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► **To cite this version:**

Elisa Gomes, Jean-François Lemaître, Valentina Rodriguez-Rada, François Débias, Emmanuel Desouhant, et al.. Foraging at night under artificial light: impacts on senescence and lifetime reproductive success for a diurnal insect. *Animal Behaviour*, 2024, 210, pp.85 - 98. 10.1016/j.anbehav.2024.01.025 . hal-04476841

HAL Id: hal-04476841

<https://hal.science/hal-04476841v1>

Submitted on 25 Feb 2024

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Foraging at night under artificial light: impacts on senescence and lifetime reproductive success for a diurnal insect

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ARTICLE INFO

Article history:

Received 1 August 2023

Initial acceptance 17 October 2023

Final acceptance 2 January 2024

MS. number: 23-00405

Keywords:

egg-laying behaviour

fitness

life span

light pollution

night-time feeding

Venturia canescens

The increasing use of artificial light at night (ALAN) is an anthropogenic disturbance with evolutionary consequences for both nocturnal and diurnal organisms. It has been hypothesized that light pollution could create a 'night-light' niche providing new opportunities for diurnal organisms to forage and reproduce at night, with fitness consequences still scarcely explored. We exposed diurnal parasitoid wasps (*Venturia canescens*) to control (0 lx), low (0.7 lx) or high (20 lx) intensity of light at night throughout their lives and monitored changes in behavioural and life history traits. Light pollution influenced the night-time activity of wasps, with increased feeding and egg laying at night and a tendency for higher night-time reproductive success under a high intensity of light pollution. Surprisingly, high light pollution also increased the wasps' life span. Light pollution did not significantly affect lifetime reproductive success but did affect the distribution of ovipositions between day and night. Additionally, we showed that reproductive senescence occurred in *V. canescens* and that offspring development time was influenced by light pollution, in interaction with maternal age. These findings highlight the use of the 'night-light' niche in a diurnal insect exposed to light pollution, with potential implications for population dynamics, especially in natural conditions.

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Ecosystems undergo numerous human-induced environmental changes such as habitat loss, chemical pollution or climate change (Sih et al., 2011). Similar to these changes, artificial light at night (ALAN) is particularly pervasive and rapidly expanding (Falchi et al., 2016). The rise of ALAN during the 19th century and its strong increase with the development of electric lighting profoundly altered natural light cycles. Daily and seasonal cycles of light and dark, as well as lunar light cycles, are predictable environmental variations that act as major cues for organisms (Gaston et al., 2017; Kronfeld-Schor et al., 2013). Their disruption by ALAN therefore has multiple ecological and biological impacts for the living world (Sanders et al., 2020) as well as potentially important evolutionary consequences (Davies & Smyth, 2018; Desouhant et al., 2019; Swaddle et al., 2015).

Initially, studies on the detrimental effects of ALAN were solely focused on nocturnal organisms, such as bats, moths or fireflies, which were more likely to suffer from behavioural disturbance (Deora et al., 2021; Firebaugh & Haynes, 2016; Russo et al., 2017). However, diurnal organisms are also impacted by illuminated

nights since artificial lighting creates new opportunities for diurnal species to forage or display reproductive behaviours at night ('night-light' niche, Longcore & Rich, 2004). So far, evidence of the use of the 'night-light niche' comes mostly from diurnal vertebrate species, such as birds with an advanced onset of activity (de Jong et al., 2016; Dominoni et al., 2014) or an increase in night-time activity (Ouyang et al., 2017). In the common swift, *Apus apus*, high intensity of light at night during the breeding season led birds to be active throughout the night instead of roosting in their nest (Amichai & Kronfeld-Schor, 2019). In the European blackbird, *Turdus merula*, individuals exposed to rather dim levels of ALAN (about 0.15 lx) extended their foraging activity in the evening compared to individuals in darker areas (Russ et al., 2015). Observations also showed that diurnal species can take advantage of light sources, which attract arthropods, to forage during the night (e.g. several bird species, Lebbin et al., 2007; two lizard species, *Anolis leachii* and *Anolis wattsi*, Maurer et al., 2019; an arthropod, *Platycryptus undatus*, Frank, 2009). Interestingly, diurnal arthropods can also use the night-light niche. For instance, a mesocosm field study suggested that some diurnal parasitoid species may extend their parasitism activity into the night when exposed to low levels of

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ALAN (Sanders et al., 2018). In a laboratory experiment on the same biological system, Kehoe et al. (2020) showed that both ALAN and longer daylength increased parasitism rates. Accurately quantifying the impact of artificial lighting on fitness-related traits at night and during the day is now essential to fully understand the ecological and evolutionary consequences of ALAN on diurnal organisms, and ultimately their interaction with other species.

Lifetime reproductive success, defined as the number of offspring produced during an individual's life span, is a keystone variable to estimate fitness of organisms (Clutton-Brock, 1988). Lifetime reproductive success depends on longevity and reproductive success, two traits that we examined in this study. In the last decade, empirical studies have highlighted that the decrease in reproductive success with age (i.e. reproductive senescence or reproductive ageing) is a pervasive process that occurs in both laboratory and wild populations (Nussey et al., 2013; Zajitschek et al., 2020). Reproductive senescence patterns can differ within species, notably in response to environmental conditions (Cooper & Kruuk, 2018; Tidière et al., 2016), which can be altered by human activities. Anthropogenic disturbances may therefore ultimately impact senescence patterns. Indeed, some studies suggested a potential link between ALAN and age-related changes in biological traits, potentially mediated by increased oxidative stress following the presence of light during the night (studies on laboratory rats, El-Bakry et al., 2018; Vinogradova et al., 2009) or disruption of melatonin cycles (Reiter et al., 2017). However, a direct influence of ALAN on reproductive senescence and lifetime reproductive success is still rarely studied (but see McLay et al., 2018).

The aim of this study was hence to test whether ALAN affected day- and night-time activity, the pattern of reproductive senescence, longevity and lifetime reproductive success of a diurnal parasitoid wasp, *Venturia canescens*. We designed an experiment that allowed us to consider both nocturnal and diurnal foraging behaviours separately. Indeed, while *V. canescens* is a diurnal species showing no activity in the dark (in the absence of any stimulus related to feeding and oviposition), it has previously been demonstrated that females exposed to ALAN moved during the night (Gomes et al., 2021). ALAN could therefore allow the wasps to exploit the night-light niche (i.e. to forage at night), which could consequently boost their lifetime reproductive success. We thus predicted that wasps exposed to ALAN would feed and lay eggs at night, unlike wasps not exposed to light at night. In addition, ALAN has also been shown to alter the diurnal behaviours of females: wasps exposed to light at night preferred to search for hosts rather than for food during the day and tended to produce more offspring when given a single occasion to parasitize a host aggregate (Gomes et al., 2021). We therefore predicted that wasps exposed to ALAN would have a higher parasitism rate and thus a greater reproductive success during the day and at night (but with fewer offspring produced at night than during the day) compared to wasps without light at night. In addition, wasps exposed to ALAN seem to allocate more to immediate reproduction (Gomes et al., 2021), so we also predicted stronger reproductive senescence in these individuals (characterized by an earlier onset of senescence and/or a steeper decline in reproductive performance), as expected under resource-based allocation trade-offs (Lemaître et al., 2015).

