A peer-reviewed version of this preprint was published in PeerJ on 9 October 2018.

View the peer-reviewed version (peerj.com/articles/5599), which is the preferred citable publication unless you specifically need to cite this preprint.

Willmott NJ, Henneken J, Selleck CJ, Jones TM. 2018. Artificial light at night alters life history in a nocturnal orb-web spider. PeerJ 6:e5599
https://doi.org/10.7717/peerj.5599
Artificial light at night alters life history in a nocturnal orb-web spider

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The prevalence of artificial light at night (ALAN) is increasing rapidly around the world. The potential physiological costs of this night lighting are often evident in life history shifts. We investigated the effects of chronic night-time exposure to ecologically relevant levels of LED lighting on the life history traits of the nocturnal Australian garden orb-web spider (Eriophora biapicata). We reared spiders under a 12-hour day and either a 12-hour natural darkness (~0 lux) or a 12-hour dim light (~20 lux) night and assessed juvenile development, growth and mortality, and adult reproductive success and survival. We found that exposure to ALAN accelerated juvenile development, resulting in spiders progressing through fewer moults, and maturing earlier and at a smaller size. There was a significant increase in daily juvenile mortality for spiders reared under 20 lux, but the earlier maturation resulted in a comparable number of 0 lux and 20 lux spiders reaching maturity. Exposure to ALAN also considerably reduced the number of eggs produced by females, largely associated with ALAN-induced reductions in body size. Despite previous observations of increased fitness for some orb-weavers in urban areas and near night lighting, it appears that exposure to artificial night lighting may lead to considerable developmental costs. Future research will need to consider the detrimental effects of ALAN combined with foraging benefits when studying nocturnal insectivores that forage around artificial lights.
Artificial light at night alters life history in a nocturnal orb-web spider

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13 ABSTRACT

14 The prevalence of artificial light at night (ALAN) is increasing rapidly around the world. The potential physiological costs of this night lighting are often evident in life history shifts. We investigated the effects of chronic night-time exposure to ecologically relevant levels of LED lighting on the life history traits of the nocturnal Australian garden orb-web spider (*Eriophora biapicata*). We reared spiders under a 12-hour day and either a 12-hour natural darkness (~0 lux) or a 12-hour dim light (~20 lux) night and assessed juvenile development, growth and mortality, and adult reproductive success and survival. We found that exposure to ALAN accelerated juvenile development, resulting in spiders progressing through fewer moults, and maturing earlier and at a smaller size. There was a significant increase in daily juvenile mortality for spiders reared under 20 lux, but the earlier maturation resulted in a comparable number of 0 lux and 20 lux spiders reaching maturity. Exposure to ALAN also considerably reduced the number of eggs produced by females, largely associated with ALAN-induced reductions in body size. Despite previous observations of increased fitness for some orb-weavers in urban areas and near night lighting, it appears that exposure to artificial night lighting may lead to considerable developmental costs. Future research will need to consider the detrimental effects of ALAN combined with foraging benefits when studying nocturnal insectivores that forage around artificial lights.

31 Keywords: orb-web spider; life history; artificial light at night; development; urbanisation
INTRODUCTION

The spread of artificial light at night (ALAN) is increasing rapidly around the globe and its presence has been linked to shifts in physiological and behavioural traits in animals (Gaston et al., 2013; Longcore & Rich, 2004). Exposure to ALAN is directly linked to changes in key life history traits, including variation in patterns of juvenile growth (Brüning et al., 2011), reductions in immune function (Bedrosian et al., 2011; Durrant et al., 2015), survival (Shah et al., 2011) and fecundity (McLay et al., 2017), as well as shifts in reproductive behaviours (Firebaugh & Haynes, 2016; McLay et al., 2017; van Geffen et al., 2014, 2015). Indirectly, where exposure to night lighting stimulates earlier maturation and smaller adult size, there may be reproductive costs due to poorer male performance (Elgar & Jones, 2008; van Geffen et al., 2014) and reduced female fecundity (Honěk & Honek, 1993; van Geffen et al., 2014). Adults that emerge earlier may benefit if this extends their potential breeding period and thus increases offspring production (Lowe et al., 2014; Schneider & Elgar, 2002). However, each sex may respond differently to the presence of ALAN, and maturation time for males and females could desynchronise (Dominoni et al., 2013; van Geffen et al., 2014).

