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Guiding lights: foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night

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Abstract

The reach of artificial light at night (ALAN) is growing rapidly around the globe, including the increasing use of energy-efficient LED lights. Many studies document the physiological costs of light at night, but far fewer have focused on the potential benefits for nocturnal insectivores and the likely ecological consequences of shifts in predator-prey relationships. We investigated the effects of ALAN on the foraging behaviour and prey capture success in juvenile Australian garden orb-web spiders (*Eriophora biapicata*). Laboratory experiments demonstrated that juvenile spiders were attracted to LED lights when choosing foraging sites, but prey availability was a stronger cue for remaining in a foraging site. Field experiments revealed a significant increase in prey capture rates for webs placed near LED lights. This suggests that any physiological costs of light at night may be offset by the foraging benefits, perhaps partially explaining recently observed increases in the size, fecundity, and abundance of some orb-web spider species in urban environments. Our results highlight the potential long-term consequences of night lighting in urban ecosystems, through the impact of orb-web spiders on insect populations.

Keywords: light pollution; trade-off; urbanisation; prey capture; web architecture; Araneidae

Introduction

The introduction of artificial light at night (ALAN) into urban areas has disrupted the natural daily and seasonal cycles of light and dark under which organisms evolved (Gaston et al., 2013; Hopkins et al., 2018). The presence of ALAN shifts the composition of invertebrate communities, including an increase in the local abundance of predatory species and their insect prey around artificial lights (Davies et al., 2013), causing changes in both foraging behaviour and foraging success of predators (Adams, 2000; Dwyer et al., 2013; Polak et al., 2011). The extent to which nocturnal predators derive benefits from the attraction of their potential prey to artificial lights depends on the responses of the predators to night lighting. While some nocturnal insectivores avoid illuminated sites (Rydell, 1992; Sparks et al., 2005), predators that do forage near lights may alter their behaviour in illuminated sites, which in turn can affect their foraging success (Elgar et al., 1996; Perry et al. 2008). For example, in ALAN affected sites, some insectivorous bats alter the altitude and speed at which they fly, which may affect their ability to encounter and capture insects (Polak et al., 2011). However, for many predatory species that forage near lights, it is unclear whether they are attracted to artificial light *per se*, or to the associated increase in prey availability.

Orb-web spiders are abundant and ecologically significant terrestrial insectivores, with diverse foraging strategies. Nocturnal orb-web spiders can derive substantial benefits from increased prey densities around artificial lights, since their foraging success depends on the frequency with which prey intercept their webs (Adams, 2000; Ceballos et al., 2005). Recent evidence suggests that some orb-web spiders have a greater fecundity in urban habitats (Lowe et al.,

2014) which may arise through an increase in prey encounter rates (Heiling & Herberstein, 1999; Lowe et al., 2014). Similarly, the densities of adult and sub-adult riparian nocturnal orb-web spiders (*Larinioides sclopetarius*) are higher around streetlights (Heiling & Herberstein, 1999), and laboratory experiments demonstrate that adult and sub-adult *L. sclopetarius* preferentially construct webs near artificial lights (Heiling, 1999). Interestingly, this pattern varies both within (Kovoor & Munoz-Cuevas, 1995), and between species (Family Araneidae - positive phototaxis: Heiling, 1999; negative phototaxis: Nakamura & Yamashita, 1997). This variation may have an ecological basis, as the attraction of *L. sclopetarius* to artificial lights is potentially related to its riparian lifestyle. Specifically, as water reflects moonlight *L. sclopetarius* might use light as a cue for wet habitats rich in insect prey. More significantly, there is a global shift towards more energy-efficient LED lighting, which has a different light spectrum than older light technologies (Gaston et al., 2012). The attraction of insects to lights varies between lighting technologies (Gaston et al., 2012), but whether similar shifts occur for their nocturnal predators is not known. It is therefore important to investigate how these newer lighting technologies affect predator-prey dynamics.

A crucial component of the foraging behaviour of web-building spiders is web site tenacity – the likelihood that a web-building spider remains at the same site on subsequent days or nights following initial web construction. After relocating to a new site, orb-web spiders may reduce silk investment in webs until they experience sufficient prey encounter rates (Nakata & Ushimaru, 1999). This suggests that web site tenacity is driven less by the cues involved in initial site selection, and more by the information gathered once at the foraging site. For example, high web site tenacity reflects high foraging success that outweighs the costs of moving, information that can only be gathered after a web is constructed in the potential foraging site (Nakata & Ushimaru, 1999). Prey capture rates appear to be higher around older artificial lighting technology (Adams, 2000; Heiling & Herberstein, 1999), and web site tenacity studies of adult spiders report a positive correlation between web site tenacity and prey capture rates (Chmiel et al., 2000; McNett & Rypstra, 1997). Hence, we would expect web site tenacity to increase around artificial lights. However, it is unclear whether the association between the presence of artificial light and prey capture success that spiders prioritise illumination over prey availability as cues for web site tenacity. Comparatively little is known about the foraging strategies of juvenile spiders, despite the impact of juvenile foraging on adult size and rates of development (Moya-Laraño et al., 2003; Neumann et al., 2017), although they appear to be less resistant to moving their webs (Chmiel et al., 2000; Enders, 1975).

