Reduced light avoidance in spiders from populations in light-polluted urban environments

Tomer J. Czaczkes[1*], Ana-María Bastidas Urrutia[2], Paolo Ghislandi[2,3], and Cristina Tuni[2]

[1] Institute of Zoology, Universität Regensburg, Universitätsstraße 31, D-93053 Regensburg, Germany

[2] Department of Biology, Ludwig-Maximilians University of Munich, Grosshaderner Str. 2, 82152 Planegg-Martinsried, Germany;

[3] Department of Bioscience, Aarhus University, Ny Munkegade 116, 8000 Aarhus C, Denmark

* Corresponding author, email tomer.czaczkes@ur.de

ORCID IDs:

TJC: 0000-0002-1350-4975

PG: 0000-0002-4713-6082

CT: 0000-0002-7190-1143

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Abstract

Increased urbanisation is leading to a rise in light pollution. Light pollution can disrupt the behaviour and physiology of animals resulting in increased mortality. However, animals may also benefit from artificial light sources, as these may aggregate prey or signal suitable environments. For example, spiders are commonly seen congregating around artificial light sources. Changes in selective pressures engendered by urban environments are driving changes in urban organisms, driving better adaptation to these environments. Here we ask whether urban populations of the synanthropic spider *Steatoda triangulosa* show different responses to light compared to rural populations. Egg-sacs from urban and rural populations were collected and incubated in a common garden setting, and the emerging spiderlings tested for light preference. While rural spiderlings avoided light (37% built webs in the light), urban spiderlings were indifferent to it (49% built webs in the light). Reduced light avoidance may benefit spiders through increased prey capture, increased movement into suitable habitats, or due to a release from selection pressure from visually hunting predators which do not enter buildings.

Key words

Light pollution; urban evolution; anthropogenic selection; urbanization; artificial light at night; *Steatoda triangulosa*

Introduction

Worldwide light regimes have undergone a dramatic change over the last century. In some regions the levels of artificial lighting are increasing by up to an estimated 20% per year (Hölker et al. 2010). Artificial light at night (ALAN) can affect animal navigation and can have large effects on species interactions such as pollination, predation, and niche partitioning (Longcore and Rich 2004; van der Putten et al. 2004; Dwyer et al. 2013; Knop et al. 2017; Sanders and Gaston 2018).

Perhaps most famously, night-flying insects such as moths are often attracted to light. Such attraction can result in direct mortality due to exhaustion or damage, but also in increased visibility and local density, consequently exposing them to predation (Turnbull 1964; Warren 1990). Night-flying insects should thus be under direct selection for reduced light attraction (Gaston et al. 2013). Altermatt and Ebert (2016) recently demonstrated that moths from urban populations showed significantly reduced flight-to-light response compared to moths from rural populations, strongly suggesting that selection pressures against flight-to-light are operating in urban settings.

By contrast, predators might benefit from attraction to light or reduced avoidance of it, as this would allow them to take advantage of locally abundant food sources and increased prey visibility. Birds, bats, and spiders have been reported to aggregate around artificial lights and then to prey on the light-attracted animals (Polak et al. 2011; Davies et al. 2012). Such predator aggregations can often be explained by learning, or by remaining in rewarding environments (Turnbull 1964). Web-building spiders, in particular, are conspicuous residents near artificial lights (Heiling 1999; Manfrin et al. 2017; Mammola et al. 2018), and likely aggregate around lights due to increased hunting success of night-flying insects (Turnbull 1964; Manfrin et al. 2017). We hypothesised that, much as urban moths show reduced light attraction (Altermatt and Ebert 2016), urban spiders may show reduced light repulsion, or increased attraction, when compared to rural spiders. Here, we test this hypothesis on the web-building behaviour of the widespread synanthropic spider *Steatoda triangulosa*.