A potential underlying mechanism for these life history shifts is that the presence of ALAN may simulate a longer day and/or mask daily and seasonal patterns of light. Changes in natural lighting drive a multitude of daily and seasonal biological rhythms, including reproduction (Nelson et al., 2010; Tauber et al., 1986), and thus ALAN may have serious consequences for juvenile development and reproductive maturation (McLay et al., 2017; Shah et al., 2011; van Geffen et al., 2014). For species that exhibit seasonal diapause or overwintering (Schaefer, 1987; Shah et al., 2011; van Geffen et al., 2014), disruption by ALAN (simulating long-day photoperiods that naturally suppress diapause; Nylin & Gotthard, 1998) can result in earlier
maturation (van Geffen et al., 2014) and may increase mortality (Shah et al., 2011). However, there is variation in these patterns across taxa, as development time may also be shortened in vertebrate species that do not exhibit diapause (Brüning et al., 2011; Dominoni et al., 2013). This suggests the effects of ALAN on life history depend on species specific physiological and life history traits.

The detrimental effects of ALAN are potentially exacerbated if animals are attracted to artificial lights. Many species exhibit positive phototaxis (for example, attraction towards natural moonlight or light reflecting off water bodies), which is an adaptive trait facilitating behaviours such as navigation (Minnaar et al., 2015; van Langevelde et al., 2011) or foraging site choice (Heiling, 1999; Rydell, 1992). For these species, ALAN may act as an ecological trap (sensu, Hale & Swearer, 2016) resulting in individuals settling in poor quality habitats (Gerhard Eisenbeis & Hänel, 2009; Gaston et al., 2012; Longcore & Rich, 2004). Conversely, nocturnal insectivores may gain direct benefits if they forage around artificial lights because increased prey densities around these lights facilitates increased foraging success (Adams, 2000; Heiling & Herberstein, 1999; Lacoeuilhe et al., 2014). However, while research demonstrates that insectivores (in particular) may gain foraging benefits from the presence of ALAN the potential physiological costs of ALAN are largely unstudied.

Spiders are an ideal taxon for investigating the relative ecological costs and benefits of the presence of ALAN. Simulated long-day photoperiods may induce shifts in a spider’s maturation period, reducing the number of juvenile instars (Miyashita & Department, 1987; Nylin & Gotthard, 1998; Schaefer, 1987); a pattern that likely varies with species and life history stage (Schaefer, 1987). Additionally, some species are urban exploiters, meaning they perform well in urban habitats (Bolger et al., 2008; Lowe et al., 2014; Shochat et al., 2004). However, it is not
always clear which urbanisation factors (e.g. light, noise, temperature and habitat fragmentation) 
or which species traits drive this urban exploitation (Trubl et al., 2012). Broadly, urbanisation 
drives shifts in temperature, prey availability, and other correlated factors that potentially alter 
spider development, including development time and total growth (Bonaric, 1987; Lowe et al., 
2014; Mayntz et al., 2003; Vollrath, 1987). The specific impact of artificial light is often omitted 
when investigating the effects of urbanisation on spiders (Dahirel et al., 2017; Lowe et al., 2014). 
This is a surprising oversight, as many orb-weavers preferentially construct their webs in open 
spaces and so are likely to be attracted to artificial lighting during foraging site choice (C. L. 
Craig & Bernard, 1990; Heiling, 1999), and importantly, artificial lights aggregate their 
night-time insect prey (Heiling & Herberstein, 1999; Kreiter & Wise, 2001; Longcore & Rich, 
2004).

We investigated the effects of lifetime exposure to ALAN on key life history traits (juvenile 
development rate, total growth and survival, as well as adult reproductive output and survival) in 
the Australian garden orb-web spider (Eriophora biapicata). These large nocturnal spiders (body 
length up to 22mm in females and 18mm in males) are prevalent in urban and suburban habitats 
and often build their webs near or on artificial lights. Additionally, they forage primarily on 
species of Lepidoptera, Coleoptera, and Diptera (Herberstein & Elgar, 1994), many of which are 
highly attracted to lights (Gerhard Eisenbeis & Hänel, 2009). In good quality foraging sites such 
as around street lights, which attract abundant nocturnal invertebrate prey, E. biapicata juveniles 
demonstrate high foraging site persistence (NJW, unpublished data). Hence, they are an ideal 
species for investigating the life history consequences of ALAN exposure, as they are likely to 
be chronically exposed to the effects of artificial light at night in urban areas.