Once a foraging site is selected, the foraging success of an orb-web spider depends upon web architecture, which may reflect local environmental conditions. Web architecture influences the process of prey capture, changing the probability of prey interception and prey retention, and often varies between individuals (Blackledge & Eliason, 2007; Sensenig et al., 2012; Walter & Elgar, 2016). While orb-web size affects intercept rates, properties of the web such as the number of radii and spiral spacing affect the ability of the web to absorb the kinetic energy of flying insects, therefore influencing prey retention in the web (Opell & Bond, 2001; Blackledge & Zevenbergen, 2006). Artificial lighting may affect these properties in a number of ways. First, spider web size may decrease in illuminated sites, because increased prey availability satiates spiders, and satiated spiders construct smaller webs (Adams, 2000; Herberstein et al., 2000). Further, reduced visibility at night allows nocturnal orb-web spiders to produce more viscid and stickier capture strands, which can affect prey-attraction (Craig & Freeman, 1991). Artificial illumination may therefore reduce prey capture rates by increasing web visibility to prey, or stimulate spiders to produce less viscid and therefore less visible webs, thereby altering prey-attraction to webs. Prey composition may also change, due to the effects of artificial light on web detection by prey depending on the variable visual systems of different prey types.

Exposure to ALAN stimulates faster maturation but a smaller adult size in *E. biapicata* when diet is controlled (Willmott et al., 2018). Maturation rate and eventual body size both depend on juvenile foraging success (Moya-Laraño et al., 2003; Neumann et al., 2017), so a more complete understanding of the impacts of ALAN on these spiders requires a comparison of the prey capture rates of juvenile spiders in illuminated and naturally dark sites.

Here, we used laboratory and field experiments to investigate the effects of the presence of artificial LED night lighting on foraging site choice and tenacity, web construction, and prey capture rates in juveniles of the Australian garden orb-web spider (*Eriophora biapicata*; Family Araneidae). We predicted that artificial light at night would attract juvenile spiders and thus influence initial web site selection, but prey availability would signal site quality and thus be a stronger predictor of web site tenacity. We predicted that webs placed near LED lights would capture more prey due to the attraction of insects to lights. Finally, we expected that light conditions during rearing and web construction would affect web architecture, and thus prey capture rates.

Methods

Study Species

The Australian garden orb-web spider (*Eriophora biapicata*; Family Araneidae) is a large nocturnal insectivore (body length up to 22mm in females and 18mm in males) (Davies, 1980). Shortly after sunset, these spiders construct large, complete orb-webs that catch nocturnal flying insects, particularly Lepidoptera, Coleoptera and Diptera, throughout the night (Herberstein & Elgar, 1994). The foraging behaviour of juveniles is not well documented, but third instar spiders disperse from the eggsac and construct small, complete orb webs (NJW, personal observation). When they have a well-formed web, juveniles can capture and consume prey up to three times their own body size (NJW, personal observation).

Collection and Housing

Experimental spiders were reared from eggsacs laid in the laboratory by wild-caught females collected in an urban park in Melbourne, Victoria (37.7911 S, 144.9515 E) in February 2016. Females were collected from sites ranging in light intensity from <0.1 lux to 40 lux. Light intensity was measured using a Skye Instruments Lux Meter at various locations in the habitat where spiders were collected, taking the brightest measurement at each point on several nights (around 22:00) that varied in cloudiness. However, the light intensity was not recorded for the location of each female's web. A total of 860 spiderlings derived from 18 wild-caught females were reared from hatching at 22°C under a 12-hour day (2000 lux;12V cool white LED strip lighting with a peak wavelength of 445nm; **Figure 1**) and a 12-hour night that was either darkness (*dark at night treatment*; 0 – 0.06 lux) or dim light at night (*light at night treatment*; 20 – 24.6 lux; 12V cool white LED strip lighting). Laboratory night-time lux levels were chosen to approximate natural darkness (dark at night treatment) and the equivalent of being directly under an urban streetlight (light at night treatment) where many of the wild-caught females were naturally located. While cool white LED lights do not provide a perfect approximation of natural sunlight and so may have affected the physiology of the spiders, both treatment groups experienced the same daylight lighting. These lighting conditions are also similar to those used for other terrestrial invertebrate systems (Durrant et al., 2015; McLay et al., 2017). We used lux (*sensu* Gaston et al., 2017) as our measure of light levels. As lux is based on human vision, this doesn't necessarily capture the relative effects of light influencing spiders *per se*, but it does provide a direct link to illuminance as commonly measured in the environment and as employed in the design and mitigation of artificial lighting systems. Offspring from each female contributed equally to each of the two light at night treatments (n=430 for each treatment). Juveniles were housed in inverted plastic cups (9cm tall, 8cm diameter at the base) under standard laboratory conditions (Henneken et al., 2015). Cups were lightly misted with water every two days and spiders were fed 3-5 *Drosophila melanogaster* per week. A sample of these spiders was used for each of the following experiments (see below). Individuals used in *Web Site Selection* and *Web Site Tenacity* experiments were not subjected to the *Web Construction* and *Prey Capture Rates* experiments. It was not possible to collect data blind to the treatment as the two treatment groups (lit or dark) were always easily distinguishable.

