



Research

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Nocturnal foraging enhanced by enlarged secondary eyes in a net-casting spider

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Animals that possess extreme sensory structures are predicted to have a related extreme behavioural function. This study focuses on one such extreme sensory structure—the posterior median eyes of the net-casting spider *Deinopis spinosa*. Although past research has implicated the importance of vision in the nocturnal foraging habits of *Deinopis*, no direct link between vision in the enlarged eyes and nocturnal foraging has yet been made. To directly test the hypothesis that the enlarged posterior median eyes facilitate visually based nocturnal prey capture, we conducted repeated-measures, visual occlusion trials in both natural and laboratory settings. Our results indicate that *D. spinosa* relies heavily on visual cues detected by the posterior median eyes to capture cursorial prey items. We suggest that the enlarged posterior median eyes benefit *D. spinosa* not only through increased diet breadth, but also by allowing spiders to remain active solely at night, thus evading predation by diurnal animals.

1. Introduction

The ability to gather and process information from the environment, made possible by an animal's sensory systems, is integral to the success and survival of all animals. Over evolutionary time, selection has presumably favoured enhancements of sensory systems that provide the greatest benefits to individuals, while also favouring low costs [1]. The often observed match between the capacities of an animal's sensory systems and the animal's apparent needs is a testament to such selection [2,3]. Thus, when we observe extreme sensory structures unique to particular animals, we often hypothesize an associated extreme sensory-specific function.

Although the majority of spiders have eight eyes, most are considered to have relatively poor eyesight [4]. Two notable exceptions are the ground-dwelling spider families Salticidae (the jumping spiders) and Lycosidae (the wolf spiders). Spiders from both families possess enlarged eyes used in foraging and mating contexts [5–10]. In stark contrast with their ground-dwelling relatives, an enhanced visual system is rare in web-building spiders, which tend to rely more on vibrational cues in their web for foraging and mating [4,11,12]. Indeed, while enhanced visual systems are uncommon across the 114 currently described families of spider [13], they are almost unheard of among web-building spiders. Members of the net-casting spider genus *Deinopis* are a rare, if not unique, exception.

Net-casting spiders get their name from their unique foraging strategy. Following sunset, individuals construct a non-sticky silk frame resembling the letter 'A' (figure 1*a*). They hang upside down from this frame, holding a rectangular capture snare made of woolly silk (figure 1*b*) with their front three pairs of legs. From this position, foraging spiders lunge towards prey, expanding the snare and actively ensnaring prey with surprising accuracy given the nocturnal nature of *Deinopis* [14]. Deinopid spiders can capture both cursorial (walking) and aerial (flying) prey items using this net-casting technique [15].

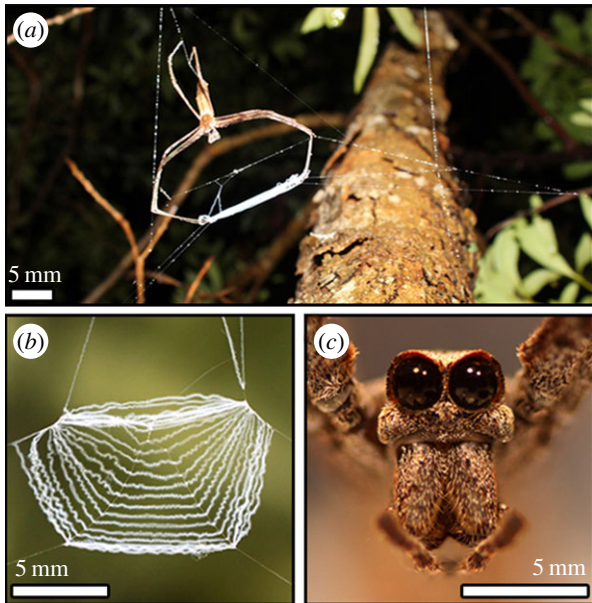


Figure 1. (a) *Deinopis* spider in foraging posture; (b) a capture snare made from woolly silk; and (c) frontal view of a *Deinopis* spider's enlarged posterior median eyes. Scale bars, 5 mm.

