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The effect of coachwhip presence on body size of North American racers suggests competition between these sympatric snakes

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Abstract

When sympatric species compete, character divergence may help maintain coexistence. Snakes are often found in species-rich assemblages while exploiting similar resources; because snake body size is a relatively plastic trait that determines the range of prey sizes an individual may consume, divergence in body size between sympatric species may arise as a result of interspecific interactions. The North American racer, *Coluber constrictor*, and the larger coachwhip, *Coluber flagellum*, have a close taxonomic relationship and similar foraging strategies. Therefore, we hypothesized that *C. constrictor* would be smaller where they co-occur with *C. flagellum*, as compared to where *C. flagellum* is absent, throughout the southeastern extent of their range. To evaluate this hypothesis, we obtained data on body size for 2321 adult *C. constrictor* and 526 adult *C. flagellum*, along with habitat data and other potentially important factors influencing body size. *Coluber constrictor* was smaller than elsewhere when in peninsular Florida, in pine forests, on hydric soils and in the presence of the larger and potentially competing *C. flagellum*. Body size of *C. flagellum* did not vary by any measured habitat variables. The trends we documented are consistent with the hypothesis that *C. constrictor* body size is influenced by several variables, including co-occurrence with *C. flagellum*.

Introduction

Given a limited resource, interspecific competition may occur between closely related species. Morphological divergence is one potential outcome of this competition (e.g. Grant & Grant, 2006), a process referred to as character displacement (Brown & Wilson, 1956). By influencing resource use, character displacement may facilitate coexistence over evolutionary time (Bowers & Brown, 1982). However, it is difficult to differentiate the past effects of competition from ongoing processes. For example, studies of resource partitioning or morphological variation may demonstrate that sympatric species use different resources or exhibit differences in morphology. However, it is often unknown whether these differences result from past evolutionary divergence to reduce competition, random processes or from plastic adaptations resulting from current interactions (e.g. Connell, 1980).

Studies that quantify both the diet and morphology of sympatric species may provide powerful evidence for character displacement (e.g. Huey, 1974). However, it is logistically challenging to measure the availability and consumption of prey on a large scale. As a result, morphological variation may be used as a proxy for resource use. If the morphological traits related to catching and consuming prey differ in relation to the presence or abundance of potential competitors, this is consistent with the hypothesis that interspecific interactions influence resource use (e.g. Simberloff *et al.*, 2000; Davies *et al.*, 2007).

Body sizes may differ among members of species-rich snake assemblages (Guyer & Donnelly, 1990). Although body size may not always be an appropriate means to infer differences in resource use among wildlife species (Wilson, 1975), snakes swallow prey whole; thus, body size has an important influence on the maximum size of potential prey (King, 2002). In

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addition, snakes possess phenotypic plasticity with regard to body size and growth rates (Madsen & Shine, 1993; Tanaka, 2011), particularly in response to diet (Forsman, 1991; Forsman & Lindell, 1996; Queral-Regil & King, 1998; Madsen & Shine, 2000); these changes may be eventually reflected in genetic divergence (Aubret & Shine, 2007). Consequently, competition between two sympatric snake species may be reflected in differences in body size arising within ecological timescales (Carroll *et al*., 2007).

As a snake increases in size, the size range of potential prey items increases (Shine, 1991); however, in general, small items within a snake's diet tend to compose a smaller portion of the diet as that snake grows larger (Arnold, 1993; King, 2002). Therefore, when two potentially competing species occur in sympatry, a divergence in body size may reduce competitive pressure. In this scenario, one species would prey largely on small items that compose a relatively small proportion of the items included in a larger species' diet. Notably, after examining geographic trends in *Coluber constrictor* body size, Rosen (1991) surmised that character displacement arising from intraguild competition with sympatric predators could have been the mechanism resulting in observed patterns.

The coachwhip, *Coluber flagellum*, and North American racer, *C. constrictor*, are closely related species that occur in sympatry in portions of their ranges. *Coluber flagellum*'s range is generally limited to the southern extent of the USA and Mexico. *Coluber constrictor* generally ranges throughout the USA with the exception of the arid south-west and is found in multiple and diverse habitats. In the south-eastern USA, the two species prefer different habitats at a large spatial scale; specifically, *C. constrictor* avoids scrub/shrub and grassland habitats, while *C. flagellum* avoids areas with a high density of wetlands (Steen *et al*., 2012). However, there is no evidence to suggest that these differences result from current interspecific competition (D.A. Steen *et al*., unpubl. data). In other words, differences in habitat use are likely due to divergence over evolutionary time and may result from processes independent from competition, potentially including random processes. Although differences in habitat use have been examined in the context of interspecific interactions (D.A. Steen *et al*., unpubl. data), comparable studies have not been conducted to examine whether these interactions are currently leading to changes in diet.