(i) Effects of Night Lighting on Web Site Choice and Tenacity

Experimental Light Arenas

Choice experiments were conducted in plastic containers (length 27cm × width 20cm × height 17cm) that were opaque to ambient light, with lightly sanded inner walls to produce a climbable surface (**Figure 2**). A small cylindrical container was locked into a portal at the centre of the base of the box, allowing spiders and prey (adult *D. melanogaster*) to be introduced as required while preventing escape. A hole was created in each corner of the ceiling of the box to allow light to enter. Light was provided by dimmable cool white LED strip lighting. As above, daytime lighting (between 08:00 and 20:00) was set at 2000 lux; night-time lighting (20:00 – 8:00 each night), where present, was set at 20 lux. Within the arena, a four-way wooden skewer scaffold provided spiders with a surface along which to climb when choosing a site and an attachment structure for web-building.

Web Site Choice

We assessed whether the presence of artificial light influenced web site selection by juvenile spiders reared under the dark at night light regime, by manipulating the amount of light from identical light sources (20 lux, cool white, turned on from 20:00 – 8:00 each night) that passed through the corner holes in the ceiling of the box (**Figure 2**). We covered two corner holes on the same side with opaque filters, and the other two corner holes with clear transparent filters (LEE Filters – 130 Clear), so only one side of the box was directly illuminated, but temperature differences between the two sides were minimised. We ran eight trials simultaneously, with half facing one way and half facing the other. We switched the side with the uncovered lights between each set of trials to avoid possible effects of variation in ambient temperature, air current, or magnetic orientation. We placed a single fifth-instar spider (dark at night treatment group; fed four *D. melanogaster* per night for three nights prior) in the portal container and released the spider at 20:00 (corresponding to the start of the natural foraging period) at the beginning of the first night. On the following morning, we recorded the location of the spider's complete orb-web. A spider was deemed to have selected the light side if their web was located in the third sector (Figure 2) of the box closest to the light.

Web Site Tenacity

We assessed the relative effects of artificial illumination and prey (*D. melanogaster*) availability on web site tenacity, by maintaining the spiders used in the *Web Site Selection* experiment in the choice chamber, with the identical lighting arrangement, for a further four days and three nights. Web site tenacity was measured as the proportion of spiders in that treatment group that remained in the same site following the treatments described below. We excluded spiders that initially built their web on the dark side because the sample size (n=3) was too small, and all of the spiders that initially selected the dark side subsequently selected the light side upon retesting. On the second night (at 20:00), individual spiders that had initially constructed their webs in an illuminated site (N=48) were allocated to one of two prey treatment groups: a "no prey" treatment that received no prey and a "prey" treatment in which each spider was fed four *D. melanogaster* on each of the second and third night of their trial. On the fourth night, spiders within each prey treatment were allocated to one of two light treatments: the lighting arrangement remained unchanged ("light-light" treatment), or the light side was switched (by moving the light covers) to the other side of the box ("light-dark" treatment) (n=12 for each light treatment × prey treatment group). It was not possible to include "dark-light" and "dark-dark" treatments because insufficient spiders initially built their web on the dark side, and no spiders moved their webs to the dark side prior to the fourth night. Web site tenacity was determined by whether the spider remained in the same side of the box (stay) or relocated to the opposite side (move) during the fourth night.

(ii) Effects of Night Lighting on Web Construction

We assessed the effects of lighting treatment during rearing and web construction on web architecture, by placing juvenile spiders (8^{th} – 10^{th} instar, inferred by moult exuviates) from both lighting treatments into individual Perspex frames (height 25cm × width 25cm × depth 10cm) under their corresponding lighting treatments: dark (0 – 0.06 lux; N = 23) or illuminated (20 lux; N=25). The lighting arrangement during web construction always matched that during rearing. Five *D. melanogaster* were released into the frames to stimulate web building, and the spiders constructed their webs overnight. After the web was constructed, we removed the spider without damaging the web. The spider was weighed, and we measured the web height and width as the distance between the edges of the capture area of the web along the vertical and horizontal planes of the web, respectively. We counted the number of radii in the web and measured spiral spacing at the midpoint between the central hub and the edge of the web.

(iii) Effects of Night Lighting on Prey Capture Rates

We tested the effects of artificial night lighting on prey capture rates by transferring frames containing webs constructed by juvenile spiders (same webs as in *Web Construction*) to the Royal Botanic Gardens, Melbourne (37.8304 S, 144.9796 E) in November and December 2016. The remains of *D. melanogaster* were removed from the frames to minimise any odour effects on prey attraction (Henneken et al., 2017), and all spiders had experienced an equal number of flies the previous evening. The experimental area was a riparian rainforest gully habitat that received no direct overhead lighting and minimal interference from sky glow (brightest ambient light measured from the web was <0.1 lux). The habitat consisted of an enclosed, sloped area of diverse vegetation and a small stream, and it supported large numbers of *Eriophora biapicata* prior to and during the trials (personal observations). Webs constructed by light at night and dark at night spiders were allocated to either a dark foraging (light at night N = 12; dark at night N = 11) or light foraging (light at night N = 13; dark at night N = 12) treatment: light foraging treatment webs were directly lit by a cool white LED camp light attached to nearby vegetation and measured as 20 lux at the frame (TechLight 0.5W camping light globe; 4500 Kelvin); dark foraging treatment webs were not directly lit and received <0.1 (measurements ranged from 0 to 0.05) lux of artificial light. Each frame was attached to a tripod embedded in the ground so that the frames were approximately 1.4m above the ground and 1.5m from the light source (which was ~50cm higher than the frame), varying slightly due to the terrain. At each of the ten sites (five light and five dark) we placed one web constructed by a dark at night rearing treatment spider and one web constructed by a light at night rearing treatment spider (**Figure 3**).

