Biological Conservation 144 (2011) 2274–2281

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Effect of spectral composition of artificial light on the attraction of moths

Frank van Langevelde [a], Jody A. Ettema [a,b], Maurice Donners [c], Michiel F. WallisDeVries [b,d], Dick Groenendijk [b,*]

[a] Resource Ecology Group, Department of Environmental Sciences, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands
[b] Dutch Butterfly Conservation, P.O. Box 506, 6700 AM Wageningen, The Netherlands
[c] Philips Lighting, Mathildelaan 1, 5611 BD Eindhoven, The Netherlands
[d] Laboratory of Entomology, Department of Plant Sciences, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands

ARTICLE INFO

Article history:
Received 17 February 2011
Received in revised form 31 May 2011
Accepted 4 June 2011
Available online 29 June 2011

Keywords:
Light pollution
Cascading effects
Body-size dependent effect
Ecology of the night
Lepidoptera

ABSTRACT

During the last decades, artificial night lighting has increased globally, which largely affected many plant and animal species. So far, current research highlights the importance of artificial light with smaller wavelengths in attracting moths, yet the effect of the spectral composition of artificial light on species richness and abundance of moths has not been studied systematically. Therefore, we tested the hypotheses that (1) higher species richness and higher abundances of moths are attracted to artificial light with smaller wavelengths than to light with larger wavelengths, and (2) this attraction is correlated with morphological characteristics of moths, especially their eye size. We indeed found higher species richness and abundances of moths in traps with lamps that emit light with smaller wavelengths. These lamps attracted moths with on average larger body mass, larger wing dimensions and larger eyes. Cascading effects on biodiversity and ecosystem functioning, e.g. pollination, can be expected when larger moth species are attracted to these lights. Predatory species with a diet of mainly larger moth species and plant species pollinated by larger moth species might then decline. Moreover, our results indicate a size-bias in trapping moths, resulting in an overrepresentation of larger moth species in lamps with small wavelengths. Our study indicates the potential use of lamps with larger wavelengths to effectively reduce the negative effect of light pollution on moth population dynamics and communities where moths play an important role.

1. Introduction

During the last decades, artificial night lighting has increased globally (Cinzano et al., 2001; Garstang, 2004). The use of street lighting, security lighting and other urban light sources negatively affected many animal and plant species (Rich and Longcore, 2006), and it is considered to be one of the major threats to moth populations (Frank, 2006; Conrad et al., 2006; Groenendijk and Ellis, 2011). Only recently, the effects of artificial night lighting on individuals (e.g. flight-to-light behavior, Frank, 1988), population dynamics (e.g. reduced reproduction, De Molenaar et al., 2000) and communities of nocturnal species (e.g. increased predation, Gotthard, 2000) are getting more attention (Longcore and Rich, 2004; Rich and Longcore, 2006; Settele, 2009).

Artificial night lighting attracts many moths, especially light with high ultraviolet (UV) emission (Frank, 1988, 2006; Nowinszky, 2003). A common, but still not fully convincing and complete explanation for their flight-to-light behavior is that moths mistake a strong light source for the moon and fly to it (Hsiao, 1973). This artificial lighting might have several effects on foraging and reproduction activities of moths and their interspecific interactions (Frank, 2006). For example, moths flying around streetlights at night may experience increased predation by bats and other nocturnal and diurnal predators which have learnt to take advantage of these artificial feeding stations (Rydell, 1992, 2006; but see Kuijper et al., 2008).

As different types of artificial lights are being used, knowledge about the effects of different types of lights on moths is important for their conservation. These light sources might largely differ in intensity and spectral composition, which determine their attraction to insects (Mikkola, 1972; Eguchi et al., 1982; Kelber et al., 2002). For example, it has been shown that high pressure sodium lights attract moths, because of the presence of ultraviolet wavelengths, while low pressure sodium lights of the same intensity, but not producing ultraviolet light, attract less (Rydell, 1992; Eisenbeis and Hassel, 2000; Eisenbeis, 2006). Moreover, artificial light with high ultraviolet emission could affect visual images perceived by moths, for example by accentuating ultraviolet markers which serve as "nectar guides" (Barth, 1985). It has been suggested for the protection of moths that these low pressure sodium vapor lamps should be used, while mercury vapor lamps and other lamp

---

[*] Corresponding author. Tel.: +31 0317 467346.
E-mail address: dick.groenendijk@vlinderstichting.nl (D. Groenendijk).

0006-3207/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2011.06.004

types with high ultraviolet emissions should be avoided or equipped with filters to block ultraviolet light (Frank, 2006). However, the effect of the spectral composition of artificial lighting on moth species richness and moth abundance has not been studied systematically (Johnsen et al., 2006).

Several studies document differences in the species' tendency to fly to light (Kolligs, 2000; Nowinszky, 2003). Some moth species are highly attracted to artificial lights, whereas others almost never come to these light sources, even though they occur in the direct vicinity (Kolligs, 2000; Frank, 2006). To predict effects of artificial lighting on moth species richness and moth abundance by attracting individuals, it is important to know which species are attracted and might experience high mortality. This attraction is thought to be determined by their sensitivity to light, which might be related to body size as larger eyes have higher light sensitivity than smaller eyes (Moser et al., 2004; Yack et al., 2007). This is supported by the findings that larger insect species have more sensitive vision than smaller species (Zollikofer et al., 1995; Jander and Jander, 2002; Spaethe and Chittka, 2003), which is also found in butterflies (Rutowski et al., 2009). If some moth species are more attracted to light than others, the traits related to this attraction could help us to predict effects of artificial light on communities of nocturnal species (Frank, 2006).

In this study, we tested the hypotheses that (1) artificial light with smaller wavelengths attracts higher species richness and higher abundances of moths than light with larger wavelengths, and (2) this attraction is correlated with morphological characteristics of moths, especially their eye size.

