2015. Journal of Arachnology 43:214–219

Cave-epigean behavioral variation of the whip spider *Phrynus longipes* (Arachnida: Amblypygi) evidenced by activity, vigilance, and aggression

Kenneth James Chapin: Department of Ecology & Evolutionary Biology, University of California, Los Angeles, 612 Charles E. Young Drive East, Los Angeles, CA 92704-7246. E-mail: chapinkj@gmail.com

Abstract. Caves are peculiar ecosystems; they are most often small, isolated habitats that lack the energy that sunlight provides. Cave-adapted species, isolated from epigean (i.e., surface) selection pressures, have been discovered with aphotic adaptations like blindness, depigmentation, and enhanced extra-optic sensory systems. This evolutionary process, however, only occurs in a fraction of cave ecosystems. Many cave species, especially those in tropical latitudes, occur with epigean conspecifics with ongoing gene flow and epigean migration. This includes populations of the amblypygid *Phrynus longipes* (Pocock 1894), which occur in both epigean and cave environments. I hypothesized that cave and epigean populations exhibit behavioral variation to meet the selection pressures of their respective environments. I conducted open-arena and interaction behavioral assays to test for behavioral variation between populations. Assays revealed that cave and epigean amblypygids exhibited environment-specific behavioral variation. Cave animals were more vigilant and engaged in hunting behaviors, but were less active in general, relative to epigean conspecifics. Comparative modeling indicated that aggressive behaviors during agonistic interactions were the best predictors of environment. Indeed, epigean interactions escalated to physical aggression sooner and included longer weaponry displays than did the interactions of cave conspecifics. Trial design allowed for measurements of territorial behavior, which showed that residency effects were more profound in epigean interactions than in those of cave conspecifics. The high density of amblypygids in the cave population may have resulted in more tolerant, less aggressive behaviors relative to epigean conspecifics. Thus, these findings fit the ecological and demographic conditions of each environment.

Keywords: Agonistic, personality, populations, Puerto Rico, speleology, territory

Our understanding of adaptation to cave environments is dominated by the morphological consequences of aphotic conditions, including eye reduction or loss, depigmentation, and advanced extra-optic sensory systems (Montgomery et al. 2001; Culver & Pipan 2009). Caves, of course, are not only of note for their darkness; cave ecosystems are rare and fragile (Elliott 2005), with constituents seeded from, and nourished by, the surface environment. Cave-living species were once thought of as the result of regressive evolution or relaxed selection (Barr 1968; Romero 2009). We now understand caves as unique ecosystems with their own selective pressures and important connections with the surrounding surface environment (Krajick 2001). Despite this, the relationship of cave populations with epigean (surface-dwelling) conspecifics has rarely been investigated (Culver & Pipan 2009).

Darkness is the ubiquitous feature of the ecosystems, but darkness has farther-reaching effects than just promoting the evolution of extra-optic sensory systems. Darkness means that cave systems lack the energy source of nearly all other ecosystems: the sun. Instead, trophic levels begin with an influx of energy from animals that forage in epigean environments but defecate in caves, usually bats or birds (Culver & Pipan 2009). The number of trophic levels and population sizes at each are determined by this initial energy influx, which can vary widely depending on the population size of the energy transport species. Additionally, cave species richness is often small, following species-area theory (Arrhenius 1921; Christman & Culver 2001). This results in simplified ecosystems (at least among macroorganisms) that can support large populations of relatively few species (Culver & Sket 2000; Culver & Pipan 2009).

The stark contrast between the cave and epigean environments suggests that cave animals should adapt behaviorally to a subterranean life history. Indeed, many of the most studied caves are found to house hypogean (cave-dwelling) endemics (Culver & Sket 2000). Cave populations at tropical latitudes, however, are much less studied but are likely to have epigean conspecifics; glaciation did not extirpate epigean populations, as is the hypothesized case for temperate caves (Niemiller et al. 2008). Thus, many tropical cave communities include the same species as epigean environments, but with greatly different selection pressures that potentially promote behavioral variation.

