SHORT COMMUNICATION

A test of the light attraction hypothesis in camel spiders of the Mojave Desert (Arachnida: Solifugae)

Matthew R. Graham¹, Michelina B. Pinto¹ and Paula E. Cushing²: ¹Department of Biology, Eastern Connecticut State University, 83 Windham Street, Willimantic, CT 06226, U.S.A.; E-mail: grahamm@easternct.edu; ²Department of Zoology, Denver Museum of Nature & Science, 2001 Colorado Boulevard, Denver, Colorado 80205 U.S.A.

Abstract. Research progress on the order Solifugae, commonly known as camel spiders, has been hindered by challenges inherent in collecting these fast-moving, nocturnal predators. Recently, pitfall trapping combined with artificial light lures showed promise for improving capture rates, but the hypothesis that camel spiders are attracted to light traps (positive phototaxis) has never been tested. We constructed short pitfall trap arrays with and without lights across the Mojave Desert to test the light attraction hypothesis. Nearly all camel spiders we collected were found in traps with suspended lights, lending strong support for positive phototaxis. Distance from the lights within trap arrays does not appear to be correlated with the success of individual pitfall traps. Excitingly, our short pitfall light arrays, or Caterpillar light traps, were relatively easy to install and yielded an order of magnitude more camel spiders per effort hour than previously reported techniques.

Keywords: Drift fence, Mojave Desert, pitfall trap, solifuges, solpugids, sun spiders, wind scorpions

The arachnid order Solifugae, commonly referred to as camel spiders, sun spiders, or wind scorpions, are notoriously difficult to collect and study, and few laboratories worldwide have focused on their biology. Progress is underway, however, as articles have recently been published on camel spider morphology and histology (Cushing et al. 2005, 2014; Klann et al. 2008, 2009; Klann & Alberti 2010; Cushing & Casto 2012; Bird et al. 2015; Franz-Guess & Starck 2016; Franz-Guess et al. 2016), systematics (Cushing et al. 2015; Botero-Trujillo et al. 2017; Maddahi et al. 2017), and collecting techniques (Cushing & González-Santillán 2018). Improvements in collecting techniques are especially exciting, as collecting difficulty has long hindered research on this important arachnid order.

Earlier this year, novel trapping methods were introduced that combine pitfall traps and drift fences with artificial light lures (Cushing & González-Santillán 2018). The technique works by luring camel spiders to traplines with artificial lights suspended over or near drift fences. Presumably, camel spiders that encounter a drift fence try to skirt the barrier by running parallel to it, causing them to fall into a pitfall trap. We hereafter refer to this combined light lure and pitfall trap approach as "pitfall light trapping."

Pitfall traps, drift fences, and lights can be arranged in a variety of ways, but two designs have been used with some success; the Butterfly Light Trap and the Caterpillar Light Trap (Cushing & González-Santillán 2018). The Butterfly Light Trap is an arrangement of pitfalls and drift fences curved as semi-circles around a central light source, whereas the Caterpillar Light Trap uses lights to illuminate short drift fences interspersed with pitfall traps. Both techniques operate under the assumption that the lights entice more camel spiders into the traps. But why would nocturnally foraging arachnids like camel spiders be attracted to artificial sources of light?

We were curious if the success of pitfall light trapping was due to camel spiders randomly encountering the trap arrays while foraging, and not a result of an attraction to lights (positive phototaxis). If true, then artificial lights, which are costly and require frequent battery or fuel replacements, would not be needed to effectively capture camel spiders with pitfall arrays. Although authors have encouraged the use of lights to attract camel spiders for years (i.e., Pocock 1897; Turk 1947; Cloudsley-Thompson 1961, 1977; Punzo 1998; Conrad & Cushing 2011), no formal study has directly tested whether lights make pitfall traps more effective.