2. Methods

2.1. Experimental field study

To test the hypotheses, we conducted a field experiment to attract moths with 18 Heath's collapsible portable traps with 6 Watt T5 fluorescent lamps. We used six lamp types that varied in spectral composition (Fig. 1, thus $n = 3$ per lamp type). Besides the standard warm white (Philips color \29, lamp *c* in Fig. 1) and Actinic (lamp *a*) lamps, four custom made lamp types were used. Lamp *b* contained only the green phosphor CBT ((Ce, Gd)MgB5O10:Tb),

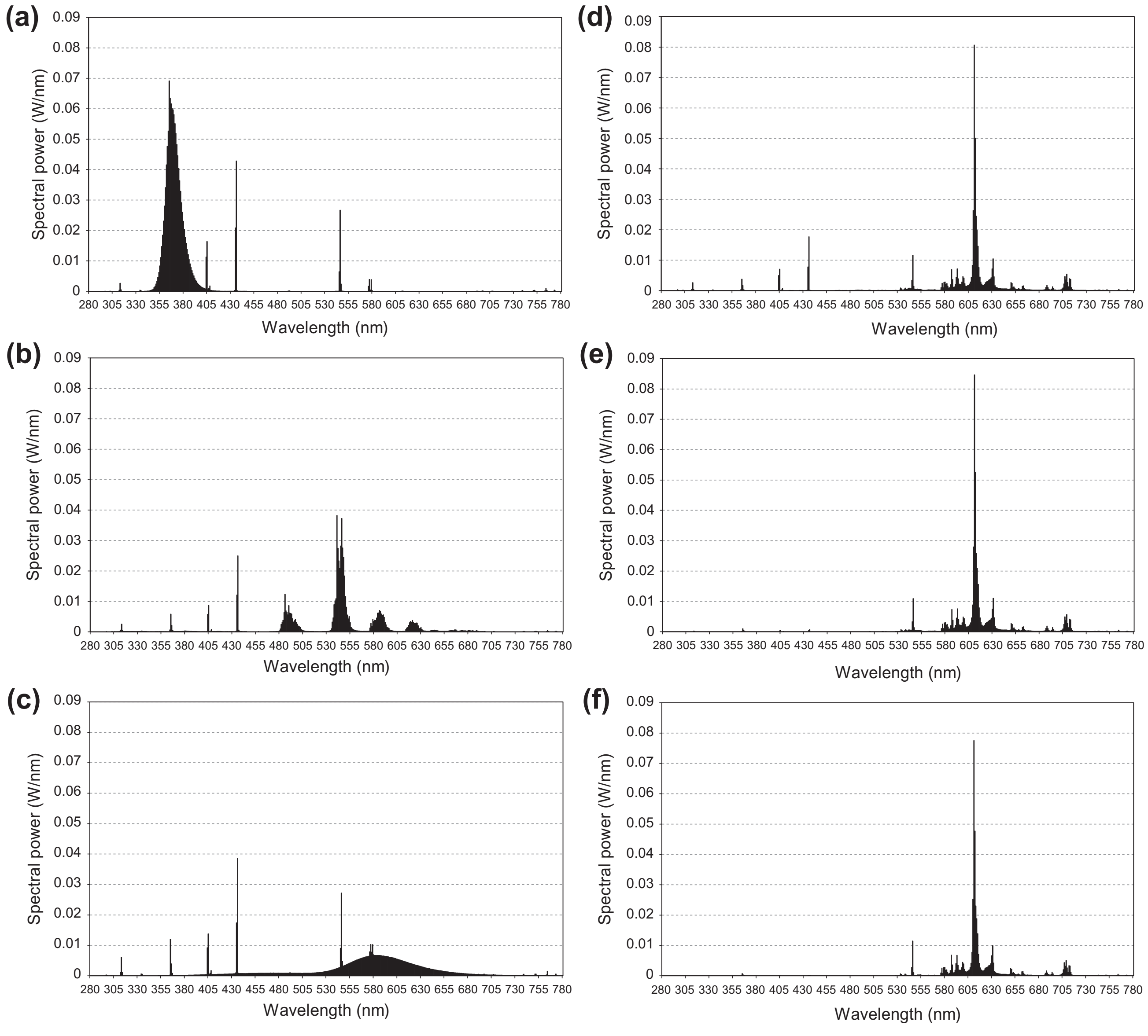

Fig. 1. Spectral power distribution (W/nm) of the six lamp types (with the weighted mean wavelength of the lamp types): *a* (381.8 nm), *b* (534.3 nm), *c* (554.0 nm), *d* (597.1 nm), *e* (616.6 nm) and *f* (617.6 nm).

with a peak wavelength at 542 nm. Lamp types *e* and *f* were all based on the red emitting phosphor YOX (Y_2O_3:Eu) with a peak wavelength of 612 nm. Lamp types *d* and *f* also contained small amounts of a white phosphor mix using BAM ($BaMgAl_{10}O_{17}$:Eu) and CAT ((Ce, Gd)$MgAl_{11}O_{19}$:Tb). The lamp types *d*–*f* were coated with a high-pass filter layer, effectively blocking all radiation below 520 nm. Apart from the actinic lamp, none of the lamps emitted significant amounts of UV (below 380 nm) (Table 1). The different lamp types can be described by the flux (in lumens), correcting for the human eye sensitivity resulting in a measure of brightness as perceived by humans; the number of photons emitted per second; and the spectral power, or radiant flux, which is the power of the radiation emitted by the lamp (in Watt). These properties are determined in the wavelength range from 380 to 780 nm. Ps, Pm and Pl denote the fraction of the spectral power emitted in the ranges 380–504 nm, 505–589 nm and 590–780 nm, respectively. As shown in Fig. 1, each lamp type contains peaks at different wavelengths. To characterize the spectral composition of the different lamp types with a single value, i.e. the dominant wavelength, we calculated the mean of the wavelengths weighted for the spectral power per wavelength (W/nm) (see Fig. 1 for values). As can be expected, the weighted mean wavelength is negatively correlated with Ps (Pearson correlation coefficient $r = -0.998$, $P < 0.001$, $n = 6$) and positively correlated with Pl (Pearson correlation coefficient $r = 0.869$, $P < 0.024$, $n = 6$), but not correlated with Pm (Pearson correlation coefficient $r = -0.089$, $p = 0.867$, $n = 6$).

