

Ecology, 0(0), 2020, e03111
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When the hunter becomes the hunted: foraging bat attacked by pit viper at frog chorus

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Manuscript received 6 March 2020; revised 24 April 2020; accepted 5 May 2020. Corresponding Editor: John Pastor.

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Citation: Szczygiel, H. A., and R. A. Page. 2020. When the hunter becomes the hunted: foraging bat attacked by pit viper at frog chorus. *Ecology* 00(00):e03111. 10.1002/ecy.3111

Bats contend with a great diversity of predators, though predation on bats is considered to be opportunistic and the frequency at which it occurs is unknown. Snake-on-bat predation in the New World is increasingly well documented, though records are largely limited to arboreal colubrids and boids hunting in caves (Esbérard and Vrcibradic 2007). Here we report predation of what was likely a fringe-lipped bat (*Trachops cirrhosus*) by a fer-de-lance (*Bothrops asper*) (Fig. 1). *Trachops cirrhosus* is an extensively studied bat, known for its predation of túngara frogs (*Engystomops pustulosus*; Fig. 2; Tuttle and Ryan 1981, Page and Jones 2016). Our observation of bat predation in túngara habitat by a terrestrial snake has implications for potential risks incurred by gleaning bats as they approach the ground to forage.

On 5 October 2019, a subadult *B. asper* was spotted via eyeshine in a stream near Pipeline Road, Soberanía National Park, Panama, as it was beginning to swallow a bat. Calling túngara frogs and their tadpoles were observed in the immediate vicinity of the snake on the night of the observation, as well as on all subsequent visits. The predation event occurred ~70 m from a culvert under Pipeline Road known to host roosting *T. cirrhosus*, a distance well within the foraging range of this bat (Jones et al. 2017). Although we were not able to make a definitive identification, the bat's morphology—specifically its overall size (roughly 30–35 g), its long uropatagium, its furry forearm, and its long tibia—points to identification as *T. cirrhosus*. Subsequent camera trapping confirmed nightly túngara choruses with bats circling calling túngara frogs at this location, suggesting that the bat was foraging for frogs when it was caught by



FIG. 1. (a) Fer-de-lance (*Bothrops asper*) eating what is likely a fringe-lipped bat (*Trachops cirrhosus*). Note the parasitic flies on the bat. (b) Photo taken ~14 min after initial observation. (c) Photo taken shortly before the snake regurgitated the bat, 35 min after initial observation. Photos by Hubert A. Szczygie.

the snake. Although it is possible that the snake found a dead bat, the presence of live streblid flies, a common ectoparasite on *T. cirrhosus*, still present and moving in the bat's fur, and the absence of rigor mortis strongly suggest that the bat was freshly killed.

The initial observation occurred at 20:05, when the bat was already dead or immobilized and oriented head-first in the mouth of the snake, with the shoulders still visible. Over the next 37 min, the *B. asper* dragged its prey away from the stream, moving backwards, possibly in an attempt to arrange the wings to make the bat easier



FIG. 2. (a) Male túngara frog (*Engystomops pustulosus*) calling. (b) Fringe-lipped bat (*Trachops cirrhosus*) eating a túngara frog. (c) Young fer-de-lance (*Bothrops asper*) found on Pipeline Road, Gamboa, Panama. Photos by Hubert A. Szczygiel.

to swallow or to consume the bat in a less open area. The mass and/or size of the bat were such that the *B. asper* struggled to move it. The bat remained oriented head-first in the snake's mouth throughout the consumption attempt. After 35 min of attempting to swallow the bat, when the widest part of the belly and wings were in its mouth, the *B. asper* regurgitated the bat and moved away. Neither the snake nor the regurgitated bat were collected.

Juvenile *B. asper* are opportunistic hunters with a diet dominated by ectotherms, transitioning to a largely endothermic diet as they grow (Kuch et al. 2004). Bats were not reported in the Farr and Lazcano (2017) review of *B. asper* prey, though Villa and Lopez-Forment (1966) noted *B. asper* predation on the nectar-feeding bat, *Glossophaga soricina*. *Bothrops asper* are highly terrestrial (Fig. 2) with adults rarely found off the ground on fallen trees or on roots, and subadults/juveniles, which have greater climbing abilities, rarely found more than a meter up on branches or in shrubs. *Bothrops asper* are sedentary for pit vipers, typically moving less than 10 m between their daytime refuges and their nocturnal ambush site(s) (Sasa et al. 2009). They use the same daytime refuge for days or weeks at a time and have smaller home ranges than other pit vipers, ranging between 3.71 and 5.95 ha (Sasa et al. 2009). Consequently, it is likely that the *B. asper* described here had been using the same ambush site for days, and may have encountered hunting bats previously.

