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COPPERHEADS ARE COMMON WHEN KINGSNAKES ARE NOT: RELATIONSHIPS BETWEEN THE ABUNDANCES OF A PREDATOR AND ONE OF THEIR PREY

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Abstract: Common Kingsnakes (formerly known collectively as *Lampropeltis getula*) are experiencing localized declines throughout the southeastern United States. Because there have been limited studies to determine how snakes regulate prey populations, and because Kingsnake declines may result in ecosystem impacts, we evaluated the hypothesis that Kingsnakes regulate the abundance of one of their prey, the venomous Copperhead (*Agkistrodon contortrix*). We generated a database of captures of the two species across the southeastern United States and, while controlling for large-scale habitat preferences, identified a negative relationship between the relative abundance of Kingsnakes and the relative abundance of Copperheads. Our results are correlative but consistent with the hypothesis that Copperhead populations experience a release from predation pressure where Kingsnake abundances are low. We suggest that Kingsnake declines, which are occurring for unknown reasons, are having ecological effects in affected ecosystems. We further highlight the potential role that snakes play in influencing the population dynamics of their prey.

Key words: *Agkistrodon contortrix*; Community ecology; Interspecific interaction; *Lampropeltis*; Population; Predation; Snake

An increasing amount of snake ecology research is being conducted (Shine and Bonnet, 2000) and this research has helped identify the important roles snakes play as predators in ecological systems (e.g., Weatherhead and Blouin-Demers, 2004). Although there is a growing body of knowledge regarding how snake growth, reproduction, and survival might be influenced by prey abundance and quality (e.g., Madsen and Shine, 2000; Lourdais et al., 2002; King et al., 2006; Sperry and Weatherhead, 2008), population-level responses are elusive, likely because of the difficulties inherent in characterizing snake abundances (Steen, 2010; Steen et al., 2012a). In addition, there have been limited studies quantifying impacts of snake predation on prey populations in natural systems (but see Lindell and Forsman, 1996). Nevertheless, invasive snakes have been implicated in the decline or extinction of multiple native species (Campbell et al., 2012; Dorcas et al., 2012), attesting to the potential for snakes to exert significant influences as predators in ecosystems.

Kingsnakes (*Lampropeltis* spp.) are distributed throughout North America and relative capture rates in traps suggest abundances can be high compared to other large-bodied snakes in the same area (Linehan et al., 2010; Steen et al., 2012a; Sutton et al., 2013). Kingsnakes are habitat generalists, although they may prefer some forested habitats over others (Steen et al., 2010a, 2012b); in addition, the species feeds on a wide variety of prey, including other snakes

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(Ernst and Ernst, 2003). Despite their generalist nature, species within this genus are experiencing localized declines in the southeastern United States (Krysko and Smith, 2005; Winne et al., 2007; Stapleton et al., 2008). For example, the Eastern Kingsnake (*L. getula*) was one of the most commonly encountered snakes within the Conecuh National Forest, Alabama, in the 1970s (Mount, 1980). Thirty years later, however, the species is considered either extirpated or nearly so at that site (Guyer et al., 2007). Over the same time period, the Copperhead (*Agkistrodon contortrix*) has changed from being an infrequently observed snake in Conecuh National Forest to the most commonly encountered species (e.g., Guyer et al., 2007). Because of the Kingsnake's well-documented habit of eating Copperheads (Ernst and Ernst, 2003; Sutton et al., 2006), a hypothesis emerged that suggested increases in Copperhead populations have resulted from a release from predation pressure in the near absence of Kingsnakes (although habitat change over this time period in relation to preferred snake habitat has not been evaluated).