The study was carried out in Kampina, a nature reserve situated in the province of Noord Brabant in The Netherlands (51°34′13.43″N, 5°16′08.59″E), from July 12 until August 25, 2009. This site is a homogeneous area to avoid differences in moth species richness and moth abundances between the individual lamps. During these six weeks, we trapped moths twice per week (thus 12 trapping moments). Each trapping night, the lamps were randomly distributed over 18 pre-selected locations. These trapping locations were all situated in the same wet meadow system of 2.3 ha surrounded by trees, and the distance to the surrounding trees was kept constant at 10 m for each location. According to Baker and Sadovy (1978), trapping with a 125 W mercury vapor lamp situated at 60 cm above ground level generates an effective response by moths at a distance of 3 m on a moonless night. Our traps were situated on the ground and located at least 50 m from a neighboring trap to prevent light interference. Traps were set at least 60 min before sunset and checked for moths at about one hour after sunrise. Each trap contained three glasses with 50 ml ethyl acetate which was used to prevent moths from escaping the trap once they entered. After each trapping night, the traps were removed from their location, the caught moth species identified to species level, and the number of individuals per species counted.

As moth activity might be influenced by environmental conditions (Frank, 2006; Reardon et al., 2006), we collected data on the mean daily wind speed, mean daily temperature at 10 cm above ground, mean cloud cover and mean daily relative humidity from a weather station of the Royal Netherlands Meteorological Institute (KMNI) at Eindhoven which is approximately at 15 km distance from the study site. Given the potential effect of moon phase on collecting moths, we tested for possible differences between the collection nights.

2.2. Allometric relationships of moth traits

We measured forewing length and width, dry body weight and eye diameter of the males of 40 moth species found in the traps. Pictures of moth eyes were taken using a CANON 350D with a Tamron 100 mm lens and a Tamron 1:1 macro converter at a minimum distance of 15 cm. Each moth's eye diameter was measured from these photographs using ImageJ. Forewing length and width were measured using a ruler up to 0.1 mm. For dry weight determination, each specimen was dried in an oven at 80 °C for 12 h and weighed using a 0.00001 g balance. Moth species characteristics represent means taken from at least three individuals.

2.3. Statistical analysis

A general linear model (GLM) was used to test for differences in overall moth species richness and moth abundance between the six light types, which was also separately done for the main moth families in our traps. In these analyses, we tested the effect of trap location (as random factor) and the average environmental conditions during the trapping moments to account for differences between these moments (as covariates). If needed, data were ln-transformed to satisfy the assumption of normality of the residuals. We used the Bonferroni test for multiple comparisons between the lamp types.

Using Reduced Major Axis regression (RMA regression, as our independent variable body mass is measured with an error, Sokal and Rohlf, 1995), we tested the allometric relationships for the measured morphological characteristics of the moth species. We calculated the abundance weighted mean for each of the morphological characteristics for the species that were caught in the traps for each lamp type and for which we measured the morphological characteristics. Again, we used RMA regression to test the relationship between the spectral composition of the lamps and these abundance weighted mean morphological characteristics.

3. Results

3.1. Moth species richness and moth abundance

A total number of 112 moth species were caught in 18 traps during 6 weeks. There was a strong correlation between overall moth species richness and moth abundance caught in each trap per trapping moment (Pearson correlation coefficient $r = 0.917$, $P < 0.001$, $n = 212$). For moth species richness, a significant differ-

Table 1

Photometrical properties of the six lamps used in the experiment: flux, photon flux and spectral power emitted by the lamps between 380 and 780 nm. Ps, Pm and Pl denote the fraction of the spectral power emitted in the ranges 380–504 nm, 505–589 nm and 590–780 nm, respectively. The weighted mean wavelength is calculated as the mean of the wavelengths weighted for the spectral power per wavelength. The spectral composition of the lamps is given in Fig. 1.

Lamp	*a*	*b*	*c*	*d*	*e*	*f*
Flux (lm)	22	293	297	162	153	143
Photons (mol/s)	3332	2953	3848	2818	2540	2366
Spectral power (W)	1.04	0.66	0.83	0.56	0.49	0.46
Ps	0.84	0.25	0.20	0.08	0.00	0.00
Pm	0.13	0.61	0.42	0.12	0.12	0.12
Pl	0.03	0.14	0.38	0.80	0.88	0.88
Weighted mean wavelength (nm)	381.8	534.3	554.0	597.1	616.6	617.6

ence was found between the six lamp types ($F_{5,121.2} = 10.264$, $P < 0.001$), whereas there was neither a significant difference between the trap locations ($F_{17,110.8} = 1.001$, $P = 0.463$) nor an interaction between lamp type and trap location ($F_{73,116} = 0.622$, $P = 0.985$). After removing trap location as random factor, our model contained lamp type ($F_{5,205} = 14.034$, $P < 0.001$) and relative humidity (more species with greater humidity) as covariate ($F_{1,205} = 5.077$, $P = 0.025$). The other environmental variables did not contribute significantly to this model. Lower species richness of moths was found in traps with lamps that emit light at larger wavelengths (Fig. 2). A similar pattern was found for the species richness of the Noctuidae, the Geometridae and the Arctiidae. Note that the latter family is now no longer considered a separate family but is included in the Noctuidae. For the Pyralidae, there were hardly any differences in species richness between the lamp types.

