

SHORT COMMUNICATION

Guano deposition predicts top predator (Amblypygi: Phryniidae) abundance in subtropical caves

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Abstract. Absence of light is a fundamental characteristic of subterranean ecosystems; thus, productivity must be supported indirectly by influx of detritus from effluent environments. I examined how this influx impacts the carrying capacity of a cave predator: the whip spider *Phrynus longipes* (Pocock, 1894). Although solitary, territorial and cannibalistic, this species occurs at extremely high densities in caves. To test the hypothesis that this is an effect of nutrient flow and not cave structure, I examined whether guano deposition at cave entrances predicted estimated population sizes of whip spiders. I found a strong correlation, suggesting that whip spider carrying capacities are at least partly determined by nutrient influx to the cave ecosystem. Larger guano deposits support a larger community of arthropod detritivores, which act as prey to this top predator in a bottom-up effect. This highlights the importance of considering surface environmental and population health along with commercial guano harvesting when studying and conserving caves and the species therein.

Keywords: Epigeal, food web, speleology, subterranean, whip spider

Nearly all terrestrial ecosystems rely on sunlight as the primary source of energy, and caves are no exception. Caves, however, have the additional challenge of accessing the sun's energy indirectly—caves are typified by darkness. This problem is overcome by transport of detritus into caves from surface environments, where sunlight is abundant. Cross-habitat detritus influx can occur via periodic flooding, streams carrying material, or organisms accidentally falling into cave entrances. The most productive caves, however, receive the sun's energy stored as guano (Polis et al. 1997; Vanni et al. 2004; Culver & Pipan 2009). Bats and birds use cave ceilings as roosting sites, where they defecate, resulting in piles of nutrient-rich and biologically available resources on the cave floor. Many organisms rely directly on guano piles for food and microhabitats (Ferreira & Martins 1998; Ferreira et al. 2000; Ferreira & Horta 2001; Moulds 2004; Gnaspini 2012). In fact, several species are specialized in consuming guano, including salamanders and ants (Fenolio et al. 2005; Moulds 2006; Gnaspini 2012).

It is generally understood in food web theory that energy influx increases primary productivity, which can have bottom-up effects on the community (Paine 1966; Matson & Hunter 1992; Rosemond et al. 2001). How detrital-based webs function has gained recent research interest (Rosemond et al. 2001; Moore et al. 2004; Mammola 2018; Venarsky et al. 2018). Caves are eminently suited to address this topic because they are relatively simple systems that oftentimes rely exclusively on detritus, not primary productivity, for energy. Further, caves in the karst belt of Puerto Rico vary greatly in bat abundance, ranging from very few bats, as in Cueva Larvas, to huge, multispecies bat populations exceeding 300,000 individuals across three families, as in Cueva de los Culebrones (Rodríguez-Durán 1998). This variation has warranted a special delineation in tropical and subtropical caves: hot vs. cold caves. Hot caves are those with such an abundance of bats that their body heat and guano decomposition heat the cave, sometimes to temperatures in excess of 40°C (Ladle et al. 2012). These systems generally have higher biodiversity and more endemics than cold caves (Ladle et al. 2012).

The amblypygid *Phrynus longipes* (Pocock, 1894) occurs in both hot and cold caves in Puerto Rico (Esposito et al. 2015). Amblypygi is an order of large, nocturnal, predatory arachnids, including several species of which reside facultatively in caves. They generally feed on

arthropods of sufficient size but will also consume vertebrates (Fig. 1; Chapin & Hebets 2016). *Phrynus longipes* is a highly territorial and cannibalistic species found in both cave and surface environments in Puerto Rico (Chapin 2015). Some Puerto Rican caves host huge populations of *P. longipes* at high densities. For example, previous research at Cueva de los Culebrones estimated a density of two individuals m⁻² (Chapin 2015). Given that the adult leg span of *P. longipes* can reach 70 cm, this is an extremely high density, where practically all territories abut each other. As such, cave *P. longipes* must negotiate frequent interactions with territorial (Chapin & Hill-Lindsay 2016) and cannibalistic (Chapin & Reed-Guy 2017) conspecifics in darkness. On the surface, however, *P. longipes* are sparsely distributed across limiting, patchy microhabitats, rarely interact, and fall prey to a diversity of predators absent from the cave environment.

