

Effect of bulb type on moth trap catch and composition in UK gardens

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Abstract

1. Light traps are a key method for monitoring moth populations. A wide variety of light sources are employed for this purpose, differing in brightness and spectrum. Relatively little is known about how this affects the resulting sample.
2. We analyse seven moth trap bulb types using ten years of records from the Garden Moth Scheme (GMS) to provide the largest and most comprehensive comparison of moth trap bulb types to date.
3. The total abundance of moths caught by a trap is strongly linked to bulb wattage and brightness. We estimate that Heath traps catch fewer moths than Robinson or Skinner-style traps.
4. Ordination models indicated that Mercury Vapour bulbs collected a distinct fauna to Actinic bulbs. Species composition also varied between Actinic bulbs which differ in brightness, with brighter Actinic traps tending to collect a larger proportion of large-winged species.
5. We develop hypotheses whereby large-winged, strong flying moths are more strongly affected by artificial light (arising from moth traps or other sources). We explore how this hypothesised mechanism may result in negative fitness effects for larger, mobile moth species. Our findings have significant consequences for survey design, citizen science projects, and for understanding the impact of ALAN on the moth community.

Introduction

As the largest single radiation of plant-feeding insects (Mitter et al., 2017), the order Lepidoptera comprises one tenth of all described species on Earth, the vast majority of which are moths (van Nieukerken et al., 2011; Wagner et al., 2021). Butterflies are frequently employed as an indicator of the health of insect communities and of biodiversity more generally (Fleishman and Murphy, 2009). Moths share many of the features which make butterflies attractive in this regard: Lepidoptera tend to respond rapidly to environmental change (New, 1997) and are distributed globally (Fleishman and Murphy, 2009). Relative to other insect groups, moth species are readily identified owing to the presence of distinctive wing patterns (Thomas, 2005) and the availability of exceptional identification resources (e.g. Sterling and Parsons, 2023; Waring and Townsend, 2018). However, moths can serve as particularly effective indicators of insect diversity due to their substantially greater species richness compared to diurnal Lepidoptera (Wagner et al., 2021) and the ease with which they can be collected in large numbers using light traps - even in highly anthropogenically modified environments such as gardens (Bates et al., 2013).

Standardised recording of moths in the UK is conducted through the long-running Rothamsted Insect Survey, which uses a 112-node network of 200W clear tungsten filament moth traps to measure changes in abundance throughout the country (Bell et al. 2020; Conrad et al., 2006). In addition to standardised monitoring, as many as 2000 volunteers regularly run moth traps in the UK, many of which submit their records to biodiversity databases or other citizen science organisations (Fox et al., 2011). However, standardised Rothamsted traps are rarely used by citizen scientists or in field experiments due to their large size, mains power requirements and relatively inefficient 200W tungsten bulb. Instead, a great variety of alternative designs and light sources are employed, hampering standardization and therefore wider use of community science datasets to monitor moth abundance. In contrast to butterflies, for which standardised 'Pollard walks' (Pollard and

Yates, 1993) facilitate straightforward inclusion of volunteer records in large-scale abundance monitoring, volunteer moth records have only recently been included in Butterfly Conservation's annual survey detailing *The State of Britain's Larger Moths* (Fox et al., 2021). This has been made possible through the application of occupancy models (Dennis *et al.*, 2017). These methods control for variation in moth trap type by treating all records as 'opportunistically gathered', such that citizen science records convey information only on the occurrence or non-occurrence of a species in a location. In this process, all information on species' relative abundance is obscured. Given the central role played by the abundance of common species in ecosystem service delivery (Winfree et al. 2015; Winfree et al. 2025) and recent interest in monitoring insect abundance trends (e.g. Duchenne and Fontaine, 2024; Müller *et al.*, 2024; Seibold *et al.*, 2019), methods capable of estimating moth abundance trends from semi-standardised citizen science records could unlock a novel data source of wide interest and relevance to understanding the status of insects in the UK and more widely. The first step to broader use of citizen science data for monitoring the abundance of moths is to develop a more complete understanding of the various methods used to collect moths in these surveys.

Many smaller studies have sought to compare one or several moth trap bulb types and receptacle designs to one another in the field. For example, Williams (1951) found that compared to a 125W MV Robinson-style traps, Rothamsted-style traps using the same bulb collected 63.82% fewer moths, while Rothamsted-style traps using 200W 'ordinary' (presumably tungsten filament) bulbs caught 91.44% fewer moths. Williams (1955) found that 200W 'ordinary' bulbs collected 37.5% fewer moths than 125W MV, while use of Rothamsted-style trap designs reduced catch by 25% compared to Robinson designs. Heath (1966) found that 15W blacklight bulbs collect 3.3% more moths than 15W bulbs and Waring (1980) found that a 6W Actinic heath trap caught 35.30% of the macrolepidoptera collected by a 125W Robinson MV. More recent work has shown that various trap parameters can impact catch size, including receptacle design (e.g. Robinson, Heath, Skinner, Rothamsted;

Bates *et al.*, 2013), period of the night for which the trap is running (Axmacher and Fiedler, 2004; Nowinszky *et al.*, 2007), time at which the trap is emptied (discussed in Fry and Waring, 2020), presence and colour of vanes (Singh *et al.*, 2022), height of the trap (Intachat and Woiwod, 1999), presence and position of packing material (usually egg boxes) inside the trap (discussed in Fry and Waring, 2020), manual versus automatic collection of samples (Axmacher and Fiedler, 2004) and, perhaps most importantly, the brightness and emission spectra of the light source used (Bates *et al.*, 2013; Donners *et al.*, 2018; Fayle *et al.*, 2007; Somers-Yeates *et al.*, 2013; van Grunsven *et al.*, 2014; van Langevelde *et al.*, 2011).

Further, as moth species are thought to differ in their attraction to light (Merckx and Slade, 2014), mediated by variation in mobility (van de Schoot *et al.* 2024) and possibly spectral sensitivity (Somers-Yeates *et al.*, 2013), it is likely that the species composition, as well as total abundance, of trap catches will be affected by the bulb type used (Donners *et al.*, 2018; Somers-Yeates *et al.*, 2013; van Langevelde *et al.*, 2011). Anecdotal evidence from naturalists has long suggested that traps using different bulbs will produce different samples (Altermatt and Ebert, 2016; Frank, 1988). At the very least, some species are rarely collected at light but appear more abundant using other collection methods (see Sterling and Parsons, 2012). However, as Brehm (2017) notes, field comparisons regularly find little compositional differences between bulbs with fundamentally different light spectra. For example, Infusino *et al.* (2017) found localized habitat conditions to be a stronger determinant of moth trap composition than light source, and the geometrid assemblages attracted to MV in comparison to incandescent lamps have been found to be surprisingly similar (Intachat and Woiwod 1999; Jonason *et al.* 2014). In the more controlled environment of an indoor choice experiment, Brehm *et al.* (2021) found that moths are preferentially attracted to lamps that emit a high proportion of short-wave radiation. However, in a similar field-based comparison, Niermann and Brehm, (2022) found that different LED lamps collected similar numbers and assemblages of moths, independent of whether strong or weak lights were used or if the lamps were of a mixed radiation or UV type, despite the traps

86 being placed close together (26.4 m - 46.9 m). It therefore appears that small variations in
87 microhabitat can obscure differences between bulb types, especially in short-term
88 experiments. Additionally, the effective range of moth traps appears to vary between families
89 (Merckx and Slade, 2014) and traps placed close together will suffer from light competition
90 effects (Brehm et al. 2021). These difficulties make designing a field experiment capable of
91 detecting abundance and compositional differences between moth trap light sources a
92 significant logistical challenge, which is yet to be overcome in a comprehensive comparison
93 of commonly used bulb types.

