex used in experiment; No. measur, total number of individual measurements per sex; M, males; F, females; BRA, brachypterous females; APT, apterous females.
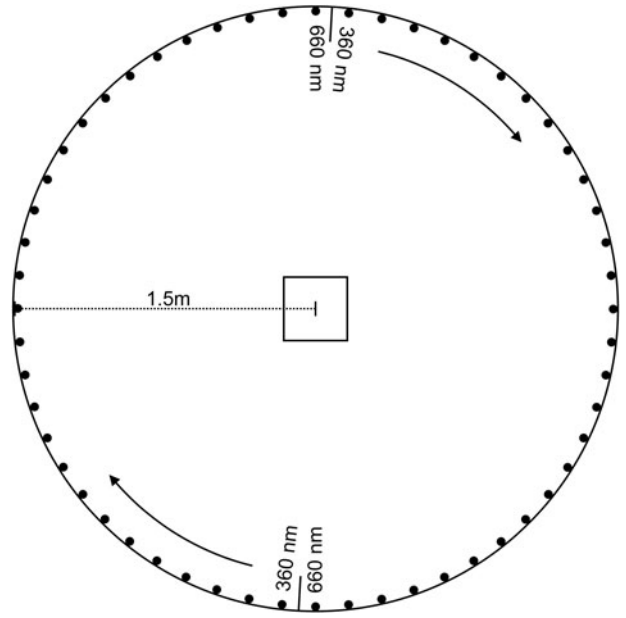

Fig. 1. Schematic representation of the experimental light arena. Dots indicate positions of monochromatic LEDs around the walls (separated by approximately 17 cm). Arrows show the direction of increasing light-wavelengths in 10 nm increments. The inner square indicates the position of the starting box.

held for 15 min in order to adapt to internal conditions and become orientated.

To test attraction, an electromagnetic stimulus having its main portion in the visible light range and the remainder within the UV region (360–660 nm) was selected. The test spectrum was divided into two repetitions, each of which was subdivided into 28 spectral vectors (fig. 1). Each spectral vector was emitted from a monochromatic light-emitting diode (LED) with a specific wavelength of radiated light. To avoid possible influences caused by differences in radiant flux of one wavelength of LED versus others (Cowan & Gries, 2009), the radiative flux of each LED was calibrated to 2.5 mW. LEDs were installed around the inside perimeter of the arena in order to maintain an equal distance (17 cm) between each succeeding LED, and separate vectors were linked to one another by their progressively increasing wavelengths (fig. 1). This placement of lights allowed moths gradually to choose the most attractive narrow parts of radiation. To minimalize the effects of reflected light on selectiveness of LEDs, together with small radiative flux, the light was emitted from sources in narrow viewing angle (maximally 30°) orientated directly to the starting place in the centre of arena.

Moths were tested always in the night following their collection and during the time of their natural activity (twilight to midnight). Each night, experiments were made first with males and then with females. After completing the experiments, the entirety of the inner walls and starting box was cleaned with 70% ethanol. During each experiment, up to four individuals of the same sex and species were tested together. Each was marked using a permanent marker to ensure its consistent identification. After assimilation in the starting box, moths were released and the precise spectrum of the LED reached was recorded. When tested moths reached a certain diode, the measurement was recorded as positive reaction

Table 2. Results of general linear mixed-effects models showing the relationships between response variable (LENGTH) and tested predictors. Random effects in models were INDIVIDUAL and TRIAL RUN within the measurements of each individual.

Model formula (fixed effects)	Deviance	AIC	Model significance			Random effects	
			χ^2	d.f.	P	Variance	SD
~NULL	7265.5	7273.5				6.759e-08	0.0002600
~SEX	7232.4	7242.4	33.1134	1	***	5.993e-08	0.0002448
~SPECIES	7255.7	7279.7	9.799	8	ns	6.527e-08	0.0002555
~SEX + SPECIES	7230.6	7256.6	1.807	8	ns	5.951e-08	0.0002439
~SEX + SPECIES + SEX:SPECIES	7228.8	7270.8	1.827	8	ns	5.925e-08	0.0002434

AIC, Akaike information criterion; NULL, null model only with random effect.
***$P < 0.001$, ns – $P > 0.05$.

to the light source and the exact spectrum of LED was noted. If there was no reaction within 15 min after release (i.e. a moth remained at the starting point), the measurement was recorded as negative. Four consecutive measurements were made for each individual.