Behavioral phenotypes, being highly labile, are often the first to change in a new environment (Mayr 1963; Blomberg et al. 2003). For example, animals that colonize new habitat (Duckworth 2006) or occur along an altitudinal gradient (Purcell & Aviles 2007) exhibit behavioral variation across habitats, the presumed consequences of which are behavioral trade-offs suited for one environment but not the other. In this scenario, natural selection for either cave-adapted behavioral phenotypes or behavioral plasticity could result in distinct behavioral variation between cave and epigean populations. Indeed, tropical cave systems may house cryptic species only diagnosable by behavioral variation or genetic analyses. Alternatively, tropical cave systems with migration between cave and epigean environments may support metapopulations with limited, but measurable, behavioral variation.

In the Puerto Rican karst caves of this study, arachnids make up the majority of predators in high energy caves, with amblypygids (Arachnida: Amblypygi) being the large majority. Amblypygi is a pantropical order of some 160 nocturnal, and often cannibalistic, predators outfitted with extremely elongate front legs used to sense their environment and raptorial, claw-like pedipalps used for ambush prey capture (i.e., ‘‘sit-and-wait’’ predation) and defense (Weygoldt 2000).

Figure 1.—The cave population of *Phrynus longipes* occurs at extreme densities. Individuals are commonly found within antenniform legspan of each other.

Amblypygids have gained attention for their exceptional neurobiology and sensory systems (Strausfeld 1998; Hebets & Chapman 2000; Foelix & Hebets 2001; Santer & Hebets 2008, 2011). More recent research has made advances in connecting these proximate studies with ultimate, field-based research (Bloch & Weiss 2002; Hebets 2002; Chapin 2011, 2014; Carvalho et al. 2012; Porto & Peixoto 2013, Hebets et al. 2014). The amblypygid *Phrynus longipes* (Pocock 1894) appears to reach extreme population densities (Fig. 1) in high-energy Puerto Rican caves. This observation, while anecdotal, is surprising, given the solitary, aggressive, and cannibalistic nature of the species. Thus, I hypothesized that cave animals exhibit more tolerant behaviors to meet the high conspecific density of the cave environment. Cannibalism may be a greater threat to cave amblypygi, while interspecific predators are likely more important for surface conspecifics. Indeed, patterns of reduced aggression in cave animals have been shown in disparate taxa (Burchards et al. 1985; Parzefall 2001). Thus, I hypothesized that cave populations of *P. longipes* exhibit distinctly different behaviors characterized by tolerance and reduced aggression.

METHODS

Study site.—Assistants and I collected cave and epigean *P. longipes* by hand from Cueva de los Culebrones and the surrounding forest at Mata de Plátano Natural Reserve (MPNR) in the karst belt of Puerto Rico (generally located at 18.414°N, 66.726°W) in September 2012. Cueva de los Culebrones is a hot subtropical cave with an enormous and diverse bat population estimated at 300,000 individuals across six species (Rodríguez-Durán 1996; Puente-Rolón & Bird-Picó 2004). The cave houses a simple environment, with bat guano supplying initial energy instead of sunlight. Cockroaches dominate as the primary consumer macroinvertebrates, and serve as the main prey items for *P. longipes*, which are the dominant predators. Amblypygids are commonly found in a myriad of cracks and crevices in the cave wall. Data loggers placed in and outside the cave recorded $\bar{x} \pm$ sd temperatures of 26.68°C ± 0.43 (range: 25.56 – 28.89°C) within the cave and 24.57°C ± 1.92 (21.11 – 30.56°C) in the epigean environment. Relative humidity was recorded at 99.36% ± 1.33 (91.50 – 100%) in the cave and 93.23% ± 3.44 (74.50 – 96.50%) on the surface. Temperature increased linearly an estimated 0.06°C per meter into the cave ($\beta = 0.06$, Adjusted $R^2_{11} = 0.96$, $P < 0.0001$). The amblypygid population terminated at a portion of the cave with low oxygen, termed the dead zone, beginning at ca. 120 m from the entrance. The cave continues for several hundred meters, but amblypygids were never found beyond this point. The floor of the cave entrance was generally steep and muddy, but amblypygids could move between cave and epigean environments via large connected rock outcroppings on either side of the main entrance.