METHODS

Biological Model and Rearing Conditions

Venturia canescens is a solitary endoparasitoid hymenopteran (Ichneumonidae). It attacks lepidopteran larvae such as Pyralidae (Salt, 1975), in their second to fifth instar (Harvey & Thompson, 1995). Parasitoid females locate hosts thanks to a mandibular

gland secretion released by the lepidopteran larvae when feeding (Castelo et al., 2003). The species is prosynovigenic (Jervis et al., 2001), which means that the females emerge with an initial load of mature eggs, but additional eggs are also produced throughout their adult life. The eggs are hydropic (i.e. yolk-deficient) which means that they do not store nutrients (Le Ralec, 1995). Eggs are therefore not energetically costly to produce (Pelosse et al., 2011) and the lifetime reproductive success of *V. canescens* is expected to depend mostly on their longevity (approximately 3 weeks in the laboratory) and ability to find and parasitize hosts. As feeding influences longevity (wasps feeding every 48 h lived six times longer than wasps feeding at longer intervals, Desouhant et al., 2005), giving females a longer period of time to parasitize hosts should therefore increase their fecundity (Harvey et al., 2001).

We used wasps of a thelytokous (i.e. parthenogenesis in which females produce only daughters from unfertilized eggs) strain established from about 70 wild females trapped near Valence (southern France) during the summer of 2016. The strain was maintained under controlled conditions (25 ± 1 °C, $60 \pm 5\%$ relative humidity, 12:12 h light:dark) in boxes containing larvae of *Ephestia kuehniella* (Lepidoptera: Pyralidae) as hosts and organic wheat semolina as feeding medium for the host larvae. The adult wasps were fed ad libitum with honey diluted 1:1 with distilled water, because in natural conditions *V. canescens* frequently has access to nectar or honeydew as food sources (Desouhant, Lucchetta, et al., 2010).

Light Conditions

We created three experimental groups of wasps exposed to different intensities of light at night. The wasps were kept in three thermostat-controlled chambers (Sanyo Electric Co., Ltd, Tokyo, Japan; model number: MLR-351H) providing a temperature of 25 °C and a relative humidity of 60%. Daytime light intensity (3500 lx) was provided by neon tubes and, together with the light cycle (12:12 h light:dark), was similar in all three chambers. Each chamber was equipped with white LED lights (ribbon of LED SMD 5050, 6000–6500 K, Sysled, Madrid, Spain) on the ceiling to provide either a high intensity of light at night (20 lx, equivalent to the intensity of a street lamp; hereafter 'high ALAN' condition) or a low intensity of light at night (0.7 lx, equivalent to the intensity of a city skyglow, Bennie et al., 2016; hereafter 'low ALAN' condition). The emission spectrum of these LED lights, which was measured using a spectrometer (AvaSpec-3648 Fiber Optic Spectrometer, Avantes, Apeldoorn, Netherlands), is given in Appendix Fig. A1. These lighting systems were switched on in two of the three chambers, the third being used for the 'control' condition (0 lx, total darkness at night). We measured light intensities to the nearest 0.01 lx with an illuminance meter (T-10MA, Konica Minolta, Tokyo, Japan) before the experiment, and checked light intensity every time we switched light conditions between the thermostat-controlled chambers (see below). Light intensity in the chambers was measured inside the clear plastic boxes containing the insects during the experiments. We alternated the light conditions between chambers every 2 weeks to prevent any 'chamber effect'.

Experimental Set-up

We aimed to count the offspring produced by the wasps (exploiting host patches during the day and at night), as well as their feeding behaviour, daily. We therefore designed an experimental set-up to quantify egg laying and feeding activities while distinguishing between daytime and night-time activities. Host and food patches (see below) were placed on a Plexiglas plate in a standardized way ('bottom plate' in Appendix Fig. A2a). Right

above, the wasps were individually kept in clear plastic boxes on a white Plexiglas plate ('top plate' in Appendix Fig. A2b), which was drilled with holes exactly fitting into the location of the host and food patches on the bottom plate. A coarse mesh was stretched under the top plate to prevent the wasps from escaping through the holes (see Appendix Fig. A3). When the top plate was lowered, the wasps could feed and parasitize hosts through the mesh (Appendix Fig. A3b). The mesh had no effect on the wasp's ability to lay eggs or acquire food (E. Gomes, personal observation on 10 wasps, data not shown). The top plate was lifted (Appendix Fig. A3a) to replace food and host patches with new ones when needed (see further details in the Appendix).

Preparation of Host and Food Patches

Host patches consisted of 15 third-instar larvae in a petri dish (55 mm diameter) filled with semolina and covered by a piece of organza. They were prepared 7–10 days before they were used to allow the semolina to become impregnated with host kairomones.

Food patches were prepared by soaking cotton wool with 8 ml of sucrose solution (40%) in a petri dish (35 mm diameter). The sucrose solution was dyed blue with food dye (1% v/v), so we could easily determine whether the insects ate it by looking at the colour of their abdomen (see also in Desouhant et al., 2005). Food patches were prepared daily, just before their use in the experiment.

Effect of ALAN on Night-time Feeding Behaviour

Under the three night-time light conditions, the wasps had access to food either during the day or at night, alternately, followed by a 24 h period without food (see Table 1). This experimental design aimed to test whether the wasps fed during daytime or night-time when exposed to light. The 24 h period without food, as well as food provided either during the day or at night, was planned to prevent a state of satiety that would have prevented the wasps from feeding on the following days. We assessed food intake after each period during which wasps had access to food (i.e. at 2000 when food was available during the day and at 0800 when food was available during the night).

Effect of ALAN on Lifetime Reproductive Success and Reproductive Senescence

Our experimental design consisted of three 2-week experimental sessions, during which we recorded longevity and reproductive success of 74 wasps exposed to the three night-time light conditions ($N = 25$, 25 and 24 in the control, low ALAN and high ALAN conditions, respectively) to estimate reproductive senescence patterns as well as lifetime reproductive success.

For every experimental session, we took newly emerged wasps, and individually provided them with a new host patch every day (from 0800 to 2000) and every night (from 2020 to 0800 the next day) until death. There was a dark habituation period from 2000 to 2020, to prevent any behaviour due to the handling of the experimental set-up. Host larvae were concealed in the substrate (here,

wheat semolina), and in the low and high ALAN conditions, each host patch used during the night-time period was exposed to ALAN for 12 h. It was therefore assumed that ALAN had no consequences for hosts in our experiment. Age of death was recorded for each wasp, and those that were not yet dead after 2 weeks were integrated as censored individuals in the survival analysis ($N = 12$ of 74 wasps in total; there were three, two and seven censored wasps in the control, low ALAN and high ALAN conditions, respectively). Wasps were then kept at -20°C to measure their body size, because this trait can positively influence longevity and reproductive success in *V. canescens* (Pelosse et al., 2011). We measured the tibia length as a proxy of body size as commonly done in this species (e.g. Harvey & Vet, 1997). For each wasp, we took a picture of the left hind tibia under a binocular magnifier coupled with a camera and measured its length to the nearest 0.01 mm with the software Motic Image Plus 2.0 (Motic, Hong Kong). We also measured the egg load at death by counting the mature eggs under a microscope. There was no difference in egg load at death between light conditions (data not shown; mean egg load at death \pm SE = 86.7 ± 4.6). This means that potential differences in offspring production between light conditions were not due to egg limitation and variation in egg maturation during our experiments. We therefore used only body size as a covariate in analyses, to control for differences between individuals when assessing the effect of ALAN on lifetime reproductive success, longevity and reproductive senescence.

Each potentially parasitized host patch was kept in the rearing room (12:12 h light:dark, without light at night) and offspring emergences were counted for 7 weeks (see Offspring production throughout life span for a more detailed description). Classically, the development from egg to adult lasts 21 days in *V. canescens*. However, we extended the monitoring period because mother's night-time light condition, in interaction with mother's age, has been shown to prolong offspring development time by up to 60 days (Gomes et al., 2021). Overall, our experimental design allowed us to measure longevity and daily reproductive success of each wasp, distinguishing between daytime and night-time egg laying.