After the experiment, the moths were euthanized by chloroform and eye diameter (EYE SIZE) and dry body mass (MASS) were measured. Each individual was dried in an oven at 80°C for 12 h and weighed on an analytical scale (Van Langevelde *et al.*, 2011). Moths were then decapitated and EYE SIZE was measured by cellSens Entry 1.6 (Olympus, Tokyo, Japan) using DP73 camera attached to Olympus SZX16 stereomicroscope.

Data analysis

We used generalized linear mixed-effects models (GLMM) for hypothesis testing. All models were analysed using gamma distribution of errors. All analyses were run in the program R (R Development Core Team 2012) using the lme4 package (Bates *et al.*, 2014).

A first analysis focused on the differences between species and/or sexes in their reaction to lights of various wavelengths. The spectral length (LENGTH) for the LED reached by the moths in each individual experiment was the dependent variable. In view of the fact that multiple measurements were made for a given individual, which were possibly able to change the selection of the lights after the first experience with the conditions of the arena, the identity of the exact individual (INDIVIDUAL) and trial run (TRIAL RUN) within the measurements of the same individual were specified as a random effects. Thus, the model distinguish the intra-individual effects. SPECIES and SEX (male, female) were added as the fixed effects of main interest.

A second analysis endeavoured to explain EYE SIZE as a possible response to continuous wing reduction. In these models, precise eye size was used as the dependent variable, whereas species was taken as a random effect. Wings type (WING) was specified as FULL (fully developed wings in males), BRACHYPTERY (at least small remnants in females), or APTERY (without any wings in females) and used as a fixed effect. In addition, as the eye size depended strongly on discrete body size due to allometry (Shingleton *et al.*, 2008), MASS was added as another fixed effect in the first position of the model. A similar model with SPECIES as random factor was fitted to test the dependence of MASS on WING type. Tukey's HSD tests were used to examine the differences between levels of significant factorial predictors.

The most parsimonious models were selected by comparing AIC values of model fits. This procedure compared models by balancing their complexity and goodness of fit (Akaike, 1974). Null models with random effects were fitted first, and then these were mutually compared with the more complex models with fixed effects and their interactions. Those models with the lowest AIC and with ΔAIC $\leq$ 2 were selected as best fitting to the data. We used a χ^2 test as a probability function to express significance of the models.

To distinguish whether or not some precise wavelengths are preferred by individuals with different eye size and wing type, a canonical correspondence analysis (CCA) was run in Canoco for Windows 4.5 (Ter Braak & Smilauer, 2002). As response variables (referred to in the software as 'species data'), the light wavelength preferences (measured as the number of observations with positive reactions to each light per each individual) were used. The predictors ('environmental data' in the software) used were relative eye size (expressed as RATIO between EYE SIZE and MASS) and wing type (FULL, BRACHYPTERY or APTERY). The full model was then simplified by forward selection procedure and only significant predictors were selected. A Monte Carlo permutation test (999 runs, full model) was used to express the significance of final ordinations containing only significant predictors. All models were fitted with and without affinity of individuals to SPECIES to check the possible influence at species level.

Results

Overall, the experiment evaluated a sample of 204 individuals (112 males, 92 females [73 brachypterous, 19 apterous]) of nine geometrid species collected under natural conditions (table 1). Sexes differed in their reaction during experiments. Only five individual measurements of males from a total of 448 were negative, while in the case of females 144 measurements (from 368) were negative. Overall, 443 of the individual measurements of males and 224 of those for females were positive (table 1).