Population density estimate.—I conducted mark-recapture surveys to estimate cave population density in September 2012 from ca. 2000 to 0400 h along five cave sections by capturing all observed *P. longipes* and marking them with paint on the prosoma dorsum. Animals were recaptured the following night and the proportion of marked and unmarked captures were used in population estimates. The short latency between marking and recapture surveys allowed for Chapman-Peterson estimates, which assume closed populations (i.e., no birth, death, migration, or mark loss). Population estimates for the surface were also conducted in this manner, but individuals were too uncommon and dispersed in the forest to meet the assumptions of population estimate statistics, so minimum number known alive was calculated instead.

Behavioral trials.—I tested cave and epigean individuals for behavioral variation via two successive assays. First, a 10 min open-arena assay assessed activity level, vigilance, and sit-and-wait responses when exposed to a novel environment. Next, a 45 min agonism assay assessed latency to physical aggression and weaponry displays of paired individuals from the same environment. Open-arena assays were scored using three groups of behaviors developed from direct observation of *P. longipes* and published ethograms of other Amblypygi species (Fowler-Finn & Hebets 2006; Walsh & Rayor 2008): sit-and-wait, vigilance, and activity. Behaviors were pooled by function, which coincided with the morphology involved in the behavioral action. The sit-and-wait category included grooming and prey-waiting behaviors. Both of these behaviors only occur when animals are not exploring their environment or threatened. Grooming is achieved via specialized combing structures on the pedipalps that clear the antenniform and walking legs of debris (Weygoldt 2000). Since amblypygids are sit-and-wait predators, they often sit for hours with pedipalps extended awaiting prey (Weygoldt 2000). Thus, these behaviors are indicative of a calm or at-rest state (Weygoldt 2000). The vigilance category included tactile and olfactory exploration

Table 1.—Mark-recapture population estimates (Chapman-Peterson estimate ± 95% confidence interval), minimum number known alive (MNKA), and individual per area estimates for five sections of the cave wall 0–2 m from the cave floor. Overall, there are estimated to be approximately two whip spiders m^{-2}.

	Section 1	Section 2	Section 3	Section 4	Section 5	Overall
Section depth	43.6	50.7	60.8	74.1	84.5	84.5
MNKA	36	28	31	62	53	237
MNKA m^{-2}	0.41	1.97	1.53	2.33	1.12	1.40
Estimate	56 ± 107	42 ± 73	39 ± 66	90 ± 221	63 ± 121	335 ± 1541
Estimate m^{-2}	0.64	2.95	1.93	3.38	3.03	1.98

with the antenniform legs. Amblypygids rely primarily on olfactory and tactile cues via the antenniform legs to gain information from their environment (Weygoldt 2000; Fowler-Finn & Hebets 2006; Santer & Hebets 2009). Thus, scanning and making contact with antenniform legs were measured to record vigilant behaviors. Lastly, the activity category included walking, running, and climbing using the walking legs. These behaviors are consistent with exploring the environment, and represent the activity level of individuals.

Behaviors recorded during agonistic interactions included the duration and latency (from the beginning of the interaction) of pedipalp displays, touching with the antenniform legs, flicking, fencing, and physical contact (see Fowler-Finn & Hebets 2006 for a description of these behaviors). My focus was to measure the latency to escalate agonistic interactions and the duration of displays. Agonism opponents were collected from their respective environments and randomly paired. Thus, I assumed that individuals were naïve about their opponents.