Each web was checked every half hour over a two-and-a-half-hour period (21:00-23:30), and the identity (classified to order), size, and position in the web of captured prey were recorded. This procedure was repeated over three nights. The locations of the LED lights were switched between nights such that light and dark sites were alternated between nights to ensure the full range of habitat conditions were experienced by all four treatment groups. The sky was clear on all three nights; the moon was new, first quarter, and waxing crescent and the temperature (start point and end point) was 18°C - 14°C, 19°C - 14°C, and 22°C - 16°C on nights one to three, respectively.

Statistical Analysis

Statistical analyses were carried out using R version 3.1.2 (R Core Team, 2014). Web site selection and tenacity were tested using Chi-squared tests, with the two prey treatments analysed separately. No spider was used for more than one replicate, and spiders were excluded from the analysis if they failed to construct webs on the initial or any following nights; moulted or died during a trial; or were in the prey treatment but failed to capture flies. Spiders that were excluded from web site tenacity trials were still included in analyses of web site selection. Measures of web construction were analysed using two-sample two-sided t-tests. We used generalised linear mixed models (GLMMs) to assess the effects of light conditions during web construction (fixed factor) and during foraging (fixed factor) on the number of small prey captured and the prey size-weighted total capture, with web area and spider weight as random factors in each model. To determine the contribution of each factor, we compared the full model with reduced models (one omitting web construction, one omitting foraging, and one omitting web area) using ANOVAs. Captured prey were classified as "small" (body length < 5mm), "medium" (body length 5mm – 15mm), or "large" (body length > 15mm). To create size-weighted values, small prey items were ranked as 1, medium prey as 2 (each medium prey item was given the same value as two small prey), and large prey as 3 (equivalent to three small prey), and the values were then summed for each web to give a proxy measure for total prey capture.

Results

(i) Effects of Night Lighting on Web Site Choice and Tenacity

Web Site Selection

A total of 51/64 spiders successfully constructed a complete orb-web at one end of the box; nine spiders failed to construct a complete orb-web, and four spiders constructed orb-webs in the centre of the box and were therefore deemed to show no clear preference. Of the 51 spiders that selected a side, 48 (94%) constructed their web on the light side of the arena (Chi-squared test: $\chi^2 = 32.96$, $df = 1$, $P < 0.001$).

Web Site Tenacity

Prey availability had a clear effect on web site tenacity. Spiders provided with access to prey for two nights did not subsequently change the location of their web on the fourth night, regardless of lighting treatment ("light-light" $N = 14$; "light-dark" $N = 10$; **Figure 4**). In contrast, the spiders showed a significant preference for building webs near lights in trials where no prey items were provided on nights two and three: two of 13 individuals in the "light-light" treatment moved on the fourth night, compared with nine of 11 individuals in the "light-dark" treatment (Chi-squared test: $\chi^2 = 8.09$, $df = 1$, $P = 0.004$) (**Figure 4**).

(ii) Effects of Night Lighting on Web Construction

There was no significant difference in juvenile body mass between the two treatment groups (dark at night = 67.49 ± 0.6 mg; light at night = 67.47 ± 0.55 mg; t-test: $t_{46} = 0.03$, $P = 0.98$). There were no significant differences between the two treatment groups in any of the measures of web architecture (**Table 1**). The total web area was always smaller than the maximum size allowed by the frame (height 25cm × width 25cm); adults of this species constructed larger webs in frames of the same size (NJW unpublished data), indicating that juveniles could have built larger webs but did not, and so web size was not constrained by frame size.

(iii) Effects of Night Lighting on Prey Capture Rates

The rate of small prey capture in the field was significantly higher in the illuminated foraging treatment compared with the dark foraging treatment (GLMM: χ^2 = 15.54, *df* = 1, *P* < 0.0001) (**Figure 5**). Medium and large prey were only captured in illuminated sites, although only two large prey were caught overall. The size-weighted total capture was higher in illuminated sites (mean ± standard error weighted value for illuminated sites = 1.58 ± 0.31 prey per hour; dark sites = 0.23 ± 0.08 prey per hour; χ^2 = 15.72, *df* = 1, *P* < 0.0001). However, prior experience of a light environment did not influence prey capture rates: webs constructed by juveniles in the light and dark rearing treatment groups captured similar numbers of small (χ^2 = 2.85, *df* = 1, *P* = 0.09) and total prey (χ^2 = 0.91, *df* = 1, *P* = 0.34) items. Web area did not significantly affect the number of small prey (χ^2 = 1.17, *df* = 1, *P* = 0.28) or total prey (χ^2 = 0.91, *df* = 1, *P* = 0.34) captured. Webs in the dark foraging treatment primarily caught only Diptera, whereas webs in the light foraging treatment additionally caught Coleoptera, Hymenoptera, and one Isoptera (an alate termite). Although moths were observed flying around the webs and towards the lights, none were captured.