Offspring Production Throughout the Life Span

All host patches were monitored twice a week to count the daily offspring production throughout the wasps' life span as well as the total number of offspring per wasp. In addition, we also wanted to determine the development time of offspring depending on mother's age. For this purpose, we monitored the development time of offspring emerging from host patches parasitized by 1- 4-, 7- and 10-day-old wasps. We monitored the patches parasitized during both daytime and night-time. Offspring emerging from these patches were stored frozen dry at -20°C to measure their body size (see protocol in the paragraph above).

Ethical Note

The parasitoid wasp *V. canescens* is not under ethical regulation in Europe (Directive 2010/63) or in France. The experiments were nevertheless carried out in accordance with the three Rs principles for ethical animal experimentation. The use of live insects was obligatory, as the study focused on the behavioural responses to ALAN ('Replacement'). However, for the experiments, we used the minimal number of individuals necessary to obtain reliable and statistically robust results ('Reduction'). These numbers, given in the Methods, were based on previous experiments focusing on behaviours of *V. canescens*. In the laboratory, insects were housed in climate-controlled conditions and provided with food and hosts. During the behavioural experiments, the insects were handled in such a way as to minimize stress as far as possible. When insects had

Table 1
Schedule of the periods when the wasps were allowed to feed during a 2-week experimental session

Day	Daytime (0800 to 2000)	Night-time (2020 to 0800)
Day 0	Food	No food
Day 1	No food	Food
Day 2	No food	No food

This sequence of feeding (Day 0 to Day 2) was repeated until day 13.

to be killed at the end of the experiments, we used a method ensuring that death is instantaneous (freezing at -80°C ; 'Refinement').

Statistical Analysis

We performed the statistical analyses with R 4.0.2 (R Core Team, 2020). Throughout the statistical analyses, we used the packages *lme4* (Bates et al., 2014) and *nlme* (Pinheiro et al., 2019) to build linear models (LMs), generalized linear models (GLMs) and linear mixed models (LMMs).

For the analysis of night-time behaviours and lifetime reproductive success, we built GLMs in which, unless otherwise specified, we included body size, light condition and thermostat-controlled chamber, as well as their two-by-two interactions, as explanatory variables. From the full models, we used a backward model selection approach to select the best model. When needed, we computed post hoc comparisons between factor modalities using the package *emmeans* (Lenth, 2020). Cohen's *h* (Cohen, 1992) was computed to estimate effect sizes between proportions, using the *pwr* package (Champely, 2020). Magnitude of effect sizes was assessed according to the following thresholds: $|h| < 0.2$: negligible; $0.2 \leq |h| < 0.5$: small; $0.5 \leq |h| < 0.8$: medium; $|h| \geq 0.8$: large (Cohen, 1992).

Night-time feeding and egg-laying behaviours

To assess whether light condition influenced the wasps' night-time feeding and egg-laying behaviours, we fitted (quasi)binomial GLMs (logit link). For each wasp, we computed the proportion of nights with access to food during which the focal individual actually fed. With regard to the egg-laying behaviour, we analysed the proportion of wasps that exploited host patches at least one night with the binary variable 'Patch exploitation behaviour at night' ('Yes' or 'No') as response variable. As for night-time feeding, for each wasp, we also computed the proportion of nights on which the focal individual laid eggs during its lifetime. Daytime behaviours were not affected by light condition during the night because all females fed and laid eggs during the day.

Effect of ALAN on lifetime reproductive success

We analysed night-time reproductive success and daytime reproductive success (see definitions in Table 2) by fitting negative binomial GLMs (log link) that account for overdispersion in the data. Lifetime reproductive success (see Table 2) was also analysed with a negative binomial GLM (log link). Finally, we analysed the distribution of egg-laying events between day and night (see Table 2) by fitting a quasibinomial GLM (logit link). Two outliers (in terms of offspring number) were removed from the analyses.

Effect of ALAN on life span and reproductive senescence

We investigated the effect of light condition on life span using survival analysis (package *survival*; Therneau, 2015). We fitted Cox

proportional hazards models including light condition (factor with three modalities, 'Control', 'Low ALAN' and 'High ALAN'), body size and thermostat-controlled chamber (factor with three modalities, 'Chamber1', 'Chamber2' and 'Chamber3'), as well as their two-by-two interactions as explanatory variables. We selected the best model based on the Akaike information criterion (AIC). When models had a ΔAIC (i.e. difference between their AIC and the AIC of the best model) lower than 2, we selected the simplest model to satisfy parsimony rules (Burnham & Anderson, 2002). The full list of fitted Cox models is provided in Appendix Table A1. We used the package *rms* (Harrell, 2021) to compute post hoc comparisons between factor modalities in the best Cox model selected.

We tested the effect of light condition on reproductive senescence using three reproductive traits: the daily reproductive success, offspring quality and offspring development time (log-transformed to meet the assumption of normality; see Table 2). Age-related changes in these traits were assessed by building LMMs with the daily number of offspring, offspring body size or offspring development time as response variable, and mother's age and light condition, as well as their interaction, as explanatory variables. For the daily number of offspring, we compared three types of age function: linear, quadratic and threshold. For the threshold function, the threshold value was determined by fitting a piecewise regression over a range of values between 1 and 14 days of age and selecting the value that gives the lowest residual deviance (Ulm & Cox, 1989). The best model selected had a threshold value set at 5 days. For offspring quality and development time, individuals whose mothers were 7 or 10 days old were grouped into the same age class of '7+ days' because of small sample sizes, leading to three age classes. Age was therefore included as a factor (with three modalities, '1 day', '4 days' and '[7–10] days') in the models for these two response variables. Mother's identity was included in all the models as a random effect to account for confounding effects of pseudoreplication (*sensu* Hurlbert, 1984). Mother's longevity was also included as a fixed effect to control for selective disappearance (e.g. if 'low-quality' individuals with a low reproductive success die younger, causing older age classes to have a high reproductive success; Nussey et al., 2008). Finally, the total number of offspring produced was included as a covariate in the models for offspring body size and development time, to account for the potential trade-off between offspring quantity and quality (Berrigan, 1991; Godfray et al., 1991). The number of offspring for each mother's age and light condition is given in Table 3, as well as the number of females by which these offspring were produced.

As for Cox models, we selected the best model for daily reproductive success based on AIC. The full list of fitted models for daily reproductive success is provided in Appendix Table A2. For offspring quality and development time, the statistical significance of explanatory variables was based on the *F* statistic with adjusted degrees of freedom (following Kenward & Roger, 1997).

Table 2

Definition of the variables used to assess the effects of artificial light at night on lifetime reproductive success, life span and reproductive senescence in our study

Name	Definition
Night-time reproductive success	Total number of offspring that emerged from all the host patches exploited during the night throughout a wasp's life
Daytime reproductive success	Total number of offspring that emerged from all the host patches exploited during the day throughout a wasp's life
Lifetime reproductive success	Total number of offspring produced from daytime and night-time host patches added together
Distribution of egg-laying events between day and night	Relative proportion of daytime and night-time reproductive success in lifetime reproductive success
Life span	Age at death
Daily reproductive success	Daily number of offspring produced from daytime and night-time host patches added together
Offspring quality	Body size, estimated using tibia length (mm) as a proxy
Offspring development time	Number of days between egg laying and offspring emergence

Table 3
Total number of offspring in each cross-modality of artificial light at night (ALAN) condition and mother's age

		Mother's age		
		1 day	4 days	[7–10] days
Light condition	Control	121 (22)	17 (5)	12 (4)
	Low ALAN	98 (26)	12 (9)	10 (2)
	High ALAN	100 (21)	31 (12)	9 (5)

The number of mothers is given in parentheses.

RESULTS

Night-time Feeding and Egg-laying Behaviours

Light conditions influenced the percentage of nights with access to food during which the wasps fed ($F_{2,66} = 3.78$, $P = 0.03$), which were, on average, 63%, 51% and 81% in the control, low and high ALAN conditions, respectively (Fig. 1). Post hoc tests showed that the only significant difference was between low and high ALAN conditions ($z = 2.80$, $P = 0.02$) with a biological difference considered as medium (effect size: Cohen's $h = 0.65$; Fig. 1). However, the effect size between control and high ALAN conditions (Cohen's $h = 0.43$) suggested that the difference, albeit not statistically significant (post hoc test: $z = 1.96$, $P = 0.10$), was also moderately biologically relevant.