It remains unclear why *P. longipes* can achieve such high densities in caves. I hypothesized that this huge density of predators is explained, and thus limited by, energy influx into the cave ecosystem in the form of bat and bird guano. As such, I predicted that guano deposition rates would correlate positively with population estimates. Alternatively, whip spider population densities could be limited by space. If this is the case, then I expect cave depth to predict population estimates.

Assistants and I conducted mark-recapture surveys to estimate cave population densities across four caves in the karst belt of Puerto Rico (generally located at 18.414°N, 66.726°W) in August 2014: Cueva de los Culebrones, Cueva Maria Soto, Cueva Matos, and Cueva Larvas. I explored the extents of all caves to determine the range of *P. longipes* for each site. Populations were delineated by cave extents, except in Cueva de los Culebrones, where a dead zone (i.e., a zone of low oxygen) limited the species range to the first ca. 120 m (Chapin 2015).

I estimated populations across three nights from 18:00 to as late as 04:00. On the first night, assistants and I captured *P. longipes* and marked them with Testors brand enamel paint on the prosoma dorsum. For the remaining two nights, I recaptured amblypygids, marked unmarked individuals, and counted marked individuals. The short latency between marking and recapture surveys allowed for Lincoln-Petersen estimates (Seber 2002). I used the Chapman



Figure 1.—The amblypygid *Phrynus longipes* eating a primary consumer (Blattodea; top panel) in Cueva de los Culebrones, Aricebo, Puerto Rico, USA. Increased guano deposits support more primary consumers (bottom inset), which allows for enormous whip spider populations (bottom panel).

estimator, which is an estimator similar to Lincoln-Petersen, but with less bias at small sample sizes (Chapman 1951). This estimate assumes closed populations with no birth, death, immigration, or mark loss. These assumptions are realistic for this system, since dispersal is low and surveys were conducted on consecutive nights.

I measured guano deposition by placing six metal trays (20 cm diam.) evenly spaced across each cave entrance. I weighed each tray before leaving them at cave entrances for 24 h to collect guano. I then placed the metal trays in a drying oven at 60°C for 7 d before weighing them again. I averaged the change in tray weight for each cave and tested if guano deposition predicted *P. longipes* population sizes via linear regression. Further, I measured the depth of each cave to the nearest meter to test if cave size predicted *P. longipes* populations.

This was done in a separate model. I performed analyses in the programming language R 3.5.1 (R Core Team 2014).

Assistants and I collected 1,271 *P. longipes* across the four caves. The cave-wide population estimates varied from nearly 50 to over 500 individuals (Chapman-Petersen estimate \pm 95% CI). Cueva Matos and Cueva de los Culebrones had the highest population sizes and the greatest guano deposition (Table 1; Fig. 2). These two caves had large populations of bats, especially when compared to Cueva Maria Soto and Larvas, which had very few bats; Cueva Maria Soto was mostly used by cave-dwelling sparrows. Ceuvas Culebrones and Matos could be considered hot caves for this reason (Ladle et al. 2012). Mean guano deposition was highly predictive of cave population sizes ($m = 5.74 \pm 0.77$, $R^2 = 0.97$, $F_{1,2} = 55.45$, $P = 0.018$), such that larger guano deposition supports larger populations of *P. longipes*. Cave size alone,

Table 1.—*Phrynus longipes* population estimates and mean guano deposition for four Puerto Rican caves. Mark-recapture population estimates are Chapman estimators for population size with 95% confidence intervals., minimum number known alive (MNKA) is the total number of individuals observed during collection, guano deposition are averages of 6 collection trays placed at the entrance of each cave, and length of the cave or cave section occupied by *P. longipes*.