In analysing attractiveness of lights with different wavelengths, SEX was the only significant predictor and no effect of SPECIES was detected (table 2). All other tested models had ΔAIC > 2 and did not improve significance over the previous model. Males and females differed strongly in their reactions to light sources (fig. 2). While males rather preferred lights with shorter wavelengths (mean ± SD: 402 ± 51 nm), females varied much more in their light selection (mean ± SD: 478 ± 104 nm) and it was impossible to detect any preferred spectral area for them.
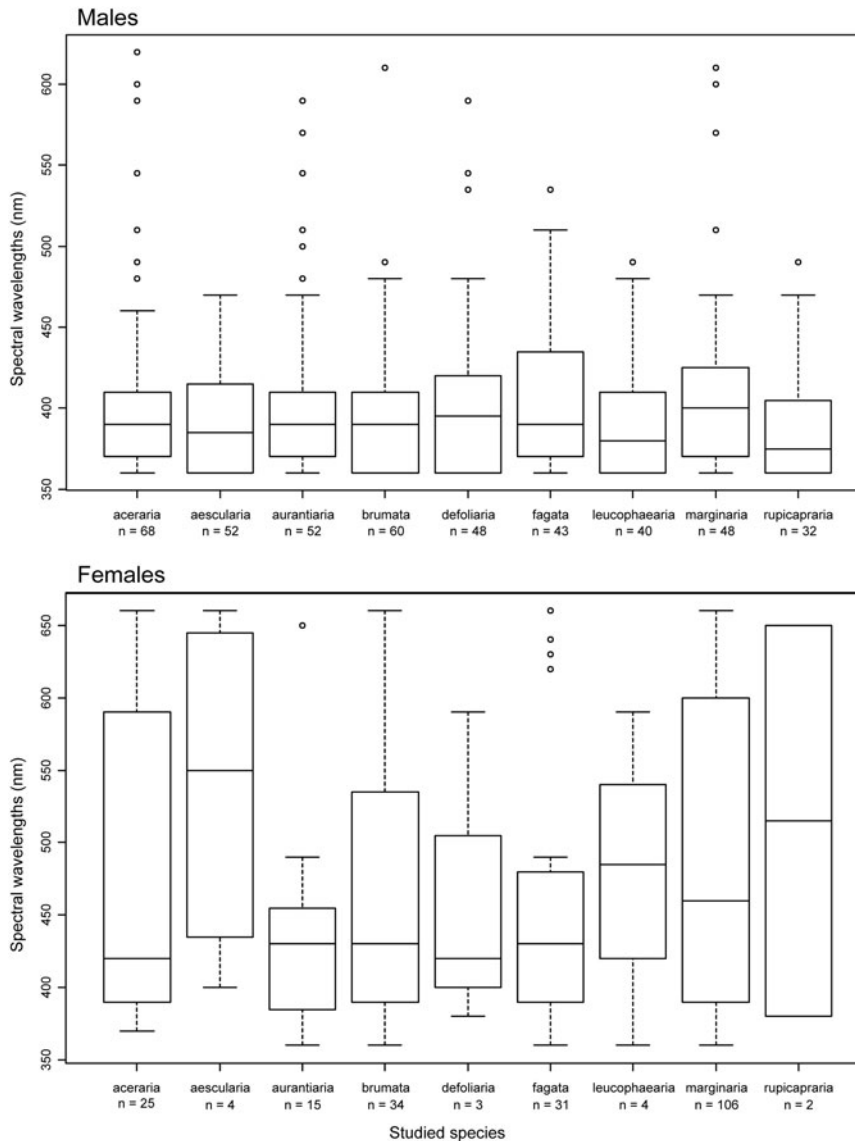
Fig. 2. Comparison of the preference for lights with distinct spectral composition by males and females in nine studied geometrid species. n – number of individual measurements for each species. Box-plot attributes: minimum value, 25th percentile, median, 75th percentile, maximum value and outliers (empty circles) are shown.