With regard to the night-time egg-laying behaviour, light condition influenced the percentage of wasps that exploited host patches (i.e. that have had offspring) at least one night: 76%, 80% and 100% in the control, low and high ALAN conditions, respectively ($\chi^2_2 = 9.38$, $P = 0.009$). Effect sizes suggested a strong effect of the high ALAN condition compared to the control (Cohen's $h = 1$) and low ALAN (Cohen's $h = 0.95$) conditions. However, light condition had no effect on the percentage of nights on which the wasps laid eggs during their lifetime ($F_{2,67} = 0.30$, $P = 0.74$), which were, on average, about 33%, 33% and 40% in the control, low and high ALAN conditions, respectively.

Effect of ALAN on Lifetime Reproductive Success

Daytime reproductive success was not statistically different between light conditions ($\chi^2_2 = 1.03$, $P = 0.60$; Fig. 2). However,

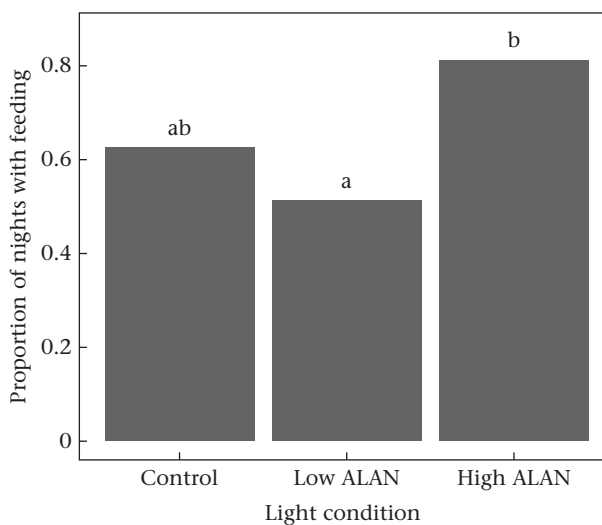


Figure 1. Proportion of nights with access to food during which wasps fed, for the control and artificial light at night (ALAN) conditions. Different letters show a significant statistical difference at the 0.05 level.

there was a tendency for light condition to influence the night-time reproductive success ($\chi^2_2 = 4.37$, $P = 0.11$; Fig. 2). The mean night-time reproductive success almost doubled between control and high ALAN conditions (3.96 ± 1.03 and 7.22 ± 1.06 offspring on average, respectively), and between low and high ALAN conditions (3.96 ± 0.82 and 7.22 ± 1.06 offspring on average, respectively).

When considering the overall lifetime reproductive success, no influence of light condition was detected ($\chi^2_2 = 2.27$, $P = 0.32$). Only body size had a positive effect on the total number of offspring produced throughout a wasp's life ($\chi^2_1 = 3.90$, $P = 0.05$). However, light condition influenced the respective contribution of daytime and night-time reproductive success to lifetime reproductive success ($F_{2,65} = 2.63$, $P = 0.08$). Offspring coming from host patches exploited during night-time represented, on average, 23% ($\pm 5\%$), 26% ($\pm 5\%$) and 41% ($\pm 4\%$) of the total number of offspring for the females in the control, low ALAN and high ALAN conditions, respectively (Fig. 3). Post hoc tests showed that only the difference between high ALAN and control conditions was significant ($z = -2.60$, $P = 0.03$), but with a small effect size (Cohen's $h = 0.29$).

Effect of ALAN on Life Span and Reproductive Senescence

Life span

While low and high ALAN conditions did not influence the life span in *V. canescens* compared to the control condition (Table 4, Fig. 4), contrast analysis showed that the difference in life span between the low and high ALAN conditions was significant ($z = 2.5$,

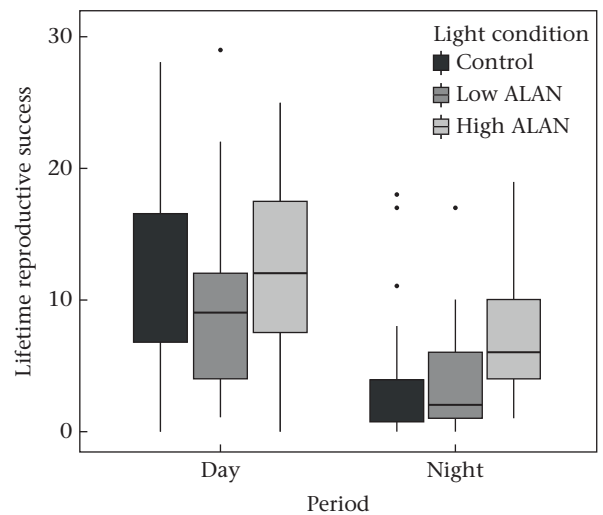


Figure 2. Lifetime reproductive success, estimated by the total number of offspring emerging from the host patches exploited either during the day or at night throughout the life of the wasps, for the control and artificial light at night (ALAN) conditions. The boxes represent the interquartile range (IQR) between the first quartile (Q1) and the third quartile (Q3), and the vertical lines below and above the boxes extend to the smallest ($Q1 - 1.5 \times IQR$) and largest ($Q3 + 1.5 \times IQR$) values, respectively. The box plot black lines represent the median lifetime reproductive success, and outliers are displayed as points.

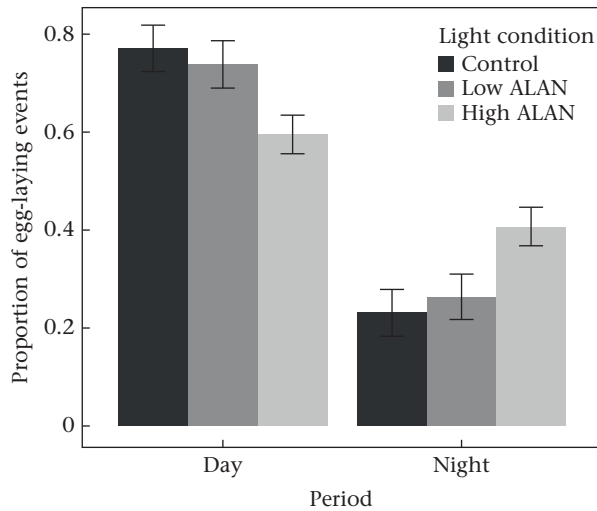


Figure 3. Proportion of egg-laying events that occurred during the day and during the night, illustrating the respective contribution of daytime and night-time reproductive success to lifetime reproductive success for control and artificial light at night (ALAN) conditions.

$P = 0.01$). The median longevity was 4.3 (95% confidence interval, CI = [2.9 ; 7.4]), 2.9 (95% CI = [2.9 ; 4.3]) and 6.2 (95% CI = [4.3 ; NA]) days in the control, low ALAN and high ALAN conditions, respectively. Body size also had a significant effect on the wasps' longevity, with a larger body size reducing the risk of death by a factor of 0.01 (Table 4).

Reproductive senescence

The best model selected to describe the changes in daily reproductive success with age included only a linear effect of age and no significant effect of light at night (Table 5, Fig. 5a).