The interaction between túngara frogs and fringe-lipped bats has become a textbook example of the conflicting selection pressures faced by sexually signaling males. To attract a mate, male frogs produce conspicuous advertisement calls, which in turn attract the attention of eavesdropping bats that use these calls to locate their prey. *Trachops cirrhosus* typically emerge from their day roosts between 18:20 and 19:20, and travel an average of 218 m to forage (Jones et al. 2017). They are perch hunters that spend most of the night hanging from a perch, punctuated by short flights of less than a minute to catch prey (Kalko et al. 1999).

Snake predation on roosting bats has been well documented in arboreal snakes such as boids, which take advantage of concentrated numbers of bats in permanent roosts such as large caves. Esbérard and Vrcibradic (2007) identified 20 species of snakes (6 boids, 10 colubrids, 4 vipers) and 16 species of bat involved in snake–bat predation events. Most observations are of predation on roosting bats or predation on bats as they enter or leave the roosts, though many instances of predation were observed indirectly from dissections of preserved snakes, where the bat's behavior during capture cannot be ascertained. Five species in the family Viperidae were recorded as bat predators, though these data are almost exclusively derived from dissections rather than direct observation, so bat behavior at the time of capture (foraging versus roosting) cannot be determined (Esbérard and Vrcibradic 2007, Venegas et al. 2019). The only

definitive record of a Neotropical snake preying on a foraging bat we found occurred in 1979 when a boid was observed capturing a nectar-feeding bat (*Phyllostomus discolor*) at a *Parkia nitida* flower (Hopkins and Hopkins 1982). Although other records indicate possible predation on foraging bats (Groves 1962), definitive evidence to this effect is lacking.

Predation of foraging bats is less well documented than predation on roosting bats largely because it is difficult for potential predators (and for observing researchers) to predict exactly where and when a bat will forage. Given that *T. cirrhosus* only spends 11% of the night in flight (Jones et al. 2017), there was a narrow window in which the *B. asper* could have caught the bat. Predation risk, however, has potentially important implications for foraging behavior. Flight cage observations show that *T. cirrhosus* is often reluctant to land on the ground, even though frogs calling from ground level are common prey (R. A. Page, unpublished data). In their review of foraging behavior in *T. cirrhosus*, Page and Jones (2016) mention that the conspicuous movement involved in prey pursuit and capture may draw the attention of other predators and turn the bat from hunter to hunted. The field observation reported here suggests support for this hypothesis.

To our knowledge, the landscape of fear model (Laundré et al. 2001) has not been applied to bat foraging behavior. We propose that *T. cirrhosus* faces conflicting selection pressures as it forages. It must navigate a landscape of opportunity (as a predator) as well as a landscape of fear (as prey), which may overlap to its disadvantage. Frogs are an excellent food source that are relatively easy for bats to find because of their loud, species-specific mating calls (Tuttle and Ryan 1981), their dynamically moving vocal sacs (Gomes et al. 2016), and the ensuing ripples that emanate from the calling male over the water surface (Halfwerk et al. 2014). Although hunting near the ground has high potential rewards, it is possible that bats using this foraging strategy face greater risks of predation. There is also the potential for indirect effects of the bat landscape of fear on túngara behavior, as frogs may favor calling in habitat bats perceive as dangerous. Adding a terrestrial predator—a ground-dwelling snake—as an additional level of complexity to study of bat–frog predation will provide deeper insight into this well-established study system and expand upon the relatively new study of the landscape of fear.

ACKNOWLEDGMENTS

We thank the Smithsonian Tropical Research Institute for logistical support; Gregg Cohen for scouring the forest for the bat carcass after the observation; and Alison Davis Rabosky,

Harry Greene, Karen Warkentin, Marco Tschapka, Michael J. Ryan, and two anonymous reviewers for their helpful comments.

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