Analogous situations have been observed at two other sites. In South Carolina (Ellenton Bay on the Savannah River Site, Aiken County), Kingsnake declines have been documented (Winne et al., 2007), whereas a previously rare congener of Copperheads (i.e., Cottonmouths, *Agkistrodon piscivorus*) has increased in numbers to the point that it is one of the most commonly encountered species (Willson et al., 2006). Similarly, although once abundant at Paynes Prairie (Alachua County, Florida), Kingsnakes are now considered extirpated as a result of habitat change, collecting, road mortality, and possibly, invasive fire ants (*Solenopsis invicta*; Krysko and Smith, 2005). Meanwhile, numbers of Cottonmouths have apparently increased there over the last few decades (Smith and Dodd, 2003). In both cases, the ultimate cause of these shifts in relative abundance is unknown but could include responses to habitat change. At least for South Carolina, one hypothesis suggested that Cottonmouths were increasing in number because of a decline in predation from Kingsnakes (Winne et al., 2007).

The ongoing and widespread declines of reptiles constitute a global crisis (Gibbons et al., 2000) and we have little information regarding how snake declines might be affecting the ecosystems in which they occur. The enigmatic declines of Kingsnakes in the southeastern United States provide a means to both identify ecological effects of a snake predator on populations of its prey and describe potential impacts of this ongoing conservation crisis. Therefore, we examined captures of Kingsnakes and Copperheads across the southeastern United States and incorporated large-scale habitat preferences into analyses to evaluate the hypothesis that decreased Kingsnake relative abundances are associated with increased relative abundances of Copperheads.

Materials and Methods

We solicited data from snake surveys that used drift fences in combination with pitfall, box, and/or funnel traps (e.g., Burgdorf et al., 2005; Sutton et al., 2010; Steen et al., 2010b) for at least 2 yr (excluding months when snakes are inactive) throughout the southeastern United States. Our study encompassed portions of the geographic ranges of three currently recognized species (i.e., Eastern Kingsnake [*Lampropeltis getula*], Speckled Kingsnake [*Lampropeltis holbrooki*], and Eastern Black Kingsnake [*Lampropeltis nigra*]) that had previously been considered subspecies of *L. getula* (Pyron and Burbrink, 2009a,b). Because precise geographic boundaries among these species are unknown and, importantly, they are ecologically similar, we did not distinguish among them in our analyses and hereafter refer to these species collectively as Kingsnakes.

Data were generated via independent long-term monitoring projects (Table 1). We compiled the number of Kingsnakes and Copperheads captured within each trap over the course of a given study/project. Our study area encompassed sites where Kingsnake populations are not thought to have declined (e.g., Ichauway, Georgia; Linehan et al., 2010) as well as areas where it is thought that they have declined precipitously (e.g., Conecuh

TABLE 1.—Geographic areas and sampling effort of snake-trapping projects in the southeastern United States that generated data used to examine the relationship between relative abundances of Copperheads, *Agkistrodon contortrix*, and Kingsnakes, *Lampropeltis* spp.

Location	State	Total traps	Trap type	Years monitored	Reference
Fort Stewart Military Reservation	Georgia	5	Funnel	1999–2000	Stevenson et al. (2003)
Conecuh National Forest	Alabama	12	Box	2005–2006	Guyer et al. (2007)
DeSoto National Forest (and surrounding areas)	Mississippi	5	Funnel	2004–2006	Baxley and Qualls (2009)
Camp Shelby Joint Forces Training Center	Mississippi	34	Box	2005–2009[a]	Lee (2009)
Joseph W. Jones Ecological Research Center (Ichauway)	Georgia	16	Box	2005–2008	Linehan et al. (2010)
Eglin Air Force Base	Florida	19	Box	2009–2010	Steen et al. (2013b)
William B. Bankhead National Forest	Alabama	6	Box	2005–2008[b]	Sutton et al. (2010)
Eastern Texas and western Louisiana (various)		272	Box	1992–2009[c]	Rudolph et al. (2006)
Western Louisiana, private industrial timberlands		8	Box	2007–2009[d]	

[a] Sixteen traps were monitored for 2 yr and 18 traps were monitored for 3 yr during this time period.
[b] Individual traps were monitored for a total of 3 yr each during this 4-yr period.
[c] Individual traps were monitored from varying periods of time, from 2 to 7 yr.
[d] Rudolph et al. (2006) can be consulted for comparable methodology.

National Forest, Alabama; Guyer et al., 2007). Trapping design and sampling effort varied among projects. These differences do not bias the relative numbers of Copperheads and Kingsnakes detected in a given trap, however, and these were the numbers we used to identify any relationships between the two species.