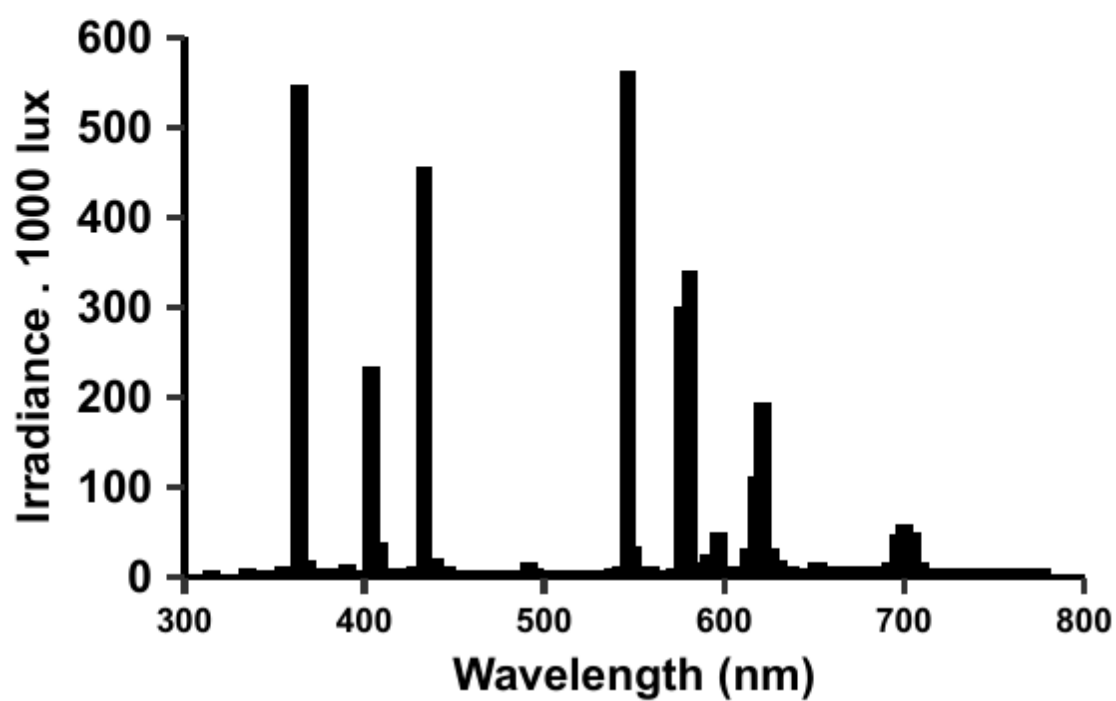
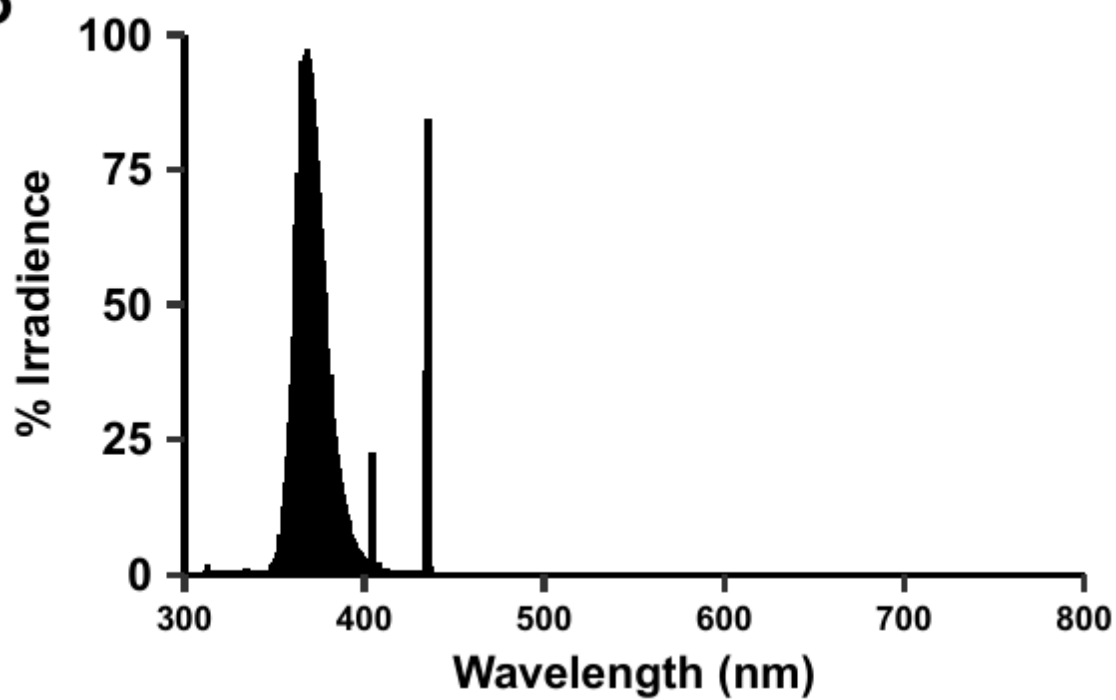
A**B**

Figure 1. A: Spectral power distribution of a 125W Mercury Vapour lamp manufactured by Philips, normalised to an irradiance of 1000 lux in 5nm wavelength bands. B: Generic spectral power distribution of Actinic lamps across wattages produced by Philips in 5nm wavelength bands. Irradiance is expressed as a portion of the total irradiance produced, which varies between lamps. The most frequently used lamp type used in the GMS, 125W MV emits light at a much broader spectrum than Actinic lamp (data sourced from Philips Lighting, 2025; 2024).

Describing catch size and compositional differences in insect communities is important for monitoring programmes and the design of ecological experiments, and it is important that any biases in widely used sampling methods are fully understood. However, variation in the composition of moth trap samples across trapping methods can also be used to make inferences about the impact of artificial light at night (ALAN) on the moth community. This is because near-identical mechanisms are responsible for both the functioning of moth traps and the disruptive effects of ALAN. As such, while Actinic and Mercury Vapour bulbs are not commonly employed as street lighting, various traps of different spectra are frequently used to explore the effect of ALAN on moths in choice experiments (e.g. Altermatt and Ebert, 2016; Brehm et al. 2021; Somers-Yeates et al. 2013; van Langevelde et al. 2011).

Here, 10 years of records collected through the Garden Moth Scheme (GMS) in a single land use type (gardens in the United Kingdom) from seven bulb types and three trap designs are used to explore the impact of spectrum and brightness on the attraction of moths to artificial light. We use weather, bulb type and trap type variables to examine how moth abundance changes night-to-night and collate garden habitat variables with information about surrounding land uses to partition garden-to-garden variation attributable to bulb type, urbanisation, and distance to street lighting. As such we provide the largest comparison of moth trap types to date, producing estimates of how moth trap and bulb types compare to one another in terms of catch size, with the aim of assisting in the development of standardised monitoring programs and the selection of moth trap types for field studies.

Exploring the species-composition of moth trap catches, we also test two hypotheses regarding the impact of ALAN on moths. Firstly, we hypothesise that moths display species-specific responses to artificial light of different spectra. This leads to the prediction that moth traps of different spectra will sample different sections of the moth fauna and collect different species. We test this hypothesis by comparing species composition from traps using Actinic to those using Mercury Vapour bulbs. Secondly, we explore the “reduced mobility hypothesis”, described by van de Schoot (2024). Altermatt and Ebert (2016) find that spindle ermine moths (*Yponomeuta cagnagella*) exhibit reduced wing size in areas impacted by ALAN compared to pristine populations. Investigating the mechanism behind this reduced flight-to-light response, van de Schoot et al. (2024) find that urban individuals of this species had on average smaller wings than those emerging from dark, pristine environments. This “reduced mobility hypothesis” states that ALAN exerts selective pressure against mobility in moths, mediated by evolutionary changes in wing size. Here, we develop this hypothesis further. We expect that larger, more mobile moths are more strongly attracted to moth traps, but that this effect will be stronger for brighter light sources. We hypothesise that brighter traps will be able to be perceived by moths from further distances, but that only highly mobile moths will be able to travel to the trap and become caught. We therefore predict that dimmer bulbs will collect a higher proportion of smaller, less mobile species, while brighter bulb types will collect a higher proportion of larger, more mobile species. We test this mobility hypothesis by comparing the size distribution of samples from different bulb types and different levels of ALAN exposure while controlling for other habitat, landscape and geographic variables in ordination models.

Methods

The Garden Moth Scheme dataset

The Garden Moth Scheme (GMS) is a semi-standardised citizen science surveying project (2003 – present), which asks participants to sample moths with a light trap in their garden each Friday between March and November. Participants are encouraged to report all

records (including trap nights where no moths were recorded), to sample regardless of weather conditions (barring extreme or dangerous weather) and are given a prescribed list of readily identifiable species on which to focus. The scheme has engaged hundreds of participants, producing a large collection of c.36-week time-series of moth trap catches from a variety of trap types, distributed across Great Britain, Ireland and the Channel Islands. Participants also report information about their garden: the distance to green space, farmland, street lighting, water, woodland and to the coast. Participants provide a list of their garden microhabitats: presence of a bird table, Buddleia, compost heap, >25 m² lawn, log pile, long grass, pussy willow, trees over 10 m, oak trees over 10 m, wild honeysuckle, wild ivy, wildflower meadow are recorded.

Statistics

All analyses were conducted in R version 4.4.3 (R Core Team, 2025). The percentage landcover in a 100m radius surrounding each site was extracted from the UK CEH Land Cover Map 2022 (25m rasterised pixels; Marston et al., 2024) dataset for each of the 21 landcover classes. Daily 1km resolution rainfall volume and minimum temperature variables were extracted from the CEDA Archive HadUK Gridded Climate Observations v1.2.0 (Hollis et al., 2019). Moon phase was gathered for each sample night using the package ‘moonlit’ (Śmielak, 2023), which calculates the percentage of full moonlight intensity based on moon phase, elevation, latitude, and longitude (compared to the average full moon value of 0.32 lx), not accounting for cloud cover.

To estimate differences in catch between a range of trap types across each covariate (Model 1) a generalised linear mixed model (GLMM) was fit to time series from each site meeting a set of filtering criteria. Firstly, we separate all GMS records by site (participants’ gardens) and year. We filter to include only site-years in Great Britain (excluding records from Ireland and Northern Ireland) in which at least 34 weeks of sampling were conducted. We remove any additional samples taken in winter outside of the GMS sampling window. We exclude

timeseries which employed multiple trap or bulb types. Using participant's reported collection method, we identify seven frequently used bulb types (125W Mercury Vapour, 80W Mercury Vapour, 60W Actinic, 40W Actinic, 20W Actinic, 15W Actinic, 6W Actinic) and three frequently used trap types (Heath, Robinson, Skinner), excluding all records that fall outside these categories. This excludes a small number of participants who used home-made or unconventional traps and bulbs. This produces a dataset of 34–36-week timeseries from seven bulb and three trap categories in Great Britain. Individual gardens may include between 1 and 10 years of records. Graphical description of the spread of trap and bulb categories and covariates in the unfiltered dataset are provided in Supplementary Information Figures 1-5.

To these data we fitted a generalised linear mixed model (GLMM) using package glmmTMB (Brooks et al. 2017; McGillicuddy et al. 2025) including variables describing bulb type (125W Mercury Vapour, 80W Mercury Vapour, 60W Actinic, 40W Actinic, 20W Actinic, 15W Actinic, 6W Actinic), trap type (Robinson, Heath, Skinner), week of the year, maximum daily temperature, rainfall volume (in log cubic millimetres) and percentage full moonlight intensity. We model crossed random effects for 'site' (garden) and 'year' (2013-2022) to account for repeated measures and interannual variation in insect abundance.

We undertook extensive residual simulations throughout the modelling process using R package DHARMA (Hartig, 2024) to refine model specification. Data consisted of counts (total number of moths caught in a single trap over one night of sampling) which in preliminary Poisson models indicated overdispersion. As such, a type I negative binomial error term with a log link function was selected (Ver Hoef and Boveng, 2007), coupled with a dispersion model including the variables bulb type, maximum daily temperature, site ID and week of the year. To assess any potential residual non-linearity, we plotted residuals against each covariate individually. This procedure indicated non-linearity between maximum daily temperature and moth abundance. We also found complex multimodal non-linearity between

moth abundance and week of the year, corresponding to seasonal variation in moth abundance. We captured this non-linearity using natural splines using 20 degrees of freedom for week of the year and 5 degrees of freedom for maximum daily temperature.