Both *C. flagellum* and *C. constrictor* are diurnal active foragers that feed on a wide variety of prey. However, the two species may partition prey, to some degree, where they co-occur (Halstead, Mushinsky & McCoy, 2008). *Coluber flagellum* is generally larger than *C. constrictor* (Ernst & Ernst, 2003), suggesting that *C. flagellum* may consume larger prey. These morphological differences could have evolved to minimize competition. However, we hypothesized that interactions on an ecological timescale may amplify existing morphological differences. Specifically, we hypothesized that *C. constrictor* body size would be smaller in sites co-occupied with *C. flagellum* than in sites where *C. flagellum* was absent. If *C. constrictor* was smaller in sites occupied by *C. flagellum* than in sites where they are absent, we interpreted these differences in body size as evidence of competition for prey. Because *C. constrictor* is common and found in many habitats, it was not possible to identify enough sites with *C. flagellum*, but not *C. constrictor*, to measure how body size of the former may vary in relation to the latter.

Materials and methods

Data collection

We solicited data from researchers that collected snout-vent length (SVL) and body mass for *C. flagellum* and/or *C. constrictor* as components of prior mark-recapture research efforts in the south-eastern USA (Table 1). We attempted to obtain data only from areas within the geographic range of both species, although there were only a limited number of sites where only *C. constrictor* was found. We therefore included data from north Alabama and portions of Louisiana, which were slightly outside the known range of *C. flagellum* (Ernst & Ernst, 2003). Snakes were generally captured with drift fences in association with funnel or box traps. We also included some snakes collected incidentally within discrete geographic areas (e.g. Savannah River Site). We obtained further data for *C. constrictor* from Louisiana State University (LSU) museum specimens due to low numbers of *C. constrictor* captured in areas where *C. flagellum* did not occur. Individual records from the Louisiana museum collection were designated as allopatric or sympatric based on the known ranges of the species (Ernst & Ernst, 2003) and expert opinion (J. Boundy, LSU Museum of Natural Science, personal communication).

With the exception of the LSU records, our snake data originated from collecting efforts conducted within the discrete geographical areas (hereafter, sites), listed in Table 1. With regard to the two species of interest, we defined a site as allopatric if only *C. constrictor* was detected there. Therefore, we use 'allopatric' and 'sympatric' to describe individual sites, all of which were generally within the geographic range of both species.

Only adults were included in the analyses. Although size at maturity may vary geographically, we considered *C. constrictor* as adult if they were ≥600 mm SVL (Fitch, 1999) and *C. flagellum* as adult if they were ≥900 mm SVL (Wright & Wright, 1957; Stebbins, 1985). It is difficult to standardize methods of obtaining snake lengths; for example, certain observers may stretch snakes to varying lengths when taking measurements (Natusch & Shine, 2012). Therefore, some caution is warranted; however, due to the vast extent of our database, we suggest that our results are useful for examining general trends in body lengths.

Use and availability of resources may be influenced by factors other than competition (Toft, 1985), and body size may be influenced by multiple factors (Olalla-Tärraga, Rodríguez & Hawkins, 2006). Therefore, we qualitatively categorized the habitat features at the location of each snake capture by recording dominant habitat type (Pine Forest, Oak Forest or Scrub) and soil type (well-drained, moderately drained or poorly drained, hereafter, Xeric, Mesic or Hydric, respectively) and by estimating canopy cover (Low = 50% or

Table 1 Sources of data used in analysis of North American racer, *Coluber constrictor*, and coachwhip, *Coluber flagellum*, body sizes within the south-eastern extent of their range