We excluded recapture events on sites where individuals were marked, but this was not possible at 272 of 377 sites. Because of the low recapture rates at sites where all animals were marked (e.g., <10%, Linehan et al., 2010), we suggest this discrepancy does not substantially alter our analysis. In addition, we included traps located in the Florida Panhandle, where Kingsnake declines are suspected but where the Copperhead is at the southern limit of its geographic distribution. We conducted an exploratory post hoc analysis that excluded the traps where individuals were not marked, as well as the traps within the Florida Panhandle, and our results were not qualitatively altered. So, we suggest that these data do not bias our findings and include all observations in our results.

We used the number of captures of a given species as an index of relative abundance. In general, this is a questionable practice because it does not consider how variation in detection probability has influenced observed values (Anderson, 2001). Estimates of snake relative abundances are difficult to quantify, however, in large part because of low detection probabilities (Steen, 2010; Steen et al., 2012a). Until improved methods emerge to address low detection, we make the simplifying assumption that detections of each species reflect their relative abundances.

With the use of an information-theoretic approach, we examined the effects of Kingsnake abundance on the abundance of Copperheads by extending the models hypothesized by Steen et al. (2012b) to describe the distributions of terrestrial snakes in the southeastern United States. Specifically, Steen et al. (2012b) used 2001 National Land Cover Data (NLCD, 30-m pixels; Homer et al., 2004) to characterize the land cover surrounding each of the traps contributing data to the current study and found that Copperhead occupancy was best described by two models that included landscape characteristics (i.e., scrub/shrub, total forest, and open water) within 500 m of each trap (Table 2). In this study, we assumed that habitat features selected by the species were also the important habitat features that influenced abundance.

We used Generalized Linear Mixed Models with a Poisson distribution fit with the Laplace approximation as implemented by the package nlme in R v2.15 (Bates et al., 2011). Each model contained a random intercept for the site in which an individual trap was located. We built models to explain abundance that contained covariates from the two best models that Steen et al. (2012b) used to describe Copperhead occupancy, both with and without a covariate representing the abundance of

TABLE 2.—Models used to evaluate the relationship between the relative abundances of Kingsnakes (*Lampropeltis* spp.) and Copperheads (*Agkistrodon contortrix*) throughout the southeastern United States. k = number of parameters and w_i = model weight.

Model	k	logLik	AIC	ΔAIC	w_i
Kingsnake + scrub/shrub	3	−777.89	1563.78	0	0.99
Scrub/shrub	2	−783.93	1573.85	10.07	0.01
Kingsnake + forest + water	4	−809.38	1628.76	64.98	0
Forest + water	3	−816.26	1640.51	76.73	0
Kingsnake	2	−850.56	1707.12	143.34	0
Null	1	−857.52	1719.04	155.26	0

Kingsnakes. We also evaluated a model that contained only the Kingsnake abundance covariate, as well as a null model (Table 2). We then ranked and compared models with the use of Akaike's Information Criterion (Akaike, 1974).

We further examined whether the relationship between Kingsnake and Copperhead abundances was influenced by habitat quality by testing for relationships between abundances of the two species within areas considered to be high- and low-quality habitat for Copperheads (following Burkett-Cadena et al., 2013). Specifically, because the analysis described above, and Steen et al. (2012b), suggested that Copperhead habitat quality is largely influenced by the amount of scrub/shrub surrounding a trap, we examined the relationship between Kingsnake and Copperhead abundances in traps with high and low amounts of scrub/shrub habitat surrounding them, separately. To do so, we divided the data set into high and low scrub/shrub areas, and into traps with high and low Kingsnake abundance with the use of K-means clustering. We then developed a mixed Poisson model similar to the ones described above to test for differences in abundance of Copperheads in areas with high and low Kingsnake abundance within high and low scrub/shrub areas, separately (Burkett-Cadena et al., 2013).