MATERIALS & METHODS
Collection and Housing

Experimental spiders were obtained from eggsacs laid in the laboratory by 18 wild-caught *Eriophora biapicata* females collected from sites ranging in light intensity from <0.1 lux to 40 lux (Skye Instruments Lux Meter) in an urban park in Melbourne, Victoria (37.7911 S, 144.9515 E) in February 2016. Spiderlings from these 18 families were reared from hatching at 22°C under a 12-hour day (2000 lux; 12V cool white LED strip lighting; Figure S1) and a 12-hour night that was either darkness (0 lux treatment; n = 215; 0 – 0.06 lux) or dim light at night (20 lux treatment; n = 235; 20 – 24.6 lux; 12V cool white LED strip lighting). Offspring from each family contributed equally to each of the two light treatments. At 14.95 ± 1.47 (mean ± SE) days after emergence from the egg sac, juvenile spiders were transferred to inverted plastic cups and maintained until death under standard laboratory conditions (Henneken et al., 2015). To maintain humidity, cups were lightly misted with water every two days. Young juveniles (hatching until 7th instar) were provided with three to five *Drosophila melanogaster* per week; older juveniles (7th instar to penultimate instar) were fed three to five house flies (*Musca domestica*) per week; and, adults were fed one juvenile cricket (*Acheta domesticus*) equal to their body size twice a week. All spiders were provided with equal food appropriate to their size and stage regardless of treatment group.

Development, Growth, and Survival

To assess the effects of the presence of ALAN on development rates and survivorship, spiders were checked every two to three days and any moults or deaths were noted. The date of death after maturation was taken as a measure of adult lifespan. The age (in days) at which a spider completed its final moult was defined as its age at maturation. Once spiders reached maturity, we
measured their body mass (mg) and the length of the tibia (mm) on the front left leg, and used these to determine total life-time growth.

Reproductive Success

We assessed whether exposure to ALAN during development affected reproductive success by providing spiders with mating opportunities within their own light treatment groups and measuring the number of offspring produced. Mating pairs were age-matched to ensure senescence (days since maturation) differed as little as possible between treatment groups (mean ± SEM senescence at mating: 0 lux males = 20.32 ± 2.36; females = 8.14 ± 0.81; 20 lux males = 18.96 ± 2.56; females = 10.40 ± 2.17). Prior to each mating trial, we allowed the female to build a web in a rectangular Perspex frame (58cm × 58cm × 15cm) after ‘sunset’ in the laboratory. Following web construction, we placed the male in the bottom corner of the frame furthest from the hub of the female’s web to allow mating. Following mating, both males and females were returned to their normal housing conditions. For each mated female, we recorded the time between mating and production of the first eggsac, the number of eggsacs laid, the number of spiderlings that emerged, and the average mass of individual spiderlings in the first eggsac produced by each female; spiderling mass in subsequent eggsacs were not measured due to time constraints. To separate reproductive costs of ALAN due to physiological disruption, independent of reproductive costs due to shifts in body size, we calculated the number of eggs produced per mg of female body mass for each mated female.

Statistical Analysis

Statistical analyses were carried out using R version 3.4.2 (R Core Team, 2017). We used a generalised linear mixed model (with an assumed logit link) to compare the proportion of
juveniles in each treatment group surviving to maturity, and linear mixed models for measures of
age at maturation, length of the intermoult period, number of recorded moults, body mass, and
tibia length in adults. Treatment (0 lux vs. 20 lux) was a fixed factor, while family was a random
factor in these models. Sex was a fixed factor in these models (except for the model for
proportion surviving). In the case of a significant treatment × sex interaction, we analysed the
effect of light treatment separately for each sex and the effect of sex separately for each light
treatment. Due to the strong correlation between treatment group and age at maturation,
relationships between age at maturation and body mass, tibia length, or number of juvenile
moults were analysed separately. The marginal ($R^2_m$) and conditional ($R^2_c$) R-squared values are
presented for these analyses. Survival curves (for entire lifespan and separately for adult
longevity only) for each treatment group were built using a Kaplan-Meier survival analysis
(lifespan or adult longevity as response, light treatment as fixed factor, family as random factor;
sex was a fixed factor for the analysis of adult longevity), and curves were compared using a log-
rank test (survival package in R; Therneau, 2015). Linear mixed models were used to test the
effects of light treatment and family on the number of eggsacs produced, the number of
spiderlings per eggsac, the time to the first eggsac, and the mass of spiderlings in the first eggsac.