Similar results were found for differences in moth abundance between lamp types. A significant difference was found between the six lamp types ($F_{5,112.5} = 10.774$, $P < 0.001$). There was no significant difference in moth abundance between the trap locations ($F_{17,103.8} = 0.635$, $P = 0.857$), and also the interaction between lamp type and trap location was not significant ($F_{73,116} = 0.741$, $P = 0.768$). After removing trap location as random factor, the model contained lamp type ($F_{5,205} = 12.895$, $P < 0.001$) and relative humidity as covariate (with a positive sign, $F_{1,205} = 6.514$, $P = 0.011$). The highest abundances were found in the traps with the lamps that emit light with the shortest wavelengths, whereas

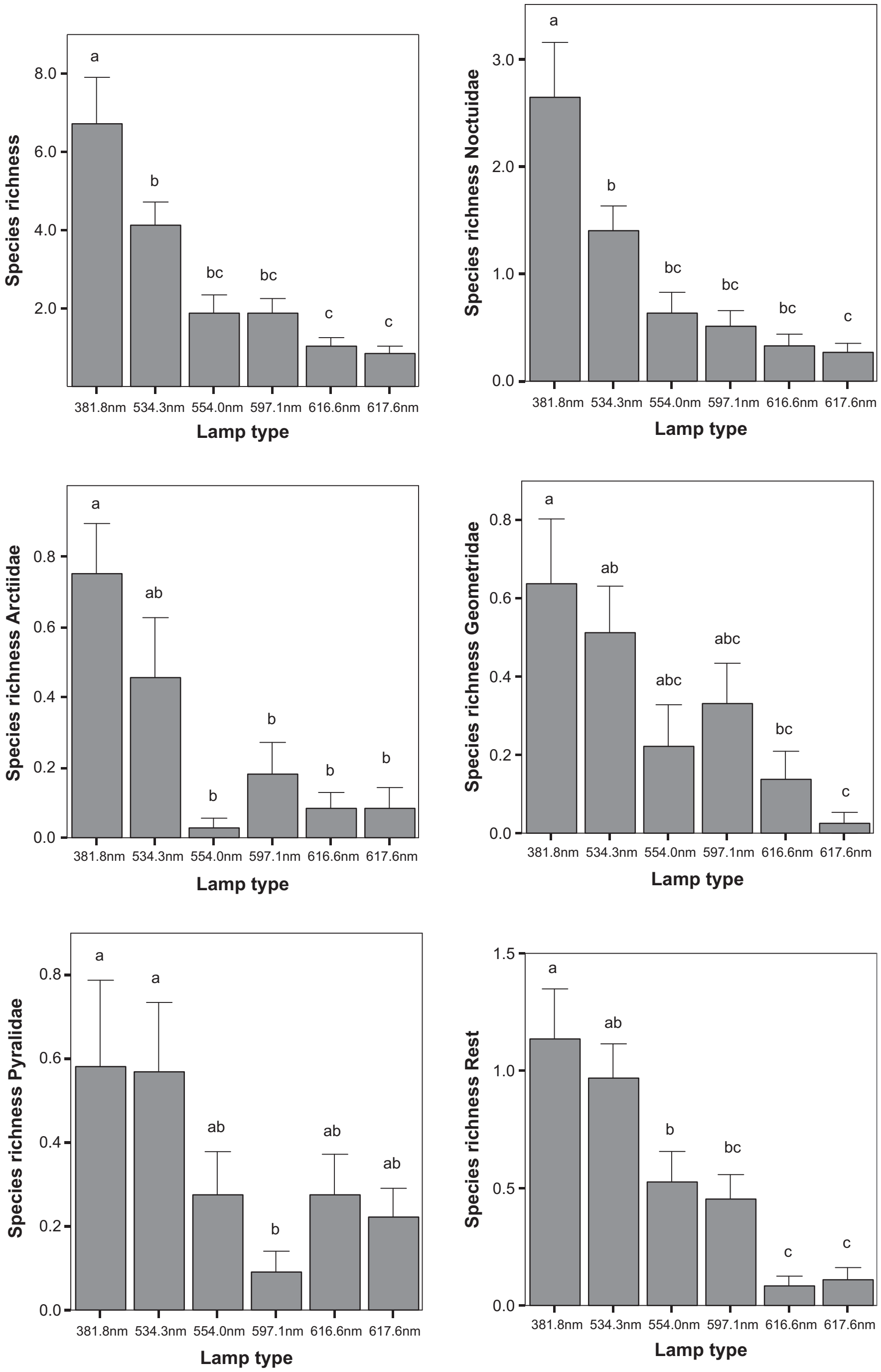

Fig. 2. Mean moth species richness (± s.e.) for the different lamp types, which can be characterized by the weighted mean wavelength (see Fig. 1). Letters indicate significant differences between the lamp types.

there were no differences between the other lamp types (Fig. 3). Again a similar pattern was found for the abundances of the Noctuidae, and the abundances of the Geometridae and Arctiidae decreased for lamp types with larger wavelengths. For the Pyralidae, no differences in abundances were found between the lamp types.