Discussion

This study has three key findings. First, we found that while juvenile *Eriophora biapicata* preferred to construct their webs near artificial LED lights, their decision to remain at a foraging site was determined primarily by past foraging success rather than the presence of artificial light, despite the otherwise strongly attractive nature of artificial light. Second, field experiments demonstrated a potential fitness benefit of the attraction to artificial lights: webs constructed by juveniles and then placed near artificial lights caught significantly more prey, which potentially translates into greater foraging success. Third, our data suggest that web architecture and prey capture rates of juvenile spiders are not affected by long-term lighting conditions during the immature stages of development.

Foraging Site Choice and Tenacity

Web site tenacity in orb-web spiders involves two phases, which can be mediated by different cues: initially, spiders may use environmental cues to locate web sites (e.g. Heiling & Herberstein, 1999; Elgar et al., 2016), with their subsequent, ongoing decision to remain at that site depending upon their foraging success (Chmiel et al., 2000; McNett & Rypstra, 1997; Nakata & Ushimaru, 1999). Correlational field studies report higher spider densities around lights in nocturnal orb-web spiders (Heiling & Herberstein, 1999) and diurnal jumping spiders (Frank, 2009; Wolff, 1982). However, these studies did not distinguish between initial site choice and web site tenacity. Our data suggest that juvenile *E. biapicata* preferentially built their webs near artificial lights, demonstrating an innate attraction to artificial light itself (Gaston et al., 2013). Attraction to artificial lights by riparian orb-web spiders (*Larinioides sclopetarius*) is attributed to streetlights acting as a super-stimulus, mimicking moonlight reflected off river water and thereby indicating areas of high prey value (Heiling, 1999). As *E. biapicata* is not a specialist riparian species, the attraction may be a response to light indicating an open space where a web can be built and through which insects are likely to fly (Craig & Bernard, 1990; Heiling, 1999). Negative phototaxis has been observed in the orb-web spider *Argiope amoena* (Nakamura & Yamashita, 1997), showing variation in phototaxis within the Family Araneidae and this may be a result of variation in the spectra of lights used in these experiments, differences in background illumination, or other differences between species. For subsequent web site tenacity, our experiments showed that spiders would remain in the same web site if they caught prey, regardless of light treatment, but light treatment only affected web site tenacity in the absence of prey. Hence, food availability was a stronger predictor than ALAN for the likelihood of a juvenile spider remaining in the same foraging site. Using prey availability as the primary cue for web site tenacity represents a more adaptive strategy, as illuminated sites with low prey availability would otherwise act as ecological traps (*sensu* Hale & Swearer, 2016), attracting spiders into poorer quality foraging sites.

Web Architecture

Orb-web architecture can be influenced by foraging history (Adams, 2000; Schneider & Vollrath, 1998; Tso et al. 2007; Blackledge & Zevenbergen, 2007), and ambient lighting (Elgar et al., 1996). However, contrary to our predictions, juveniles of *E. biapicata* maintained under different light regimes did not adjust the size and structure of their webs. In contrast to our findings, adults of the orb-web spider *Neoscona crucifera* constructed smaller webs around artificial lights in the field, likely stimulated by greater satiation in such field sites (Adams, 2000; see also Blackledge & Eliason, 2007). In our experiment, both treatment groups received the same quantity and type of food prior to web architecture measurements. As recent prey capture history influences web architecture (Adams, 2000; Blackledge & Zevenbergen, 2007), this may have encouraged similar architecture between the two treatment groups. Orb-web spiders may shift web decorating behaviours and web width in response to ambient illumination containing UV wavelengths (Elgar et al., 1996), although behavioural responses to LED lights, which lack UV light, are untested. Dahirel et al. (2017) found that spiders alter their web architecture to increase prey capture rates in response to shifts in the types of prey available in urban areas. However, they did not investigate such shifts in relation to artificial lights, which alter insect community composition (Davies et al., 2012), and hence prey availability. Further studies will need to separate lighting conditions during development from lighting conditions during web construction to discern behavioural responses to local illumination, as differences in web architecture observed in field experiments may result from shifts in available prey around artificial lights (Adams, 2000; Davies et al., 2012).

Shifts in Perception of Webs by Prey

An illuminated night-time environment can also alter the nature of the predator-prey interaction through shifts in other web properties. Nocturnal spiders may be able to produce more viscid silk than their diurnal counterparts, because less viscid silk reflects less light, and is thus less visible to prey under brighter conditions (Ceballos et al., 2005; Craig & Freeman, 1991; Heiling & Herberstein, 1999). Thus, artificial lighting may increase the visibility of silk produced by nocturnal spiders and thus reduce foraging efficiency. This may explain our observation of moths flying around the webs in the field but never making contact. The failure of experimental webs to capture moths may alternatively be due to a change in silk composition, as our spiders were reared on a diet of Diptera as juveniles, which may alter silk odour (Henneken et al., 2017). This is of potential ecological importance, as moths form an important component of the diet of *E. biapicata* (NJW personal observations) and the ecologically similar *E. transmarina* (Herberstein & Elgar, 1994).