RESULTS

Maturation Time and Survival

The probability that a juvenile reached maturity was comparable for the two light treatments (72
of 215 0 lux spiders; 64 of 235 LaN spiders; GLMM: $\chi^2 = 2.54$, df = 1, $P = 0.11$).
However, 20 lux spiders matured significantly earlier (Table 1a) and required fewer moults to
reach maturity (Table 1b) compared with 0 lux spiders. The intermoult interval (days) was
comparable for 20 lux and 0 lux spiders (Table 1c). There was a positive relationship between
time to maturation and the recorded number of moults ($F_{(1,131)} = 109.1, P < 0.0001$; Figure 1).

Overall, the total number of days survived (from emergence from the egg to death) by 20 lux spiders was less than 0 lux spiders (log-rank test: $\chi^2 = 10.90, df = 1, P < 0.001$; Figure 2) but adult survival was comparable for the two light treatments ($\chi^2 = 0.001, df = 1, P = 0.97$).

Regardless of lighting treatment, males matured earlier than females (Table 1a) and required fewer moults to reach maturity (Table 1b). The intermoult interval (days) was shorter for females compared to males (Table 1c) and adult females lived longer than males ($\chi^2 = 41.85, df = 1, P < 0.0001$; Figure 3).

**Body size**

There were significant main effects of light treatment and sex on body mass at maturation, and a significant interaction between light treatment and sex (Table 1d). Treatment-specific analyses revealed while female body mass was significantly greater than male body mass in both light treatments, this difference was larger in the 0 lux group ($LaN$: estimate ± SE = -37.15 ± 12.30, $F_{(1,50)} = 8.79, P < 0.004$; 0 lux: estimate ± SE = -174.96 ± 23.70, $F_{(1,58)} = 52.10, P < 0.0001$).

Additionally, sex-specific analyses confirmed that 20 lux spiders were significantly smaller than 0 lux spiders, with a bigger effect in females (males: estimate ± SE = -163.82 ± 17.10, $F_{(1,76)} = 87.550, P < 0.0001$; females: estimate ± SE = -296.66 ± 21.63, $F_{(1,56)} = 215.01, P < 0.0001$).

There was a significant main effect of light treatment, but not sex, on tibia length, and a significant treatment-sex interaction (Table 1e). Treatment-specific analyses demonstrated that male tibia length was greater than female tibia length for 20 lux spiders ($F_{(1,50)} = 15.95, P = 0.0002$) but the sexes were comparable in 0 lux spiders ($F_{(1,58)} = 0.84, P = 0.36$). Sex-specific analyses found that tibia length was significantly greater in 0 lux compared to $LaN$ spiders in both males ($F_{(1,76)} = 117.47, P < 0.0001$) and females ($F_{(1,56)} = 215.01, P < 0.0001$). There was a
positive relationship between time to maturation and adult body mass ($F_{(1,131)} = 262.35, P < 0.0001$; Figure 4) and adult tibial length ($F_{(1,131)} = 40.55, P < 0.0001$; Figure 5).

Reproductive Success

The number of eggsacs laid per female was comparable across light treatments (Table 2a), but LaN females produced fewer spiderlings overall (Table 2b). On average, LaN females produced 63.96% fewer spiderlings per eggsac (main effect: $\chi^2 = 218.35, df = 1, P < 0.0001$; Table 2c). The number of spiderlings per eggsac declined with eggsac number (main effect: $\chi^2 = 30.07, df = 1, P < 0.0001$), doing so faster in 0 lux females (interaction: $\chi^2 = 8.42, df = 1, P < 0.004$; Figure 6). The egg to mass ratio (the ratio of the number of eggs per eggsac to female body mass at maturity) was not significantly different between treatment groups ($0 \text{ lux} = 2.11 \pm 0.12; \text{LaN} = 1.84 \pm 0.16$ eggs per mg of female; $t_{45} = 1.33, P = 0.19$). The time between mating and laying the first eggsac was comparable between treatment groups (mean ± SEM days: $0 \text{ lux} = 28.54 \pm 2.54; \text{LaN} = 22.92 \pm 2.15; F_{(1,49)} = 2.83, P = 0.1$). There was no significant effect of light treatment on the mass of individual spiderlings in the first eggsac (Table 2d).

