Received: 23 August 2024 | Accepted: 11 December 2024
DOI: 10.1111/een.13421

SHORT COMMUNICATION

Ecological Entomology

Predation of the white-lined sphinx moth (*Hyles lineata*) is dependent upon time of day but not human disturbance

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Funding information
The College of Science at The University of Texas at El Paso; National Science Foundation, Grant/Award Number: Chihuahuan Desert Biodiversity Research Experience for Undergraduates

Associate Editor: Gina Marie Wimp

Abstract

1. Human settlements and urbanisation are increasing globally, with more than half of the Earth's terrestrial surface being impacted by humans. This development has resulted in numerous anthropogenic stressors including nocturnal sensory pollution (i.e. light pollution), which is a key driver of insect declines.
2. Nocturnality is hypothesized to reduce predation risk from visually-guided diurnal predators. More than half of all insect species, and 80% of Lepidoptera, are estimated to be nocturnal.
3. Predation rates on insects are likely a result of habitat, time of day and the local predator composition. We investigated how predation rates on plasticine moth replicas differed between urban and rural sites, and between night and day.
4. Visually matching paper-winged, clay-bodied replicas of the white-lined sphinx moth, *Hyles lineata*, were placed in a natural area within the city of El Paso, Texas, and in remote Chihuahuan Desert with minimal human disturbance. These replicas were checked during dawn and dusk for 3 days.
5. Predation rates were significantly lower at night than during the day regardless of location, and predator composition differed between sites. Insectivorous birds were the primary diurnal predators in both locations, whereas nocturnal predators were represented primarily by insects at the rural site and by mammals at the urban site.
6. These findings support the hypothesis that visually-guided predators, such as birds, exert higher predation pressures during the day, and supports the hypothesis that insect biodiversity, especially of predaceous insects, is affected by urbanisation.

KEYWORDS
urbanisation insects, nocturnal, predator community, prey, temporal niche

INTRODUCTION

Predation risk is hypothesised to shape the long-term evolution of temporal niche partitioning in animals and diel cycles (McCauley et al., 2012). Nocturnality in many species has been attributed to avoidance of visually-guided diurnal predators, such as birds (Maor et al., 2017). Yet, predator behaviour and survival have also been shaped by prey activity patterns and environmental conditions for millennia. However, the nocturnal environment is drastically changing in the Anthropocene as more than 23% of Earth's terrestrial surface no longer experiences natural darkness (Falchi et al., 2016) and over 50% consists of human-altered environments (Riggio et al., 2020). These changes to the environment and the nocturnal niche have resulted in many diurnal species becoming nocturnal, thus altering the evolutionary trajectories of night-time communities (Gaynor et al., 2018; Seymoure et al., 2023). For example, diurnal, urban birds have increased foraging activities into the night hours (Dominoni & Partecke, 2015), as well as increased overall prey consumption (Titulaer et al., 2012). Lastly, 50% of insects are estimated to be nocturnal, with one of the most speciose orders, Lepidoptera, containing 80% nocturnal species (Hölker et al., 2010). As insects are key ecosystem service providers and are experiencing substantial declines (Wagner, 2020), investigating the role that temporal niches, the built environment and predator assemblages play in insect survival is fundamental to understanding entomology in the Anthropocene.

Insects, especially palatable moths, are profitable prey items for numerous carnivorous and omnivorous species, including all classes of vertebrates, insects and myriad other arthropods (Wagner, 2020). These predators occupy different temporal niches; many insectivorous birds are crepuscular and diurnal, and mostly rely upon vision for prey detection. Most insectivorous mammals (e.g. bats and rodents) are nocturnal and guided by non-visual modalities for prey detection. Insectivorous arthropods occupy all temporal niches and rely upon numerous sensory modalities for prey detection. However, diurnal insectivorous species are altering their activity patterns to become more nocturnal and crepuscular due to light pollution and other human disturbances (Dominoni, 2017). Thus, visually-guided predator–prey interactions are likely changing in the built environment across the 24-hour light cycle.