Consequences of Increased Prey Capture Rates

Our experiments demonstrate a foraging benefit derived directly from the presence of artificial lighting. Artificial lights attract insects, which then aggregate around the lights (Longcore & Rich, 2004). Accordingly, webs constructed near these lights will experience increased encounter rates with flying insects compared with webs in dark sites. We found that webs placed near lights captured more prey, regardless of the lighting conditions in which the webs were built, and this was not significantly affected by web size. Presumably the higher prey capture rate reflects greater prey numbers around the lights and therefore increased interception of prey by webs. There was no difference in body size between light treatment groups for juveniles, although spiders exposed to ALAN mature at a smaller body size (Willmott et al., 2018), suggesting that consequences for foraging dynamics will depend on the age of the spiders. Given the strong physiological impact of the presence of ALAN on growth and reproduction in this species (Willmott et al., 2018), increased prey capture rates are likely to translate to increased growth and reproductive output (Higgins & Goodnight, 2011), potentially explaining field observations of larger spiders in illuminated areas (Heiling & Herberstein, 1999). However, long-term declines in insect populations have been attributed to night lighting (Longcore & Rich, 2004). The shift towards LED lights means a change in the spectrum produced by artificial lights, and the larger blue peak of LED lights at night time has been linked to stronger physiological impacts on animals (Gaston et al., 2012). Our data indicate that the LED spectrum is strongly attractive to many insects, so this shift in ALAN spectrum may drive changes in insect community compositions.

The longer-term impacts at the population and community level are unclear. Nocturnal orb-web spiders, like other nocturnal insectivores, aggregate around artificial lights, as do their insect prey. As invertebrate distributions become patchier, insects may experience increased predation pressure, further compounding the physiological costs of ALAN. Urban insect communities appear to be declining around the globe (Fox, 2013; Longcore & Rich, 2004; Eisenbeis et al., 2009), and the compounding costs of ALAN may accelerate these declines. Similarly, the physiological costs experienced by insects appear to be experienced by spiders: *E. biapicata* reared under ALAN mature earlier and at a smaller size (Willmott et al. 2018). These developmental shifts are likely to affect the ability of predators to capture prey and the predation pressure they consequently place on declining insect communities. Future research should consider the long-term impacts of anthropogenic light on predator-prey relationships to better understand the likely consequences for urban ecosystems.

Ethical Approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Table 1 Measures (mean ± SE) of web architecture in dark webs (constructed by dark-reared spiders under dark conditions) and light webs (constructed by light-reared spiders under light conditions) and the results of t-tests. Web area was calculated as π × height × width. Comparisons were made using two-sample t-tests

	Dark Webs (N = 23)	Light Webs (N = 25)	Statistic	P-value
Web Height (cm)	18.87 ± 0.48	20.14 ± 0.42	t_{46} = 0.90	0.13
Web Width (cm)	17.57 ± 0.56	18.64 ± 0.43	t_{46} = 0.87	0.16
Web Area (cm^2)	263.79 ± 13.92	296.97 ± 11.67	t_{46} = 0.94	0.08
Capture Spiral Spacing (cm)	0.33 ± 0.01	0.35 ± 0.02	t_{46} = 0.55	0.60
Radii Number	18.30 ± 0.35	18.32 ± 0.39	t_{46} = 0.33	0.98

Figure Captions

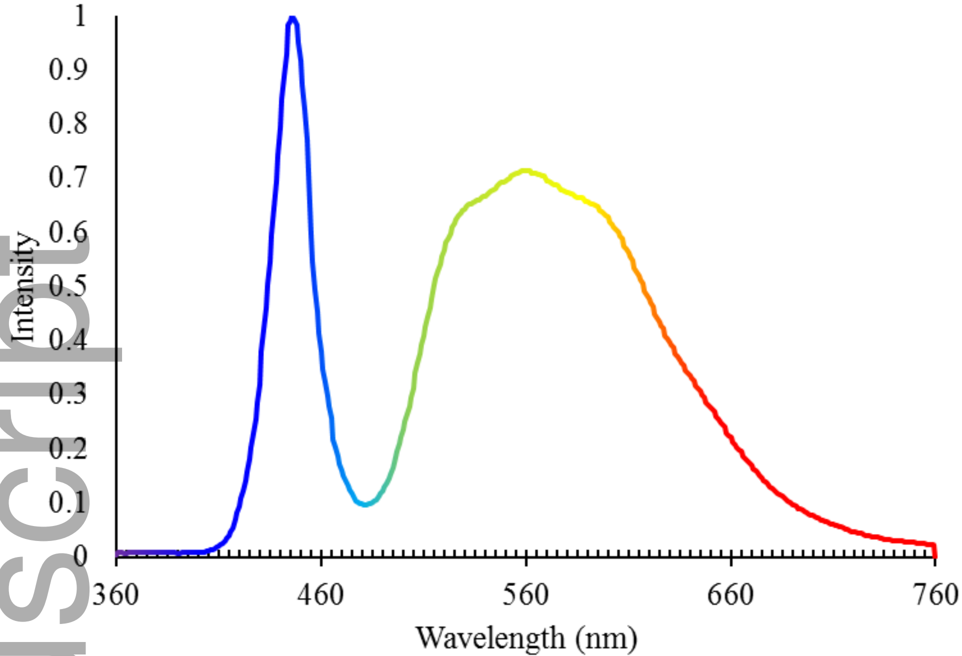
Fig. 1 Spectral composition of the cool white LED lights (12V DC cool white LED strip lighting supplied by World of Thought, Victoria, Australia) used during rearing, site choice, web construction, and prey capture rate experiments. The blue peak wavelength is 445nm