Site	MNKA	Recapture success rate	Estimate ± CI	\bar{x} deposition (mg)	Occupied cave length (m)
Cueva Larvas	51	0.62	48 ± 5.3	0.0	53
Cueva Maria Soto	253	0.62	352 ± 35.4	43.3	289
Cueva de los Culebrones	359	0.39	441 ± 45.4	75.0	104
Cueva Matos	608	0.38	576 ± 12.4	85.0	118

however, did not predict amblypygid population sizes ($F_{1,2} = 0.04, P = 0.86$).

Bat and bird guano deposits, but not cave size, correlated with *P. longipes* populations across four caves, suggesting that prey abundance limits whip spider population sizes. Thus, it seems that bottom-up effects impact top predator carrying capacities in these systems. Guano deposition has been shown to increase population sizes of primary producers in a similar manner (Polis et al. 1997). For example, seabird deposits improve soil nitrogen on desert islands (Sánchez-Piñero & Polis 2000; Wait et al. 2005) and the bats of Bracken cave, home to ca. 20 million Mexican free-tailed bats, provide important nutrients to invertebrate communities (Iskali & Zhang 2013). Food web theory predicts that cave guano increases primary consumers and, indirectly, predators of those consumers, thus having bottom-up effects on the cave trophic pyramid. Bottom-up effects have been shown in similar systems. For example, adding detritus increases top arthropod predator abundance in leaf-litter forest communities (Chen & Wise 1999). Future research that manipulates energy influx into caves could provide valuable insights into these effects.

The close correlation between guano deposition and population size suggested that *P. longipes* population sizes are limited by bat population sizes. This link between two secondary consumers from disparate food webs highlights the importance of understanding cave-surface interactions in both research and conservation. Surely, the persistence of *P. longipes* cave populations depends on the bats and birds using caves, and human impacts to bats will likely impact entire subterranean ecosystems. Population health of threatened cave species may be improved by supporting bat and bird populations. Further research is needed on the interdependence of surface and cave

ecosystems and the use of guano estimates as proxies for prey abundance. In particular, guano estimates can enable research where prey populations are exceedingly difficult to measure, like invertebrate communities in cave systems. Studies comparing a large number of caves could reveal more complex patterns of cave energy-influx.

Some cave populations were exceptionally dense, and Cueva Matos is the largest estimated Amblypygi population to date (Bloch & Weiss 2002; Carvalho et al. 2012; Chapin 2015). Cave amblypygids are clearly impacted by increased interaction rates with conspecifics relative to surface populations (Chapin & Hill-Lindsay 2016). This, combined with low predator abundance in caves, makes cannibalism a primary risk for cave amblypygids (Chapin & Reed-Guy 2017). Increased cannibalism risk seems to have presented selection pressure for agonism avoidance, less aggressive encounters, or other tolerant behaviors (Chapin 2015). However, evolutionary research on the system to understand how this variation is maintained remains wanting.

The estimates of guano deposition occurred over only a short time period and across a small number of caves. Further research could examine how behavioral changes of guano depositors through time impact cave ecosystems. Behaviorally-mediated seasonality could occur in caves if behavior changes energy influx, e.g., with migrating species. I also did not measure the intermediate consumer in the system. Examining temporal variation at all trophic levels would be a fruitful endeavor. Further, whip spiders are reclusive, and caves are replete with cracks and crevices in which they retreat. While the population estimates achieved small confidence intervals, estimates are likely conservative.

Phrynus longipes cave populations are limited by prey, the abundance of which is determined by bats and birds transporting energy from surface ecosystems into darkness. This system serves as an example for how cave ecosystems depend on surface environments for energy and nutrients. As such, conserving caves requires both the conservation of surrounding land, and the conservation of organismal movement between surface and cave environments. Further, this work suggests that that cave ecosystem productivity is limited by guano, which is an economically valuable agricultural fertilizer (Kunz et al. 2011; Sothearen et al. 2014). Caves stripped of guano have their trophic pyramid base pulled from under them, which is sure to have devastating bottom-up impacts on the community therein.