Animals were housed individually in plastic terraria with paper used for walking and hiding for 24 h prior to trials. All trials were conducted in the laboratory of MPNR after dark, in 85–95% RH and 23–27°C from 2000–0400 h. The behavioral arena was a 70 cm × 30 cm × 33 cm glass enclosure divided into two equal halves by a removable acrylic sheet and with a paper substrate. After the 10 min open-arena assay, the acrylic divider was lifted and animals were able to interact for the 45 min interaction assay. Arenas were washed with 70% isopropyl alcohol between trials (sensu Fowler-Finn & Hebets 2006). Trials were conducted in total darkness under 920 nm peak wavelength infrared LED lights using an infrared digital camera recording 640 × 480 p at 30 fps. Behaviors were recorded to the nearest frame.

Statistical analyses.—A nonmetric multidimensional scalar (NMDS) ordination using binomial deviance dissimilarity (a likelihood based version of the improved Bray-Curtis measure; Millar & Anderson 2004) was used to test if cave and epigean amblypygids exhibited distinct behaviors in open-arena assays. A NMDS was preferred over factor analyses like principle component analysis because it does not assume multivariate data normality or linearity. I compared these data in an analysis of similarity (ANOSIM) to test if cave and epigean individuals exhibited distinct behavioral repertoires. I tested interaction assays for behavioral variation using a multimodel comparative approach with logistic regressions predicting location (cave or surface; n = 42). I randomly selected one of the two opponents from each trail to be included in the analysis to avoid pseudoreplication. I chose predictor variables that lacked collinearity and represented the diversity of behavioral displays that occurred during agonistic interactions. These included pedipalp display and flicking duration, and latency to physical aggression. I then compared this global model to more parsimonious iterations using Akaike's Information Criterion corrected for small sample size (AICc) and Akaike Weights (w_i). Reviews of this information-theoretic, multimodel statistical approach can be found in Richards (2005) and Symonds & Moussalli (2011). The initial open-arena assay caused a territorial residency effect in subsequent interactions (unpublished data). Thus, I tested the effect of residency (i.e., if individuals on their side of the arena were more likely to win than when on the opponent's side) between cave and epigean populations with Wilcoxon tests. Lastly, I compared aggression levels in subsequent interactions with χ^2 tests. I conducted all statistics using R 3.0.1 and the R package vegan (Oksanen et al. 2013).

RESULTS

Population density.—The cave-wide population estimate was 335 ± 1541 (Chapman-Peterson estimate ± 95% CI) individuals in a 2 m × 123.5 m area of cave wall or a density of ca. 2 individuals m^{-2}. Densities increased with cave depth (Table 1). The minimum number known alive (MNKA) for the cave transect was 237 individuals (1.40 m^{-2}). The survey area was searched in five sections, with a two-person search time of less than 1 h per section. Comparatively, only 25 surface individuals were found during a two-person search over 12 nights lasting ca. 4 hours each night. I never found surface animals in spatial association. Thus, the cave population was extremely dense relative to epigean populations.

Behavioral trials.—The NMDS of open-arena assay behaviors produced a low stress statistic of 0.06 with two dimensions, suggesting a good fit. An ANOSIM indicated that cave (n = 70) and epigean (n = 20) individual behaviors are distinct (R = 0.14, P = 0.010, 10,000 permutations). Cave animals exhibited more vigilant and sit-and-wait behaviors, while epigean conspecifics had higher activity levels (Fig. 2).

Comparative analyses of logistic regressions of agonistic interactions found that native environment (cave or epigean) was best predicted by latency to physical aggression and duration of pedipalp displays (w_i = 0.487; Table 2). Models without pedipalp displays were only slightly worse at predicting native environment, while a model without aggression suffered substantially, with an AICc close to that of a null model (ΔAICc = 8.15).