DISCUSSION

Our study demonstrated dramatic shifts in key life history traits of *Eriophora biapicata* resulting from chronic exposure to artificial light at night (ALAN). Exposure to ALAN reduced the number of juvenile instars, which resulted in earlier maturation at a smaller body size and ultimately led to a significant reduction in reproductive output. Mortality rates were higher in spiders exposed to ALAN, although earlier maturation meant there was no significant difference between treatment groups in the proportion that reached maturity. Here, we discuss the consequences of these life history shifts in the context of increased foraging success for spiders.
that build their webs near artificial lights, as we predict this may counter the physiological costs observed.

**Effects of ALAN on Spider Life History Traits**

Seasonal shifts in temperature and daily photoperiod regulate patterns of growth and development in the majority of animals (Adkisson, 1966; Fonken & Nelson, 2014; Navara & Nelson, 2007). Spiders exposed to ALAN, which may emulate the longer photoperiod normally associated with spring and summer, progressed through fewer juvenile moults and matured earlier. This is consistent with similar observations of extended photoperiods reducing instar number and stimulating earlier maturation in the house spider *Achaearanea tepidariorum* Koch 1841 (Miyashita, 1987). Similarly, ALAN exposure triggers shortened seasonal diapause and earlier maturation in other arthropod species (Shah et al., 2011; van Geffen et al., 2014), and overwintering as early instar juveniles is documented for several spider species (Schaefer, 1987). One possible explanation is that spiders exposed to ALAN may skip several winter moults as the nocturnal photic cues they experience mimic spring and summer photoperiods. In our study, we did not observe an overwintering period during which spiders did not moult for either treatment group. It is possible that moulting occurs during natural overwintering, but these moults are likely associated with only small increases in body mass. This shift in the rate of development may be related to a documented physiological effect of ALAN: its suppression of the nocturnal synthesis of melatonin (Jones et al., 2015). Melatonin is a highly evolutionarily conserved molecule (Vivien-Roels & Pévet, 1993) that is linked to circadian rhythms and appears to have a regulatory function for moulting in arthropods (Girish et al., 2015), although its functions in spiders are largely untested.
Earlier maturation has potential consequences for body size, as a shorter development time affords less time to accumulate body mass. Here, 20 lux spiders were smaller at maturity, largely due to their earlier maturation. However, when maturation time was statistically controlled spiders (particularly females) reared under light at night were also smaller than 0 lux spiders, suggesting that ALAN may directly affect growth rate in this species. This contrasts with a previous study in the cabbage moth which found no evidence that exposure to ALAN affected rates of body mass growth (van Geffen et al., 2014), but such effects have received little attention across other invertebrate taxa. In our spiders, the critical body mass at which moulting is triggered (Nijhout, 2003) may have been altered by exposure to ALAN. Further, artificial light potentially impaired their ability to consume food, or to convert food into body mass. Food consumption was kept as similar as possible between the two treatment groups, so a physiological disruption is the most likely explanation. Exposure to ALAN can increase food intake and growth in vertebrates through effects on hormones that regulate hunger and satiety (Challet, 2015; Fonken & Nelson, 2014). To our knowledge, the effects of ALAN on these hormones have not been explicitly tested in arthropods, but analogues of some of these hormones have comparable physiological roles in insects (Mataruga et al., 2009).

A major cost of exposure to ALAN is an increase in mortality (Eisenbeis & Hassel, 2000; Longcore & Rich, 2004). Spiders exposed to ALAN exhibited higher lifetime mortality rates but, as ALAN also stimulated earlier maturation, the number of spiders that reached maturity and adult longevity were both comparable across the two groups. This increase in mortality may have been driven by increased oxidative stress, as is suggested for other species (Jones et al., 2015). Alternatively, it may have resulted from their accelerated development, as resources were diverted from growth and maintenance into reproductive development (Boggs, 1992). In contrast
to previous studies (McLay et al., 2017), there was no effect of ALAN on adult longevity. This can be explained by a trade-off between the deleterious effects of aging and the benefits of accruing more body reserves. Spiders in the 0 lux treatment aged more prior to maturing, so their adult lifespan would be shortened; however, they also had greater body reserves, prolonging their adult lifespan.