Here, we investigated how urbanisation and time of day affected predation rates on sedentary plasticine replicas of the white-lined sphinx moth (Lepidoptera: *Hyles lineata*). *Hyles lineata* is an appropriate study organism for testing differential predation temporally and spatially as *H. lineata* is mostly crepuscular but active during day and night, and is a profitable prey item that is common in both urban and undeveloped locations across Central and North America (Tuttle, 2007). Following from the hypothesis that visually-guided predation is enhanced in brighter conditions, we predicted that *H. lineata* will have higher predation rates during the day than at night. Also, as urban predators are hypothesized to be shifting to nocturnal niches due to increased lighting from light pollution as well as other anthropic factors (Dominoni, 2017; Gaynor et al., 2018), we predicted that urban moths will have higher nocturnal predation than rural moths. Lastly, as urban environments have reduced biodiversity and fewer predators (Simkin et al., 2022), we predicted that predator composition will be more varied in rural habitats compared with urban habitats.

METHODS

Plasticine replicas

To quantify predation rates and predator composition between time of day and urbanisation, we developed visually accurate plasticine replicas of adult *Hyles lineata*. Eight *H. lineata* moths in pristine condition were selected from the University of Texas at El Paso Biodiversity Collections. Following Troscianko and Stevens (2015) and Da Cunha et al. (2024), we quantified wing coloration with a UV/VIS Samsung NX1000 camera. We photographed moth specimens both dorsally and ventrally with a UV-suitable grey standard (Spectralon; Labsphere; 40% reflectance) under clear skies between 13:15 and 14:15 in February and March. We then printed moth replica wings on White, Letter Paper (Office Depot® Multi-Use Printer & Copy Paper, White, Letter 8.5″ × 11) using a Xerox C310 printer. Photographs of moth specimens and paper wings were compared for spectral match. We adjusted the brightness and RGB values of the paper wing reflectance using the photo editing software General Image Manipulation Program (GIMP) to ensure a close spectral match to the moth specimens. This process was repeated until reflectance values were similar between moth wings and paper wings: see Figures 1 and S1. Paper wings were then cut to the correct shape and size, and inserted into 4.5 g of non-toxic brown clay (Brown Craft Smart Oven Baked Polymer) moulded to the shape of *H. lineata*'s body. Finally, twist ties were used to attach clay replicas to branches.

Study sites and replica deployment

For moth deployment, we selected one urban site within El Paso, TX—Knapp Land Nature Preserve (KLNP; 31.864035, −106.465106)—and one rural site, Indio Mountains Research Station (IMRS; 30.776681, −105.016751), which is approximately 180 km from El Paso, TX. KLPN is 143 hectares of protected Chihuahuan Desert with high human disturbance, whereas IMRS consists of 161 km^2 of undisturbed Chihuahuan Desert. Additionally, KLNP is adjacent to Franklin Mountains State Park, which consists of 9182 hectares of preserved Chihuahuan Desert. However, both KLNP and adjoining Franklin Mountains State Park are centrally located within El Paso and receive high levels of light and noise pollution, as well as other urban impacts.

During dusk on June 8, 2023, 200 moth replicas were placed on native plants at each site, 400 in total, at least 50 m apart from other replicas. Replicas were then checked every dawn (approximately 04:58–06:00) and dusk (approximately 20:10–21:12) for attack marks for 72 h. Attacks recorded at dawn indicated a nocturnal attack and attacks at dusk indicated a diurnal attack. All attacked replicas were removed from the study and photographed. We categorised attacks as bird, mammal, insect or unknown based on the indentations left on the clay replicas (see Low et al., 2014 and Figure S2).

Statistical analysis

Differences in survival probabilities after 72 h between the two sites were tested using Kaplan–Meier survival analysis with the log-rank test 'survival' package in R (Therneau, 2015). Missing replicas were incorporated into the Kaplan–Meier survival analysis as censored individuals (Seymoure et al., 2024). Chi-square analyses were used for