We tested for multicollinearity using variance inflation factors implemented in R package performance (Lüdecke et al. 2021). All variables took values less than 3. Bulb type, trap type, rainfall, and moon phase took values between 1.08 and 1.66, while natural spline terms week of the year and maximum daily temperature took values of 2.75 and 2.82 respectively.

The variance explained by fixed effects (marginal R^2) was calculated using a likelihood-ratio test implemented in package MuMIn (Bartoń, 2025). This test compares the fitted model to a null model including only an intercept, the random effects (site and year) and dispersion model to estimate the variance explained by fixed effects only. Predictions were made using package marginalesffects (Arel-Bundock et al., 2024) and converted to a percentage of the mean 125W MV prediction for comparability. Post-hoc pairwise comparisons between estimated marginal mean values for bulb and trap-type categories was conducted using package emmeans (Lenth, 2024).

Ordination was conducted on samples pooled by site and year to examine species composition variation attributable to bulb type. Only sites with complete GMS microhabitat information were used ($n = 34$ -36-week timeseries). Categorical distance to feature variables were converted to numerical by taking an average of the distances in the range category.

The furthest option in the survey response, ">2km", was converted to equal 2km. To determine the ordination method, Decorana (DCA) was performed on the log-transformed species matrix as a measure of heterogeneity. A DCA axis 1 value of 2.54 indicated beta-diversity was suitably homogenous for constrained linear ordination (RDA rather than CCA).

Using the function 'ordiR2step' with 49,999 permutations (Oksanen et al., 2022), a global model with all available variables was compared to an intercept-only model using forward

selection to identify and remove extraneous variables. In this procedure variable selection stops if a new variable is either non-significant or if the adjusted R^2 of the model including the new variable exceeds that of the global model. The function provides a test of the significance of each variable to the selected model with an ‘ANOVA-like’ Monte-Carlo test using 999 permutations (Oksanen et al., 2022), which was then adjusted for multiple comparisons using Holm’s correction. Multicollinearity was assessed with variance inflation factors. Percentage suburban landcover had a variance inflation factor of 12.43 and was removed, lowering the variance inflation factors of all variables to below 2.4. All variables excluding suburban landcover were therefore selected. Ten variables with the highest contribution to model adjusted R^2 are provided in Table 1. A full list of selected variables is provided in Supplementary Table 1.

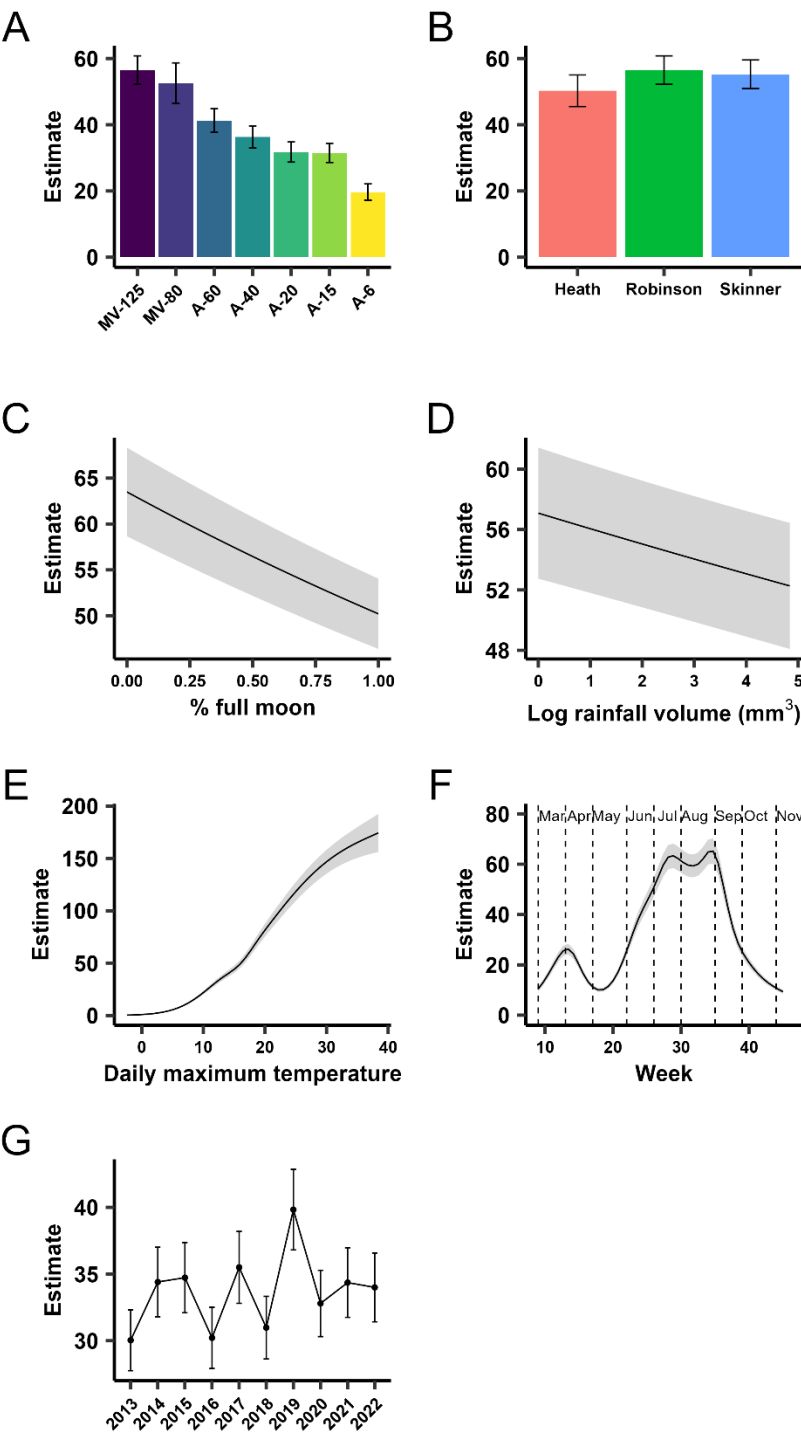
After initial model selection, partial ordination was used to identify the effect of bulb type on species composition. In a partial ordination, conditioning variables (selected CEH landcover variables, latitude, longitude, year, the GMS microhabitat variables and GMS distance to feature variables) are ‘partialled out’ before analysis by comparing models with and without the variables, leaving only the contribution of the selected constraining variable(s) (Borcard et al., 2018). Following this procedure, the ‘mobility hypothesis’ (van de Schoot et al. 2024) was tested by regressing species’ typical wing size on to RDA axes one and two using vegan function ‘envfit’. This function is suitable for calculating the regression of supplementary variables which pertain to species by setting the ‘display’ argument to ‘species’ (Oksanen et al., 2022). Typical wing size was calculated by averaging minimum and maximum forewing length gathered from Cook et al., (2021) with additional data from Waring and Townsend (2018) and Sterling and Parsons (2012). These data are provided in the Supplementary Information Table 3. Significance of these trait variables were assessed by Monte Carlo simulation (999 permutations). We assess differences in RDA scores across moth families using a Kruskal–Wallis test. Post hoc pairwise comparisons were conducted using Dunn’s test with Holm correction to control the family-wise error rate.

265

266 The inertia explained by the selected model was evaluated by calculating an unconstrained
267 (PCA) model with no explanatory variables and extracting the first two axes (Zelený 2022).
268 PCA axes were then used as variables in an RDA to determine the maximum inertia that
269 could be explained by the theoretical best orthogonal explanatory variables. The model R^2
270 value was then calculated as a proportion of this maximum explicable variation. Significance
271 of the R^2 value was evaluated by comparison to the distribution of 999 R^2 values generated
272 by Monte Carlo simulation using randomised environmental variables, implemented in vegan
273 function 'anova' (Oksanen et al., 2022).

274

275 **Results**



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277

278 *Figure 2. Predicted number of moths caught in a single trap-night by bulb type (A),*
279 *trap type (B), percentage full moon (C) log-transformed rainfall volume (D), daily*
280 *maximum temperature (E), week of the year (F), and year (G).*

Abundance analysis

In total, 3,801,663 individual moths were included in the abundance analysis across 86,062 trap nights and 575 individual gardens. The mean number of years surveyed per garden was 4.33.

The GLMM Model 1 fixed effects' (daily rainfall volume, maximum daily temperature, trap type, bulb type, week of the year) marginal R^2 was 56.65%. Percentage 125W MV catch is provided in Table 1 to facilitate comparison of abundance between traps. All bulb categories showed significant ($p < 0.0001$) effects relative to the 125W MV reference category, except for 80W MV, which was not statistically significant ($p = 0.175$). Predicted values show catch increased with wattage (Fig. 2a; Table 1). Marginal mean predictions were not significantly different in pairwise comparisons between 80W MV and 125W MV ($p = 0.7171$) and between 15W Actinic and 20W Actinic bulbs ($p = 0.9999$). All other pairwise comparisons were significant ($p < 0.0025$).

Following an early low peak in March, catch was highest in midsummer, generally decreased with rainfall, increased with minimum temperature, and decreased with moonlight (Fig. 2C, D, E, F; SI Table 1.) Total abundance of moths across all GMS sites fluctuated between 2013 and 2022, lacking a clear trend (Fig 2. G)

Trap type had a significant effect on moth trap catch ($p < 0.001$). Pairwise marginal mean comparisons indicated that Heath traps caught the fewest moths. Heath traps were predicted to catch 11.05% fewer moths than Robinson traps ($p = 0.0004$) and 9.03% fewer moths than Skinner traps ($p = 0.0022$). There was no significant difference between Robinson and Skinner traps ($p = 0.3770$).