In an effort to minimize costs and maximize trapping efficacy for a new four-year project on North American camel spiders, we conducted a simple field test of the light attraction hypothesis. We set up pitfall traps with lights ('lighted' traps) and without lights ('dark' traps) at four sites spanning the Mojave Desert (Fig. 1). If camel spiders do exhibit positive phototaxis, then lighted traps should capture significantly more individuals than dark traps.

We used a modified Caterpillar Light Trap array design (Cushing & González-Santillán 2018) with one 3 m drift fence (landscape edging) and three 10 cm x 10 cm x 5 cm pitfall traps (plastic food storage containers) set into the ground. One pitfall was sunk at each end of 3 m drift fence and one cup was set under the middle of the fence (Fig. 1). An equal number of lighted and dark arrays were set up at each site. Trap arrays were spaced at least 30 m apart, alternating between lighted and dark traps. There was no significant difference in the quality or character of the habitat (e.g., substrate consistency or flora) where the lighted and dark arrays were installed. Batterypowered camping lanterns with adjustable luminosity (1750 Lumen LitezAll) were hung on stakes 0.50-0.75 m over the middle of each lighted array. The lanterns were set to 750 lumens at dusk, which allowed them to run continuously throughout each night. Batteries (four D cells) were replaced each day to ensure similar luminosity across nights and study sites. We poured RV & marine antifreeze into each pitfall trap to a depth of 3-4 cm. RV & marine antifreeze is primarily ethanol and propylene glycol, both of which have been demonstrated to effectively preserve arachnid tissues for molecular analyses (Vink et al. 2005) while still safe for vertebrate wildlife.

Trap arrays were each set for a single trap night and disassembled in the morning. Camel spiders and arthropod bycatch were then transferred to ethanol (95% and 75% respectively) and sent to the Denver Museum of Nature & Science for curation and identification. Our trapping effort resulted in a total of 22 pitfall arrays, 11 lighted and 11 dark, at the following four sites from 29 July to 3 August 2018:

U.S.A.: California: San Bernardino County, Newberry Springs, Newberry Springs Road, N 34.806282°, W 116.662672°, 29 July – 30 July 2018. Photosphere: online at https://goo.gl/maps/XvDa6BsRKPp

U.S.A.: Nevada: Nye County, Mecca Road E, 10.8 km N Longstreet Inn & Casino, N 36.505612°, W 116.409261°, 30 July – 31 July 2018. Photosphere: online at https://goo.gl/maps/kPJr9Q18Buu



Figure 1.—Examples of short pitfall traps set with artificial lights (lighted trap; left) and without lights (dark trap; right). Both photographs were taken southwest of Las Vegas, Nevada. Compass readings, elevations, bearings, coordinates, altitudes, and time/date stamps were generated in the field using the Solocator camera app (online at http://solocator.com).

U.S.A.: Nevada: Clark County, 7.1 km W Enterprise, S Hualapai Way, N 36.011691°, W 115.321091°, 31 July – 1 August 2018. Photosphere: online at https://goo.gl/maps/ZyEijbfBQ622

U.S.A.: California: San Bernardino County, 10.4 km NE Oro Grande (straight line distance), Powerline Road, N 34.650895°, W 117.239619°, 1 August – 2 August 2018. Photosphere: online at https://goo.gl/maps/CHhLRYjPjet

Our lighted arrays proved incredibly effective, with 49 camel spiders collected from the 11 arrays. Conversely, the 11 dark arrays only trapped a single specimen. A two-way ANOVA indicated that capture rate was similar among the four study locations ($F_{3,14}=0.9$, P=0.47). Capture rate in lighted arrays (4.5 ± 0.9 individuals / session) was significantly greater than that in dark arrays (0.1 ± 0.1 individuals / session; $F_{1,14}=24.2$, P<0.001). The positive effect of light on capture rate was detected among all study locations (location × treatment interaction: $F_{3,14}=0.7$, P=0.54), thereby failing to reject the light attraction hypothesis. Remarkably, we discovered at least one camel spider in all 11 lighted arrays, with a maximum of 11 and an average of 4.5 per array (Table 1). The lighted arrays also resulted in significantly more insect bycatch, although we did not quantify the difference.

