Size and Growth in Two Populations of Black Kingsnakes, *Lampropeltis nigra*, in East Tennessee

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Size and Growth in Two Populations of Black Kingsnakes, *Lampropeltis nigra,* in East Tennessee

Ted M. Faust[1,*] and Sean M. Blomquist[2]

Abstract - This paper reports information on size and growth of snakes in two populations of *Lampropeltis nigra* (Black Kingsnake) over 20 years of study and provides a comparative analysis that builds on the work of Jenkins et al. (2001). During a 7-year study (1990–1996) at the Anderson County Wildlife Sanctuary (ACWS) and a 13-year study (1997–2009) at the University of Tennessee Forestry Resources Research and Education Center (FES) in Oak Ridge, TN, we captured 265 individual Black Kingsnakes a total of 556 times. The size of Black Kingsnakes in these two populations are the smallest reported for this species, with mean (± SD) snout-to-vent length (SVL) of 66.9 ± 24.5 cm (maximum = 112 cm) at ACWS and 55.8 ± 16.8 cm (maximum = 87 cm) at FES. At FES, the mass-SVL relationship is represented by an exponential equation (mass [g] = 0.0004 SVL [cm]$^{2.98}$) similar to ACWS (mass [g] = 0.0005 SVL [cm]$^{2.95}$). Across both sites, juvenile kingsnakes grew 1.1 cm/mo faster than adult individuals. There was a significant decline in body condition index (BCI) in the combined population during 1990–2009, with BCI declining by 0.960 units annually at ACWS and by 0.981 units annually at FES over the respective study periods. Declines in BCI may be a precursor to a decline in abundance.

Introduction

Many reptiles are long lived, and thus require analysis of long-term datasets (>5 years) in order to gain insight into their ecology (Gibbons et al. 2000, Madsen and Shine 2001). Short-term studies of growth can produce misleading results due to seasonal variation in availability of prey and other resources (Madsen and Shine 2001), whereas comparative, long-term studies more accurately evaluate differences in size and growth among snake populations (Hill and Beaupre 2008, Jenkins et al. 2001). Recent reports of *Lampropeltis getula* L. (Eastern Kingsnake) population declines throughout the southeast (Krysko and Smith 2005, Stapleton et al. 2008, Winne et al. 2007) as well as general declines in herpetofauna worldwide (Gibbons et al. 2000, Reading et al. 2010) further exemplify the need for both comparative and long-term studies concerning ecology and habitat use. While reasons for declines remain enigmatic, habitat loss and degradation, environmental pollutants, and other anthropomorphic factors are often credited as likely factors influencing declines in population health and abundance (Krysko and Smith 2005, Winne et al. 2007).

The *Lampropeltis getula* species complex was recently split into five species including *Lampropeltis nigra* Yarrow (Black Kingsnake, formerly *Lampropeltis getula nigra*; Pyron and Burbrink 2009a, b). Black Kingsnakes range from the Mississippi River east to the Appalachian mountains and from the Gulf coast

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north to southern Illinois (Pyron and Burbrink 2009a). This complex was split based on genetic and morphological evidence (Pyron and Burbrink 2009a), with ecological differences and allopatric geographic distributions supporting the new species (Pyron and Burbrink 2009b).

Kingsnakes spend much of their time underground (Linehan et al. 2010) and often use small-mammal burrows for refuge sites (Steen et al. 2010) and movements (J. Byrd, Clinch River Environmental Studies Organization [CRESO], Clinton, TN, pers. comm.). Species within the *Lampropeltis getula* complex are commonly found in loose, dry soil types that allow burrowing in edge areas of natural pine and hardwood forest macrohabitats which contain sufficient levels of ground-cover microhabitat (i.e., coarse woody debris, leaf litter, ground vegetation; J. Byrd, pers. comm.; Plummer 2010; Steen et al. 2010).