Cave territory residents were 20% more likely to win territorial contests than cave intruders. Epigean residents,

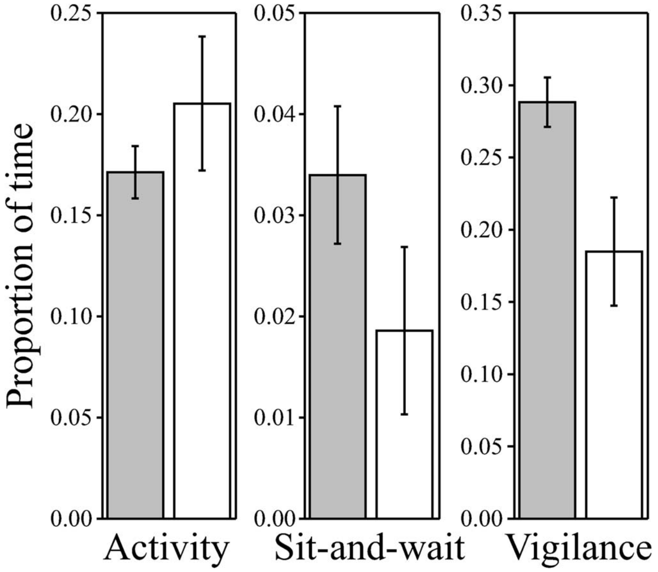

Figure 2.—The proportion of time that cave (grey) and epigean (white) animals spent enacting behaviors within three groups. Activity behaviors including walking, running, and climbing walls are measures of activity level and exploration. Sit-and-wait behaviors, including grooming and opening the pedipalps to await prey, are indicative of being at rest. Lastly, vigilance behaviors included scanning the environment and investigating points in the arena with the antenniform legs. Bars represent mean proportions spent performing each category of behavior and lines represent standard errors of the mean.

however, were 400% more likely to win than epigean intruders. Furthermore, epigean interactions escalated to physical aggression sooner ($\bar{x}$ ± SE: 3.24 s ± 1.79) than cave conspecifics (23.24 s ± 4.91; $W = 733$, $P = 0.044$). Epigean animals were not more likely to initiate agonistic interactions prior to physical contact (21.05% of trials) relative to cave conspecifics (9.84%; $\chi^2_1 = 1.66$, $P = 0.197$). Similarly, I failed to detect a difference between the latency for cave and epigean animals to escalate to physical aggression in subsequent interactions (17% vs. 36%; $\chi^2_1 = 1.94$, $P = 0.164$).

DISCUSSION

Cave and epigean individuals exhibited distinct behavioral variation; cave animals were tolerant and vigilant while epigean conspecifics were exploratory and aggressive. Additionally, cave agonistic interactions led to physical attack sooner and individuals displayed weaponry longer than cave conspecifics. The most important parameter for predicting native environment was physical aggression (Table 2). Epigean amblypygids escalated to physical aggression sooner than cave conspecifics, which was also the most important parameter for predicting native environment.

These results support the hypothesis that the high conspecific density of caves promoted conspecific tolerance. Conspecific density affects aggression levels in several other animal groups as well. For example, rodents (Davis 1958; Sachser 1986), felines (Benson et al. 2006), birds (Craig 1979), fish (Plath et al. 2003), and insects (Simpson et al. 1999) all show increased tolerance with density. For cave *P. longipes*, the high conspecific density of caves and resultant higher frequency of aggressive interactions may select for tolerance or less costly interactions. Indeed, agonistic interactions in *P. longipes* are costly both energetically and due to the risk of injury. Amblypygids may engage in less aggressive ways of negotiating agonistic interactions if they occur too frequently.

Table 2.—Logistic regression with total pedipalp display time, latency to physical aggression, and flicking during agonism assays as predictor variables, and location (cave or epigean) as the response variable ($n = 42$).