Bulb	Trap nights	Estimate	Std.error	Statistic	P value	CLD	Percent 125W MV catch
Intercept (125W MV)	47565	-2.72	0.14	-19.83	0.00	a	100.00
MV 80	1437	-0.07	0.05	-1.36	0.17	a	93.25
Actinic 60	8884	-0.33	0.03	-11.19	0.00	b	71.85
Actinic 40	8193	-0.51	0.04	-13.92	0.00	c	60.30
Actinic 15	12622	-0.60	0.04	-16.62	0.00	d	54.76
Actinic 20	4336	-0.60	0.04	-14.56	0.00	d	54.73
Actinic 6	2071	-1.09	0.06	-19.04	0.00	e	33.46

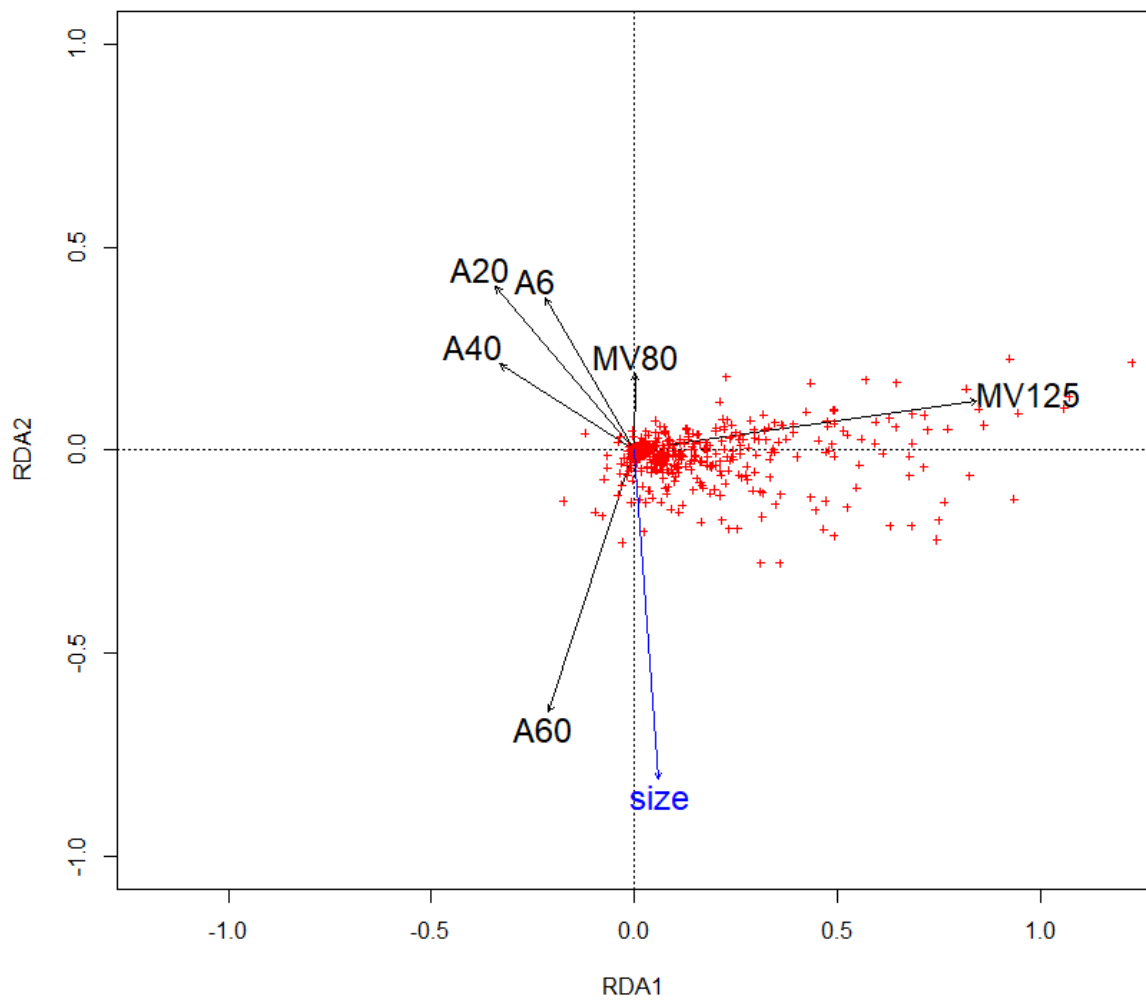
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308 *Table 1. GLMM model 1 bulb categories with total number of trap-nights and predicted*
309 *values for each bulb category. Population-level predictions are provided (setting random*
310 *effects to 0) using all covariates at their mean values. Compact letter display (CLD) indicates*
311 *pairwise comparisons in which estimated marginal means were significantly different from*
312 *one another. Bulbs which share a CLD were not significantly different from one another.*
313 *Extended version including all covariates is provided in Supplementary Table 1.*

314

315 Species composition.

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317

318 *Figure 3. Model 2 partial log-transformed RDA ordination with regressed arrow for size. The*
 319 *effect of all sample variables besides bulb category was 'partialled out' before plotting. Arrow*
 320 *'size' shows the effect of species' forewing length regressed on to the ordination result.*

321

The overall unconditioned RDA model was highly significant ($p < 0.001$, $\text{adj-}R^2$ was 0.29). In this model, all included variables were selected and highly significant ($p < 0.006$). Based on adjusted R^2 , bulb category made the single largest contribution to compositional differences observed in the GMS ($\text{adj-}R^2 = 0.0619$), followed by latitude ($\text{adj-}R^2 = 0.0589$) and distance to farmland ($\text{adj-}R^2 = 0.0473$).

Variable	Cumulative $\text{adj}R^2$	Adj R^2	Df	AIC	F	Pr(>F)	Source
Bulb category	0.0619	0.0619	6	15268.43	32.47	0.00112	GMS
Latitude	0.1208	0.0589	1	15083.9	192.20	0.00112	
Distance to farmland	0.1681	0.0473	1	14926.7	163.19	0.00112	GMS
Longitude	0.2054	0.0373	1	14796.34	135.00	0.00112	
Year	0.2210	0.0156	1	14740.7	58.00	0.00112	
Garden size	0.2302	0.0092	3	14709.73	12.34	0.00112	GMS
Distance to woodland	0.2380	0.0079	1	14681.37	30.36	0.00112	GMS
% Suburban landcover	0.2443	0.0063	1	14658.7	24.64	0.00112	CEH
Distance to coastline	0.2499	0.0057	1	14638.19	22.46	0.00112	GMS
Soil Type	0.2554	0.0054	2	14619.41	11.36	0.00112	GMS

Table 2 Source, significance, adjusted R^2 , AIC, F values of the 10 variables with the largest impact on moth community composition, measured by adjusted R^2 . Variables were evaluated OrdR^2step with 49,999 permutations. R^2 was adjusted using Holm's correction ($\text{adj}R^2$). Degrees of Freedom (Df), AIC (Akaike Information Criterion), F-statistics (F), and F-statistic p-values (Pr(>F)) are provided. GMS variables originate from the Garden Moth Scheme survey dataset; CEH variables were extracted from the 2021 CEH Landcover map. A full list evaluated variables is available in Supplementary Information Table 2.

Model 2 (Fig. 3) was generated by conditioning variance attributed to all variables aside from bulb category, which was constrained. Model 2 was highly significant ($p < 0.001$). 26.57% of

the inertia was conditioned and 4.40% was constrained. The adjusted R^2 was 0.044, representing 29.71% of the maximum variation explicable by two axes. For constrained axes, Eigenvalues were 8.78 for RDA1, 0.515 for RDA2, and 0.233 for RDA3.

Variation between MV and Actinic traps aligned with RDA1 (which contained the majority of the total model variance), while centroids of Actinic traps were similar in RDA1, but showed variation in RDA2 (Figure 3). The higher wattage Actinic traps took lower RDA2 scores, but broadly similar RDA1 scores.

The average of each species' reported minimum and maximum forewing length (size) was then regressed onto the ordination axes. Species' position on the ordination was significantly related to their size ($p > 0.023$, $r = 0.065$). The regression aligned with RDA2, the axis partitioning Actinic bulbs by brightness. Size was aligned with the ordination arrow for 60W Actinic bulbs and positioned opposite to lower Actinic bulbs and 80W MV bulbs. Extracting species' RDA scores (Fig. 4), a Kruskal–Wallis test indicated a significant difference in RDA1 scores across moth families, $H(3) = 9.08$, $p = 0.028$. Post-hoc Dunn's test with Holm's correction indicated no significant pairwise differences in RDA1 scores between families (all $p > 0.06$). A Kruskal-Wallis test indicated a significant difference in RDA2 scores across families, $H(3) = 14.94$, $p = 0.0018$. Post-hoc Dunn's test using Holm's correction indicated a small significant difference in RDA2 between Noctuidae and Erebidae ($p = 0.0018$; Erebidae median = 0.00441, Noctuidae median = -0.00649), but no significant differences between any other pairwise comparison of families.