3.2. Relation between moth morphological characteristics and light attraction

The dry weight of the measured 40 moth species varied between 0.004 g (*Cabera exanthemata*; Geometridae) and 0.375 g (*Laothoe populi*; Sphingidae). We found allometric relationships for eye diameter (range 0.67–3.54 mm), forewing length (range 0.98–3.70 cm) and width (range 0.35–1.85 cm). For eye diameter, the intercept of the RMA regression was 6.118 (S.E. = 0.140, $P < 0.001$) and the slope was 0.347 (S.E. = 0.038, $P < 0.001$) with $R^2 = 0.54$, resulting in the allometric relationship $454 \times \mathrm{BM}^{0.347}$ (BM is body mass in g). The relationship between body mass and forewing length could be described by the equation $4.25 \times \mathrm{BM}^{0.262}$ (both coefficients $P < 0.001$, $R^2 = 0.45$), and forewing width by $2.77 \times \mathrm{BM}^{0.368}$ (constant $P = 0.122$, coefficient for forewing width $P = 0.004$, $R^2 = 0.20$). We found strong negative relationships between the weighted mean wavelength of the lamp

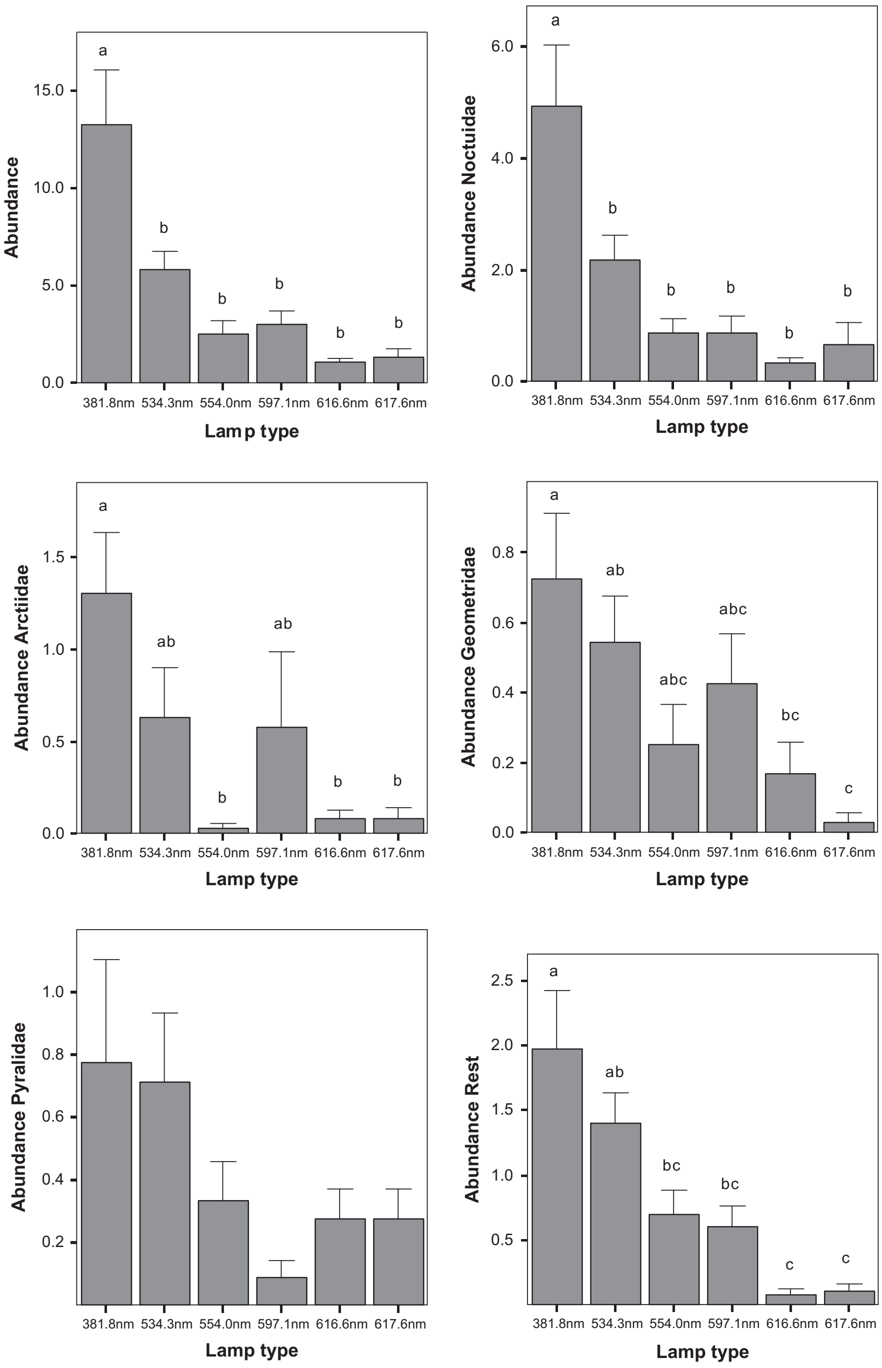

Fig. 3. Mean moth abundance (± s.e.) for the different lamp types. The weighted mean wavelength of the lamp types are given (see Fig. 1). Letters indicate significant differences between the lamp types.

Table 2
The effects of the dominant wavelength of the different lamp types on moth morphological characteristics ($n = 16$ lamps, as two lamps provided insufficient data for the analysis). The dominant wavelength is calculated as the weighted mean of the wavelengths for each lamp type, and the moth characteristics are calculated as the abundance-weighted mean for the species that were caught in the traps for each lamp type.

Moth characteristics	R^2	Slope (± s.e.)	P
Forewing length	0.70	−0.030 (± 0.005)	<0.001
Forewing width	0.66	−0.015 (± 0.003)	<0.001
Dry weight	0.42	−0.001 (± 0.0002)	0.007
Eye diameter (ln-transformed)	0.46	−0.002 (± 0.001)	0.005

types and the moth morphological characteristics (Table 2). Moths with larger body mass, larger wing dimensions and larger eyes were attracted to light dominated by smaller wavelengths.