Fig. 2 Design of light box for assessing initial web site selection and subsequent web site tenacity. Spiders enter the box through a portal at the base, which is also an access point for *D. melanogaster* prey. The portal is sealed by a cylindrical plastic capsule. = 2000 lux, 8:00 – 20:00 light; = 20 lux, 20:00 – 8:00 light. = clear filter, = opaque covering. Yellow lines represent the wooden skewer scaffold

Fig. 3 Experimental design for the light site. Webs constructed under dim light conditions by light at night treatment spiders (light-reared web) and webs constructed under dark conditions by dark at night treatment spiders (dark-reared web) were placed at equal heights (~1.4m) from the ground at equal distances (~1.5m) from the light source (cool white LED camping globe fixed to a plant). Lights were ~0.5m higher off the ground than the webs. Dark sites were set up identically but without the light source

Fig. 4 Proportion of spiders that stayed (dark grey) or moved (light grey) on the fourth night of the experiment. In the "light-light" group, the position of the light source was not changed, whereas in the "light-dark" group, the source of light was swapped to the other side of the container. "Prey" treatment spiders received four *D. melanogaster* on each of nights one and two, whereas "no prey" spiders received no food. Sample sizes: light-light+prey (n=14), light-dark+prey (n=10), light-light+no prey (n=13), light-dark+no prey (n=11). All included spiders initially built their webs in the light. * denotes a significant difference ($P < 0.05$), tested using Chi-squared tests

Fig. 5 Prey capture rates (per hour) (mean ± SE) for webs placed in dark sites and illuminated sites in the field. Dark-reared webs were those constructed by dark-reared (0 lux at night) spiders under dark conditions, while light-reared webs were constructed by light-reared (20 lux at night) spiders under light conditions. Sample sizes: light-reared+light-site (n=13), light-reared+dark-site (n=12), dark-reared+light-site (n=12), dark-reared+dark-site (n=11). There was a significant difference ($P < 0.05$) between Dark Sites and Illuminated Sites, but not between Dark Webs and Light Webs within sites



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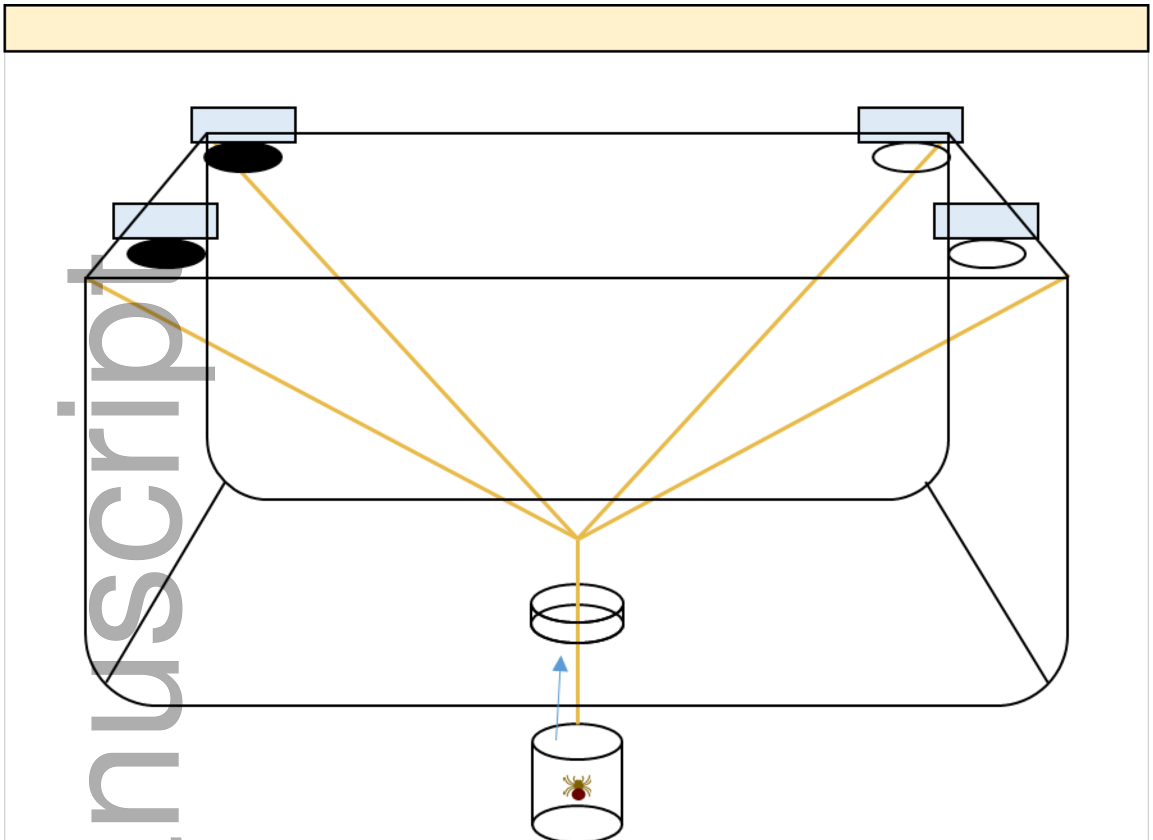