Net-casting spiders in the genus *Deinopis* possess uniquely enlarged eyes that appear physiologically well suited for detecting movement in low-light-level conditions [16]. Unlike the enlarged primary eyes of jumping spiders, it is a pair of secondary eyes, the posterior median eyes, of *Deinopis* spiders that are greatly enlarged (figure 1c). These eyes are reported to be 2000 times more sensitive to light than human eyes [16] and are presumed to aid in their unique 'net-casting' foraging strategy [14,15], but this function has yet to be tested directly. To this end, we use repeated-measures, visual occlusion experiments in the field and in the laboratory to test the hypothesis that the posterior median eyes of *D. spinosa* function to increase visually based nocturnal foraging efficacy.

2. Material and methods

(a) Field experiment

Field trials were conducted during Spring 2013 at Paynes Prairie State Park located in Micanopy, FL, USA. A total of 29 *D. spinosa* were used in field trials (eight mature females, eight penultimate females, eight penultimate males and five juveniles). Mature males do not engage in net-casting, and thus were not included in this experiment.

Each field-collected individual was observed during natural foraging behaviour under two separate conditions: (i) visually occluded and (ii) sham/non-visually occluded, hereafter referred to as 'control'. Following Zurek *et al.* [17], we temporarily occluded posterior median eyes by applying opaque dental silicone using a wooden toothpick. Foraging behaviour was recorded using portable infrared cameras. We quantified multiple variables from the recorded foraging trials: prey capture success (yes/no within a trial), number of prey captures, prey type (cursorial versus aerial) and estimated prey size. Generalized linear mixed models were used to compare treatment effects on within-individual foraging trial outcomes. Related samples McNemar tests were used to compare the effects of treatment on the likelihood to capture either cursorial or aerial prey items. A Mann-Whitney *U* test was performed to compare size between cursorial and aerial prey items captured. For additional methodological and statistical details, see the electronic supplementary material.

(b) Laboratory experiment

To control for foraging site location and prey abundance, we conducted follow-up visual occlusion trials in a laboratory setting. A total of 16 *D. spinosa* were used in laboratory trials (six mature females, three penultimate females, five penultimate males and two juveniles).

Similar to field trials, we recorded two foraging bouts per focal spider: (i) visually occluded and (ii) control. We adopted identical manipulation protocols and recording methods from field trials. Following manipulation, spiders were placed in cylindrical testing arenas, one spider per arena. Crickets, *Acheta domesticus*, were used as prey with one cricket per trial. Variables quantified from recorded video include: prey capture success (yes/no within a trial) and latency to prey capture (in seconds). A generalized linear mixed model was used to compare within-individual capture latencies between treatments. A related samples McNemar test was used to compare the effects of treatment on the likelihood to capture prey. For additional methodological and statistical details, see the electronic supplementary material.

3. Results

(a) Field experiment

Individual *D. spinosa* were less effective at foraging when their enlarged posterior median eyes were occluded. Visually occluded spiders showed a significantly lower likelihood to catch prey ($B = 1.92$, $Z = 2.78$, $p = 0.005$, figure 2a) as well as a lower quantity of prey items caught ($B = 1.22$, $Z = 2.406$, $p = 0.016$). Regarding prey item type, visually occluded spiders were less likely to capture cursorial prey ($N = 29$, $\chi^2 = 5.143$, $p = 0.016$, figure 2b), whereas visual occlusion did not affect a spider's ability to capture aerial prey ($N = 29$, $\chi^2 = 0.444$, $p = 0.508$, figure 2c).

Cursorial prey were significantly larger than aerial prey ($N = 21$, $Z = 2.537$, $p = 0.011$; average prey length of cursorial: 6.03 mm (s.d. = 2.17 mm) versus aerial: 3.27 mm (s.d. = 1.55 mm)). Prey capture success and number of prey items were neither affected by treatment order, sex, life stage nor size (see the electronic supplementary material).

(b) Laboratory experiment

Similar to field trials, *D. spinosa* were less likely to capture prey while visually occluded during laboratory trials ($N = 16$, $\chi^2 = 7.111$, $p = 0.004$). In all cases of successful foraging by visually occluded individuals, prey walked into the support threads of the web ($N = 7$). For the spiders that captured prey under both visual occlusion and control treatments ($N = 7$), the time to prey capture was greater when visually occluded ($B = 2.15$, $Z = 51.70$, $p < 0.0001$; visual occlusion 784 ± 638 s versus control: 76 ± 60 s) and this latency to prey capture was not affected by treatment order, sex, life stage or size (see the electronic supplementary material).