4. Discussion

4.1. Effects of spectral composition

In this study, we manipulated the spectral composition of artificial light and recorded the number of moth species and moth abundances that were attracted to these lights. We found that the lamp types that are dominated by smaller wavelengths attracted higher species richness and abundances of moths. This agrees with studies on the effects of streetlight where more insects were found in traps with high pressure mercury vapor lamps, followed by high pressure sodium–xenon vapor lamps, and then by high pressure sodium vapor lamps (Eisenbeis and Hassel, 2000; Eisenbeis, 2006). Our results also agree with a study in the City of Düsseldorf where they found the least insects attracted by LEDs that did not emit any UV (Eisenbeis and Eick, 2010). In the traps with a mean weighted wavelength of around 382 nm (lamp type *a*), we caught the highest overall moth species richness and abundance. This lamp type, the Actinic lamp (type *a*), had a large UV-part, which may account for the strong attraction of moths. This agrees with the findings of Cowan and Gries (2009), who found in a laboratory experiment that light of 400–475 nm wavelength attracted more individuals of the Indian meal moth (*Plodia interpunctella*, Pyralidae) than other wavelengths (475–600 nm, 575–700 nm and 590–800 nm). Light of 405 nm wavelength attracted the most individuals compared to the 435, 450 or 470 nm light. Moreover, they found in electroretinogram recordings that light of 405 nm wavelength elicited significantly stronger receptor potentials from both female and male eyes than light of 350 nm. Although we did not find an effect of lamp type on the species richness and abundance of moths of the Pyralidae, the study of Cowan and Gries (2009) clearly shows that some species of the Pyralidae do respond to the spectral composition of light. Besides the finding that moths are attracted to light dominated by smaller wavelengths, our results also show that artificial lights with mean weighted wavelengths of around 617 nm (lamp types *e* and *f*) attract the lowest moth species richness and moth abundance.

We also found that artificial light dominated by smaller wavelengths attracted relatively larger moth species and a higher abundance of these larger species. The high correlation between species richness and abundance stresses the negative effects of the lamp types: not only more species with on average a larger body mass, but also more individuals of these species are attracted. This size-dependent attraction could be explained by findings that larger insect eyes, i.e. larger insects have generally larger eyes (Jander and Jander, 2002; Rutowski et al., 2009), are more sensitive to light (Moser et al., 2004; Yack et al., 2007). Because lamps with short wavelengths are still commonly used (Eisenbeis, 2006), their great attraction of larger moth species might have significant consequences for the ecology of the night.

4.2. Cascading effects of size-dependent mortality

Because moths attracted to artificial lights suffer an increased mortality (Frank, 1988, 2006; Warren, 1990; Nowinszky, 2003; Longcore and Rich, 2004), the trait(s) related to this attraction will be under selection. Our results suggest indeed a possible selection pressure from artificial light on body size of moth species, as it favors individuals of smaller moth species that are less inclined to fly to light than individuals of larger moth species. We therefore hypothesize that relatively smaller moth species are found with relatively higher abundances in areas with high light pollution compared to areas with low artificial light emission during the night. Moreover, we hypothesize that this size-dependent mortality has cascading effects for both trophic interactions and ecosystem services where moths are involved.

It has indeed been recognized that artificial light can have a large effect on interspecific interactions resulting in ecosystem effects (Longcore and Rich, 2004). A large part of the diet of many spider, bird and bat species may contain moths or their caterpillars (Sierro and Artellaz, 1997; Visser et al., 2006; Rydell, 2006; Whittaker and Karatas, 2009). Although hardly quantified, it is likely that a significant part of the diet of some of these predatory species contains larger moth species (Sierro and Artellaz, 1997). For example, the diet of the Brown long-eared bat (*Plecotus auritus*) includes almost exclusively larger moth species from the Noctuidae (83%). The dominant moth species in the diet was the relatively large *Anaplectoides prasina* (Rostovskaya et al., 2000). Another example is the migratory bird European nightjar (*Caprimulgus europaeus*), which mainly feeds on moths during its presence in northwestern Europe from late April to early September (Sierro et al., 2001). The adult birds feed their young mainly with individuals of larger moth species as the breeding season progresses in summer (Cramp, 1985). The widespread decline in larger moth species in The Netherlands and the United Kingdom is expected to have strong effects on this bird species (Groenendijk and Ellis, 2011), as many passerine birds feed their young with caterpillars (Visser et al., 2006). The decrease in larger moth species due to attraction to artificial light could cause a change in the size distribution of prey species, which might have large consequences for predatory species. We expect that declining abundances of larger moth species due to light pollution might result in food reductions for these predatory species, with subsequent decreases in their abundance.

Some moth species are important pollinators (Boggs, 1987; Pettersson, 1991), but effects of artificial light on pollination are hardly known. Besides the misleading effects on the visual images perceived by moths by high ultraviolet emission (Barth, 1985), size-dependent mortality of moths might reduce pollination by larger moth species. For example, the moth *Hadena bicruris* (relatively large moth species from the Noctuidae) is known to be the main pollinator of *Silene latiflora*, a short-lived perennial plant (Jürgens et al., 1996), and the orchid *Platanthera bifolia* is mainly pollinated by moths of the Sphingidae and Noctuidae, which contain mainly large species (Nilsson, 1983). Another example is *Silene sennenii*, only occurring in the north-eastern Iberian Peninsula, which also largely depends on larger moth species for its pollination (Martinell et al., 2010). A decline in such specialist pollinators due to light pollution might lead to a decline in the density of the plant species. Besides pollination, herbivory is another effect that moths can have on the vegetation (Bernays et al., 2004). As the larvae of the majority of larger moth species have a generalized spectrum of host plants (Groenendijk and Ellis, 2011), the decline in their abundance due to light pollution might translate in a general decline in herbivore pressure. Further experiments should reveal the effects of a reduction in larger moth species and their abundances on the vegetation.