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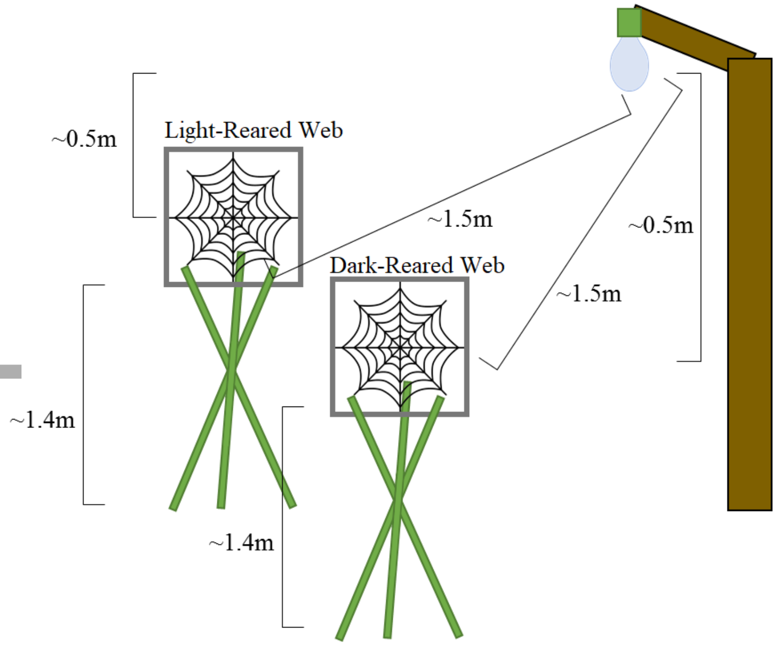

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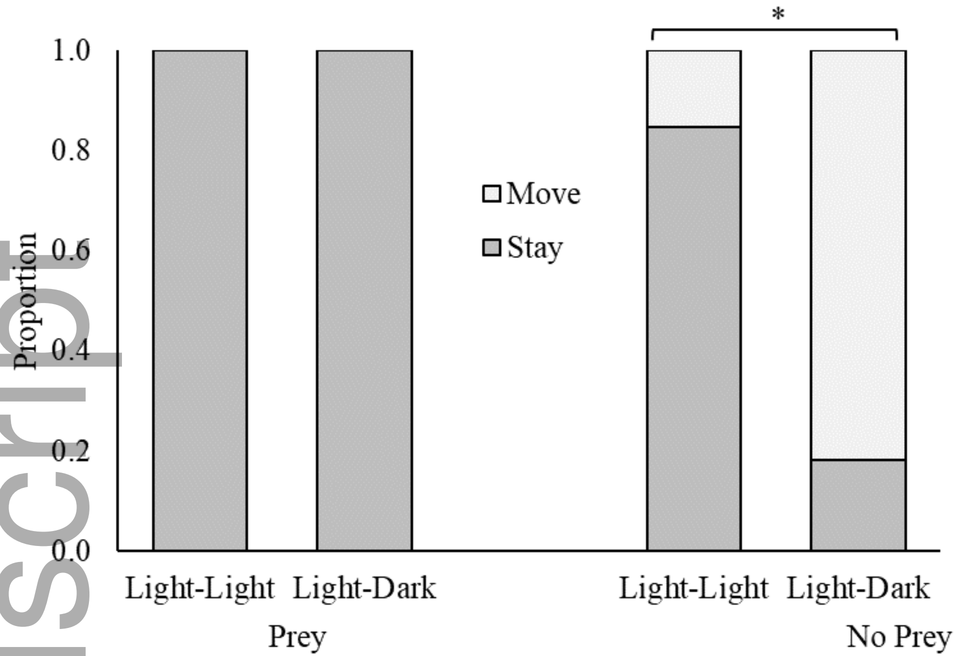

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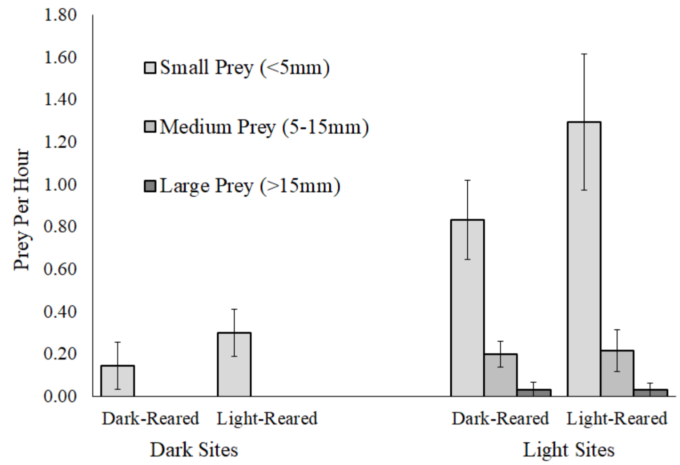

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