Evidence from field surveys suggest that there may be a correlation between the distance from the light source within individual pitfall arrays and the number of camel spiders collected, with more specimens in traps closer to light sources. Given the design of our lighted arrays, with a single lantern suspended above the middle pitfall trap, we were able to explore this idea. A one-tailed t-test indicated that the average number of camel spiders collected from middle pitfalls (2.55 per trap) was indeed significantly greater (P =0.032) than that of the outer pitfalls (0.95 per trap). This should be expected, however, because the drift fences could lead the camel spiders into the middle pitfalls from both sides, so we should expect nearly twice as many samples in the middle pitfalls even without a light attraction effect. After correcting for this by treating the pair of outer pitfalls in each array as a single trap, more camel spiders were still collected in the middle pitfalls than outer pitfalls, but the difference was no longer significant (P = 0.232). Furthermore, one middle pitfall at our site near Victorville, California contained 11 camel spiders, which is considerably greater than any other pitfall trap in our study. Nine of the 11 samples were early instars, perhaps individuals of the same brood that recently hatched nearby. If we exclude this outlier, then the number of camel spider collected in middle cups and outer cups is identical (19 each). Thus, our data do not suggest a negative correlation between the effectiveness of pitfall traps and their distances from artificial light sources. We caution, however, that this result could be caused by using short drift fences, as

Table 1.—Number of lighted and dark pitfall arrays installed at four sites spanning the Mojave Desert, and the number of camel spiders collected in middle and outer pitfall traps at each site.

| Survey Location | Treatment | # of trap arrays | # in middle traps | # in outer traps | Mean # per middle trap | Mean # per pair of outer traps | Total |
|----------------------|-----------|---------------------|----------------------|---------------------|---------------------------|--------------------------------------|-------|
| Newberry Springs, CA | lighted | 2 | 3 | 4 | 1.5 | 2.0 | 7 |
| | dark | 2 | 0 | 0 | 0.0 | 0.0 | 0 |
| Mecca Road, NV | lighted | 3 | 1 | 7 | 0.3 | 2.3 | 8 |
| | dark | 3 | 0 | 0 | 0.0 | 0.0 | 0 |
| Enterprise, NV | lighted | 3 | 11 | 5 | 3.7 | 1.7 | 16 |
| | dark | 3 | 0 | 1 | 0.0 | 0.5 | 1 |
| Oro Grande, CA | lighted | 3 | 13 | 5 | 4.3 | 1.7 | 18 |
| | dark | 3 | 0 | 0 | 0.0 | 0.0 | 0 |
| All Sites Combined | lighted | 11 | 28 | 21 | 2.6 | 1.9 | 49 |
| | dark | 11 | 0 | 1 | 0 | 0.1 | 1 |

the outer pitfall traps were still well-illuminated by the lanterns hung in the middle of each array. We predict that pitfall arrays with longer drift fences might still benefit from the use of multiple lights strung along the trapline.

The success of the pitfall light trapping approach is exciting and could revitalize the study of camel spiders. Given our success, we recommend the use of these modified Caterpillar Light Trap designs with short 3-pitfall drift fences, a single light lure, and a single line of fencing, as they require fewer supplies and less time to install than longer, multi-light Caterpillar Light Traps. In addition, short arrays are easier to place along the contours of rugged terrain and can be quickly set up in a variety of habitats to maximize the number of species collected in an area. It only took us about an hour, working as a team of two, to set up six pitfall arrays. With 49 camel spiders from 11 lighted arrays, we collected an astonishing 26.7 specimens per twoperson hour of effort. This rate is close to an order of magnitude greater than collection rates using previous approaches; such as actively searching near permanent lights (3.8 ± 3.10 per hour) and waiting for camel spiders to approach temporary light sources (1.2 \pm 1.9 per hour) (Cushing & González-Santillán 2018).