ACKNOWLEDGMENTS

This research was funded by an Animal Behavior Society Student Research Grant, the American Philosophical Society Lewis and Clark Fund for Exploration and Research, the Explorers Club Exploration Fund, the UCLA Latin American Institute via a donation from the Faucett Catalyst Fund, the UCLA Edwin W. Pauley Fellowship, and the Department of Ecology and Evolutionary Biology Fellowship, UCLA. Thanks to field assistants Alma Basco, Laura Caicedo, Patrick Casto, Kimberly Dolphin, Jose Sánchez-Ruiz, Chelsea Vretenar, and Daniel E. Winkler. Research was conducted under

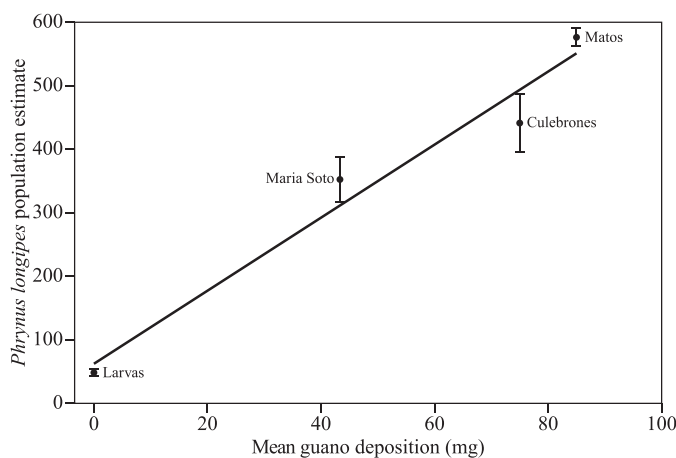


Figure 2.—Mean guano deposition predicting *Phrynus longipes* population estimates across four caves in Puerto Rico. Mean guano deposition was highly predictive of cave population sizes ($m = 5.74 \pm 0.77, R^2 = 0.97, F_{1,2} = 55.45, P = 0.018$).

the Puerto Rico Department of Natural Resources and the Environment permit numbers 2012-IC-064 and 2013-IS-075.