Offspring size was not influenced by either mother's age ($F_{2,373} = 1.40$, $P = 0.25$) or light condition ($F_{2,63.5} = 0.75$, $P = 0.48$; Appendix Fig. A4). In contrast, the effect of light condition on offspring development time depended on mother's age ($F_{4,332.5} = 8.67$, $P < 0.01$). More precisely, for offspring whose mothers were in the '7+' age group, individuals in the control condition took significantly longer to develop than those in the low ALAN condition (about 9 days longer on average; post hoc test: $t = 4.0$, $P < 0.01$; Fig. 5b). However, the difference in development time was not significant between individuals in the control and high ALAN conditions (about 6 days on average; post hoc test: $t = 1.85$, $P = 0.16$), and only marginally significant between individuals in the low and high ALAN conditions (about 2 days on average; post hoc test: $t = -2.38$, $P = 0.05$). For offspring from both 1-day-old and 4-day-old mothers, there were no significant differences in development time between light conditions.

DISCUSSION

Our study highlights that the diurnal wasps, when exposed to ALAN, were able to use the 'night-light niche' as illustrated by the increase in feeding and egg-laying activity at night in exposed

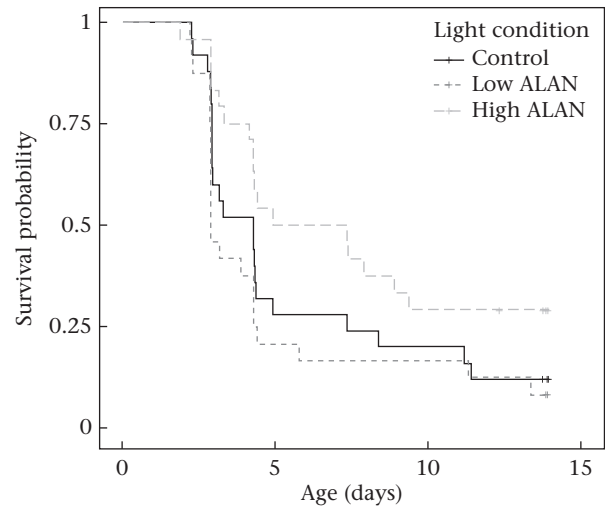


Figure 4. Survival curves for the control, low artificial light at night (ALAN) and high ALAN conditions.

individuals. However, the night-time activity induced by ALAN did not affect the wasps' lifetime reproductive success. We nevertheless detected that ALAN influenced the distribution of egg-laying events, by increasing the contribution of night-time reproductive success to lifetime reproductive success. Moreover, our results suggested that reproductive senescence occurs in *V. canescens* and is modulated by the degree of light exposure during the night when focusing on offspring development time.

Presence of ALAN led *V. canescens* females to use the 'night-light niche'. This phenomenon had rarely been reported and quantified in insect species until recently. A recent study showed that parasitism rate of an aphid parasitoid (*Aphidius megourae*) almost doubled when individuals were exposed to low levels of light at night (between 0.1 and 5 lx; Sanders et al., 2018). The authors also showed that *A. megourae* did not attack hosts during the night in the absence of ALAN. Another study on *A. megourae* showed that ALAN, as well as longer daylength, increased the daily parasitoid parasitism rate (Kehoe et al., 2020).

However, most of the studies did not differentiate between daytime and night-time parasitism activity in the light-polluted conditions. Even though a study showed that *V. canescens* did not move in the dark (Gomes et al., 2021), in our control condition wasps fed and laid eggs during the night despite the absence of light. This 'overestimation' of nocturnal activity in the control condition (which could lead to an underestimation of the effect of ALAN) may be due to the easy access to both food and hosts in our experimental set-up, whereas in field conditions, resources may be more difficult to reach in the dark, because the wasps use habitat structure to navigate (Desouhant et al., 2003). Nectar can be produced at night (Antoñ et al., 2017), and visual cues are involved in foraging in *V. canescens*, with wasps being capable of associative learning between colour cues and a food or host reward (Desouhant, Navel, et al., 2010; Lucchetta et al., 2008). Such visual cues probably increase the efficiency of females for finding hosts or

Table 4
Semiparametric Cox proportional hazards (PH) model selected for the longevity data

Type	Variable	Coefficient \pm SE (hazard ratio)	z	P
Semiparametric Cox PH	Body size	-4.89 ± 1.3 (0.01)	-3.8	<0.01
	Light condition (Low ALAN)	0.47 ± 0.3 (1.46)	1.5	0.13
	Light condition (High ALAN)	-0.35 ± 0.3 (0.67)	-1.1	0.29

The best model was selected based on the Akaike information criterion (AIC). The full list of fitted models is provided in Appendix Table A1.

Table 5

Linear mixed-effects model selected for investigating the senescence pattern in daily reproductive success

Trait	Age function	Variable	Parameter estimate \pm SE	<i>t</i>
Daily number of offspring	Linear	Age	-0.38 \pm 0.04	-9.74

The best model was selected based on Akaike Information Criterion (AIC). The full list of fitted models is provided in [Appendix Table A2](#).

food, but their use in the absence of light might be less efficient. Conversely, temperature was held constant between day and night in our experiment, which could have exacerbated the consequences of ALAN for parasitoid activity. Indeed, [Kehoe et al. \(2020\)](#) showed that a drop in night-time temperatures can moderate the effect of ALAN on parasitism rate. Further experiments combining temperature variation and exposure to light at night should clarify how ALAN and temperature interact to regulate lifetime reproductive success. This will also allow a better understanding of potential cocktail effects of anthropogenic disturbances.

Changes in activity patterns may have consequences for lifetime reproductive success. In *V. canescens*, lifetime reproductive success was not affected by ALAN, despite changes in feeding behaviour, intensification of night-time egg-laying behaviour and differences in life span. Surprisingly, wasps exposed to high ALAN lived longer than those exposed to low ALAN in our experiment, which may be linked to the observed increase in night-time feeding. Light at night has been shown to modify food intake in vertebrates, but also to cause various metabolic disorders (e.g. weight gain, lipid accumulation in the liver, impaired glucose tolerance; [Batra et al., 2019](#); [Fleury et al., 2020](#); [Fonken et al., 2010](#); [Masís-Vargas et al., 2019](#)). Even though we did not detect a negative effect of ALAN on the life span of *V. canescens* in our study, changes in the timing of feeding and potential metabolism alterations due to light at night may affect fitness, and more specifically reproductive traits ([Xu et al., 2011](#)). Daytime reproductive success was not statistically different between light conditions, and there was only a tendency for ALAN to increase the night-time reproductive success. This tendency was nevertheless supported by a shift in the distribution of egg-laying events between day and night for the wasps exposed to ALAN. One way to confirm or invalidate this tendency could be to provide more hosts to the wasps to allow a greater variability in the number

of offspring produced and therefore detect clear differences in the reproductive success of *V. canescens* between light conditions. Several studies have assessed the fitness differences under various regimes of light at night in the laboratory, with various outcomes. In *Drosophila melanogaster*, a species that has an optimal oviposition behaviour at dusk or early night, chronic exposure to dim light at night significantly reduced (by 20%) the proportion of ovipositing females and the number of eggs laid ([McLay et al., 2017](#)). A subsequent study showed that the negative consequences of light at night persisted as females aged ([McLay et al., 2018](#)), confirming the probable fitness costs of ALAN in this species. However, some species seem to benefit from the presence of light at night, such as the diurnal lizard *Anolis sagrei*. In this species often found in urbanized habitats, females exposed to ALAN increased their reproductive output by laying more eggs at a higher rate, without cost in terms of offspring quality ([Thawley & Kolbe, 2020](#)). Using mesocosms, a recent field experiment demonstrated that the performance of the parasitoid *A. megourae* decreased markedly in the long term in the presence of ALAN, suggesting that the wasps did not use the ‘night-light niche’ (even though it was not explicitly tested there) and might have impaired host-finding abilities ([Sanders et al., 2022](#)). Interestingly, the consequences of ALAN for parasitoid fitness depended on the light wavelength. While a previous study on *A. megourae* found that low levels of ALAN from cool white LEDs extended parasitoid activity and increased their efficiency ([Sanders et al., 2018](#)), ALAN from monochromatic LEDs decreased parasitoid efficiency for specific light colours (e.g. purple, blue, green and yellow), but not for others (e.g. red; [Sanders et al., 2022](#)). Regarding the LED lights used in our study, there was a peak in blue wavelengths (i.e. between 400 and 450 nm, [Fig. A1](#)), which is typical of the emission spectrum of cool white LEDs ([Elvidge et al., 2010](#)). This feature may have modified the perception of the blue-dyed food in our experimental set-up (although note that there is no innate attraction for blue colour in *V. canescens*, [Lucchetta et al., 2008](#)). However, as the spectral sensitivity of the visual system of *V. canescens* is unknown, we cannot yet predict whether this would change the foraging behaviour of the insects, and in which way. Future studies should therefore take both daytime and night-time behaviours, as well as light wavelengths, into account to fully comprehend the fitness consequences of ALAN for insects.