To the best of our knowledge this study represents only the second study to test the light attraction hypotheses in camel spiders. Linsenmair (1968) used a circular arena with a light suspended near one side to test the hypothesis that solifuges display positive phototaxis. He found that two species of Galeodidae demonstrated a menotactic orientation to the light stimulus (or a movement in a relatively constant angle towards the lit side of the arena). Previous authors appear to have known that lights attract camel spiders, but why? One hypothesis is that camel spiders navigate to and from permanent or semi-permanent burrows at night by traveling at a constant angle to the moon or stars, which they can confuse with nearby artificial lights. Trying to maintain a constant angle to the lights could cause them to spiral into the light source, a hypothesis that has been proposed to explain positive phototaxis in night-flying insects such as moths (reviewed in Frank et al. 2006). Our observations in the field, however, make this unlikely, as camel spiders seem to travel in straighter trajectories towards lights, not spirals. An alternate hypothesis is that camel spiders somehow sense the increased insect activity at lights, perhaps by visual or vibrational stimuli, and fall in the traps while trying to catch insect prey. The lighted arrays attracted more insect bycatch, providing indirect support for this hypothesis. Another hypothesis is that solifuges are attracted to light/dark contrasting stimuli in the environment since such contrasting areas may signal a hilltop or high point (such as a bush) where hilltopping insects are more likely to be found. Hilltopping is a common mating strategy for a variety of insects in low resource environments such as the desert habitats where solifuges are common (Alcock & Dodson 2008) and nocturnal hilltopping insect species are thought to also be common (Skevington 2008). Thus, solifuges may have evolved a positive attraction to light/dark contrasting areas in their environment where concentrations of insect prey are more likely and artificial lights create a superstimulus.

Additional research on collecting methodology could test these ideas and further refine pitfall light trapping designs, as several questions remain unanswered. Does fence length influence trapping success? What about light luminosity and spectral composition? We hope to see these questions explored and camel spider trap designs further optimized. Research on camel spiders has been notoriously difficult, but the future appears 'bright.'

ACKNOWLEDGMENTS

We thank George M. Graham for assistance in the field. Ryan R. Jones graciously helped us acquire permits to collect camel spiders throughout the Southwest. Funding for this project was provided by NSF grant DEB-1754030 awarded to MRG, NSF grant DEB-

1754587 awarded to PEC, and the Marc Freeman Scholarship fund at Eastern Connecticut State University awarded to MBMP. W. Brett Mattingly and two anonymous reviewers provided important comments that improved the manuscript.