RESULTS

We used data from 377 traps distributed among nine projects in our analyses. These traps were open between 2 and 7 yr (Table 1). We recorded captures of 299 Kingsnakes and 2012 Copperheads. Kingsnakes were detected at 122 traps (32%) and Copperheads were detected at 313 traps (83%); both Kingsnakes and Copperheads were caught at 109 (29%) traps. The number of captures within a given trap ranged from 0 to 12 (mean ±1 SE = 0.79 ± 0.09) and 0–89 (5.34 ± 0.35) for Kingsnakes and Copperheads, respectively.

The best model of Copperhead abundance received a majority of the model weight (w_i) and the next best model had ΔAIC > 10 (Table 2). This best model indicated that Copperhead abundance was lower in scrub/shrub habitat (β = –0.02, SE < 0.01) and declined even more so with greater Kingsnake abundance (β = –0.05, SE < 0.01; Fig. 1). Our analysis of Copperhead abundance within traps surrounded by high and low shrub/scrub and containing low and high Kingsnake abundances further revealed a negative relationship between the two species. The beta value for the factor indicating high Kingsnake abundance traps was negative in both high and low scrub/shrub areas (β = –1.10, SE =

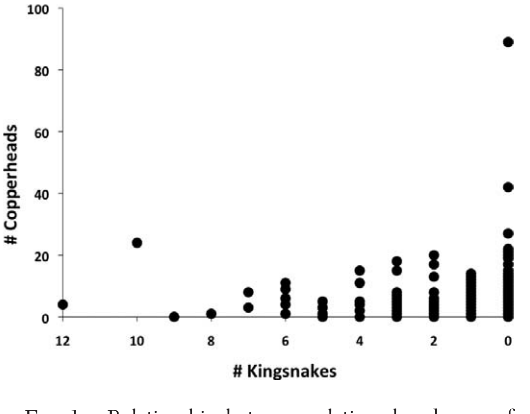

FIG. 1.—Relationship between relative abundances of Copperheads (*Agkistrodon contortrix*) and Kingsnakes (*Lampropeltis* spp.) in areas trapped for snakes throughout the southeastern United States.

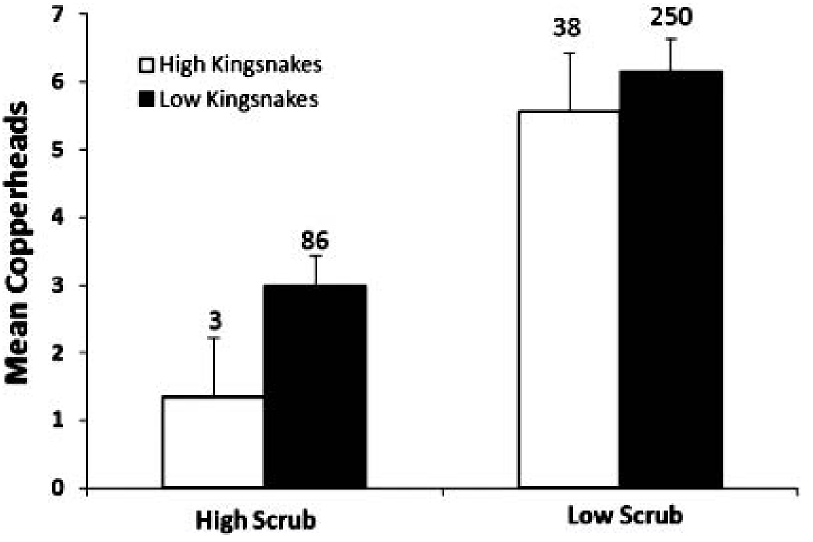

FIG. 2.—Mean number of Copperheads (*Agkistrodon contortrix*) caught in areas of high and low scrub/shrub, and high and low relative abundance of Kingsnakes (*Lampropeltis* spp.). Numbers indicate sample size (traps).

0.51; $\beta = -0.30$, SE = 0.08, respectively; Fig. 2)—suggesting a negative relationship between abundances of the two species regardless of habitat quality.