The impact of ALAN on the viability of urban spider populations depends on its effects on the reproductive fitness of individual spiders in a population. 20 lux spiders produced the same number of eggsacs but considerably fewer spiderlings compared to 0 lux spiders. The reduction in fecundity for 20 lux females was largely explained by ALAN induced differences in body mass, as similarly sized females produced comparable numbers of eggs regardless of light treatment. The lack of strong size-independent effects of ALAN on fecundity is contrary to previous results in Drosophila (McLay et al., 2017). However, our results suggest that a smaller body size due to ALAN exposure will nonetheless lead to a reduction in reproductive fitness.

There was no difference between treatment groups in adult longevity, so both groups had an equal amount of time for egg production. However, under natural conditions, predation and declining winter temperatures are major sources of mortality, so earlier maturation may extend the breeding period (Dominoni et al., 2013; Schneider & Elgar, 2002). Hence, the ALAN-induced trade-off between maturing earlier or maturing larger also implies a trade-off between a longer breeding period or producing more spiderlings per eggsac. In this study, we tested the effects of light treatment with both groups provided with the same amount of food, whereas spiders that build their webs near lights are likely to receive considerable foraging benefits (Adams, 2000; Catherine L. Craig, 1987). If greater food intake increases reproductive output (Kreiter & Wise, 2001; Reed et al., 2007), the foraging benefits associated with artificial lights
have the potential to at least partially compensate the reproductive costs of this trade-off (Lowe et al., 2014). We found no effect of light treatment on the mass of individual spiderlings. This has important potential fitness implications, as offspring size is related to offspring performance, including starvation tolerance and the ability to capture prey (Walker et al., 2003). However, further intergenerational effects may not be evident without further measurements of performance and development in subsequent generations.

CONCLUSIONS

The impacts of ALAN on orb-web spiders, and their combined direct and indirect effects on urban insect populations, depends in part on how shifts in life history patterns in these spiders affect predator-prey interactions. Increased mortality and smaller body size may reduce the predation impact spiders exert on insect populations, counteracting increases in predation due to mutual attraction of both predator and prey towards artificial lights. Artificial light at night is associated with high levels of urbanisation (Elvidge et al., 2001; Hansen et al., 2001; Longcore & Rich, 2004; Ma et al., 2012) and spiders living in urban habitats will experience not only the impacts of ALAN, but other environmental perturbations due to urbanisation. Understanding the impacts of urbanisation more generally for spider populations, and the likely consequences for insect communities, will require a more integrated consideration of these factors. Future research into the effects of ALAN on urban insectivores more generally should consider the impacts on both foraging success and development in individuals, and how these impacts translate into population-level effects.

ACKNOWLEDGEMENTS
We thank Mark Elgar for his insightful advice and manuscript comments. We thank Lucy Mc Lay, Caitlyn Perry and Po Peng for their help with spider maintenance, and Katrina-Lee Ware for counting the majority of the spiderlings.

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Table 1 (on next page)

Effects of light treatment on development time and total growth

Measures (mean ± SE) of development time and total growth at maturity for males and females in the two lighting treatment groups – dark at night (0 lux) and light at night (20 lux), and the full models for these effects. Non-significant (P > 0.1) interactions were dropped from models. Superscript letters above means and standard errors denote significant differences (P < 0.05) in treatment-specific or sex-specific comparisons.
| Models                              | 0 lux at Night | 20 lux at Night | Statistic   | P-value |
|------------------------------------|----------------|-----------------|-------------|---------|
|                                    | Males          | Females         | Males       | Females |
| a) Age at Maturation (days)        |                |                 |             |         |
| Light Treatment                    | 300.28 ± 6.22  | 334.91 ± 7.12   | 262.03 ± 6.11 | 272.35 ± 5.38 F(1,131) = 85.78 < 0.0001 |
| Sex                                |                |                 | F(1,131) = 16.97 < 0.0001 |
| b) Number of Juvenile Moults       |                |                 |             |         |
| Light Treatment                    | 11.61 ± 0.30   | 12.90 ± 0.36    | 10.33 ± 0.29 | 11.17 ± 0.34 F(1,131) = 25.28 < 0.0001 |
| Sex                                |                |                 | F(1,131) = 10.99 0.001 |
| c) Length of Intermoult Period (days) |                |                 |             |         |
| Light Treatment                    | 31.30 ± 1.17   | 30.42 ± 0.80    | 33.05 ± 1.62 | 28.01 ± 1.01 F(1,131) = 0.02 0.89 |
| Sex                                |                |                 | F(1,131) = 4.91 0.03 |
| d) Body Mass (mg)                  |                |                 |             |         |
| Light Treatment                    | 290.1 ± 14.44  | 456.07 ± 19.78  | 126.47 ± 8.70 C 162.56 ± 7.99 D F(1,131) = 247.6 < 0.0001 |
| Sex                                |                |                 | F(1,131) = 57.15 < 0.0001 |
| Light Treatment × Sex              |                |                 | F(1,131) = 23.32 < 0.0001 |
| e) Tibia Length (mm)               |                |                 |             |         |
| Light Treatment                    | 6.98 ± 0.14 A  | 6.81 ± 0.11 A   | 5.43 ± 0.11 B | 4.78 ± 0.10 C F(1,131) = 163.16 < 0.0001 |
| Sex                                |                |                 | F(1,131) = 0.52 0.47 |
| Light Treatment × Sex              |                |                 | F(1,131) = 10.71 0.001 |
Table 2 (on next page)