LITERATURE CITED

- Bloch, C.P. & 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.
- Carvalho, L.S., J.O. Gomes, S. Nickel-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 Tucuruí Dam lake, Pará, Brazil. *Journal of Natural History* 46:19–20.
- Chapin, K.J. 2015. Cave-epigeal behavioral variation of the whip spider *Phrynus longipes* (Arachnida: Amblypygi) evidenced by activity, vigilance, and aggression. *Journal of Arachnology* 43:214–219.
- Chapin, K.J. & E.A. Hebets. 2016. Behavioral ecology of Amblypygi. *Journal of Arachnology* 44:1–14.
- Chapin, K.J. & S. Hill-Lindsay. 2016. Territoriality evidenced by asymmetric intruder-holder motivation in an amblypygid. *Behavioral Processes* 122:110–115.
- Chapin, K.J. & S. Reed-Guy. 2017. Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. *Ethology* 123:772–777.
- Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. *University of California Publications in Statistics* 1:131–159.
- Chen B., & D.H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80:761–772.
- Culver, D.C. & T. Pipan. 2009. *The Biology of Caves and Other Subterranean Habitats*. Oxford University Press, Oxford.
- Esposito, L.A., T. Bloom, L. Caicedo-Quiroga, A.M. Alicea-Serrano, J. Sánchez-Ruiz, L.J. May-Collado et al. 2015. Islands within islands: Diversification of tailless whip spiders (Amblypygi, *Phrynus*) in Caribbean caves. *Molecular Phylogenetics and Evolution*. 93:107–117.
- Fenolio, B.D., G.O. Graening, B.A. Collier & J.F. Stout. 2005. Coprophagy in a cave-adapted salamander; the importance of bat guano examined through nutritional and stable isotope analyses. *Proceedings of the Royal Society B: Biological Sciences* 273:439–443.
- Ferreira, R.L. & L.C.S. Horta. 2001. Natural and human impacts on invertebrate communities in Brazilian caves. *Revista Brasileira de Biologia* 61:7–17.
- Ferreira, R.L. & R.P. Martins. 1998. Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. *Tropical Zoology* 12:231–252.
- Ferreira, R.L., R.P. Martins & D. Yanega. 2000. Ecology of bat guano arthropod communities in a Brazilian dry cave. *Ecotropica* 6:105–116.
- Gnasplini, P. 2012. Guano communities. Pp. 359–364. *In* *Encyclopedia of Caves*, 2nd ed. (W.B. White, D.C. Culver, eds.) Elsevier, Amsterdam.
- Iskali, G. & Y. Zhang. 2013. Guano subsidy and the invertebrate community in Bracken cave: the world's largest colony of bats. *Journal of Caves and Karst Studies* 77:28–36.
- Kunz, T.H., E.B. de Torrex, D. Bauer, T. Lobova & T.H. Fleming. 2011. Ecosystem services provided by bats. *Annals New York Academy of Sciences* 1233:1–38.
- Ladle, R.J., J.V.L. Firmino, A.C.M. Malhado & A. Rodríguez-Durán. 2012. Unexplored diversity and conservation potential of Neotropical hot caves. *Conservation Biology* 26:978–982.
- Mammola, S. 2018. Finding answers in the dark: caves as models in ecology fifty years after Pouson and White. *Ecography* 42:1331–1351.
- Matson, P.A. & M.D. Hunter. 1992. The relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology* 73:723.
- Moore, J.C., E.L. Berlow, D.C. Coleman, D.C. de Ruiter, Q. Dong, A. Hastings et al. 2004. Detritus, trophic dynamics and biodiversity. *Ecological Letters* 7:584–600.
- Moulds, T. 2004. Review of Australian cave guano ecosystems with a checklist of guano invertebrates. *Proceedings of the Linnean Society of New South Wales* 125:1–42.
- Moulds, T. 2006. The first Australian record of subterranean guano-collecting ants. *Helictite* 39:3–4.
- Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Polis, G.A., W.B. Anderson & R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology, Evolution and Systematics* 28:289–316.
- R Core Team. 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org.
- Rodríguez-Durán, A. 1998. Distribution and nonrandom aggregations of the cave bats of Puerto Rico. *Journal of Mammalogy* 79:141–146.
- Rosemond, A.D., C.M. Pringle, A. Ramírez & M.J. Paul. 2001. A test of top-down and bottom-up control in a detritus-based food web. *Ecology* 82:2279–2293.
- Sánchez-Piñero, F. & G.A. Polis. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* 81:3117–3132.
- Seber, G.A.F. 2002. *Estimation of Animal Abundance and Related Parameters*. 2nd ed. Blackburn Press, Caldwell, NJ, USA.
- Sothearen, T., N.M. Furey & J.A. Jurgens. 2014. Effect of bat guano on the growth of five economically important plant species. *Journal of Tropical Agriculture* 520:169–173.
- Vanni, M.J., D.L. DeAngelis, D.E. Schindler & G.R. Huxel. 2004. Overview: Cross-habitat flux of nutrients and detritus. Pp. 3–11. *In* *Food Webs at the Landscape Level*. (G.A. Polis, M.E. Power, G.R. Huxel, eds.) University of Chicago Press, Chicago, IL, USA.
- Vernarsky, M.P., J.P. Benstead, A.D. Huryn, B.M. Huntsman, J.W. Edmonds, R.H. Findlay et al. 2018. Experimental detritus manipulations unite surface and cave stream ecosystems along a common energy gradient. *Ecosystems* 21:629–642.
- Wait, D.A., D.P. Aubrey & W.B. Anderson. 2005. Seabird guano influences on desert islands: soil chemistry and herbaceous species richness and productivity. *Journal of Arid Environments* 60:681–695.

Manuscript received 17 May 2019, revised 18 July 2019.