4. Discussion

Results from both field and laboratory experiments support our hypothesized relationship between an extreme sensory structure—enlarged posterior median eyes—and an extreme behavioural function—visually based nocturnal foraging—in the net-casting spider *D. spinosa*. Our findings corroborate past suggestions of *Deinopis* spiders using visual cues in foraging behaviour and confirm the expectation that

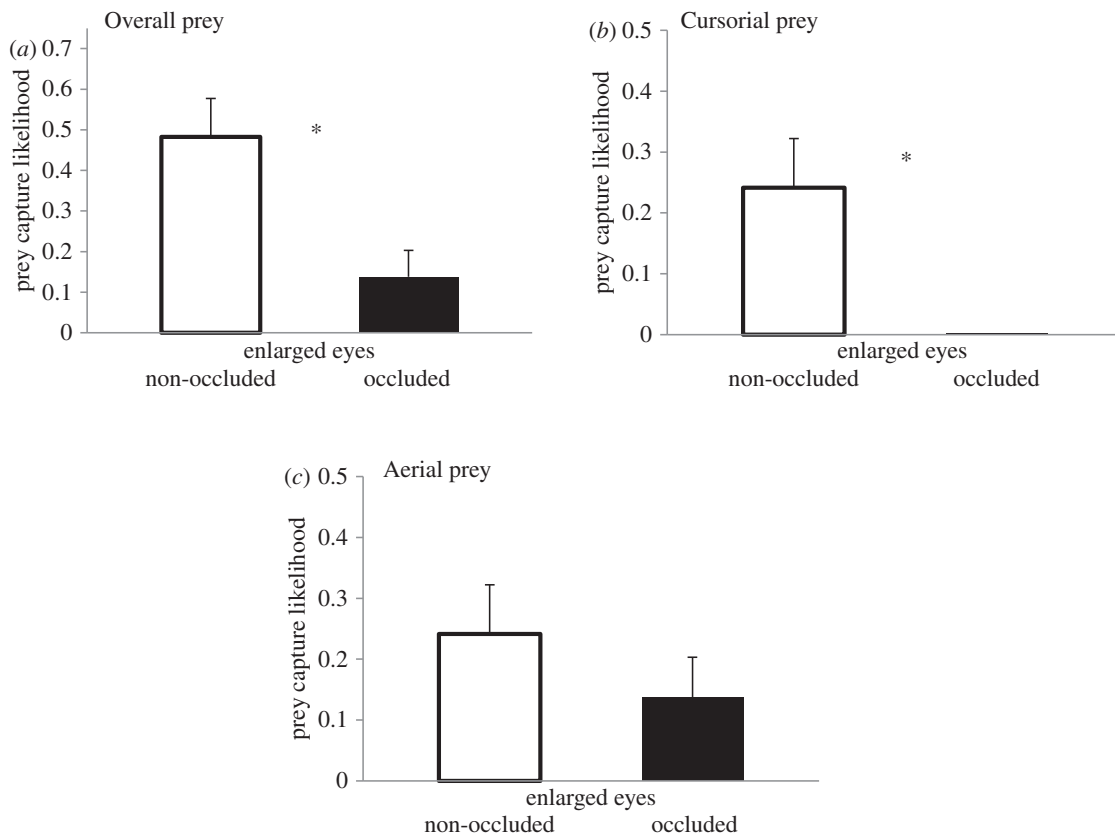


Figure 2. (a) Graphical representation of the effect of visual occlusion on overall likelihood to capture prey in the field experiment. Likelihood to capture prey was significantly lower while spiders were visually occluded. Prey item type is further subdivided by cursorial prey and aerial prey. Visually occluded spiders were unable to capture cursorial prey (b), while occlusion had no effect on likelihood to capture aerial prey (c). Asterisks represent statistically significant differences.

the posterior median eyes of *D. spinosa* are important in visually based nocturnal prey capture [14,15]. Our results suggest that *D. spinosa* depend on their enlarged eyes for cursorial, but not aerial, prey capture. We propose that the enlarged posterior median eyes of these spiders ultimately provide two related functional benefits: (i) increased diet breadth and (ii) the ability to restrict foraging to low-light (i.e. nocturnal) conditions.