Effects of light treatment on fecundity and offspring size

Measures (mean ± SE) of fecundity and offspring size for spiders in the dark at night (0 lux) and light at night (20 lux) treatments.
| Models                              | 0 lux at Night | 20 lux at Night | Statistic     | P-value |
|------------------------------------|----------------|-----------------|---------------|---------|
| a) Eggsacs per Female (count)      |                |                 |               |         |
| Light Treatment                    | 5.18 ± 0.47    | 5.40 ± 0.46     | $\chi^2 = 0.11$, $df = 1$ | 0.74    |
| b) Spiderlings per Female (count)  |                |                 |               |         |
| Light Treatment                    | 4367.92 ± 361.61 | 1471.27 ± 234.37 | $\chi^2 = 43.06$, $df = 1$ | $< 0.0001$ |
| c) Spiderlings per Eggsac (count)  |                |                 |               |         |
| Light Treatment                    | 895.07 ± 35.01 | 311.23 ± 22.33  | $\chi^2 = 183.34$, $df = 1$ | $< 0.0001$ |
| d) Individual Spiderling Mass (mg) |                |                 |               |         |
| Light Treatment                    | 2.36 ± 0.05    | 2.33 ± 0.05     | $F_{(1,45)} = 0.16$ | 0.70    |
Figure 1

Relationship between number of moults and age at which spiders reached final moult

The relationship between the number of recorded moults and age (in days) at which male and female spiders reared in the dark at night (0 lux) and light at night (20 lux) treatments completed their final moult. The black line represents the fitted regression line \( y = 0.03x + 3.13; R^2_m = 0.48, R^2_c = 0.61 \) for the overall relationship between number of moults and age at maturation.
Figure 2

Effect of light treatment on survival over the entire lifespan

Survivorship curve for dark at night (0 lux) and light at night (20 lux) treatment group spiders over their entire lifespan. Day 0 represents 14.95 ± 1.47 (mean ± SE) days since hatching, at which point spiderlings were placed individually into cups and subjected to their lighting conditions. Prior to this point, all spiderlings experienced dark at night conditions. Shaded areas represent 95% confidence intervals from a Kaplan-Meier survival analysis.
Figure 3

Effect of light treatment on adult survival

Adult longevity (survival probabilities as adults) curves for dark at night (0 lux) and light at night (20 lux) treatment males and females. Day 0 represents the day at which each spider matured. Shaded areas represent 95% confidence intervals from a Kaplan-Meier survival analysis.
Figure 4

Effect of light treatment and sex on the relationship between body mass and age at maturity

The relationship between body mass (mg) at maturity (after final moult and before feeding again) and age (in days) at which male and female spiders reared in the dark at night (0 lux) and light at night (20 lux) treatments completed their final moult. The black line represents the fitted regression line ($y = 2.76x - 560.33$; $R^2_m = 0.61$, $R^2_c = 0.75$) for the overall relationship between body mass and age at maturation.
Figure 5

Effect of light treatment and sex on the relationship between tibial length and age at maturity

The relationship between tibial length (mm) at maturity and age (in days) at which male and female spiders reared in the dark at night (0 lux) and light at night (20 lux) treatments completed their final moults. The black line represents the fitted regression line ($y = 0.02x + 0.63; R^2_m = 0.49, R^2_c = 0.65$) for the overall relationship between tibial length and age at maturation.
Figure 6

Effect of light treatment on the number of offspring produced by females

The relationship between the number of spiderlings per eggsac and the eggsac number for females in the dark at night (0 lux) and light at night (20 lux) treatments. Shaded areas represent 95% confidence bands.