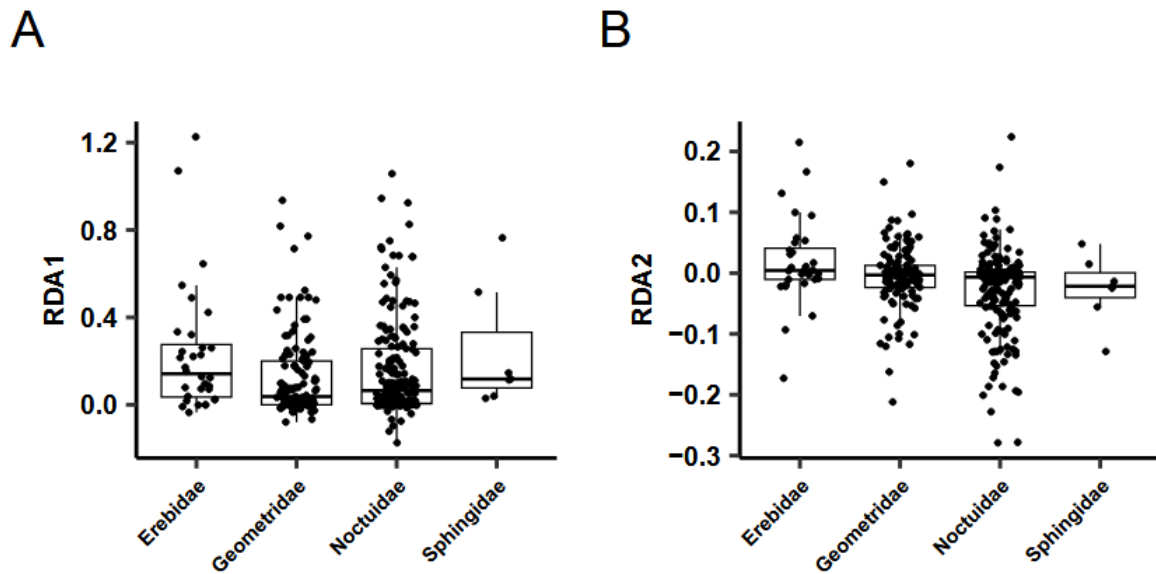


Figure 4: Comparison of RDA scores between moth families. Species of Geometridae had significantly higher RDA2 scores than those of Noctuidae. RDA scores are extract from Model 2. Higher RDA1 scores were associated with Mercury Vapor bulb types, while lower RDA2 scores were associated with brighter Actinic bulbs.

Model 3 (Fig. 5) constrained the variables 'distance to street lighting' and 'percentage urban landcover', with all other variables conditioned. The resulting ordination was highly significant ($p < 0.001$). The adjusted R^2 was 0.0033, representing 29.71% of the maximum variance explicable by two axes. Overall, 29.75% of the variance was conditioned; 0.37% of the variance was constrained. Eigenvalues for the constrained axes were: RDA1 = 0.4052; RDA2 = 0.3397. The regressed vector for species' size was significantly related to the ordination ($p = 0.0019$, $R^2 = 0.0288$) and aligned with distance to street lighting. The regressed arrows approached orthogonality to percentage urban landcover.

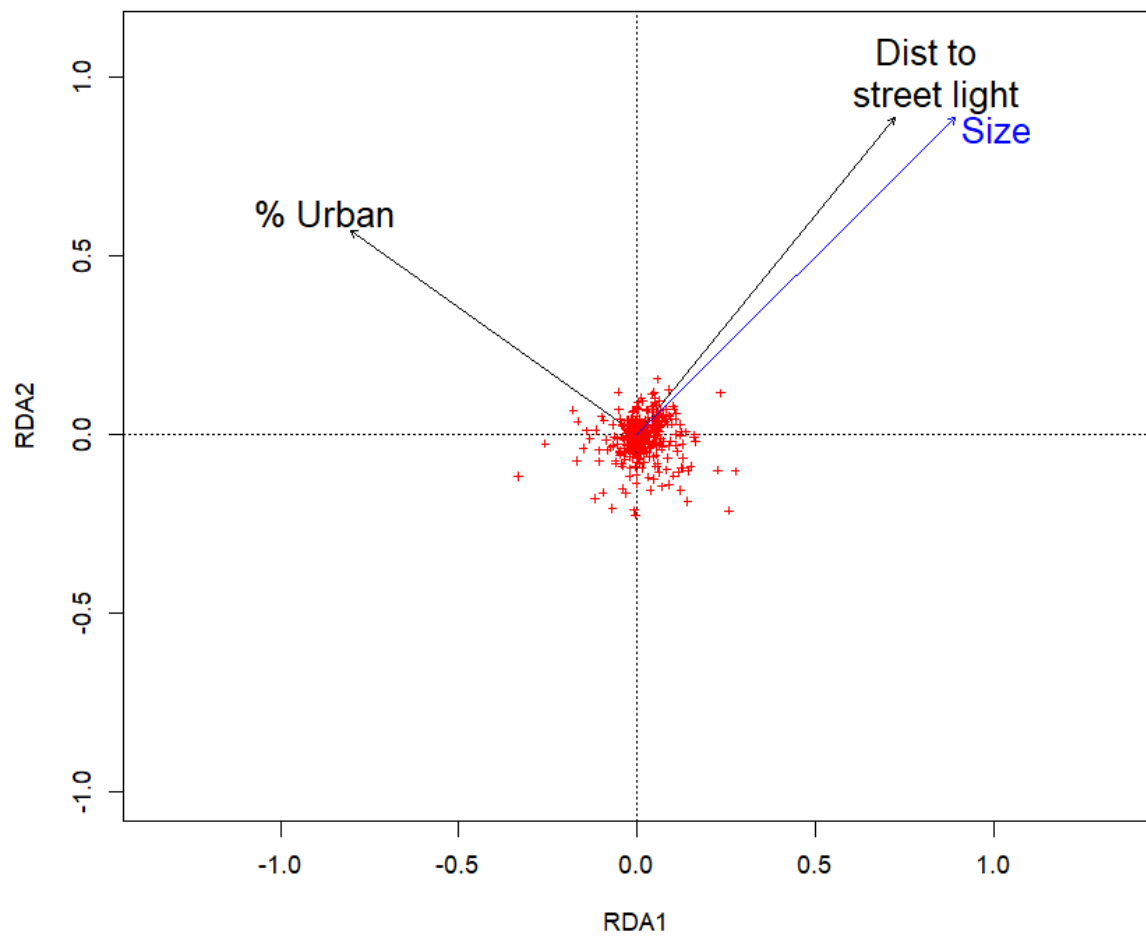


Figure 5. Model 3 RDA ordination. All variables besides percentage urban landcover and distance to streetlighting were 'partialled out' before plotting. Arrow 'size' shows the effect of species' size regressed on to the ordination result.

Discussion

We find that brighter moth trap bulbs generally collect larger numbers of moths. We find that Robinson and Skinner traps tend to collect more moths than Heath-style traps. We find some differences in species composition between bulb types. Ordination model results lead

us to hypothesise that MV traps collect a unique assemblage, and that brighter, higher wattage Actinic bulbs collect a larger proportion of large winged and mobile moth species.

Model 1 indicates that higher wattage moth traps generally collect larger numbers of moths. One bulb type, 15W Actinic, falls out of this pattern and is estimated to collect marginally more (+0.032) moths than 20W Actinic bulbs. 15W Actinic traps can be powered easily by battery, meaning that they may be more freely placed away from competing light sources within the garden. This flexibility may be conducive to higher total catches than otherwise expected by wattage alone. We estimate that Heath-style traps are likely to collect fewer moths than Robinson or Skinner style traps. However, we find no significant difference between Robinson and Skinner designs. We find that catch is negatively affected by moonlight, rainfall, and low temperature, in line with previous studies (Jonason et al., 2014; Holyoak et al., 1997; Puskas et al., 2006). However, due to the observational nature of our study, a major unmeasured source of confounding is non-random assignment of moth trap type to participants' gardens (selection effects). For instance, where competing light pollution is not an issue, participants may select a dimmer trap which can catch a manageable number of moths or will ensure a larger proportion land inside (rather than surrounding) the trap, more experienced trappers may use more powerful bulb types and participants with the means to buy more expensive traps may also have more diverse gardens (the 'luxury effect', Leong et al. 2018). We are unable to control for this confounding. Our estimates are, however, based on substantially larger sample sizes than previous field-based comparisons (e.g. Blomberg et al., 1976; Brehm, 2017; Brehm et al., 2021; Fayle et al., 2007; Infusio et al., 2017; Merckx and Slade, 2014; Niermann and Brehm, 2022; Somers-Yeates et al., 2013). We also provide improved estimates over previous analyses of GMS data (Bates et al., 2013) by parameterising the important determinants of moth abundance over 10 years.

Model 2 indicates that bulb types collect somewhat different assemblages of species.

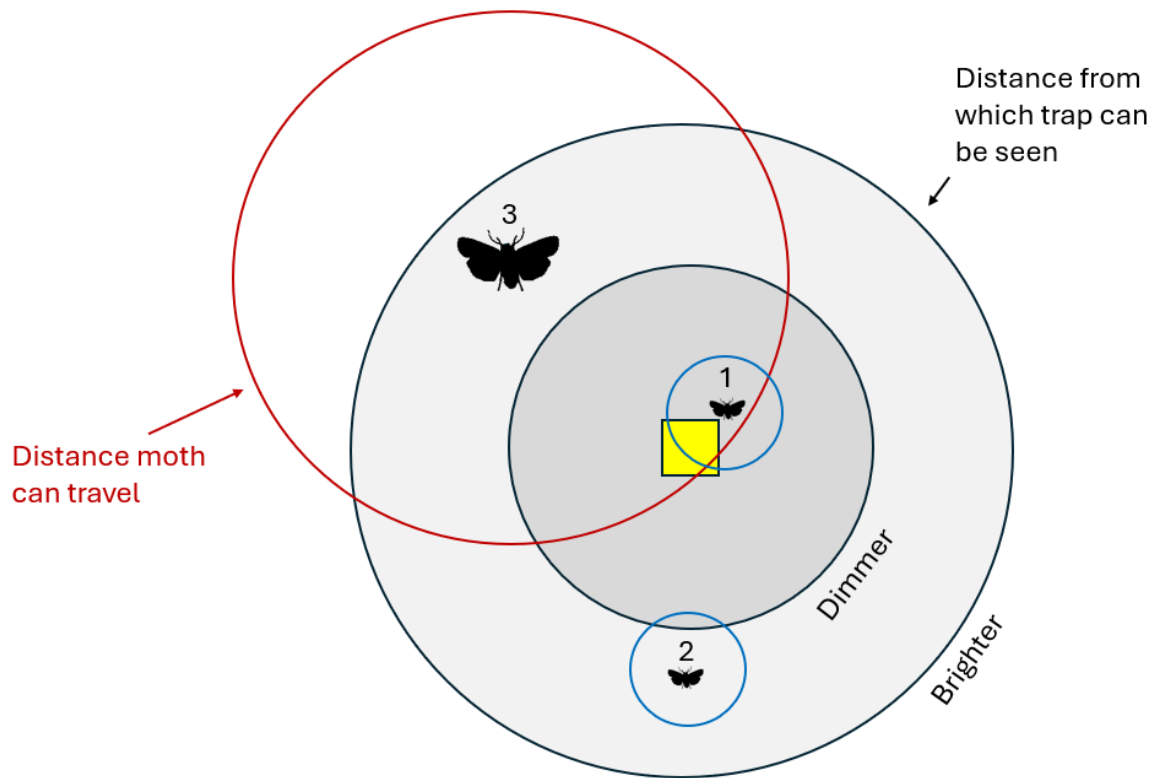
Previous reports conflict over compositional differences between moth traps. Between traps