Model	k	AICc	ΔAICc	w_i
aggression + display + flick	4	45.94	2.41	0.146
aggression + display	3	43.53	0.00	0.487
aggression + flick	3	46.88	3.35	0.091
display + flick	3	51.68	8.15	0.008
aggression	2	45.07	1.54	0.226
display	2	49.79	6.27	0.021
flick	2	52.49	8.96	0.006
intercept	1	50.40	6.88	0.016

Alternatively, other mechanisms may have promoted the observed behavioral variation. For example, losing a territory in the forest likely comes at a great cost because suitable spaces are scarce (Bloch & Weiss 2002; Hebets 2002; Chapin 2014). Comparatively, the cave presents a higher density of suitable spaces to establish territories, which might make them less valuable; contest losers are likely to attain an alternate territory, though perhaps of less value. This is indirectly supported by the result that residency had a greater effect on contest outcome for forest interactions.

Interaction assays failed to show that forest animals were more likely to initiate agonistic interactions prior to physical contact than cave conspecifics. This could be because olfaction or other non-contact sensory cues are more important for forest animals than cave dwellers. These avenues of communication are important for amblypygids (Foelix & Hebets 2001; Hebets 2002; Walsh & Rayor 2008; Hebets et al. 2014), but their usefulness may be compromised in the cave environment, where contact-based cues play a larger role. Further, airborne olfactory cues might be less useful in high-density cave populations where the environment may be oversaturated with conspecific chemical cues. Future research could elucidate differences in how cave and epigean amblypygids gather external information.

The cave population size is exceptionally large, and is certainly the largest estimated to date (Bloch & Weiss 2002; Carvalho et al. 2012). The estimate had a wide CI but is still conservative considering the elusive nature of the animals and the complex network of cracks and crevices within the cave wall in which they live. Considering that large adult *P. longipes* have an antenniform leg span of 45–50 cm (pers. obs.) and that individuals are not evenly dispersed, the surface area density estimate indicates that most, if not all, individuals were within contact distance of another individual. This is confirmed by our observations in the field. Cave amblypygids are clearly impacted by increased interaction rates with conspecifics relative to epigean individuals, which rarely come into contact. This, combined with low predator abundance in caves, likely makes cannibalism the most important factor for survivorship for cave amblypygids. Increased cannibalism risk presents selection pressure for agonism avoidance, less aggressive encounters, or other tolerant behaviors.

Phrynus longipes exhibit environment-specific behavioral variation. Cave animals exhibited more tolerant behaviors relative to epigean conspecifics that were more aggressive and active. These adaptations seem to correlate with population density—a hypothesis that can be tested by extending this research across multiple cave systems. Indeed, environment-specific behavioral variation has the potential to elucidate the mechanisms for the development and maintenance of behavioral variation within species. Understanding phenotypic variation of cave-adapted animals with epigean conspecifics is a new avenue of biospeleology that can inform management plans for cave conservation.

ACKNOWLEDGMENTS

The American Philosophical Society's Lewis and Clark Fund for Exploration and Research, the Department of Ecology & Evolutionary Biology, UCLA, and the Edwin W. Pauley Fellowship, UCLA funded this research. Thanks to Nonacs Lab members and field assistants Kimberly Dolphin, Chelsea Vretner, and Daniel Winkler. Research was conducted under a PR DRNA permit 2012-IC-064.

LITERATURE CITED

Arrhenius, O. 1921. Species and area. Journal of Ecology 9:95–99.

Barr, T.C. 1968. Cave ecology and the evolution of troglobites. Pp. 35–102. *In* Evolutionary Biology. (T. Dobzhansky, M.K. Hecht & W.C. Steere, eds.). Appleton-Century-Crofts, New York.

Benson, J.F., M.J. Chamberlain & B.D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? Animal Behavior 71:685–693.

Bloch, C. & L. Weiss. 2002. Distribution and abundance of the whip spider *Phrynus longipes* (Arachnida: Amblypygi) in the Luquillo Experimental Forest, Puerto Rico: response to natural and anthropogenic disturbance. Caribbean Journal of Science 38:260–262.

Blomberg, S.P., T. Garland & A.R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioural traits are more labile. Evolution 57:717–745.