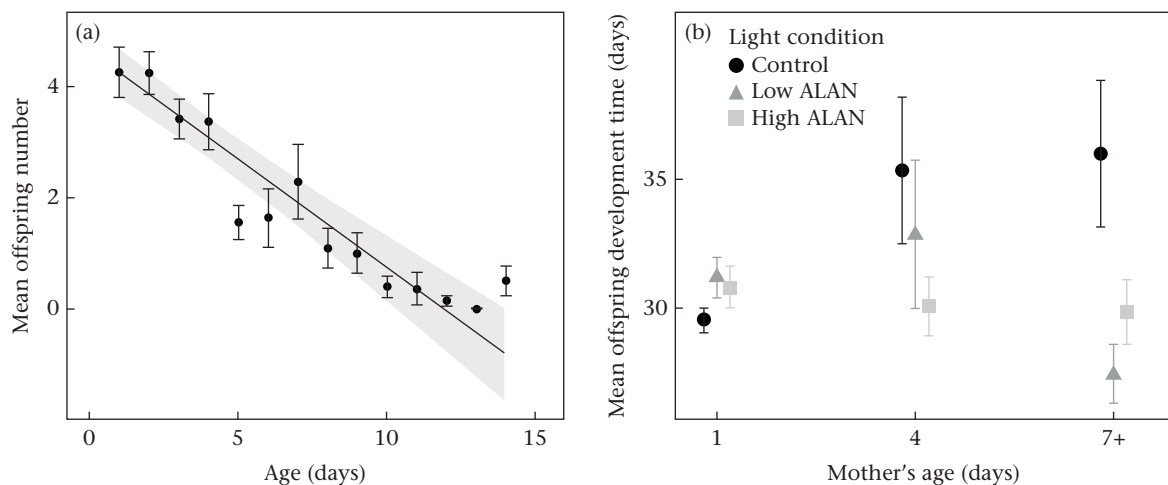


Figure 5. (a) Age-related changes in reproductive traits in *V. canescens*. The points represent the average number of offspring produced per age and the bars correspond to the standard error. The line represents the prediction from the best selected model (linear effect of age) and the shaded area the 95% confidence interval. (b) Effect of mother's age on offspring development time in the control, low artificial light at night (ALAN) and high ALAN conditions. Individuals older than 7 days of age were grouped into the ‘7+’ age class. Symbols represent mean \pm SE.

As in a number of other insect species (e.g. the cockroach *Nau-phoeta cinerea*, Moore & Moore, 2001; fruit flies, Carey & Molleman, 2010), we detected changes in reproductive performance with mother's age in *V. canescens*. However, only age-related changes in offspring development time were impacted by ALAN. Specifically, offspring development time was negatively correlated with mother's age for mothers that had been exposed to low ALAN. A previous study had found an interaction between mother's age and mother's light condition on offspring development time, but in the opposite direction (Gomes et al., 2021). Even though these results may at first appear contradictory, they arose from different experimental conditions. In the previous study, older females had no oviposition experience, in contrast to our experiment. In *V. canescens*, egg maturation occurs throughout the life of the wasps (Jervis et al., 2001). Therefore, patch exploitation activity and presence of ALAN could have altered the quality of the eggs produced by the females. These eggs do not contain energy reserves (Le Ralec, 1995), but other substances such as hormones (e.g. melatonin whose synthesis can be influenced by ALAN, Grubisic et al., 2019) could be maternally transmitted to the offspring. Moreover, although a decrease in development time did not seem to impact offspring quality (estimated by the body size of the offspring at emergence) in our study, this consequence of ALAN may affect other offspring fitness-related traits (e.g. storage of energy reserves, physiological condition) that would be relevant to explore in the future. Nevertheless, evidence of relationships between light at night and reproductive senescence is rare. A study on *D. melanogaster* found that exposure to light at night influenced (nonlinearly) age-related declines in the propensity to lay eggs and the number of eggs produced by females (McLay et al., 2018). More studies are needed to determine relationships between light at night, reproductive senescence and potential underlying mechanisms.

Even though ALAN is known to have multiple and pronounced detrimental consequences for individuals and populations (Boyes et al., 2021; Gaston et al., 2014), recent studies have also highlighted positive effects of light at night on important biological traits at the individual level (e.g. McLay et al., 2018) or on species interactions. For instance, despite an overall negative effect on diurnal plant–pollinator interactions during daytime, Giavi et al. (2021) observed increased plant–pollinator interactions under light at night for a few plant species, which can be beneficial. In our study, although we did not detect strong detrimental or beneficial consequences of ALAN for the lifetime reproductive success of *V. canescens*, we did observe behavioural changes when the wasps were exposed to ALAN. These changes (i.e. feeding and laying eggs at night) could result in a shift in the distribution of ovipositions between day and night for wasps which, in natural conditions, could become more vulnerable to predation or experience suboptimal conditions for the exploitation of hosts. Behavioural changes induced by ALAN may therefore have major consequences for population dynamics and need to be explored further.

Author Contributions

Elisa Gomes: Conceptualization, Methodology, Formal Analysis, Investigation, Writing- Original draft, Writing – Review & editing; **Jean-François Lemaître:** Formal analysis, Writing – Review & editing; **Valentina Rodriguez-Rada:** Investigation; **François Débias:** Resources; **Emmanuel Desouhant:** Conceptualization, Methodology, Writing – Review & editing, Funding acquisition; **Isabelle Amat:** Conceptualization, Methodology, Writing – Review & editing, Funding acquisition.

Data Availability

The data supporting this article are provided as [Supplementary material](#).

Declaration of Interest

The authors declare no competing or financial conflict of interest.

Acknowledgments

We thank Marc Théry for lending the illuminance meter and dedicate this work to him. We also thank Gilles Ledoux from the 'Institut Matière Lumière' (IML, University Claude Bernard Lyon 1) for measuring the emission spectrum of the LED lights. This work was funded by IDEXLyon (Scientific Breakthrough project) and is part of the project 'ALAN One Health' funded by the University Claude Bernard Lyon 1.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.01.025>.

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Appendix

In the evening, before the end of the photophase, the top plates were lifted to stop the wasps from accessing the patches. Host patches were replaced with new ones, and food patches were provided or removed, depending on the day (see Table 1). The mesh under the top plate was also changed to remove any odour deposited by the wasps during the day or kairomone and food residues. Twenty minutes after the end of the photophase, the top plates were gently lowered so that the wasps could start feeding and exploiting host patches. In the morning, access to host and food was prevented just before the onset of the photophase by lifting the top plate again. The host patches and the mesh were replaced by new ones, and food patches were provided or removed, depending on the day. We checked whether the wasps fed during the night by looking at the colour of their abdomen. Host and food were made available again for the wasps at the same time in each light condition.