Prior research had implicated the importance of visually based nocturnal foraging in net-casting spiders, yet without confirming a direct link to the unusually large posterior median eyes [14,15]. Coddington & Sobrevila [15] described two stereotyped attacks of *D. spinosa*, termed ‘forward strikes’ and ‘backward strikes’, and concluded that ‘forward strikes’ are visually guided, as spiders would net-cast downwards atop dead insects presented on a wire. Our field and laboratory trials corroborate these prior observations and highlight a previously undocumented relationship between prey niche partitioning (cursorial versus aerial) and visual input, namely that vision-based foraging may relate predominantly to cursorial prey, captured through ‘forward strikes’. Without the ability to perceive visual cues collected by the enlarged eyes, *D. spinosa* seem unable to capture cursorial prey items in their natural habitat while the occlusion of visual perception did not suppress aerial prey capture ability. As cursorial prey items were larger and potentially more nutritious than aerial prey items, we hypothesize that the posterior median eyes are the result, at least in part, of selection for increased diet breadth—the ability to incorporate larger, more nutritious cursorial prey. It has been suggested that web-building spiders depend on rare,

large prey items to survive and produce eggs ([18,19]; but see [20]); thus the unique foraging tactics and specialized visual capabilities of *Deinopsis* spiders might increase their ability to capture higher quality prey items typically out of reach of the average web-building spider. Indeed, recent phylogenetic analyses suggest that this net-casting technique arose in parallel with a vastly increased abundance of cursorial insect prey during the Cretaceous Terrestrial Revolution [21]. The recently hypothesized relationships among spider taxa indicate that deinopid spiders diverged when many orb-web lineages abandoned web-building as a foraging tactic [21], suggesting that visually guided net-casting might have been one successful, though seemingly unorthodox, strategy for taking advantage of newly available prey items.

Deinopsis spinosa is a strictly nocturnal species that spends its daylight hours mimicking palm fronds [22]. Predation pressure has been hypothesized to favour nocturnal activity patterns across diverse taxa [23]. Anecdotal daylight observations in the habitat of *D. spinosa* reveal highly cryptic spiders that remain motionless in a habitat full of diurnal, visually oriented predators, shown previously to eat or parasitize spiders (e.g. song birds [24,25], parasitoid wasps [26] and jumping spiders [8]). We hypothesize that diurnal predation risk has played a role in the evolution of the obligate nocturnal lifestyle and associated sensory specializations observed in the net-casting spider *D. spinosa*. Interestingly, not all net-casting spiders possess enlarged posterior median eyes [27], providing a natural experiment to assess relationships between predation pressure, foraging activity and sensory structures.

In summary, we have shown that a nocturnal predator heavily invested in low-light level vision through extreme

sensory structures receives significant benefits from these specializations in the form of more and potentially higher quality prey. We hypothesize that selection for both increased diet breadth and decreased predation led to this extreme sensory system. Selection for an increase in diet breadth is also proposed to have influenced the sensory specializations of the star-nosed mole, a charismatic, and now classic, example of sensory system specialization [2]. Future comparative studies across genera and species of net-casting spider will further elucidate the relative importance of distinct selective forces on the evolution of this unusual sensory system.

Ethics. The work conducted complies with the ethical regulations in the USA.

Data accessibility. Datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. J.A.S. and E.A.H. designed the experiments, J.A.S. executed the experiments, and J.A.S. and E.A.H. analysed and interpreted data. J.A.S. drafted the manuscript, which was edited by both authors. Both authors approved the current version, and agree to be accountable for its contents.

Competing interests. We have no competing interests.