of different spectra, several field experiments have found little or no difference in assemblage (Blomberg et al., 1976; Fayle et al., 2007; Merckx and Slade, 2014; Somers-Yeates et al., 2013; van Grunsven et al., 2014), while others note differences, but conflict over underlying causes (cf. Brehm, 2017; Brehm et al., 2021; Infusio et al., 2017; Niermann and Brehm, 2022; see Introduction). Model 2 indicates that there were relatively large differences in species composition between different bulb types compared to other variables examined. Based on adjusted R^2 , compositional differences attributable to bulb type were larger than any other geographic, landcover or garden microhabitat variable tested.

What underlies this compositional variation? As RDA models explained a relatively small portion of the total variation in species composition, it is not possible to draw firm conclusions on this question. We find that noctuid species took significantly lower values in RDA2 when compared to erebid species, but there was no significant difference compared to any other family tested. Regressing species' forewing length on to Model 2 indicated that species' forewing length was significantly related to their position on the ordination axes. Larger species had significantly larger negative values in RDA2, while smaller species took larger positive values in RDA2. RDA2 partitioned Actinic traps by wattage, indicating that species associated with brighter, higher wattage Actinic traps tended to have larger wings than those associated with dimmer, lower wattage Actinic bulbs.

Building on the "reduced mobility hypothesis" described by van de Schoot et al. (2024), we hypothesise that a mechanism contributing to this association is species' mobility. As trap brightness is increased, we expect that its light will be perceptible to moths from further distances, but that many of the moths which perceive the light will not reach the trap and become caught. It seems likely that a contributing factor to whether an individual moth reaches the trap and becomes caught is its size and mobility, as more mobile moths are likely to be capable of travelling further to reach the trap. If a bulb's brightness is increased one would therefore expect to sample the local (mobile and relatively immobile) fauna, plus some portion of the more distant individuals that are mobile enough to reach the trap. The

439 hypothesis is illustrated diagrammatically in Figure 6. This hypothesis predicts that large
 440 moths should be over-represented with respect to weak-flying species in bright traps, a
 441 prediction tentatively supported by our ordination results.



442

443 *Figure 6. Diagram illustrating the mobility hypothesis, building on the mobility mechanism*
 444 *described in Altermatt and Ebert (2016) and tested in van de Schoot et al. (2024). The*
 445 *central, yellow-coloured box represents a moth trap or other light source. Black circles, filled*
 446 *grey, represent the distance from which the trap can be seen; we expect brighter moth traps*
 447 *can be perceived by moths from further away. Silhouettes represent moths in proximity to*
 448 *the trap. Moths 1 and 2 represent small, relatively immobile species, whereas moth 3*
 449 *represents a more mobile species; coloured circles represent the distance a particular moth*
 450 *is capable of travelling. For the dimmer trap, only moth 1 can see the trap. Moth 1 is also*
 451 *capable of travelling to the trap, so may become caught. For the brighter trap, both moth 2*
 452 *and moth 3 can see the trap and may become attracted to it. However, moth 2, which is*

relatively immobile, is not capable of reaching the trap to become caught. In this simple graphical model, increasing the brightness of a trap will change the species assemblage collected, increasing the proportion of large species relative to small species.

While also explaining a relatively small portion of the total variation in species composition, Model 3 provides some support for the above hypotheses. In Model 3, which constrained percentage urban landcover together with distance to street lighting, species' position on the ordination was also significantly related to their size. The regressed arrow aligned with that of distance to street lighting and was orthogonal to that of urban landcover. This association indicates that traps within gardens further from street lighting tended to collect a larger proportion of large-winged moth species, whereas gardens closer to street lighting tended to collect more small-winged species. Orthogonality between the regressed size arrow and percentage urban landcover indicates that this relationship was unrelated to urbanity, a potential confounder of the effect of ALAN on species composition. It follows from the mechanism postulated above that strong-flying moth species are more likely to be caught under streetlights as well as within moth traps. Ordination Model 3 therefore leads us to tentatively hypothesise that there may be selective pressure against mobility in moths due to ALAN. Previous work also supports these hypotheses. Altermatt and Ebert (2016) established that in the spindle ermine moth (*Yponomeuta cagnagella*), ALAN exposure precipitated behavioural and morphological changes causing urban-collected individuals to display 30% reduced flight-to-light response compared to those collected in dark rural areas. Van de Schoot et al. (2024) measured the wing dimensions (length, width, and area) of these moths, finding that those collected from ALAN-affected areas showed a significant reduction in forewing length. This suggests selective pressure against mobility mediated by changes in forewing length. Findings presented here, that larger winged moths form a larger proportion of catch within brighter traps, provides some support to this hypothesis. Together, this has led us to hypothesise that ALAN can work as an ecological trap, altering moth

community composition by exerting negative fitness effects on large moth species (Figure 6), a mechanism potentially contributing to the faster decline of large species in the United Kingdom (Coulthard et al., 2019).

Another mechanism that could explain the observed patterns is allometry: all else equal, smaller eyes are less sensitive to light as they can collect and focus fewer photons (Warrant, 2017; Warrant and Somanathan, 2022). As eye size appears to scale with wing size allometrically in moths (Stöckl et al. 2022), we are unable to distinguish between these two mechanisms - both may play a role. However, previous work supports the hypothesis that mobility plays a substantial role in the flight-to-light response in moths (Altermatt and Ebert, 2016; van de Schoot et al. 2024).

Our results also suggest that MV traps collect a distinct assemblage to actinic traps (Model 2). However, factors underlying compositional differences between MV and Actinic traps are less clear than those between Actinic traps of different wattages. MV bulbs emit a larger proportion of non-UV and longer wavelength light than Actinic (Figure 1). Brehm et al. (2021), van Langevelde et al. (2011) and Somers-Yates et al. (2011) find that light sources of longer wavelength collected fewer species, suggesting the UV portion of the spectrum is most attractive to moths. Our findings support this conclusion. However, not tested is the combination of UV and longer wavelength light. Here, Model 2 showed that 80W MV bulbs were positioned closest to 125W MV bulbs along RDA1, despite lower and more variable catch size produced by 80W MV traps (Model 1). This indicates that a portion of the variation between these bulb types is attributable to emission spectra rather than simply sample size. One study, comparing blacklight-coated (excluding all but UV radiation) MV bulbs to non-coated MV bulbs (Fayle et al., 2007) found that excluding the human-visible portion of the spectrum decreased catch size and diversity. Together with ordination Model 2 presented here, this supports the hypothesis that UV in concert with longer-wavelength light produces a characteristic MV species assemblage, possibly including species which are more sensitive

to longer-wavelength light. Further work is required to evaluate traits underlying this variation.

In 2015, MV bulbs were banned in the EU for general purpose use and are no longer widely manufactured (Bates et al., 2013). Here it is shown that the trap type producing the next largest samples is 60W Actinic, but this comes with the caveat that MV and Actinic bulbs appear to sample different sections of the moth fauna. An alternative not evaluated are LED traps (White et al., 2016; Brehm, 2017; Infusino et al., 2017). These traps can be designed to output a great variety of spectra by combining diodes, are energy efficient, and typically lightweight. Several designs are currently available, such as the LepiLED (Brehm, 2017), but the ideal spectral profile of LED lamps is yet to be determined (but cf. Niermann and Brehm, 2022; Brehm, 2017). Results presented here support the idea that inclusion of longer wavelength emitting diodes are likely to broaden the fauna which LED traps sample (Brehm, 2017). Also not evaluated here are 200W tungsten bulbs used by the Rothamsted Insect Survey light trap network. These bulbs emit substantially less UV and a broader range of LW radiation than MV traps and are therefore likely to sample a distinct fauna.

Conclusions

We found that higher wattage bulbs generally collected larger numbers of moths and that different bulb types collected somewhat different sets of species. We found that Heath-style traps collected fewer moths than Robinson or Skinner style traps but found no significant difference between Robinson and Skinner trap designs.

We also used ordination to explore compositional differences between traps. We hypothesise that: (1) large winged, mobile species can travel further to light sources and are consequently more likely to be caught by moth traps or under street lighting; (2) this mechanism is a cause of the (relatively weak) patterning observed in ordination models,

which indicated brighter moth traps are characterised by a larger proportion of large-winged species; (3) this mechanism implies that the negative fitness effects of ALAN are more pronounced for large-winged moth species; (4) compositional differences between MV and Actinic traps indicate that there may be an 'MV-unique' moth assemblage, potentially caused by the broader spectral emission profile of MV bulbs in comparison to Actinic bulbs. Further work is required to explore these hypotheses in an experimental setting.

While standardised moth collection methods exist in the form of Rothamsted-style traps, these traps are rarely used by citizen scientists. Given that the most widely used MV bulbs have now been phased out of production, there is an opportunity to develop a new standardised protocol for monitoring moths akin to Pollard walks used to monitor butterflies in citizen science surveys. It is imperative that any candidate 'standard' bulb stay in production long into the future. It is also desirable that a candidate bulb is inexpensive, widely available, non-toxic, energy efficient and long-lasting. While LED moth traps are not evaluated here, potential candidate bulbs assessed include widely-used 60W Actinic bulbs for sites where mains power is available, and 15W Actinic bulbs for sites where battery power is required.