Table A1

Set of Cox models fitted to assess the effect of artificial light at night on life span in *V. canescens*

Model ID	LC	BS	TC	LC*BS	LC*TC	BS*TC	AIC	ΔAIC	Weight
9	+	+	+	NA	+	NA	431.73	0.00	0.32
12	+	+	NA	NA	NA	NA	431.88	0.15	0.30
15	NA	+	NA	NA	NA	NA	434.21	2.48	0.092
11	+	+	+	NA	NA	NA	434.33	2.60	0.087
4	+	+	+	NA	+	+	435.38	3.65	0.051
3	+	+	+	+	+	NA	435.69	3.96	0.044
6	+	+	NA	+	NA	NA	435.86	4.13	0.041
7	+	+	+	NA	NA	+	437.25	5.52	0.020
13	NA	+	+	NA	NA	NA	437.42	5.69	0.019
5	+	+	+	+	NA	NA	438.22	6.49	0.012
1	+	+	+	+	+	+	439.35	7.62	<0.01
8	NA	+	+	NA	NA	+	440.03	8.30	<0.01
2	+	+	+	+	+	+	441.03	9.30	<0.01
10	+	NA	+	NA	+	NA	442.08	10.35	<0.01
16	+	NA	NA	NA	NA	NA	444.11	12.37	<0.01
18	NA	NA	NA	NA	NA	NA	446.40	14.67	<0.01
14	+	NA	+	NA	NA	NA	447.33	15.60	<0.01
17	NA	NA	+	NA	NA	NA	450.25	18.52	<0.01

We tested the effect of light condition (LC), body size (BS) and thermostat-controlled chamber (TC), as well as their two-by-two interactions (LC*BS, LC*TC, BS*TC). The symbol + means that the focal parameter is present in the model and NA means that the focal parameter is absent from the model. ΔAIC is the difference in the Akaike information criterion (AIC) between each model and the model with the lowest AIC and weight is the AIC weight of each model. The best model selected is shown in bold.

Table A2Set of models fitted to assess the senescence pattern of daily reproductive success in *V. canescens*

Model ID	LC	Age function	LC*A	BS	LG	AIC	ΔAIC	Weight
213	NA	AL	NA	+	NA	2154.63	0.00	0.50
24	NA	AL	NA	NA	NA	2156.06	1.43	0.25
182	+	AL	NA	+	NA	2157.19	2.55	0.14
19	+	AL	NA	NA	NA	2158.79	4.16	0.06
181	NA	AL	NA	+	+	2160.63	5.99	0.03
21	NA	AL	NA	NA	+	2162.28	7.65	0.01
2	+	AL	NA	+	+	2162.99	8.35	<0.01
17	+	AL	NA	NA	+	2164.88	10.25	<0.01
141	+	AL	+	+	NA	2166.62	11.98	<0.01
143	+	AL	+	NA	NA	2168.20	13.57	<0.01
14	+	AL	+	+	+	2172.36	17.73	<0.01
142	+	AL	+	NA	+	2174.26	19.63	<0.01
40	NA	AQ	NA	+	NA	2178.20	23.57	<0.01
44	NA	AQ	NA	NA	NA	2179.22	24.59	<0.01
381	+	AQ	NA	+	NA	2181.14	26.50	<0.01
60	NA	AT	NA	+	NA	2182.22	27.59	<0.01
39	+	AQ	NA	NA	NA	2182.30	27.67	<0.01
38	NA	AQ	NA	+	+	2182.80	28.17	<0.01
64	NA	AT	NA	NA	NA	2183.13	28.49	<0.01
41	NA	AQ	NA	NA	+	2184.37	29.74	<0.01
59	+	AT	NA	+	NA	2185.26	30.63	<0.01
4	+	AQ	NA	+	+	2185.44	30.81	<0.01
58	NA	AT	NA	+	+	2185.73	31.10	<0.01
62	+	AT	NA	NA	NA	2186.29	31.66	<0.01
37	+	AQ	NA	NA	+	2187.22	32.58	<0.01
61	NA	AT	NA	NA	+	2187.25	32.62	<0.01
6	+	AT	NA	+	+	2188.49	33.86	<0.01
57	+	AT	NA	NA	+	2190.21	35.57	<0.01
542	+	AT	+	+	NA	2193.47	38.83	<0.01
541	+	AT	+	NA	NA	2194.50	39.86	<0.01
54	+	AT	+	+	+	2196.65	42.02	<0.01
543	+	AT	+	+	+	2198.35	43.72	<0.01
342	+	AQ	+	+	NA	2201.28	46.64	<0.01
341	+	AQ	+	NA	NA	2202.45	47.81	<0.01
34	+	AQ	+	+	+	2205.52	50.89	<0.01
343	+	AQ	+	NA	+	2207.32	52.68	<0.01
211	NA	NA	NA	+	+	2221.45	66.82	<0.01
22	NA	NA	NA	NA	+	2223.13	68.50	<0.01
18	+	NA	NA	+	+	2224.17	69.54	<0.01
20	+	NA	NA	NA	+	2226.04	71.41	<0.01
25	NA	NA	NA	+	NA	2233.58	78.94	<0.01
212	+	NA	NA	+	NA	2236.10	81.47	<0.01
23	+	NA	NA	NA	NA	2237.40	82.76	<0.01

We tested the effect of light condition (LC), three age functions (linear AL, quadratic AQ, threshold set at 5 days AT), the interaction between light condition and age (LC*A), body size (BS) and individual longevity (LG). The symbol + means that the focal parameter is present in the model and NA means that the focal parameter is absent from the model. ΔAIC is the difference in the Akaike information criterion (AIC) between each model and the model with the lowest AIC and weight is the AIC weight of each model. The best model selected is shown in bold.

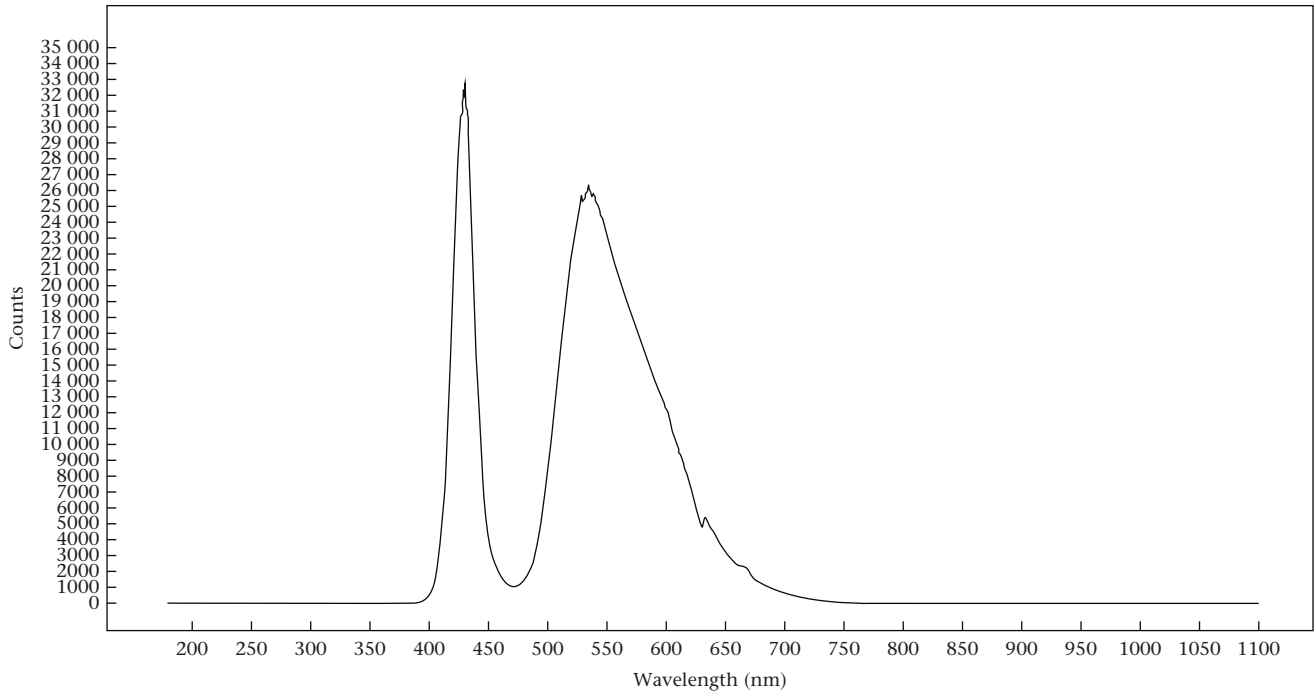


Figure A1. Emission spectrum of the LED lights used in the study.