Differences in individual EYE SIZE were best explained by a model, which contained the variables MASS, WING, and their interaction (table 3), but the interaction had only weak effect on the response of main effects (ΔAIC between the model with and without interaction is only about 3; table 3). EYE SIZE differed significantly between individuals with different wing type (Tukey's HSD test in GLMM: APTERY–BRACHYPTERY: $z = 5.20$, $P < 0.001$; APTERY–FULL: $z = 16.06$, $P < 0.001$, BRACHYPTERY–FULL: $z = 19.05$, $P < 0.001$; table 1, fig. 3A), with EYE SIZE changing from smallest in apterous females (mean ± SD: 0.5836 ± 0.0733 mm) through brachypterous females (mean ± SD: 0.6336 ± 0.0667 mm) to fully winged males (mean ± SD: 0.8366 ± 0.1164 mm). This effect was significant also after withdrawing the effects of individual MASS (table 3). Individuals with different WING type differed strongly in their MASS, but even across species this effect

related only to sex and not species (table 1, fig. 3B). While fully winged males were lighter than females (Tukey's HSD test: APTERY–FULL: $z = -5.75$, $P < 0.0001$; BRACHYPTERY–FULL: $z = -4.90$, $P < 0.0001$), apterous and brachypterous females did not differ significantly by MASS (Tukey's HSD test: APTERY–BRACHYPTERY: $z = -0.58$, $P > 0.05$).

CCA ordination pointed to differences in preferred spectral lengths by individuals with different WING types (test of significance of first axes: eigenvalue = 0.248, $F = 5.579$, $P = 0.001$. All canonical axes (trace = 0.321, $F = 3.636$, $P = 0.001$) explained the 3.49% variability in species data (fig. 4). RATIO was observed to be insignificant during forward selection ($F = 0.872$, $P = 0.635$). Thus, the fully winged males flew more often to lights with shorter wavelengths (360–510 nm) than did females. Brachypterous females tended slightly more toward shorter wavelengths than did apterous females. When filtering out

Table 3. Results of general linear mixed-effects models showing the relationships between response variable (EYE SIZE) and tested predictors. Random effect in models was SPECIES.

Model formula (fixed effects)	Deviance	AIC	Model significance			Random effect	
			χ^2	d.f.	P	Variance	SD
~ NULL	−326.28	−320.28				0.022	0.097
~ MASS	−341.77	−333.77	15.493	1	***	0.012	0.109
~ MASS + WING	−633.28	−621.28	291.503	2	***	0.004	0.063
~ MASS + WING + MASS:WING	−640.59	−624.59	7.318	2	*	0.003	0.056

AIC, Akaike information criterion; NULL, null model only with random effect.
*** $P < 0.001$, * $P < 0.05$.

Discussion

Fully winged males and flightless females differed in their reactions and preferences to lights with varying spectral composition. While males flew more often to shorter wavelengths (under 500 nm), females varied more widely in their choice. This is in accordance with the presumption that males react as flying insects and have better abilities for orientation in space (Meyer-Rochow & Lau, 2008), while wingless females are more disadvantaged by their reduction of wings and perceptions. Even though the geometrids' wingless females in the studied species may in several cases have developed independently (Snäll *et al.*, 2007; Wahlberg *et al.*, 2010), the move-to-lights differences between sexes were similar for all tested species.