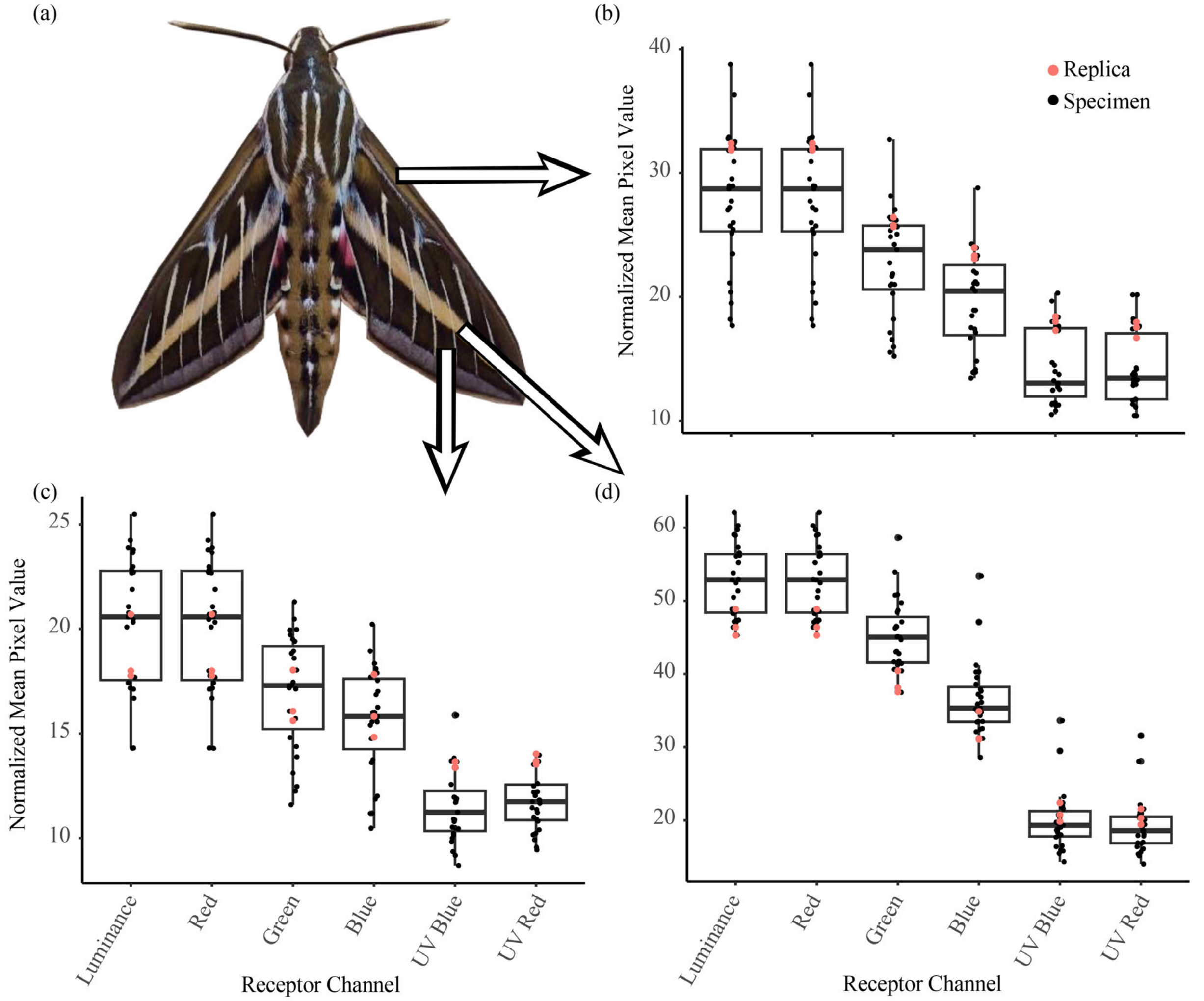

FIGURE 1 Spectral comparison of dorsal coloration between moth specimens and moth replicas. (a) The image of *Hyles lineata* used for replica construction with arrows indicating the three main regions that were assessed for colour matching between moth specimens and replicas. (b) Leading edge of the forewing, (c) brown patches surrounding white line and D) the white line. Each area was sampled in three separate regions.

testing differences in attack rates between night and day, as well as predator composition. For the temporal niche Chi-square analysis, we corrected for a longer daytime by multiplying the total number of attacks (140) by the proportion that was daytime (15 h/24 h, 0.625) and night-time (9 h/24 h, 0.375), resulting in 87.5 and 52.5 expected attacks for day and night, respectively.

RESULTS AND DISCUSSION

After 72 h of replica deployment, 35% (140/400) of the replicas were attacked and 7% (29 of 400) went missing. We found strong support for increased diurnal predation compared with nocturnal predation, as 87% (122 of 140) of the attacks occurred during the day ($X^2 = 36.27$, $df = 1$, $p < 0.001$; Figure 2a). There was no difference in survival between the rural and urban site (Kaplan–Meier, $X^2 = 1.2$, $df = 1$, $p = 0.3$; Figure 2b). Thus, predation pressures on sedentary moth replicas are four times higher during the day than at night regardless of human disturbance ($X^2 = 1.063$, $df = 1$, $p = 0.3025$). This result strongly suggests that sedentary prey occupying the nocturnal niche have decreased predation pressures. However, the replicas are only visually representative of moth prey and do not match chemical signatures or behaviours that would be exhibited by live moths (e.g. flight, leg movements, vibrational cues, pheromone secretions, etc.). Thus, nocturnal predation rates reported here are likely underestimated as many moths are predated while flying at night or parasitized through the release of chemical cues. Previous research has shown that using plasticine models can be appropriate for determining overall predation pressures on caterpillars (Seifert et al., 2016); however, unlike moths, caterpillars are relatively immobile and less likely to be predated by bats. To completely quantify predation pressures on adult moths across landscapes and temporal niches, future work involving telemetry and remote tracking is required. Lastly, these replicas were only deployed for three nights during quarter moon illumination. As