Burchards, H., A. Dölle & J. Parzefall. 1985. Aggressive behaviour of an epigean population of *Astyanax mexicanus* (Characidae, Pisces) and some observations of three subterranean populations. Behavioral Processes 11:225–235.

Carvalho, L.S., J.O. Gomes, S. Neckel-Oliveira & N.F. Lo-Man-Hung. 2012. Microhabitat use and intraspecific associations in the whip spider *Heterophrynus longicornis* (Arachnida: Amblypygi) in forest fragments formed by the Tucurui Dam lake, Para, Brazil. Journal of Natural History 46:1263–1272.

Chapin, K.J. 2011. Ecology and natural history of the tree-inhabiting social amblypygid *Heterophrynus batesii* (Butler 1873; Amblypygi: Phrynidae) in eastern Amazonian Ecuador. MS Thesis, West Texas A&M University, Canyon, Texas.

Chapin, K.J. 2014. Microhabitat and spatial complexity predict group size of the whip spider *Heterophrynus batesii* in Amazonian Ecuador. Journal of Tropical Ecology 30:173–177.

Christman, M.C. & D.C. Culver. 2001. The relationship between cave biodiversity and available habitat. Journal of Biogeography 28:367–380.

Craig, J.L. 1979. Habitat variation in the social organization of a communal gallinule, the pukeko, *Porphyrio porphyrio melanotus*. Behavioral Ecology & Sociobiology 5:331–358.

Culver, D. & T. Pipan. 2009. The Biology of Caves and Other Subterranean Habitats. Oxford University Press, New York.

Culver, D.C. & B. Sket. 2000. Hotspots of subterranean biodiversity in caves and wells. Journal of Cave and Karst Studies 62:11–17.

Davis, D.E. 1958. The role of density in aggressive behaviour of house mice. Animal Behaviour 6:207–210.

Duckworth, R.A. 2006. Behavioural correlations across breeding contexts provide a mechanism for a cost of aggression. Behavioral Ecology 17:1011–1019.

Elliott, W.R. 2005. Critical issues in cave biology. National Cave and Karst Management Symposium 2005:35–39.

Foelix, R. & E.A. Hebets. 2001. Sensory biology of whip spiders (Arachnida, Amblypygi). Andrias 15:129–140.

Fowler-Finn, K.D. & E.A. Hebets. 2006. An examination of agonistic interactions in the whip spider *Phrynus marginemaculatus* (Arachnida, Amblypygi). Journal of Arachnology 34:62–76.

Hebets, E.A. 2002. Relating the unique sensory system of amblypygids to the ecology and behaviour of *Phrynus parvulus* from Costa Rica (Arachnida, Amblypygi). Canadian Journal of Zoology 80:286–295.

Hebets, E.A., A. Aceves-Aparicio, S. Aguilar-Argüello, V.P. Bingman, I. Escalante & E.J. Gering, et al. 2014. Multimodal sensory reliance in the nocturnal homing of the amblypygid *Phrynus pseudoparvulus* (Class Arachnida, Order Amblypygi)? Behavioral Processes 108:123–130.

Hebets, E.A. & R.F. Chapman. 2000. Electrophysiological studies of olfaction in the whip spider *Phrynus parvulus* (Arachnida, Amblypygi). Journal of Insect Physiology 46:1441–1448.

Krajick, K. 2001. Cave biologists unearth buried treasure. Science 293:2378–2381.

Lind, M.I. & F. Johansson. 2011. Testing the role of phenotypic plasticity for local adaptation: growth and development in time-constrained *Rana temporaria* populations. Journal of Evolutionary Biology 24:2696–2704.

Mayr, E. 1963. Animal Species and their Evolution. Harvard University Press, Cambridge.

Millar, R.B. & M.J. Anderson. 2004. Remedies for pseudoreplication. Fisheries Research 70:397–407.