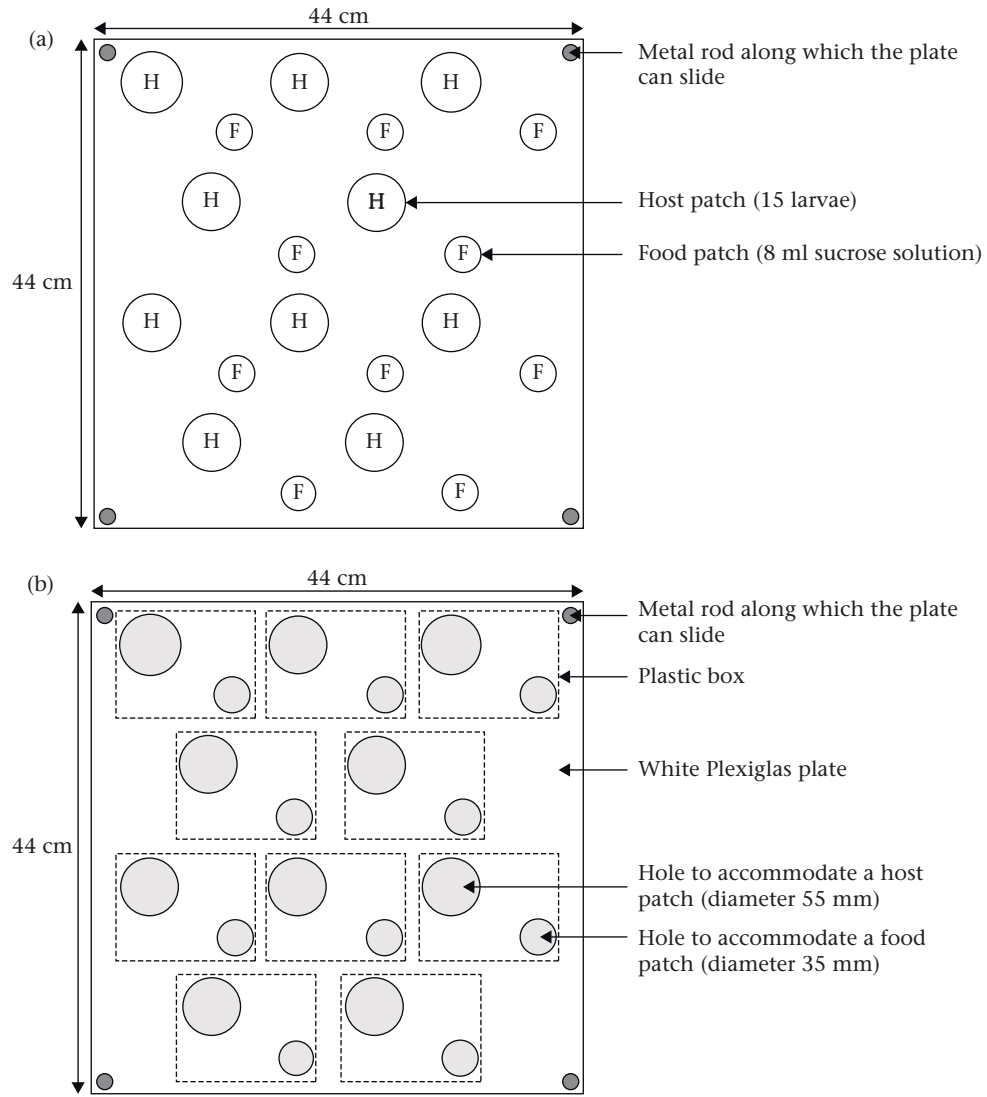


Figure A2. Diagram of the experimental set-up designed to measure the lifetime reproductive success of *V. canescens* (top view). (a) The bottom plate. (b) The top plate, with grey areas indicating empty zones (i.e. holes).

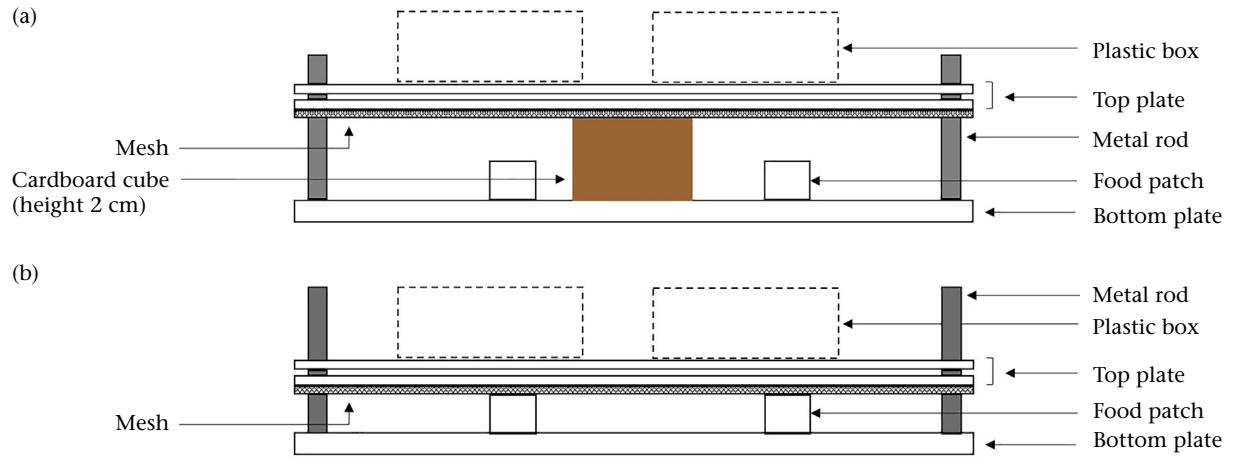


Figure A3. Diagram of the experimental set-up designed to measure the lifetime reproductive success in *V. canescens* (side view). (a) The top plate in the lifted position, which prevents the wasps accessing the food and host patches. (b) The top plate in the lowered position, which enables the wasps to feed and parasitize host patches (not shown on the diagram).

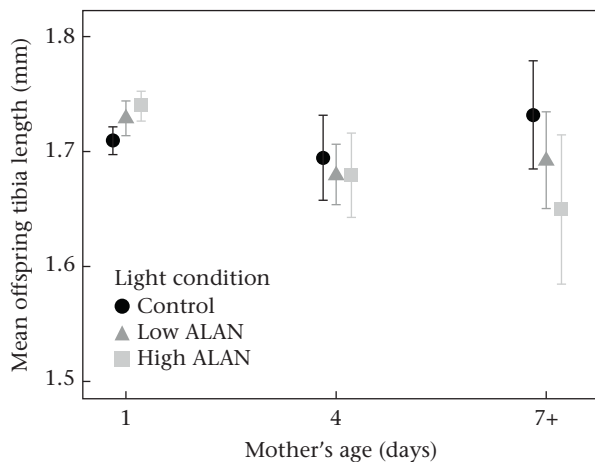


Figure A4. Effect of mother's age on offspring body size in the control, low artificial light at night (ALAN) and high ALAN conditions. Individuals older than 7 days of age were grouped into the '7+' age class. Symbols represent mean \pm SE.