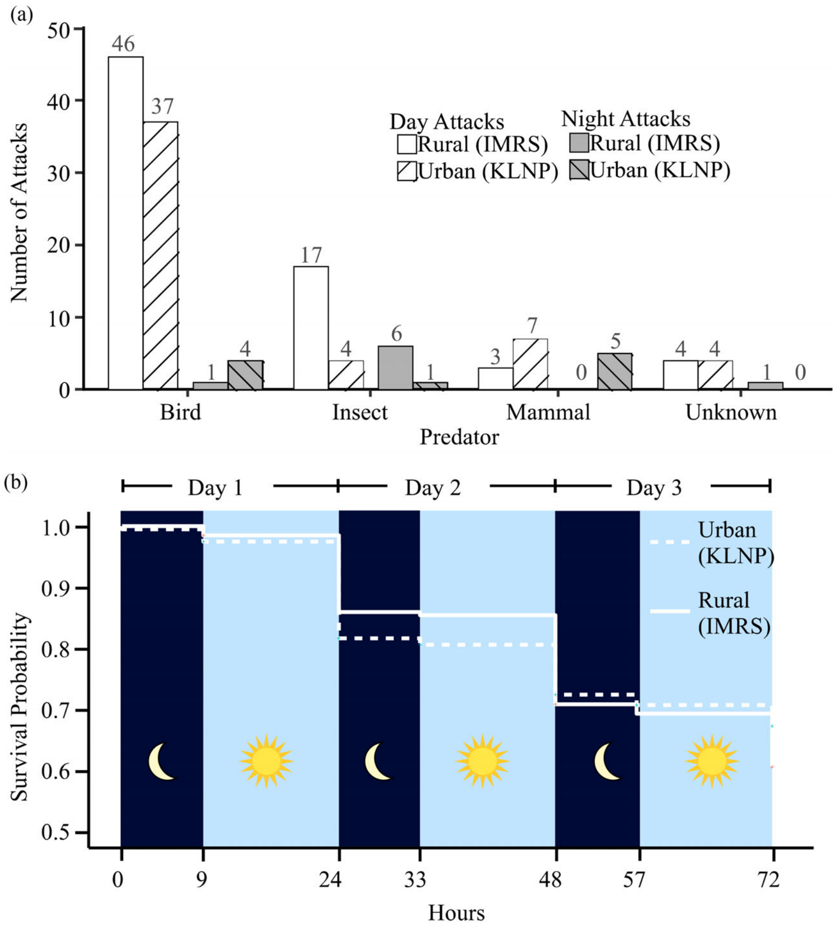

FIGURE 2 Attack results of moth replica models between urban and rural sites, and between day and night. (a) The number of attacks differs across predator class and between sites and time. Numbers above each bar represent the total number of attacks. Green bars represent the rural site and orange bars represent urban sites. Lighter bars represent daytime attacks and darker bars represent night-time attacks. (b) Survival probability between urban and rural replicas. Dark blue backgrounds represent night-time and light blue represent daytime; note that daytime is 15 h long and night-time is 9 h long. There was no significant difference in survival between sites.

predators will visually detect these replicas under ambient light conditions, there may be fewer attacks during new moon conditions and more attacks during full moon conditions. However, as full moon conditions only represent less than 10% of night-time, whereas new moon conditions represent more than half of night-time (Śmielak, 2023), the findings here could be an overestimate of nocturnal predation if light intensity is important for predator detection of sedentary moth prey.