Materials and Methods

Study populations and egg-sac collection and rearing

Steatoda triangulosa is generalist sit-and-wait predator that spins irregular webs. In the wild it is found in dark places such as under stones, and within buildings in dark corners (Blick et al. 2010). It can be found in both undisturbed and anthropogenic habitats within its natural range (the Mediterranean and Southern Europe) and outside its natural range in heated buildings. Egg-sacs were collected in March and April 2017 from rural and urban environments from six different localities (table 1). Sites were classified as rural if they were within a national park and at least 1km from the nearest settlement, and as urban if they were within a town or city, with collection occurring in or around a building. We successfully found two rural collection sites, Beigua Regional Park (Italy) and Alassio (Italy). Egg-sacs were easily found in urban environments, and sampled from locations in the broad geographic region of the two rural sites such as Milan and Finale Ligure (Italy), as well as Nice (France), and Munich (Germany). We actively attempted to sample different populations, so as to reduce the chance of extensive gene flow between rural and urban populations, so that we might detect a signal of selection on light avoidance behaviour. This constraint limited the availability of suitable rural sampling populations. Light pollution levels, sourced from https://www.lightpollutionmap.info (Cinzano et al. 2001) using the 2017 viirs (visible infrared imaging radiometer suite) data, are provided for each collection location (table 1). We collected 1-6 egg-sacs from the same web or mother, and sibling egg-sacs were noted as such. The egg-sacs were placed individually in plastic vials and brought to the laboratory at the Ludwig Maximilians University in Munich, where they were incubated in a climate chamber under constant conditions (19°C, 60% RH, constant darkness) and checked every 48 hours for spiderling emergence.

Experimental protocol

Spiderlings (n=783 were tested for web-building behaviour 1-2 days after emergence. The device used consisted of a matt-black painted plastic box (17x7x7cm), divided in the middle by an opaque polystyrene board (0.5x6x6cm) attached to the lid (figure 1). The dividing board leaves a 0.5cm gap between the board and the walls and floor, allowing spiderlings free access to both sides of the box. A small central section (2.5x1.5cm) on one end of each box was left transparent. Two rows of 40 boxes were placed with the window facing a strip of 55 lumen, 2700 Kelvin LED lights which did not produce detectable heat in the box. Thus, each box had one light and one dark side. Box arrays were maintained in conditions identical to the egg-sac incubation.

Each spiderling was placed individually in a box using a paintbrush. Only one spiderling was placed in each box. Spiderlings were randomly assigned to be placed in the dark or light side of their box. The box was closed and spiderlings allowed to choose a side to build their web. After 48 hours the boxes were inspected and the location of the web (dark or light side) noted. In cases where web was present on both sides of the box the data were discarded (12 / 783). After testing spiderlings were discarded and the box and barrier were cleaned with ethanol before reuse.

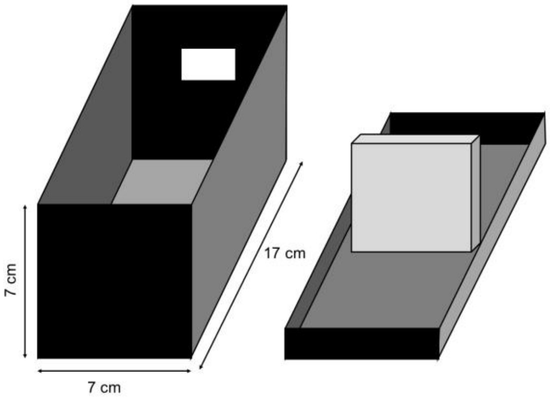

Figure 1 - Test box with lid removed. A window provides light. A central barrier affixed to the lid ensures one side of the box is darker than the other side. Spiderlings are placed in either the light or dark side, and 48 hours web location is scored.

Statistical analysis

Analyses were carried out in R 3.1.0 using Generalised Linear Mixed Models in LME4. We modelled the data using a binomial distribution and logit link function. Collection locality, egg-sac ID, and mother ID was added as random factors, with egg-sac ID nested within mother ID. To test side choice, we used the model formulae:

$$side\ choice = Population\ type\ (Rural|Urban) * Initial\ placement\ (light|dark\ side)$$
$$+ random\ effects\ (locality + MotherID[CocoonID])$$

To test likelihood of moving from initial placement side, we used the same model, but replaced the predicted variable by whether the web was found in the side in which the spiderling was placed.

The raw data is provided in supplement S1.