These similarities imply by way of the so-called 'winter moth syndrome' (Hackman, 1966; Barbosa *et al.,* 1989) a rather convergent adaptation to the environmental conditions of temperate European climate that is typical for late autumn or early spring (cold weather, insufficient nutrients for adults) with decreased adult predation by vertebrates (Buse *et al.*, 1999; Snäll *et al.*, 2007; Wahlberg *et al.*, 2010). In such conditions, males comprise the dispersed sex, which is flying in space and trying to find a female climbing on tree trunks or shrubs with which to mate (e.g. Van Dongen *et al.*, 1998; Van Dongen *et al.*, 1999). Females with reduced wings and wing muscles (Hackman, 1966; Heppner, 1991) should allocate more energy to reproduction. While polymorph females in Lepidoptera are rather rare (e.g. Heppner, 1991; Lau *et al.,* 2007), this relationship has been more studied in other insect orders with macropterous and brachypterous females (Denno *et al.*, 1989; Zera & Denno, 1997). For example, brachypterous females of the planthopper *Prokelisia dolus* have been shown to have greater overall fecundity than fully winged migrating forms (Denno *et al.*, 1989). In resolving a trade-off between flying and overall fecundity, therefore, flightless and pheromone-producing females (Svensson, 1996) reduced their sensory inputs, which would be necessary during active flight (Rydell *et al.*, 1997; Meyer-Rochow & Lau, 2008). These eventually became superfluous and so, in comparison with males, they increased their body size via hypertrophy of their reproductive organs (Hackman, 1966). The results of our experiments correspond with this knowledge, as the females tested were significantly heavier than males,

had reduced eyes, and their selection of lights spectra was poorer. The females' eyes were significantly smaller than those of the males, and according to Meyer-Rochow & Lau (2008), the eyes of flightless females also have decreased sensitivity and poorer resolution.

On the other hand, these differences in light preferences between the sexes may also be explained in part by the theory of behavioural and physiological adaptations to changes in light conditions during twilight and night (Johnsen *et al.*, 2006). Directly after sunset, the light conditions are dominated by spectra with shorter wavelengths near 450 nm and these change to longer wavelengths during the night (Johnsen *et al.*, 2006). Males of majority of the studied species are active during twilight, and, despite their lesser flying ability (Heinrich & Mommsen, 1985; Van Dongen *et al.*, 1996, Leggett *et al.*, 2011), their eyes are fully adapted to orientation in space under changing light conditions, albeit still with short wavelength dominance (Meyer-Rochow & Lau, 2008). In general, flying moths' eyes contain blue receptors sensitive to shorter wavelengths (Eguchi *et al.*, 1982; Cutler *et al.*, 1995; Briscoe & Chittka, 2001) and the fliers are better orientated in such light type (Cowan & Gries, 2009). Thus, a male preference for shorter wavelengths during the experiments should be explained by better orientation in space within which lights have such composition.

Females, meanwhile, must be active from twilight, when they are crawling on trees and attracting males (Van Dongen *et al.*, 1998), into the dark night when laying eggs. They, too, need a certain orientation in space, albeit not with such high resolution (Meyer-Rochow & Lau, 2008). This implies that during orientation, insects' eyes should be able to shift their functioning to longer wavelengths (Johnsen *et al.*, 2006). Thus, the females should be able to perform different behavioural activities under different light conditions. Moreover, females are able to change their affinity to different parts of the light spectrum according to their particular motivations. In the Indian meal moth (*Plodia interpunctella*) it has been observed, for example, that unmated females preferred slightly different wavelengths than did mated females or males (Cowan & Gries, 2009). The studied females during our experiments could have been in varying stages of the reproduction cycle (mated versus non-mated), and, inasmuch as such difference was not recognized, that could have been the reason why the females crawled toward such a wide range of the light spectrum. Moreover, it could have been that the unfertilized females were not motivated to react to any part of the light spectra whatsoever or that females were suppressed in activity and disoriented by light in general, and that accounts for the large proportion of negative reactions among females (Cowan & Gries, 2009; Van Geffen *et al.*, 2015).