LITERATURE CITED

- Alcock, J. & G. Dodson. 2008. The diverse mating systems of hilltopping insects. American Entomologist 54:80–87.
- Bird, T., R.R.A. Wharton & L. Prendini. 2015. Cheliceral morphology in Solifugae (Arachnida): primary homology, terminology, and character survey. Bulletin of the American Museum of Natural History 394: 1–355.
- Botero-Trujillo, R., R. Ott & L.S. Carvalho. 2017. Systematic revision and phylogeny of the South American sun-spider genus *Gaucha* Mello-Leitão (Solifugae: Mummuciidae), with description of four new species and two new generic synonymies. Arthropod Systematics & Phylogeny 75:3–44.
- Cloudsley-Thompson, J.L. 1961. Some aspects of the physiology and behaviour of *Galeodes arabs*. Entomologia Experimentalis et Applicata 4:257–263.
- Cloudsley-Thompson, J.L. 1977. Adaptational biology of Solifugae (Solpugida). Bulletin of the British Arachnological Society 4:61–71
- Conrad, K.R. & P.E. Cushing. 2011. Observations on hunting behavior of juvenile *Chanbria* (Solifugae: Eremobatidae). Journal of Arachnology 39:183–184.
- Cushing, P.E. & P. Casto. 2012. Preliminary survey of the setal and sensory structures on the pedipalps of camel spiders (Arachnida: Solifugae). Journal of Arachnology 40:123–127.
- Cushing, P.E. & E. González-Santillán. 2018. Capturing the elusive camel spider (Arachnida: Solifugae): effective methods for attracting and capturing solifuges. Journal of Arachnology 46:384–387.
- Cushing, P.E., J.O. Brookhart, H.-J. Kleebe, G. Zito & P. Payne. 2005. The suctorial organ of the Solifugidae (Arachnida, Solifugae). Arthropod Structure & Development 34:397–406.
- Cushing, P.E., P. Casto, E.D. Knowlton, S. Royer, D. Laudier, D.D. Gaffin et al. 2014. Comparative morphology and functional significance of setae called papillae on the pedipalps of male camel spiders (Arachnida, Solifugae). Annals of the Entomological Society of America 107:510–520.
- Cushing, P.E., M.R. Graham, L. Prendini & J.O. Brookhart. 2015. A multilocus molecular phylogeny of the endemic North American camel spider family Eremobatidae (Arachnida: Solifugae). Molecular Phylogenetics and Evolution 92:280–293.
- Frank, K.D., C. Rich & T. Longcore. 2006. Effects of artificial night lighting on moths. Pp. 305–344. *In* Ecological Consequences of Artificial Night Lighting. (C. Rich, T. Longcore, eds.). Island Press, Washington D.C.
- Franz-Guess, S. & J.M. Starck. 2016. Histological and ultrastructural analysis of the respiratory tracheae of *Galeodes granti* (Chelicerata: Solifugae). Arthropod Structure & Development 45:452–461.
- Franz-Guess, S., B.J. Klußmann-Fricke, C.S. Wirkner, L. Prendini & J.M. Starck. 2016. Morphology of the tracheal system of camel spiders (Chelicerata: Solifugae) based on micro-CT and 3D-reconstruction in exemplar species from three families. Arthropod Structure & Development 45:440–451.
- Klann, A.E. & G. Alberti. 2010. Histological and ultrastructural characterization of the alimentary system of solifuges (Arachnida, Solifugae). Journal of Morphology 271:225–243.
- Klann, A.E., T. Bird, A.V. Peretti, A.V. Gromov & G. Alberti. 2009. Ultrastructure of spermatozoa of solifuges (Arachnida, Solifugae): Possible characters for their phylogeny. Tissue and Cell 41:91–103.
- Klann, A.E., A.V. Gromov, P.E. Cushing, A.V. Peretti & G. Alberti. 2008. The anatomy and ultrastructure of the suctorial organ of

- Solifugae (Arachnida). Arthropod Structure and Development 37:3-12.
- Linsenmair, K.E. 1968. Zur Lichtorientierung der Walzenspinnen (Arachnida, Solifugae). Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 74:254–273.
- Maddahi, H., M. Khazanehdari, M. Aliabadian, H.G. Kami, A. Mirshamsi & O. Mirshamsi. 2017. Mitochondrial DNA phylogeny of camel spiders (Arachnida: Solifugae) from Iran. Mitochondrial DNA Part A 28:909–919. dOI: 10.1080/24701394.2016.1209194.
- Pocock, R.I. 1897. On the genera and species of tropical African arachnids of the order Solifugae with notes upon the taxonomy and habits of the group. Annals and Magazine of Natural History, series 6, 20:249–272.
- Punzo, F. 1998. The Biology of Camel-Spiders (Arachnida, Solifugae). Kluwer Academic Publishers, Boston/Dordrecht/London.
- Skevington, J. 2008. Hilltopping. Pp. 1799–1807. In Encyclopedia of Entomology, 2nd Edition. (J.L. Capinera, ed.) Spring Verlag, Heidelberg.
- Turk, F.A. 1947. On two new species of the family Galeodidae (Solifuga) from Asia. Journal of Natural History 14:74–80.
- Vink, C.J., S.M. Thomas, P. Paquin, C.Y. Hayashi & M. Hedin. 2005. The effects of preservatives and temperatures on arachnid DNA. Invertebrate Systematics 19:99–104.

Manuscript received 15 September 2018, revised 19 December 2018.