Location	State	Collection method	Years included	Citation	*C. constrictor*[a]	*C. flagellum*[b]
DeSoto National Forest (and surrounding areas)	Mississippi	Drift Fence	2004–2006	Baxley & Qualls 2009	57	12
Jacinto Port and Clearwater Tract	Alabama	Drift Fence	2005	J. Borden, unpubl. data	57	Absent
Camp Shelby Joint Forces Training Center	Mississippi	Drift Fence	2005–2006	Lee 2009	339	68
Conecuh National Forest	Alabama	Drift Fence	2005–2006	Guyer *et al*., 2007	57	30
Ordway-Swisher Biological Station	Florida	Drift Fence	1989–1990	Dodd Jr & Franz, 1995	90	28
Fort Stewart Military Reservation	Georgia	Drift Fence	1999–2000	Stevenson, Dyer & Willis-Stevenson, 2003	21	22
Various	Louisiana	Drift Fence	2007–2009	B. Gregory, unpubl. data	2	11
Lake Wales Ridge State Forest	Florida	Drift Fence	2004–2006	Halstead *et al*., 2008	212	32
Charleston, Dorchester, Hampton, and Jasper Counties	South Carolina	Drift Fence	2001–2003	Humphries, 2005	72	Absent
Joseph W. Jones Ecological Research Center	Georgia	Drift Fence and Incidental	2005–2008	Linehan, Smith, & Steen, 2010	222	127
Carolina Sandhills National Wildlife Refuge	South Carolina	Incidental	2000–2008	K. Messenger, unpubl. data	33	24
Various	Louisiana	Various (Museum Collection)		J. Boundy, unpubl. data	362	Not collected
Solon Dixon Forestry Education Center	Alabama	Drift Fence	2002–2004	Steen *et al*., 2010	49	15
Savannah River Site	South Carolina	Drift Fence and Incidental		J.D. Willson *et al*., unpubl. data	614	105
Eglin Air Force Base	Florida	Drift Fence and Incidental	2009–2010	Steen *et al*. in press	35	52
William B. Bankhead National Forest	Alabama	Drift Fence	2006–2008	Sutton *et al*., 2010	99	Absent

[a]Total *C. constrictor* collected ≥600 mm SVL.
[b]Total *C. flagellum* collected ≥900 mm SVL.

less vs. High = higher than 50%) for the time period when snakes were sampled. These data were not provided for LSU museum records or Savannah River Site records because many individuals were collected incidentally over relatively large areas. Based on geographic locations, we categorized each *C. constrictor* record into one of five distinct genetic lineages based on recent molecular analysis (Burbrink *et al*., 2008). Latitude may also influence body size (Ashton & Feldman, 2003); therefore, we included this information as a covariate when available. We also characterized each record as resulting from an incidental capture or from passive trapping.

Because of low capture rates, terrestrial snakes generally have low detection probabilities (Steen, Guyer & Smith, 2012); this raises the possibility that we did not detect *C. flagellum* even though it was present. However, when present, *C. flagellum* is relatively detectable in passive trapping efforts (D.A. Steen *et al*., unpubl. data) and the sampling efforts we included generally incorporated multiple seasons of trapping (Table 1). The only study conducted within a single year included 9 months of trapping. We suggest that if *C. flagellum* was not detected at a site, the population was at least at a density low enough that it was unlikely to be a significant competitor.

Analysis

We used a two-step procedure to examine the body size of *C. constrictor* in the presence and absence of *C. flagellum.* We used linear mixed-effects models with hypothesized fixed effects and a random intercept for the sites at which the snakes were collected. The first step of our analysis was to identify factors other than the presence of *C. flagellum* that may influence the size of *C. constrictor.* We built linear mixed effects models representing all possible combinations of hypothesized fixed effects, including capture method (i.e. incidental encounter vs. passive trap), sex, dominant habitat type, soil type, canopy cover, latitude and genetic clade (as described in Burbrink *et al*., 2008); study site was used as a random effect. We ranked and compared models using Akaike's Information Criterion (AIC; Akaike, 1974). We then evaluated our *a priori* hypothesis that the size of *C. constrictor* was influenced by the

presence of *C. flagellum* by adding a binary factor indicating presence/absence of *C. flagellum* to the model with the lowest AIC value from the previous step and examining the change in AIC values. This method allowed us to test for an effect of *C. flagellum* on the size of *C. constrictor* while accounting for other ecological factors.

Our study was designed to rigorously evaluate our hypothesis of interest, that is whether the size of *C. constrictor* differed in relation to the presence/absence of *C. flagellum*. However, we conducted two additional and *post hoc* analyses to identify corroborative patterns; due to model selection uncertainty, we suggest caution in interpreting these additional analyses. First, we examined factors affecting the size of *C. flagellum* using the same approach as with *C. constrictor*. We examined the size of *C. flagellum* using the same fixed effects as for *C. constrictor*, with the exception of genetic clade and sympatric/allopatric status; these effects were only available for *C. constrictor*.