Predator composition varied with birds comprising 63% of attacks, insects 20%, mammals 11% and the remaining 6% of attacks were unidentifiable ($X^2 = 112.4$, $df = 3$, $p < 0.001$; Figure 2a). Furthermore, predator attacks differed between the urban and rural sites ($X^2 = 15.87$, $df = 3$, $p = 0.001$; Figure 2a). Although birds were the main predators at both sites, the rural site had more insect attacks, and the urban site had more mammalian attacks. Both sites had negligible proportions of unknown attacks. We predicted that birds would make up more of the attacks during the night in the urban site than at the rural site due to light pollution altering circadian rhythms and foraging behaviour (Seymoure et al., 2023), and indeed this was the case as KLNP had 40% avian attacks at night compared with 12% nocturnal avian attacks at IMRS. Surprisingly, mammals comprised the most nocturnal attacks (50%) at KLNP and contributed no nocturnal attacks at IMRS. Another interesting and perhaps alarming find is that insects made up the largest proportion of nocturnal attacks at IMRS (75%), whereas insects contributed minimally to urban nocturnal attacks (10%). In fact, there were more nocturnal insect attacks at the rural site than all insect attacks at the urban site. Perhaps, these findings are evidence of insect declines in urban environments, especially those of predaceous insects (Wagner, 2020).

In conclusion, there were no differences in attack rates on profitable moth prey between urban and rural landscapes; however, rural predators comprised mainly birds and insects, whereas urban predators were predominantly birds and mammals, with almost no insect predators. Most importantly, predation rates on sedentary clay replicas of *H. lineata* were drastically lower at night than during the day, and higher in light-polluted areas than darker, pristine areas, thus supporting the hypothesis that visually-guided predation increases under brighter conditions (Beauchamp, 2007; Wcislo & Tierney, 2009).

AUTHOR CONTRIBUTIONS

Brett Seymoure: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; supervision; resources. **Braulio A. Sanchez:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing; writing – original draft. **Kajaya J. Pollard:** Conceptualization; investigation; methodology. **L. Miles Horne:** Conceptualization; investigation; writing – original draft; writing – review and editing; visualization; methodology; validation. **Elizabeth Field:** Investigation; writing – review and editing. **Ashlee D. Portz:** Investigation and writing – review and editing. **Jackson Savage:** Investigation. **Colby Smith:** Investigation; writing – review and editing. **Spencer Duffendack:** Investigation; writing – review and editing. **Elise Cotty:** Investigation. **Oliver Neria:** Investigation; writing – review and editing. **Alexander Moore:** Investigation. **Sol Saenz-Arreola:** Investigation; writing – review and editing. **Andrea Olivas:** Investigation. **Oceane Da Cunha:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing.

ACKNOWLEDGEMENTS

We are grateful for the support offered by Vicente Mata-Silva and the Indio Mountains Research Station and from the Frontera Land Alliance in El Paso, Texas, especially Rocio Ronquillo and Jenae Reneaud Field. John Deitsch was helpful in providing helpful ideas and edits throughout the writing process. This work was funded through the Department of Biological Sciences and the College of Science at the University of Texas at El Paso. Lastly, we appreciate Michael Moody and the Chihuahuan Desert Biodiversity Research Experience for Undergraduates for funding and providing opportunities to JS and SD.

FUNDING INFORMATION

This work was possible through internal funding from the College of Science at The University of Texas as well as from funds from the National Science Foundation through the Chihuahuan Desert Biodiversity Research Experience for Undergraduates.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All the predation counts are available on Dryad. Seymoure, Brett (Forthcoming 2024). Plasticine model predation of adult white-lined sphinx moths (Hyles lineata) across time and sites (urban and rural) [Dataset]. Dryad. https://doi.org/10.5061/dryad.31zcrjdx5.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

FIGURE S1. Spectral comparison of ventral coloration between moth specimens and moth replicas. (A) The image of *Hyles lineata* used for replica construction with arrows indicating the three main regions that were assessed for colour matcahing of the ventral wing between moth specimens and replicas. (B) Leading edge of the forewing, (C) brown patches surrounding white line, and (D) the white line. Each area was sampled in three separate regions.

FIGURE S2. Examples of attacks by different predators. The silhouette above each column indicates whether the attack was mammalian, insectivorous, or avian. The numbers in the photos, when present, are the ID of the model and can be ignored.

How to cite this article: Seymoure, B., Sanchez, B.A., Pollard, K.J., Horne, L.M., Field, E., Portz, A.D. et al. (2025) Predation of the white-lined sphinx moth (*Hyles lineata*) is dependent upon time of day but not human disturbance. *Ecological Entomology*, 1–6. Available from: https://doi.org/10.1111/een.13421