The effects of affinity to SPECIES in the covariate model, the explained variability of species data by WING types decreased to 2.64%. Nevertheless, this was still highly significant (test of significance of first axes: eigenvalue = 0.169, $F = 3.769$, $P = 0.001$; all canonical axes: trace = 0.233, $F = 2.613$, $P = 0.001$).
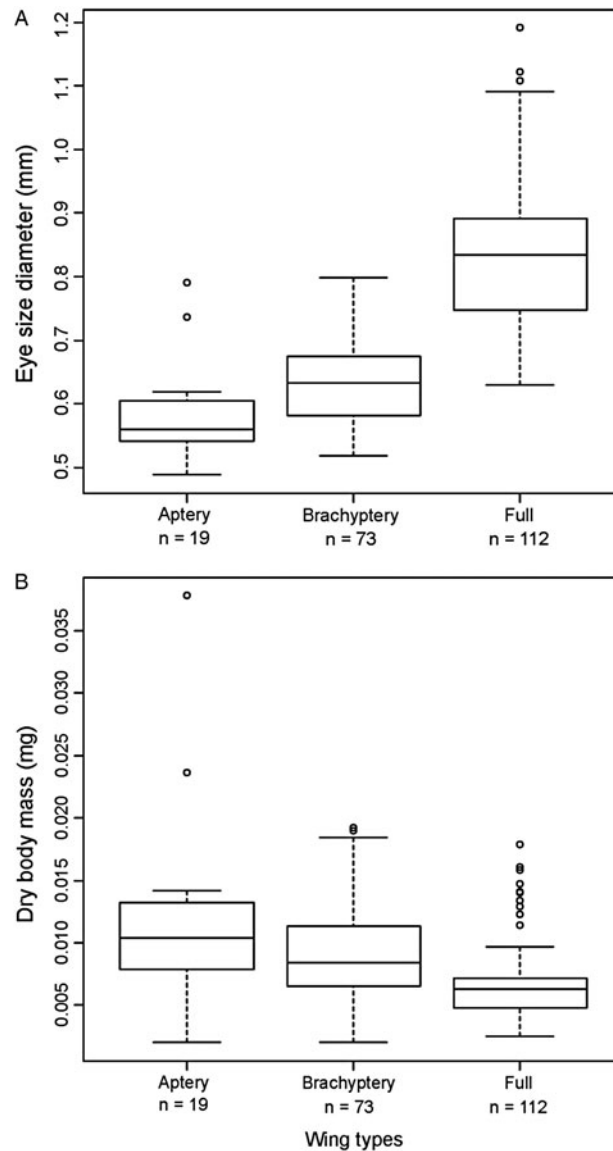
Fig. 3. Comparison of the individual morphometric attributes (A – eye size, B – dry body mass) of nine studied geometrid moth species with distinct reduction of wings. n – number of individuals for each wing type. Box-plot attributes: see fig. 1 for description.

Whereas males preferred a relatively distinct range of shorter light wavelengths – in principle across all tested species – the use of a distinct narrow spectrum of light for attracting moths could markedly enhance the effectiveness of established methods used in forest pest monitoring systems, which mainly involve species-specific pheromone attraction of males (Hand et al., 1987; Szöcs et al., 1993; Alford, 2000). A combining of these two methods has been tested, for example, on the forest pest Operophtera brumata and it was found out that more males were caught to pheromone traps illuminated by light with shorter wavelengths (Van Geffen et al., 2015). A similar mixed method (chemical and light attractant) has been tested with success also on stored-product beetle pests Tribolium castaneum (Duehl et al., 2011) and Cylas formicarius (McQuate, 2014), with increasing of the probability of adults' detection by mixed pheromone and light traps, or on

mosquitoes (Chen et al., 2011). Studies on Lepidoptera without mixed treatment have shown that light-trapping can be used with similar efficiency as other monitoring methods (Raimondo et al., 2004; Baker et al., 2011). Whereas the selected spectral range is attractive also to other groups of Lepidoptera (e.g. Van Langevelde et al., 2011), it should be expected – by using of combined pheromone-light traps – higher presence of other species in trapped samples. On the other hand, during autumn, winter, and spring only low diversity of moths occurs in forest stands of the temperate zone, and a substantial part of the trapped insects will consist, too, of such other monitored forest pests as within the genera Conistra, Orthosia or Pannolis (Alford, 2000).