We also conducted a *post hoc* analysis to identify whether body condition index (BCI; Bonnet & Naulleau, 1994) of *C. constrictor* was also influenced by the habitat variables noted earlier and the presence of *C. flagellum*. We calculated a BCI by log-transforming both SVL and mass, calculating residuals from a linear model of the two measurements and dividing residuals by the mass predicted by the model, as described in Coates *et al.* (2009; but see Peig & Green, 2009).

For all analyses, we considered covariates as useful for inference if their model-averaged 85% confidence limits did not overlap zero because model selection based on AIC favors the retention of covariates with 85% confidence limits that exclude zero (Burnham & Anderson, 2002; Arnold, 2010). We omitted all observations that did not have data for each fixed effect and log-transformed all SVL measurements before analysis to improve normality. We fit all models using maximum likelihood with package nlme (Pinheiro *et al.*, 2011) and performed all model ranking and averaging using package MuMIn (Barton, 2009) in R (R Development Core Team, 2011).

Results

We obtained size data for 2321 adult *C. constrictor* and 526 adult *C. flagellum* (Table 1), although information regarding all hypothesized factors was only available for 1005 *C. constrictor* and 304 *C. flagellum*; thus, these were the sample sizes included in our linear effects models. Of the records that did not contain data for all hypothesized factors, 64% (976 of 1538 records) were from the Savannah River Site or the LSU collection. Another 6% (99 records) were from the Bankhead National Forest; it was difficult to characterize the dominant forest cover there because of ongoing forest management. Of the 1005 *C. constrictor* for which we had complete habitat information, 889 had both SVL and body mass data, allowing us to calculate BCI. Of all *C. constrictor*, 499 were designated as allopatric with *C. flagellum* and averaged 876.7 mm SVL (standard error = 5.91); 1822 were designated as sympatric with *C. flagellum* and averaged 803.7 mm SVL (standard error = 2.69). Of *C. constrictor* included in our linear effects model, 115 were designated as allopatric with *C. flagellum* and averaged 844.9 mm SVL (standard error = 4.41); 890 were designated as sympatric with *C. flagellum* and averaged 776.9 mm SVL (standard error = 9.74, Table 2).

Table 2 Summary statistics for North American racer, *Coluber constrictor*, snout-vent length for animals captured throughout the south-eastern USA

	Mean (mm)	SE	*n*
Complete sample			
Coluber flagellum present	803.70	2.69	1822
C. flagellum absent	876.69	5.91	499
Oak	791.25	8.50	157
Pine	787.91	4.07	737
Scrub	752.14	6.61	212
Hydric soil	751.48	20.18	25
Mesic soil	790.63	6.24	323
Xeric soil	791.99	3.69	979
Central clade	853.42	9.74	174
Eastern clade	854.44	4.35	839
FL panhandle clade	793.98	5.74	377
Gulf coast clade	803.02	4.48	568
Peninsular FL clade	742.85	5.24	302
Linear effects model sample			
C. flagellum present	776.94	9.74	890
C. flagellum absent	844.92	4.41	115
Oak	793.66	9.71	133
Pine	793.38	4.35	660
Scrub	752.14	6.61	212
Hydric soil	748.88	20.87	24
Mesic soil	818.76	10.79	141
Xeric soil	780.03	3.65	840
Eastern clade	822.14	11.98	125
FL panhandle clade	808.46	6.71	293
Gulf coast clade	786.92	5.44	310
Peninsular FL clade	740.26	5.54	277

The best model for the size of *C. constrictor*, regardless of the presence/absence of *C. flagellum*, included factors for habitat, clade and type of soil (Table 3). Adding a factor for presence/absence of *C. flagellum* substantially reduced AIC (ΔAIC = 8.73) indicating that this model resulted in less loss of information in the data. Therefore, individuals of *C. constrictor* were smaller (1) in the peninsular Florida clade than the eastern clade (difference = −58.43 mm, lower confidence limit <LCL> = −97.44 mm, upper confidence limit <UCL> = −16.23 mm; Burbrink *et al.*, 2008); (2) on pine forests than hardwoods (difference = −28.05 mm, LCL = −39.85 mm, UCL = −15.98 mm); (3) on hydric soils versus mesic (difference −41.87 mm, LCL = −73.34 mm, UCL = −19.00 mm) and xeric soils (difference = −48.30 mm, LCL = −74.40 mm, UCL = −24.20 mm); and (4) in the presence of *C. flagellum* (difference = −35.31 mm, LCL = −49.70 mm, UCL = −20.54 mm). Although the mean SVL of *C. constrictor* was lower in areas where scrub was the dominant habitat type (Table 2), the only traps located in scrub-dominated areas were within a single study site (Lake Wales Ridge State Forest). Therefore, we could not independently control for the effect of the study sites with the random effect and examine the effect of scrub. Once