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Conflict of interest statement

The authors declare no conflicts of interest.

Data availability statement

Species occurrence data in this study were used under licence from a citizen science recording scheme and are available from the Garden Moth Scheme (<https://gardenmothscheme.org.uk>), subject to a data-sharing agreement. Code used to produce this manuscript are available via FigShare, <https://doi.org/10.6084/m9.figshare.27727659.v2>

References

Altermatt, F. and Ebert, D. (2016) 'Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution', *Biology Letters*, 12(4), p. 20160111. Available at: <https://doi.org/10.1098/rsbl.2016.0111>.

Arel-Bundock, V., Greifer, N. and Heiss, A. (2024) 'How to Interpret Statistical Models Using margineffects for R and Python', *Journal of Statistical Software*, 111(9), pp. 1–32. Available at: <https://doi.org/10.18637/jss.v111.i09>.

Axmacher, J.C. and Fiedler, K. (2004) 'Manual versus automatic moth sampling at equal light sources – a comparison of catches from Mt. Kilimanjaro.', *Journal of the Lepidopterists' Society*, 58(4), pp. 196–202.

Bartoń, K. (2025) *MuMIn: Multi-Model Inference*. Available at: <https://CRAN.R-project.org/package=MuMIn>.

Bates, A.J. *et al.* (2013) 'Assessing the value of the Garden Moth Scheme citizen science dataset: how does light trap type affect catch?', *Entomologia Experimentalis et Applicata*, 146(3), pp. 386–397. Available at: <https://doi.org/10.1111/eea.12038>.

Bell, J.R., Blumgart, D. and Shortall, C.R. (2020) 'Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain', *Insect Conservation and Diversity*, 13(2), pp. 115–126. Available at: <https://doi.org/10.1111/icad.12412>.

- 585 Blomberg, O., Itäemies, J. and Kuusela, K. (1976) 'Insect Catches in a Blended and a Black
586 Light-Trap in Northern Finland', *Oikos*, 27(1), pp. 57–63. Available at:
587 <https://doi.org/10.2307/3543432>.
- 588 Borcard, D., Gillet, F. and Legendre, P. (2018) *Numerical Ecology with R*. Cham: Springer
589 International Publishing (Use R!). Available at: <https://doi.org/10.1007/978-3-319-71404-2>.
- 590 Brehm, G. (2017) 'A new LED lamp for the collection of nocturnal Lepidoptera and a spectral
591 comparison of light-trapping lamps', *Nota Lepidopterologica*, 40(1), pp. 87–108. Available at:
592 <https://doi.org/10.3897/nl.40.11887>.
- 593 Brehm, G. *et al.* (2021) 'Moths are strongly attracted to ultraviolet and blue radiation', *Insect
594 Conservation and Diversity*, 14(2), pp. 188–198. Available at:
595 <https://doi.org/10.1111/icad.12476>.
- 596 Brooks, M.E. *et al.* (2017) 'glmmTMB Balances Speed and Flexibility Among Packages for
597 Zero-inflated Generalized Linear Mixed Modeling', *The R Journal*, 9(2), pp. 378–400.
598 Available at: <https://doi.org/10.32614/RJ-2017-066>.
- 599 Conrad, K.F. *et al.* (2006) 'Rapid declines of common, widespread British moths provide
600 evidence of an insect biodiversity crisis', *Biological Conservation*, 132(3), pp. 279–291.
601 Available at: <https://doi.org/10.1016/j.biocon.2006.04.020>.
- 602 Cook, P.M. *et al.* (2021) 'Traits data for the butterflies and macro-moths of Great Britain and
603 Ireland, 2021'. NERC EDS Environmental Information Data Centre. Available at:
604 <https://doi.org/10.5285/5B5A13B6-2304-47E3-9C9D-35237D1232C6>.
- 605 Coulthard, E. *et al.* (2019) 'Ecological traits predict population changes in moths', *Biological
606 Conservation*, 233, pp. 213–219. Available at: <https://doi.org/10.1016/j.biocon.2019.02.023>.
- 607 Dennis, E.B. *et al.* (2017) 'Using citizen science butterfly counts to predict species population
608 trends', *Conservation Biology: The Journal of the Society for Conservation Biology*, 31(6),
609 pp. 1350–1361. Available at: <https://doi.org/10.1111/cobi.12956>.

- 610 Donners, M. *et al.* (2018) 'Colors of attraction: Modeling insect flight to light behavior',
 611 *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329(8–9), pp.
 612 434–440. Available at: <https://doi.org/10.1002/jez.2188>.
- 613 Duchenne, F. and Fontaine, C. (2024) 'Weather explains inter-annual variability, but not the
 614 temporal decline, in insect biomass', *Insect Conservation and Diversity*, 17(6), pp. 932–937.
 615 Available at: <https://doi.org/10.1111/icad.12769>.
- 616 Fayle, T.M., Sharp, R.E. and Majerus, M.E.N. (2007) 'The effect of moth trap type on catch
 617 size and composition of British Lepidoptera', *British Journal of Entomology & Natural History*,
 618 (20), pp. 221–232.
- 619 Fleishman, E. and Murphy, D.D. (2009) 'A Realistic Assessment of the Indicator Potential of
 620 Butterflies and Other Charismatic Taxonomic Groups', *Conservation Biology*, 23(5), pp.
 621 1109–1116. Available at: <https://doi.org/10.1111/j.1523-1739.2009.01246.x>.
- 622 Fox, R. *et al.* (2011) 'Moths count: recording moths for conservation in the UK', *Journal of*
 623 *Insect Conservation*, 15(1), pp. 55–68. Available at: [https://doi.org/10.1007/s10841-010-](https://doi.org/10.1007/s10841-010-9309-z)
 624 [9309-z](https://doi.org/10.1007/s10841-010-9309-z).
- 625 Fox, R. *et al.* (2021) *State of Britain's Larger Moths 2021*. Wareham: Butterfly Conservation.
 626 Available at: [https://butterfly-conservation.org/sites/default/files/2021-](https://butterfly-conservation.org/sites/default/files/2021-03/StateofMothsReport2021.pdf)
 627 [03/StateofMothsReport2021.pdf](https://butterfly-conservation.org/sites/default/files/2021-03/StateofMothsReport2021.pdf)
- 628 Frank, K. (1988) 'Impact of Outdoor Lighting on Moths', *Journal of the Lepidopterists'*
 629 *Society*, 42(2), p. 51. Available at: <https://doi.org/10.1017/S0252921100003687>.
- 630 van Grunsven, R.H.A. *et al.* (2014) 'Spectral composition of light sources and insect
 631 phototaxis, with an evaluation of existing spectral response models', *Journal of Insect*
 632 *Conservation*, 18(2), pp. 225–231. Available at: <https://doi.org/10.1007/s10841-014-9633-9>.
- 633 Hartig, F. (2024) *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)*
 634 *Regression Models*. Available at: <https://CRAN.R-project.org/package=DHARMA>.

- 635 Heath, J. (1966) 'A Comparison of the catches obtained in insect traps fitted with 15 watt and
636 6 watt "Blacklight" fluorescent tubes', *Bulletin of Entomological Research*, 78, pp. 222–223.
- 637 Hollis, D. *et al.* (2019) 'HadUK-Grid—A new UK dataset of gridded climate observations',
638 *Geoscience Data Journal*, 6(2), pp. 151–159. Available at: <https://doi.org/10.1002/gdj3.78>.
- 639 Holyoak, M., Jarosik, V. and Novák, I. (1997) 'Weather-induced changes in moth activity bias
640 measurement of long-term population dynamics from light trap samples', *Entomologia*
641 *Experimentalis et Applicata*, 83(3), pp. 329–335. Available at: [https://doi.org/10.1046/j.1570-](https://doi.org/10.1046/j.1570-7458.1997.00188.x)
642 [7458.1997.00188.x](https://doi.org/10.1046/j.1570-7458.1997.00188.x).
- 643 Infusino, M. *et al.* (2017) 'Assessing the efficiency of UV LEDs as light sources for sampling
644 the diversity of macro-moths (Lepidoptera)', *European Journal of Entomology*, 114, pp. 25–
645 33. Available at: <https://doi.org/10.14411/eje.2017.004>.
- 646 Intachat, J. and Woiwod, I.P. (1999) 'Trap design for monitoring moth biodiversity in tropical
647 rainforests', *Bulletin of Entomological Research*, 89(2), pp. 153–163. Available at:
648 <https://doi.org/10.1017/S0007485399000243>.
- 649 Jonason, D., Franzén, M. and Ranius, T. (2014) 'Surveying Moths Using Light Traps: Effects
650 of Weather and Time of Year', *PLOS ONE*, 9(3), p. e92453. Available at:
651 <https://doi.org/10.1371/journal.pone.0092453>.
- 652 van Langevelde, F. *et al.* (2011) 'Effect of spectral composition of artificial light on the
653 attraction of moths', *Biological Conservation*, 144(9), pp. 2274–2281. Available at:
654 <https://doi.org/10.1016/j.biocon.2011.06.004>.
- 655 Lenth, R.V. (2024) *emmeans: Estimated Marginal Means, aka Least-Squares Means*.
656 Available at: <https://CRAN.R-project.org/package=emmeans>.
- 657 Leong, M., Dunn, R.R. and Trautwein, M.D. (2018) 'Biodiversity and socioeconomics in the
658 city: a review of the luxury effect', *Biology Letters* [Preprint]. Available at:
659 <https://doi.org/10.1098/rsbl.2018.0082>.