4.3. Size-biased flight-to-light behavior of moths

Light traps have been used for years 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 and Knight, 1994). Recently, it has been shown that there might be a male-biased flight-to-light behavior of moths (Altermatt et al., 2008), which affects the reliability of estimating abundances using light traps. Our study suggests that artificial lights might also cause a size-biased flight-to-light behavior, as relatively larger moth species and higher abundances of these moth species are caught in traps, especially using lamps dominated by small wavelengths. An alternative explanation for this pattern might be that we have drawn a random sample from the available species abundances, and that larger moth species occur in higher density than smaller moth species. This would contradict often found relationships between body mass and abundance that predict a decline in abundance with increasing body mass (Brown et al., 2004). Moreover, we located our traps in one site where all lamp types are exposed to the same pool of moth species. From this pool, we found that lamp types with smaller wavelengths attracted relatively more large moth species than lamp types with larger wavelengths, suggesting that there is indeed a size-bias resulting in an overrepresentation of larger moth species in lamps with smaller wavelengths. Further experimental testing of our findings is needed as this possible size-bias in flight-to-light behavior might have large implications for population and conservation biology of moths.

4.4. Synthesis

The increase in artificial night lighting (Cinzano et al., 2001) increases the urge to study effects of light pollution to support nature management options. The size-dependent attraction to artificial light we found in moths, could entail possible cascading effects for biodiversity and ecosystem services, e.g. pollination where moth species are involved, when larger moth species decline due to light pollution. To prevent these effects, this study provides evidence on spectral compositions of artificial light that have the least attraction for moths, which could be used in cities and along roads. Our results indicate the potential use of lamps with larger wavelengths to effectively reduce the negative effect of light pollution on moth population dynamics and communities that include these moths or their caterpillars.

Acknowledgements

We would like to thank Leo de Bruijn from Natuurmonumenten for giving us the opportunity to collect data, for providing free access and storing opportunities for traps at Kampina nature reserve. In addition, Jippe van der Meulen from Dutch Butterfly Conservation is kindly acknowledged for his time and efforts in the identification of the samples.

References

Altermatt, F., Baumeyer, A., Ebert, D., 2008. Experimental evidence for male biased flight-to-light behaviour in two moth species. Entomologia Experimentalis et Applicata 3, 259–265. doi:10.1111/j.1570-7458.2008.00817.x.

Baker, R.B., Sadovy, Y., 1978. The distance and nature of light-trap response of moth. Nature 276, 818–821.

Barth, F.G., 1985. Insects and Flowers: The Biology of a Partnership. Princeton University Press, Princeton, New Jersey.

Bernays, E.A., Singer, M.S., Rodrigues, D., 2004. Foraging in nature: foraging efficiency and attentiveness in caterpillars with different diet breaths. Ecological Entomology 29, 389–397.

Boggs, C.L., 1987. Ecology of nectar and pollen feeding in Lepidoptera. In: Slansky, F., Rodriguez, J.G. (Eds.), Nutritional Ecology of Insects, Mites, Spiders, Related Invertebrates. Wiley, New York, pp. 369–391.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Cinzano, P., Falchi, F., Elvidge, C.D., 2001. The first world atlas of the artificial night sky brightness. Monthly Notices of the Royal Astronomical Society 328, 689–707.

Conrad, K.F., Warren, M., Fox, R., Parsons, M., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biological Conservation 132, 279–291. doi:10.1016/j.biocon.2006.04.020.

Cowan, T., Gries, G., 2009. Ultraviolet and violet light: attractive orientation cues for the Indian meal moth, *Plodia interpunctella*. Entomologia Experimentalis et Applicata 131, 148–158. doi:10.1111/j.1570-7458.2009.00838.x.

Cramp, S. (Ed.), 1985. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic, vol. IV. Terns to Woodpeckers. Oxford University Press, Oxford.

De Molenaar, J.G., Jonkers, D.A., Henkens, R.J.H.G., 2000. Wegverlichting en natuur. I. Een literatuurstudie naar de werking en effecten van licht en verlichting op de natuur. DWW Ontsnipperingsreeks deel 34, Delft.

Eguchi, E., Watanabe, K., Hariyama, T., Yamamoto, K., 1982. A comparison of electrophysiologically spectral responses in 35 species of Lepidoptera. Journal of Insect Physiology 28, 675–682.

Eisenbeis, G., 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC, pp. 281–304.

Eisenbeis, G., Eick, K., 2010. Attraction of nocturnal insects to street lights with special regard to LEDs. Abstracts of the Society for Conservation Biology, 24th Annual Meeting: <http://www.conbio.org/activities/meetings/2010/images/abstracts.pdf> (checked 10.04.11).

Eisenbeis, G., Hassel, F., 2000. Zur Anziehung nachtaktiver Insekten durch Straßenlaternen: eine Studie kommunaler Beleuchtungseinrichtungen in der Agrarlandschaft Rheinhessens. Natur und Landschaft 75, 145–156.

Frank, K.D., 1988. Impact of outdoor lighting on moths: an assessment. Journal of the Lepidopterists' Society 42, 63–93.

Frank, K.D., 2006. Effects of artificial night lighting on moths. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC, pp. 305–344.

Garstang, R.H., 2004. Mount Wilson observatory: the sad story of light pollution. Observatory 124, 14–21.

Gotthard, K., 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. Journal of Animal Ecology 69, 896–902.

Groenendijk, D., Ellis, W.N., 2011. The state of the Dutch larger moth fauna. Journal of Insect Conservation 15, 95–101. doi:10.1007/s10841-010-9326-y.

Hsiao, H.S., 1973. Flight paths of night-flying moths to light. Journal of Insect Physiology 19, 1971–1976.

Jander, U., Jander, R., 2002. Allometry and resolution of bee eyes (Apoidea). Arthropod Structure & Development 30, 179–193.