Montgomery, J.C., S. Coombs & C.F. Baker. 2001. The mechanosensory lateral line system of the hypogean form of *Astyanax fasciatus*. Pp. 87–96. *In* The Biology of Hypogean Fishes. (A. Romero, ed.). Springer, Netherlands.

Niemiller, M.L., B.M. Fitzpatrick & B.T. Miller. 2008. Recent divergence with gene flow in Tennessee cave salamanders (Plethodontidae: Gyrinophilus) inferred from gene genealogies. Molecular Ecology 17:2258–2275.

Oksaanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin & R.B. O'Hara, et al. 2013. vegan: community ecology package. R package version 2.0-8. Online at http://CRAN.R-project.org/package=vegan.

Parzefall, J. 2001. A review of morphological and behavioural changes in the cave molly, *Poecilia mexicana*, from Tabasco, Mexico. Pp. 263–275. *In* The Biology of Hypogean Fishes. (A. Romero, ed.). Springer, Netherlands.

Plath, M., J. Parzefall & I. Schlupp. 2003. The role of sexual harassment in cave and surface dwelling populations of the Atlantic molly, *Poecilia mexicana* (Poeciliidae, Teleostei). Behavioral Ecology & Sociobiology 54:303–309.

Porto, T.J. & P.E.C. Peixoto. 2013. Experimental evidence of habitat selection and territoriality in the Amazonian whip spider *Heterophrynus longicornis* (Arachnida, Amblypygi). Journal of Ethology 31:299–304.

Puente-Rolón, A.R. & F.J. Bird-Picó. 2004. Foraging behavior, home range, movements and activity patterns of *Epicrates inornatus* (Boidae) at Mata de Plátano Reserve in Arecibo, Puerto Rico. Caribbean Journal of Science 40:343–352.

Purcell, J. & L. Avilés. 2007. Smaller colonies and more solitary living mark higher elevation populations of a social spider. Journal of Animal Ecology 76:590–597.

Richards, S.A. 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86:2805–2814.

Rodríguez-Durán, A. 1996. Foraging ecology of the Puerto Rican Boa (*Epicrates inornatus*): bat predation, carrion feeding, and piracy. Journal of Herpetology 30:533–536.

Romero, A. 2009. Cave Biology: Life in Darkness. Cambridge University Press, Cambridge.

Sachser, N. 1986. Different forms of social organization at high and low population densities in guinea pigs. Behaviour 97:253–272.

Santer, R.D. & E.A. Hebets. 2008. Agonistic signals received by an arthropod filiform hair allude to the prevalence of near-field sound communication. Proceedings of the Royal Society London B Biological Science 275:363–368.

Santer, R.D. & E.A. Hebets. 2009. Tactile learning by a whip spider, *Phrynus marginemaculatus* CL Koch (Arachnida, Amblypygi). Journal of Comparative Physiology A 195:393–399.

Santer, R.D. & E.A. Hebets. 2011. The sensory and behavioural biology of whip spiders (Arachnida, Amblypygi). Pp. 1–64. *In* Advances in Insect Physiology, Vol 41: Spider Physiology and Behaviour. (S.J. Simpson & J. Casas, eds.). Elsevier, London.

Simpson, S.J., A.R. McCaffery & B.F. Hägele. 1999. A behavioural analysis of phase change in the desert locust. Biological Reviews 74:461–480.

Strausfeld, N.J., L. Hansen, L. Yongsheng, R.S. Gomez & K. Ito. 1998. Evolution, discovery, and interpretations of arthropod mushroom bodies. Learning and Memory 5:11–37.

Symonds, M.R.E. & A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Walsh, R.E. & L.S. Rayor. 2008. Kin discrimination in the amblypygid, *Damon diadema*. Journal of Arachnology 36:336–343.

Weygoldt, P. 2000. Whip Spiders (Chelicerata: Amblypygi): Their Biology, Morphology and Systematics. Apollo Books, Stenstrup.

Manuscript received 10 January 2015, revised 9 April 2015.