Plots of Copperhead and Kingsnake abundance revealed the presence of potential outliers (Fig. 1). We therefore used the package influence.ME (Nieuwenhuis et al., 2012) to calculate Cook's distance for each observation in our data set, which identified two outliers (Cook's distance = 3.54 and 1.66). Removal of the outliers did not qualitatively affect the results for any analysis.

DISCUSSION

By quantitatively examining trends between the abundances of Kingsnakes and Copperheads on a large geographic scale, we generated results that conformed to hypotheses that had emerged from qualitative descriptions of site-specific observations. Specifically, while controlling for important large-scale habitat features, our data revealed a negative relationship between the relative abundances of Copperheads and Kingsnakes. Therefore, our results provide support for the common suggestion that Kingsnake declines in the southeastern United States, and an associated decrease in predation pressure, have caused a release of Copperhead populations.

A dense population of snakes within a given area may be able to regulate prey populations (Nowak et al., 2008) and this is likely a fruitful topic for future research. If Kingsnakes are indeed regulating Copperhead populations, the general public is likely to perceive Kingsnake foraging as a valuable ecosystem service. Indeed, some individuals already relocate incidentally encountered Kingsnakes to their property in hopes of reducing abundances of venomous snakes (personal observation); however, the efficacy of this practice is questionable and relocating Kingsnakes may increase their risk of mortality (e.g., Reinert and Rupert, 1999).

Populations of predators and prey may cyclically fluctuate over time because of multitrophic interactions (Krebs et al., 1995). We did not set out to identify whether these patterns are occurring. Our study attempted to determine whether there was an association between the relative abundance (or current absence) of Kingsnakes in a given area and the relative abundance of a known prey item, Copperheads. To date, locales that have experienced Kingsnake declines have not reported rebounds; thus, we suggest our results may not be applicable to patterns associated with cyclical fluctuations.

Because our study was correlative, we cannot rule out alternative explanations for the patterns we identified; it is important to consider that our study does not account for the complex relationships between life history, habitat change, and resource use (e.g., Durso et al., 2013) for Kingsnakes and Copperheads throughout the southeastern United States. It is possible that the patterns we observed are caused by an increase in Copperhead abundance leading to a decrease in the relative abundance of Kingsnakes. For example, an increased number of Copperheads could increase competition for certain resources (e.g., prey). Both species take a wide variety of prey, however, suggesting that individual resources are unlikely to be limiting; furthermore, Kingsnakes likely feed primarily on ectothermic prey, whereas Copperheads preferentially consume endothermic vertebrates (Ernst and Ernst, 2003). Similarly, Copperheads could be less detectable where Kingsnakes are more abundant because of changes in behavior, such as increased antipredator responses (Greene, 1988). If Copperheads are indeed less detectable where Kingsnakes are abundant, we suggest that this is probably because of the close relationship between abundance and detection (i.e., a species is less detectable when it is rare; e.g., Durso et al., 2011) and therefore consistent with our overall hypothesis. Finally, our best available data regarding Copperhead habitat preferences were based on landscape-scale information and directly relevant to species occupancy, not abundance. Informative results may be obtained from research that identifies small-scale habitat preferences and evaluates their influence on snake abundances and capture probabilities. Similarly, if long-term snake demography data were available, we might be able to investigate how habitat change has influenced snake populations over time. Those data do not currently exist on a large scale.

Although snakes can be model organisms for some ecological phenomena (Shine and Bonnet, 2000), their secretive nature makes them difficult subjects for investigations of population and community ecology (Vitt, 1987). Evidence for interspecific interactions between snakes is mounting (Luiselli, 2003, 2006; Steen et al., 2013b, 2014); however, this evidence generally pertains to the ecological process of competition. We have demonstrated that snakes may regulate populations of other snakes through predator/prey relationships. Furthermore, we describe an unanticipated outcome of the Kingsnake declines that result from unknown causes (Winne et al., 2007). Specifically, the relative abundance of Copperheads may increase across the southeastern United States if additional Kingsnake populations crash and disappear. This shifting composition of snake assemblages in the southeastern United States could have wide-ranging effects within relevant ecological systems. Given that snake populations are declining worldwide (Reading et al., 2010), similar effects might be occurring elsewhere.

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