Johnsen, S., Kelber, A., Warrant, E., Sweeney, A.M., Widder, E.A., Lee Jr, R.L., Hernández-Andrés, J., 2006. Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. Journal of Experimental Biology 209, 789–800. doi:10.1242/jeb.02053.

Jürgens, A., Witt, T., Gottsberger, G., 1996. Reproduction and pollination in central European populations of Silene and Saponaria species. Botanica Acta 109, 316–324.

Kelber, A., Balkenius, A., Warrant, E.J., 2002. Scotopic colour vision in nocturnal hawk moths. Nature 419, 922–925.

Kolligs, D., 2000. Ökologische Auswirkungen künstlicher Lichtquellen auf nachtaktive Insekten, insbesondere Schmetterlinge (Lepidoptera). Faunistisch-Oekologische Mitteilungen Supplement 28, 1–136.

Kuijper, D., Schut, J., Van Dullemen, D., Toorman, H., Goossens, N., Ouwehand, J., Limpens, H.J.G.A., 2008. Experimental evidence of light disturbances along the commuting routes of pond bats (*Myotis dasycneme*). Lutra 51, 37–49.

Longcore, T., Rich, C., 2004. Ecological light pollution. Frontiers in Ecology and the Environment 2, 191–198.

Martinell, M.C., Dötterl, S., Blanché, C., Rovira, A., Massó, S., Bosch, M., 2010. Nocturnal pollination of the endemic *Silene sennenii* (Caryophyllaceae): an endangered mutualism? Plant Ecology 211, 203–218.

Mikkola, K., 1972. Behavioral and electrophysiological responses of night-flying insects, especially Lepidoptera, to near-ultraviolet and visible light. Annales Zoologici Fennici 9, 225–254.

Moser, J.C., Reeve, J.D., Bento, J.M.S., Della Lucia, T.M.C., Cameron, R.S., Heck, N.M., 2004. Eye size and behaviour of day- and night-flying leafcutting ant alates. Journal of Zoology (London) 264, 69–75. doi:10.1017/S0952836904005527.

Nilsson, L.A., 1983. Process of isolation and introgressive interplay between *Platanthera bifolia* (L.) Rich. and *P. chlorantha* (Custer) Reichb. (Orchidaceae). Botanical Journal of the Linnean Society 87, 325–350.

Nowinszky, L. (Ed.), 2003. The Handbook of Light Trapping. Savaria University Press, Szombathely, Hungary.

Pettersson, M.W., 1991. Pollination by a guild of fluctuating moth populations: Option for unspecialization in *Silena vulgaris*. Journal of Ecology 79, 591–604.

Reardon, B.J., Sumerford, D.V., Sappington, T.W., 2006. Impact of trap design, windbreaks, and weather conditions on captures of European corn borer (Lepidoptera: Crambidae) in pheromone-baited traps. Journal of Economic Entomology 99, 2002–2009.

Rich, C., Longcore, T. (Eds.), 2006. Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC.

Rostovskaya, M.S., Zhukova, D.V., Illarionova, A.E., Ustyugova, S.V., Borissenko, A.V., Sviridov, A.V., 2000. Insect prey of the long-eared bat *Plecotus auritus* (L.) (Chiroptera: Vespertilionidae) in central Russia. Russian Entomological Journal 9, 185–189.

Rutowski, R.L., Gislén, L., Warrant, E.J., 2009. Visual acuity and sensitivity increase allometrically with body size in butterflies. Arthropod Structure & Development 38, 91–100. doi:10.1016/j.asd.2008.08.003.

Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. Functional Ecology 6, 744–750.

Rydell, J., 2006. Bats and their insect prey at streetlights. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC, pp. 43–60.

Settele, J., 2009. Ecologists should join astronomers to oppose light pollution. Nature 576, 379.

Sierro, A., Artellaz, R., 1997. Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. Acta Oecologica 18, 91–106.

Sierro, A., Arlettaz, R., Naef-Daenzer, B., Strebel, S., Zbinden, N., 2001. Habitat use and foraging ecology of the nightjar (*Caprimulgus europaeus*) in the Swiss Alps: towards a conservation scheme. Biological Conservation 98, 325–3310, doi:10.1016/S0006-3207(00)00175-0.

Sokal, R.R., Rohlf, F.J., 1995. Biometry: the principles and practice of statistics in biological research, third ed. Freeman and Co, New York.

Spaethe, J., Chittka, L., 2003. Interindividual variation of eye optics and single object resolution in bumblebees. Journal of Experimental Biology 206, 3447–3453.

Visser, M.E., Holleman, L.J.M., Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147, 164–172. doi:10.1007/s00442-005-0299-6.

Warren, A.D., 1990. Predation of five species of Noctuidae at ultraviolet light be the Western Yellowjacket (Hymenoptera: Vespidae). Journal of the Lepidopterists' Society 44, 32.

Weissling, T.J., Knight, A.L., 1994. Passive trap for monitoring codling moths (Lepidoptera, Tortricidae) flight activity. Journal of Economic Entomology 87, 103–107.

Whittaker, J.O., Karatas, A., 2009. Food and feeding habits of some bats from Turkey. Acta Chiropterologica 11, 393–403. doi:10.3161/150811009X485611.

Yack, J.E., Johnson, S.E., Brown, S.G., Warrant, E.J., 2007. The eyes of Macrosoma sp. (Lepidoptera: Hedyloidea): A nocturnal butterfly with superposition optics. Arthropod Structure & Development 36, 11–22. doi:10.1016/j.asd.2006.07.001.

Zollikofer, C.P.E., Wehner, R., Fukushi, T., 1995. Optical scaling in conspecific Cataglyphis ants. Journal of Experimental Biology 198, 1637–1646.