Table 3 Number of parameters (k), log-likelihood (LL), Akaike's Information Criterion (AIC), the difference in AIC between the model with the lowest AIC score and any given model (ΔAIC) and the model weights (wi) of linear mixed effects of the 10 models with the lowest AIC values built describing body sizes of coachwhips, *Coluber flagellum*, and North American racers, *Coluber constrictor*, and body condition index of *C. constrictor*

	Model	k	LL	AIC	ΔAIC	wi
C. flagellum	Incidental	4	387.41	–766.81	0	0.06
	Incidental + Soil	6	389.39	–766.78	0.03	0.06
	Incidental	5	388.30	–766.60	0.21	0.06
	Incidental + Soil + Canopy	7	390.14	–766.27	0.54	0.05
	Soil	5	387.90	–765.81	1.00	0.04
	Null	3	385.88	–765.76	1.058	0.04
	Incidental + Canopy + Sex	7	389.83	–765.66	1.16	0.04
	Incidental + Sex	6	388.71	–765.41	1.40	0.03
	Incidental + Sex + Soil	8	390.61	–765.21	1.60	0.03
	Incidental + Canopy + Sex + Soil	9	391.60	–765.19	1.62	0.03
C. constrictor	Clade + Habitat + Soil	10	1476.63	–2933.25	0	0.18
	Clade + Habitat + Soil + Canopy	11	1477.06	–2932.12	1.13	0.10
	Clade + Habitat + Soil + Latitude	11	1476.82	–2931.63	1.62	0.08
	Clade + Habitat + Soil + Incidental	11	1476.65	–2931.30	1.96	0.07
	Clade + Habitat + Soil + Sex	12	1477.42	–2930.85	2.41	0.06
	Clade + Habitat + Soil + Canopy + Latitude	12	1477.21	–2930.42	2.83	0.04
	Clade + Habitat + Soil + Canopy + Incidental	12	1477.09	–2930.17	3.08	0.04
	Clade + Habitat + Canopy	9	1474.03	–2930.07	3.19	0.04
	Clade + Habitat + Sex	10	1474.97	–2929.93	3.32	0.04
	Clade + Habitat + Soil + Latitude + Incidental	12	1476.84	–2929.68	3.57	0.03
Body Condition Index	Clade + Soil + Latitude	9	2627.56	–5237.12	0	0.07
	Clade + Soil + Canopy	11	2628.96	–5235.91	1.21	0.04
	Clade + Canopy	9	2626.95	–5235.90	1.22	0.04
	Clade + Soil	8	2625.94	–5235.87	1.25	0.04
	Clade + Soil + Latitude + Sex	11	2628.89	–5235.78	1.34	0.04
	Clade + Soil + Habitat	10	2627.87	–5235.75	1.37	0.03
	Clade + Soil + Latitude + Incidental	10	2627.61	–5235.22	1.90	0.03
	Clade	6	2623.61	–5235.21	1.91	0.03
	Clade + Sex + Habitat	10	2627.59	–5235.17	1.95	0.03
	Clade + Soil + Sex + Habitat	12	2629.57	–5235.13	1.99	0.03

we removed the confounding effect of scrub, an effect of pine forests became apparent. The only factor in the best model for the size of *C. flagellum* (Table 3) indicated that snakes caught incidentally were larger than those that were trapped (difference = 86.09 mm, LCL = 14.91 mm, UCL = 161.31 mm).

The best model for BCI (Table 3), regardless of the presence/absence of *C. flagellum*, revealed body condition (1) decreased with latitude ($\beta = -0.002$, LCL = –0.003, UCL < –0.001); (2) was lower on xeric soils than hydric soils (difference = –0.005, LCL = –0.008, UCL = –0.002); and (3) was higher for individuals of the Gulf Coast clade (difference = 0.008, LCL = 0.006, UCL = 0.011), the Eastern clade (difference = 0.012, LCL = 0.006, UCL = 0.018) and the peninsular Florida clade (difference = 0.007, LCL = 0.001, UCL = 0.013) than the Florida panhandle clade. The addition of a factor indicating the presence/absence of *C. flagellum* resulted in an increase in AIC (ΔAIC = 1.98) indicating a less parsimonious model.