Our results show there to be differences in move-to-light reactions between the sexes and continual changes in relative eye size and body mass and thus continual repression of
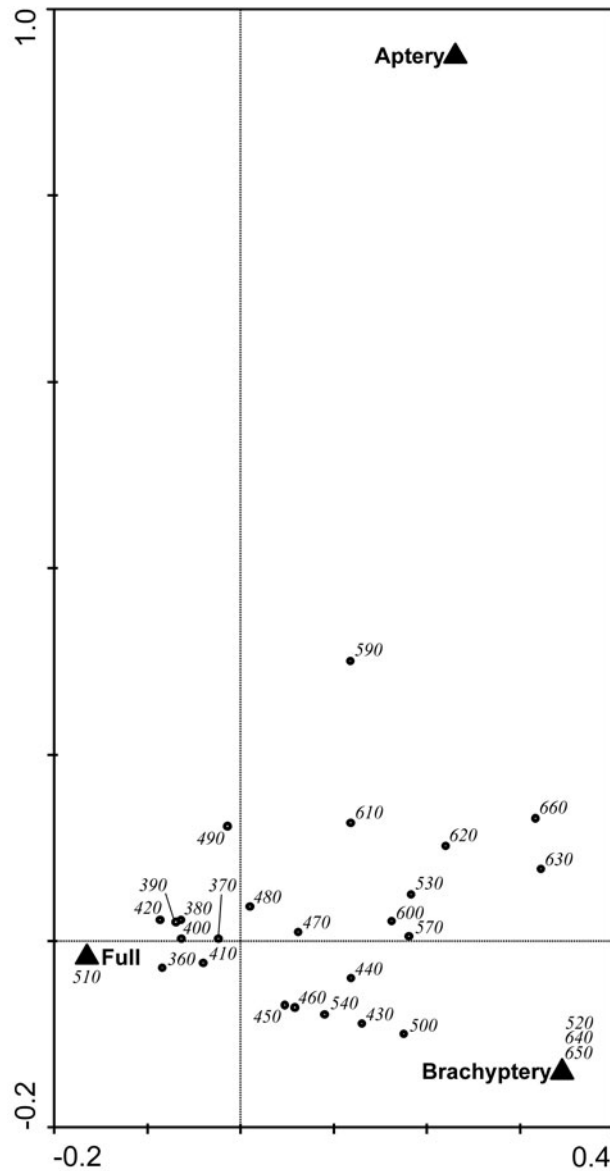
Fig. 4. Canonical correspondence analysis diagram of relationship between lights with specific wavelengths reached by moths with different wing types (triangles). Monte-Carlo test with 999 permutations: test of significance of first axes: eigenvalue = 0.248, $F = 5.579$, $P = 0.001$; all canonical axes: trace = 0.321, $F = 3.636$, $P = 0.001$.

both sexes, especially females, using light-trapping methods, (iii) whether or not the two types of females differ in their fecundity, and (iv) whether or not they differ in their nocturnal activity under residual light with long wavelengths. As implied by the multivariate analysis, the two types differ very slightly in response to spectral range. One explanation could lie in different timing of activity during night-time, but this should be more species specific, as, for example, wingless of *Phigalia pilosaria* females are active directly at twilight while the females of *E. defoliaria* are more active later in the night (Pikner M., personal observation). If such differences would be proven, then the 'mobile-type' of flightless females (Hackman, 1966) should be divided into two different groups of females having different vision abilities and reproduction success.

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redundant senses. In view of the fact that females (and males) should be able to spend only energetic resources allocated during the larval stage (Van Dongen *et al.*, 1999; Jervis *et al.*, 2005), brachypterous females should be more penalized in their overall fecundity than apterous females (Rhainds *et al.*, 2008). We should note that we recognize that our results can be biased by unequal data, and especially for females.

A number of questions arise for further research in this area, including (i) how these findings might need to be adjusted after including observations for heavy apterous females (e.g. *E. defoliara* and the genera *Lycia* and *Phigalia*), (ii) are we able to improve efficiency of existing monitoring systems in

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