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References

- Niven JE, Laughlin SB. 2008 Energy limitation as a selective pressure on the evolution of sensory systems. *J. Exp. Biol.* **211**, 1792–1804. (doi:10.1242/jeb.017574)
- Catania KC. 2012 Evolution of brains and behavior for optimal foraging: a tale of two predators. *Proc. Natl Acad. Sci. USA* **109**, 10 701–10 708. (doi:10.1073/pnas.1201885109)
- Warrant EJ, Johnsen S. 2013 Vision and the light environment. *Curr. Biol.* **23**, 990–994. (doi:10.1016/j.cub.2013.10.019)
- Foelix R. 2010 *Biology of spiders*. Oxford, UK: Oxford University Press.
- Land MF. 1969 Structure of the retina of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J. Exp. Biol.* **51**, 443–470.
- Rovner JS. 1993 Visually mediated responses in the lycosid spider *Rabidosia rabida*: the roles of different pairs of eyes. *Mem. Qld Mus.* **33**, 635–638.
- Rovner JS. 1996 Conspecific interactions in the lycosid spider *Rabidosia rabida*: the roles of different senses. *J. Arachnol.* **24**, 16–23.
- Jackson RR, Pollard SD. 1996 Predatory behavior of jumping spiders. *Annu. Rev. Entomol.* **41**, 287–308. (doi:10.1146/annurev.en.41.010196.001443)
- Clemente CJ, McMasters KA, Fox E, Meldrums L, Stewart T, Main BY. 2010 The visual system of the Australian wolf spider *Lycosa leuckartii* (Araneae, Lycosidae): visual acuity and the functional role of the eyes. *J. Arachnol.* **38**, 398–406. (doi:10.1636/B09-96.1)
- Taylor LA, McGraw KJ. 2013 Male ornamental coloration improves courtship success in a jumping spider, but only in the sun. *Behav. Ecol.* **24**, 955–967. (doi:10.1093/beheco/art011)
- Clemente CJ, McMaster KA, Fox L, Meldrum L, Main BY, Stewart T. 2005 Visual acuity of the sheet-web building spider *Badumna insignis* (Araneae, Desidae). *J. Arachnol.* **33**, 726–734. (doi:10.1636/S04-35.1)
- Herberstein ME, Wignall AE, Hebets EA, Schneider JM. 2014 Dangerous mating systems: signal complexity, signal content and neural capacity in spiders. *Neurosci. Biobehav. Rev.* **46**, 509–518. (doi:10.1016/j.neubiorev.2014.07.018)
- Natural History Museum, Bern. 2015 *World Spider Catalog, Version 16.5*. Bern, Switzerland: Natural History Museum.
- Robinson MH, Robinson B. 1971 The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). *Am. Midland Nat.* **85**, 85–96. (doi:10.2307/2423914)
- Coddington JA, Sobrevila C. 1987 Web manipulation and two stereotyped attack behaviors in the ogre-faced spider *Deinopis spinosus* Marx (Araneae, Deinopidae). *J. Arachnol.* **15**, 213–225.
- Blest AD, Land MF. 1977 The physiological optics of *Dinopis subrufus* (L. Koch): a fish-lens in a spider. *Proc. R. Soc. Lond. B* **196**, 197–222. (doi:10.1098/rspb.1977.0037)
- Zurek DB, Taylor AJ, Evans CS, Nelson XJ. 2010 The role of the anterior lateral eyes in the vision-based behaviour of jumping spiders. *J. Exp. Biol.* **213**, 2372–2378. (doi:10.1242/jeb.042382)
- Venner S, Casas J. 2005 Spider webs designed for rare but life-saving catches. *Proc. R. Soc. B* **272**, 1587–1592. (doi:10.1098/rspb.2005.3114)
- Blackledge TA, Kuntner M, Agnarsson I. 2011 The form and function of spider orb webs: evolution from silk to ecosystems. *Adv. Insect Physiol.* **41**, 175–262. (doi:10.1016/B978-0-12-415919-8.00004-5)
- Eberhard WG. 2013 The rare large prey hypothesis for orb web evolution: a critique. *J. Arachnol.* **41**, 76–80. (doi:10.1636/B12-34.1)
- Garrison NL *et al.* 2015 Spider phylogenomics: untangling the Spider Tree of Life. *PeerJ PrePrints* **3**, e1852. (doi:10.7287/peerj.preprints.1482v1)
- Getty RM, Coyle FA. 1996 Observations on prey capture and anti-predator behaviors of ogre-faced spiders (*Deinopis*) in southern Costa Rica (Araneae, Deinopidae). *J. Arachnol.* **24**, 93–100.
- Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. 2014 *Visual ecology*. Princeton, NJ: Princeton University Press.
- Durst SL, Theimer TC, Paxton EH, Sogge MK. 2008 Age, habitat, and yearly variation in the diet of a generalist insectivore, the southwestern willow flycatcher. *Condor* **110**, 514–525. (doi:10.1525/cond.2008.8493)
- Thiollay JM. 1998 Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. *Oikos* **53**, 17–30. (doi:10.2307/3565658)
- Coville RE. 1987 Spider-hunting sphecid wasps. In *Eco physiology of spiders* (ed. W Nentwig). New York, NY: Springer.
- Coddington JA, Kuntner M, Opell BD. 2012 Systematics of the spider family Deinopidae with a revision of the genus *Menneus*. *Smithson. Contrib. Zool.* **636**, 1–61. (doi:10.5479/si.00810282.636.1)