Discussion

We suggest that we have obtained evidence consistent with the hypothesis that differences in body size between two predators are amplified due to interspecific competition, a pattern also observed among a well-studied group of squamates, Caribbean anoles (*Anolis* spp., reviewed in Dayan & Simberloff, 2005). *Coluber constrictor* body size, which we consider a proxy for resource use, was influenced by the presence of *C. flagellum*. Specifically, on a site-by-site basis, *C. constrictor* was smaller when *C. flagellum* was present than when *C. flagellum* was absent. The observed divergence may result from a limit in *C. constrictor* body size when *C. flagellum* is present or an increase in *C. constrictor* body size when *C. flagellum* is absent. There are several criteria necessary to demonstrate whether observed patterns are due to character displacement; for example, researchers must document a genetic basis for specific morphological differences and consider relative survival rates of invading individuals (Schluter & McPhail, 1992). We did not address them within our study; thus, the mechanisms behind the differences we observed in body size cannot be conclusively attributed to this process.

We calculated BCI for *C. constrictor* because BCI is an effective method for measuring body reserves (Bonnet & Naulleau, 1996). Although we demonstrated shifts in body size in relation to the presence of *C. flagellum*, we did not find significant changes in BCI. Therefore, we did not obtain evidence that

the presence/absence of *C. flagellum* influenced body condition of *C. constrictor*. This is consistent with the suggestion that there is no apparent cost to smaller body sizes when in the presence of a larger competitor. This is to be expected if smaller body sizes facilitated population persistence, rather than being solely a reflection of depleted resource levels.

We cannot discount the potential that there are variables that we did not measure that resulted in the patterns we observed. This is particularly important because all of the allopatric *C. constrictor* we included in the linear effects model were collected from only two sites (although trends within this restricted sample are consistent within the entire sample; Table 2). Snakes with wide geographic ranges are likely to exhibit variation in prey taken (e.g. Luiselli, Filippi & Capula, 2005; Fleet *et al*., 2009) and prey availability and associated nutrient content influences snake body size. There is the potential that *C. constrictor* is responding to populations of prey at the different sites rather than interspecific interactions with *C. flagellum*. However, although there is some diet partitioning between *C. constrictor* and *C. flagellum*, there is considerable overlap in types of prey consumed (Halstead *et al*., 2008); therefore, it is likely that variation in prey populations among sites would influence both species similarly, yet we documented no change in *C. flagellum* body size in relation to any of the measured habitat variables.

Our conclusions would be strengthened by information on the actual prey items consumed by each species at the different sites. For example, although previous research describing morphological variation between sympatric mustelids suggested that character displacement likely resulted from competition for resources (Dayan & Simberloff, 1994), empirical diet data were not consistent with this hypothesis (McDonald, 2002). Interspecific aggression was suggested as an alternative explanation for the differences in morphology observed between mustelids. However, we know of no evidence for direct interactions of this type between *C. constrictor* and *C. flagellum*.

Large-scale studies have examined geographic variation in diet among populations of *C. constrictor* (reviewed in Rosen, 1991), including in areas where they co-occur with *C. flagellum* (Halstead *et al*., 2008), but the relationship between the diet of this species and the presence of potential predators remains elusive. To evaluate whether *C. constrictor* diet changes in response to the presence of *C. flagellum* would require a large-scale sampling effort that quantifies both prey availability and prey consumption/selection at sites where *C. flagellum* did and did not occur. Powerful evidence for interspecific interactions that influence diet could also be generated by experimentally manipulating the density of either *C. flagellum* and/or resource levels in areas where *C. flagellum* co-occurs with *C. constrictor* and then identifying how body size and prey consumption change. Such studies would be fascinating but completing them would be extremely challenging in terms of the scale of effort needed to capture snakes across their range while identifying and quantifying their diet. These studies would be even more difficult because captured snakes often do not have gut contents (e.g. Shewchuk & Austin, 2001). However, molecular techniques (e.g. Farrell, Roman & Sunquist, 2000) may hold promise for future descriptions of snake diet.

If squamates partition resources, these resources are likely to include habitat and diet (Toft, 1985). Large-scale studies have suggested that differences in resource use among present-day squamates are due largely to their evolutionary past (Vitt & Pianka, 2005), and interspecific competition is thought to structure their assemblages (Luiselli, 2006). However, there are few studies that examine whether resource use changes in relation to the presence of potential competitors (e.g. Luiselli, 2003). We suggest that the trends we documented are consistent with the hypothesis that interspecific competition between morphologically and taxonomically similar species influences body size on an ecological timescale. This divergence may be the mechanism leading to the evolutionary process of character displacement.

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