Results

Urban spiderlings were more likely to build webs in the light side of the assay box than rural spiderlings (GLMM, z = 2.193, p = 0.028, OR = 1.89, 95% C.I.= 1.07 to 3.33, see figure 2A). While rural spiders build fewer webs in the light (37%, z = 3.02, p = 0.0025), urban spiders show no side preference (49%, z = 0.41, p = 0.68). The initial placement location was also a driver of side choice, with spiderlings more likely to build a web in the light side if they were initially placed there (z = 2.54, p = 0.01, OR = 2.17, 95% C.I. = 1.2 to 3.94). The interaction between initial placement and urban/rural origin was not significant (z = -0.70, P = 0.49, OR = 0.78, 95% C.I. 0.39 to 1.56).

Whether a web was built in the side a spiderling was placed was also affected by urban or rural origin, and original placement side, with a significant interaction between these terms (z = -2.85, p = 0.0043, OR = 0.37, 95% C.I. = 0.19 to 0.73). Rural spiders placed in the dark side were likely to build a web there, while over half the rural spiders placed in the light side eventually built webs in the dark side. By contrast, urban spiders were equally likely to build their webs in the other side regardless of light conditions (figure 2B). The individual terms of the interaction were also significant: urban spiders were more likely to build a web in the non-initial placement position (z = 2.3, p = 0.02, OR = 2.0, 95% C.I. = 1.11 to 3.26), and webs were more likely to be built in the same initial placement position if the spiderlings were initially placed in the dark (z = 3.61, p = 0.0003, OR = 2.95, 95% C.I. = 1.64 to 5.3).

The addition of locality as a fixed (as opposed to random) shows no systematic effect of locality beyond the urban/rural dichotomy (for all localities z < 1.61, P > 0.11).

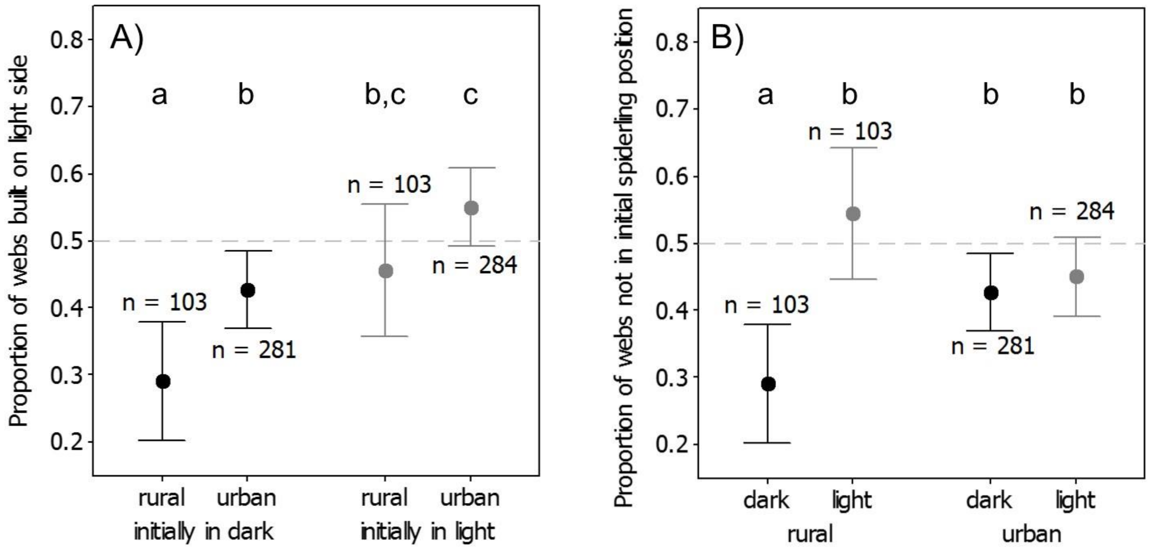

Figure 2 – Proportion of spiderlings A) building their web in the light side of the choice box and B) building their web in the other side of the box from which they were initially placed, depending on origin (urban or rural) and their initial side placement in the choice box (light or dark side). Whiskers are 95% C.I. for the mean. Different letters signify significant differences ($p < 0.05$) between groups (see S2 for details).