- 660 Lüdecke, D. *et al.* (2021) 'performance: An R Package for Assessment, Comparison and
 661 Testing of Statistical Models', *Journal of Open Source Software*, 6(60), p. 3139. Available at:
 662 <https://doi.org/10.21105/joss.03139>.
- 663 Marston, C.G. *et al.* (2024) 'Land Cover Map 2022 (25m rasterised land parcels, GB)'.
 664 NERC EDS Environmental Information Data Centre. Available at:
 665 <https://doi.org/10.5285/c9449bf5-b8f6-4a1c-b3eb-0d70575cba39>.
- 666 McGillicuddy, M. *et al.* (2025) 'Parsimoniously Fitting Large Multivariate Random Effects in
 667 glmmTMB', *Journal of Statistical Software*, 112(1), pp. 1–19. Available at:
 668 <https://doi.org/10.18637/jss.v112.i01>.
- 669 Merckx, T. and Slade, E.M. (2014) 'Macro-moth families differ in their attraction to light:
 670 implications for light-trap monitoring programmes', *Insect Conservation and Diversity*, 7(5),
 671 pp. 453–461. Available at: <https://doi.org/10.1111/icad.12068>.
- 672 Mitter, C., Davis, D.R. and Cummings, M.P. (2017) 'Phylogeny and Evolution of Lepidoptera',
 673 *Annual Review of Entomology*, 62(1), pp. 265–283. Available at:
 674 <https://doi.org/10.1146/annurev-ento-031616-035125>.
- 675 Müller, J. *et al.* (2024) 'Weather explains the decline and rise of insect biomass over 34
 676 years', *Nature*, 628(8007), pp. 349–354. Available at: [https://doi.org/10.1038/s41586-023-](https://doi.org/10.1038/s41586-023-06402-z)
 677 [06402-z](https://doi.org/10.1038/s41586-023-06402-z).
- 678 New, T.R. (1997) 'Are Lepidoptera an effective 'umbrella group' for biodiversity
 679 conservation?', *Journal of Insect Conservation*, 1(1), pp. 5–12. Available at:
 680 <https://doi.org/10.1023/A:1018433406701>.
- 681 Niermann, J. and Brehm, G. (2022) 'The number of moths caught by light traps is affected
 682 more by microhabitat than the type of UV lamp used in a grassland habitat', *European*
 683 *Journal of Entomology*, 119, pp. 36–42. Available at: <https://doi.org/10.14411/eje.2022.004>.

- 684 Nowinszky, L. (2007) 'The hourly distribution of moth species caught by a light-trap', *Applied*
 685 *Ecology and Environmental Research*, 5(1), pp. 103–107. Available at:
 686 https://doi.org/10.15666/aeer/0501_103107.
- 687 Oksanen, J. (2022) 'Package 'vegan''. Available at: [https://cran.r-](https://cran.r-project.org/web/packages/vegan/vegan.pdf)
 688 [project.org/web/packages/vegan/vegan.pdf](https://cran.r-project.org/web/packages/vegan/vegan.pdf)
- 689 Philips Lighting. (2024) 'HPL-N 125W E27 SG 1CT/24 Standard High Pressure Mercury
 690 lamp datasheet'. Available at:
 691 [https://www.lighting.philips.com/api/assets/v1/file/Signify/content/928052007399_EU.en_AA.](https://www.lighting.philips.com/api/assets/v1/file/Signify/content/928052007399_EU.en_AA.PROF.FP/Localized_commercial_leaflet_928052007399_en_AA.pdf)
 692 [PROF.FP/Localized_commercial_leaflet_928052007399_en_AA.pdf](https://www.lighting.philips.com/api/assets/v1/file/Signify/content/928052007399_EU.en_AA.PROF.FP/Localized_commercial_leaflet_928052007399_en_AA.pdf) (Accessed: 1 July 2025)
- 693 Philips Lighting. (2025) Actinic BL TL 6W/10 1FM/10X25CC datasheet. Available at:
 694 [https://www.lighting.philips.com/api/assets/v1/file/Signify/content/928000501030_EU.en_AA.](https://www.lighting.philips.com/api/assets/v1/file/Signify/content/928000501030_EU.en_AA.PROF.FP/Localized_commercial_leaflet_928000501030_en_AA.pdf)
 695 [PROF.FP/Localized_commercial_leaflet_928000501030_en_AA.pdf](https://www.lighting.philips.com/api/assets/v1/file/Signify/content/928000501030_EU.en_AA.PROF.FP/Localized_commercial_leaflet_928000501030_en_AA.pdf) (Accessed: 1 July 2025)
- 696 Pollard, E. and Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation: the*
 697 *British Butterfly Monitoring Scheme*. Chapman and Hall Ltd.
- 698 Puskas, J., Nowinszky, L. and Makra, L. (2006) 'Joint influence of meteorological events on
 699 light trapping of turnip moth (*Scotia segetum* Schiff)', *Zbornik Matice srpske za prirodne*
 700 *nauke*, (110), pp. 259–266.
- 701 R Core Team (2025) 'R: a language and environment for statistical computing.', *R*
 702 *Foundation for Statistical Computing*.
- 703 van de Schoot, E. *et al.* (2024) 'Evolutionary change in flight-to-light response in urban
 704 moths comes with changes in wing morphology', *Biology Letters*, 20(3), p. 20230486.
 705 Available at: <https://doi.org/10.1098/rsbl.2023.0486>.
- 706 Seibold, S. *et al.* (2019) 'Arthropod decline in grasslands and forests is associated with
 707 landscape-level drivers', *Nature*, 574(7780), pp. 671–674. Available at:
 708 <https://doi.org/10.1038/s41586-019-1684-3>.

- 709 Singh, R.P., Böttger, D. and Brehm, G. (2022) 'Moth light traps perform better with vanes: A
710 comparison of different designs', *Journal of Applied Entomology*, 146(10), pp. 1343–1352.
711 Available at: <https://doi.org/10.1111/jen.13068>.
- 712 Śmielak, M.K. (2023) 'Biologically meaningful moonlight measures and their application in
713 ecological research', *Behavioral Ecology and Sociobiology*, 77(2), p. 21. Available at:
714 <https://doi.org/10.1007/s00265-022-03287-2>.
- 715 Somers-Yeates, R. *et al.* (2013) 'Shedding light on moths: shorter wavelengths attract
716 noctuids more than geometrids', *Biology Letters*, 9(4), p. 20130376. Available at:
717 <https://doi.org/10.1098/rsbl.2013.0376>.
- 718 Sterling, P., Parsons, M. and Lewington, R. (2023) *Field guide to the micro-moths of Great*
719 *Britain and Ireland*. Second edition. London: Bloomsbury Wildlife.
- 720 Stöckl, A. *et al.* (2022) 'Allometric scaling of a superposition eye optimizes sensitivity and
721 acuity in large and small hawkmoths', *Proceedings of the Royal Society B: Biological*
722 *Sciences*, 289(1979), p. 20220758. Available at: <https://doi.org/10.1098/rspb.2022.0758>.
- 723 Thomas, J. (2005) 'Monitoring change in the abundance and distribution of insects using
724 butterflies and other indicator groups', *Philosophical Transactions of the Royal Society B:*
725 *Biological Sciences*, 360(1454), pp. 339–357. Available at:
726 <https://doi.org/10.1098/rstb.2004.1585>.
- 727 Van Nieuwerkerken, E.J. *et al.* (2011) 'Order Lepidoptera. Linnaeus, 1758.', *Zootaxa*, 3148(1).
728 Available at: <https://doi.org/10.11646/zootaxa.3148.1.41>.
- 729 Ver Hoef, J.M. and Boveng, P.L. (2007) 'Quasi-Poisson Vs. Negative Binomial Regression:
730 How Should We Model Overdispersed Count Data?', *Ecology*, 88(11), pp. 2766–2772.
731 Available at: <https://doi.org/10.1890/07-0043.1>.

- Wagner, D.L. *et al.* (2021) 'A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous', *Proceedings of the National Academy of Sciences*, 118(2), p. e2002549117. Available at: <https://doi.org/10.1073/pnas.2002549117>.
- Waring, P. (1980) 'Comparison of the Heath and Robinson M.V. Moth Traps', *The Entomologists Record*, 92. Available at: <https://www.biodiversitylibrary.org/page/29886446#page/406/mode/1up> (Accessed: 1 July 2025).
- Waring, P. and Townsend, M. (2018) *Field Guide to the Moths of Great Britain and Ireland*. 3rd edn. London: Bloomsbury.
- Warrant, E. and Somanathan, H. (2022) 'Colour vision in nocturnal insects', *PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES*, 377(1862). Available at: <https://doi.org/10.1098/rstb.2021.0285>.
- Warrant, E.J. (2017) 'The remarkable visual capacities of nocturnal insects: vision at the limits with small eyes and tiny brains', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1717), p. 20160063. Available at: <https://doi.org/10.1098/rstb.2016.0063>.
- Williams, C.B. (1951) 'Comparing the Efficiency of Insect Traps', *Bulletin of Entomological Research*, 42(3), pp. 513–517. Available at: <https://doi.org/10.1017/S000748530002890X>.
- Williams, C.B., French, R.A. and Hosni, M.M. (1955) 'A second Experiment on testing the relative Efficiency of Insect Traps', *Bulletin of Entomological Research*, 46(1), pp. 193–204. Available at: <https://doi.org/10.1017/S0007485300030844>.
- Winfree, R. *et al.* (2015) 'Abundance of common species, not species richness, drives delivery of a real-world ecosystem service', *Ecology Letters*, 18(7), pp. 626–635. Available at: <https://doi.org/10.1111/ele.12424>.

756 Winfree, R., Reilly, J.R. and Genung, M.A. (2025) 'Biodiversity–ecosystem function research
757 must consider abundance and not just diversity', *Nature Reviews Biodiversity*, 1(6), pp. 347–
758 348. Available at: <https://doi.org/10.1038/s44358-025-00040-1>.

759 Zelený, D. (2022) *Explained variation in constrained ordination*. Available at:
760 https://www.davidzeleny.net/anadat-r/doku.php/en:expl_var?do= (Accessed: 1 July 2023).

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