Sampling location	coordinates	Rural or Urban	Light pollution level (W/cm^2)	Number of spiderlings tested	N non-sibling egg-sacs collected
Alassio	44.105387, 8.159594	Rural	0.47	64	3
Beigua Regional Park	44.554885, 8.653581	Rural	0.49	147	5
Finale Ligure	44.177826, 8.328891	Urban	28.15	293	7
Milan	45.427895, 9.300442	Urban	27.4	108	3
Bealieu-sur-mer, Nice	43.708142, 7.332682	Urban	71.91	87	2
Munich	48.111193, 11.460662	Urban	16.94	84	3

Table 1 - Locations sampled, the light levels of the local area, and number of tested spiderlings originating from each sampling location

Discussion

While *Steatoda triangulosa* spiderlings from less-disturbed rural populations are repulsed by light, spiderlings from light-polluted urban areas were not. We suggest that the difference in web-building behavior between the urban and rural spiders is most parsimoniously explained by changes in selective pressures in light-polluted anthropic environments: spiders in urban environments have been selected for reduced light repulsion, much as moths from urban environments have been selected for reduced light attraction (Altermatt and Ebert 2016). These findings are set within the broader picture of many organisms evolving behavioural, developmental, and physiological adaptations to coping with the urban environment (McDonnell and Hahs 2015; Johnson and Munshi-South 2017).

Since we raised all spiders from early-stage egg-sacs to hatching under common garden conditions in the laboratory, environmental factors during development are unlikely to play a role in our results, although they cannot be excluded. We also cannot exclude non-genetic maternal effects – it is possible that spider mothers which live in light environments somehow modify the phenotype of their offspring to show decreased light avoidance. Nonetheless, we believe selective pressure is the most parsimonious explanation for our results.

Why should *S. triangulosa* benefit from reduced light repulsion? We propose three non-mutually exclusive possibilities. Firstly, due to the tendency for insects to be attracted to light, by building webs near light sources spiders can increase their prey capture success (Heiling 1999) but see (Yuen and Bonebrake 2017). The reduced repulsion we describe may be the beginnings of evolution towards light attraction, as light sources predict high local prey abundance. Lower light repulsion may lead to higher food intake, which results in higher fecundity, thus selecting for light attraction. Secondly, *S. triangulosa* is especially preadapted to anthropic environments (McDonnell and Hahs 2015). Indeed, *S. triangulosa* is often found in buildings well north of its natural range (Blick et al. 2010), where it most likely cannot survive in the wild. In such situations, repulsion from light may well be fatal. A reduced repulsion from these environments may make it more successful in finding a suitable habitat, and may not be related to any direct benefits of light. Thirdly, and related to the previous point, repulsion from light is usually considered an adaptation for avoiding predation by visual predators (Ringelberg 1991), which is likely why rural spiders show light repulsion. As birds and many other visual predators of spiders rarely enter buildings, selection for light avoidance may have been relaxed.

In this study, we examined the very first web building choice of spiderlings. This is a key decision in the life of a spider: web is expensive to produce (Opell 1998), and so for newly emerged spiderlings with limited resources a good web location is crucial. Web relocation can also be very dangerous, with mortality of 40% being recorded during web relocations in *Latrodectus revivensis* (Lubin et al. 1993). Spiders decide where and how to build their webs depending on many factors such as foraging success, predator exposure, wind direction, temperature, humidity, and light levels (Turnbull 1964; Lubin et al. 1993). As humans change the environment, the fitness consequences of traits change (Johnson and Munshi-South 2017). Physical changes, the selection for melanism in moths for example, are more easily observed (Kettlewell 1955). However, behavioural changes may have even more far-reaching consequences. These include ecologically important changes in range, ecosystem species composition, and species interactions (Davies et al. 2012; Wong and Candolin 2015; Manfrin et al. 2017; Knop et al. 2017). The long-term impacts of these behavioural changes may be far reaching, but as yet we still know little about them, let alone their effects.

Author contributions

TJC conceived of the study, wrote the manuscript, and analysed the data. TJC and CT coordinated the study. CT provided logistical support and laboratory space. PG collected the spiders. AMB collected the data. All authors helped design the study and gave final approval for publication.

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