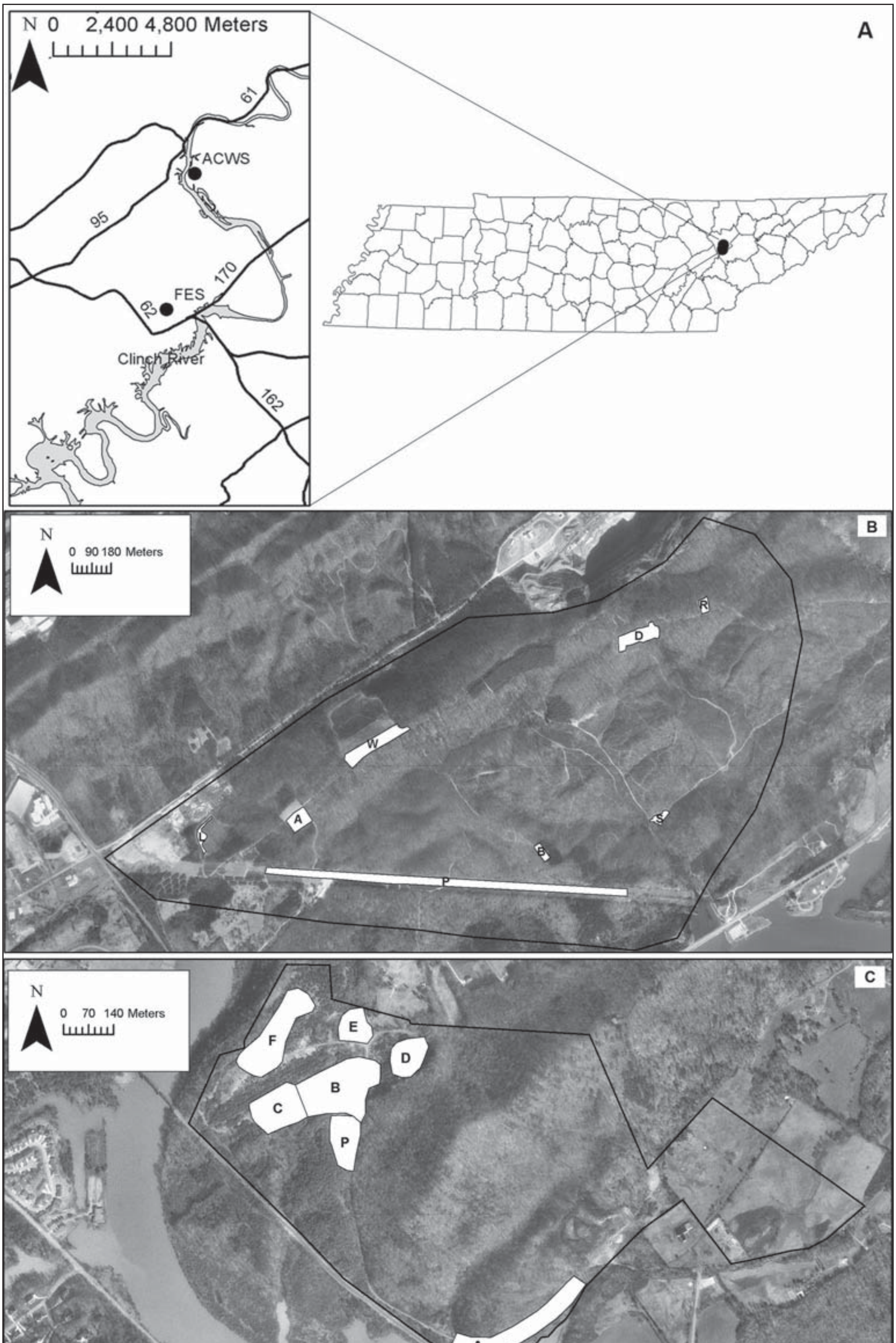
Our study focuses on size and growth of Black Kingsnakes and will help further the knowledge of (e.g., general physiology and potential habitat factors affecting size and growth) and assist in possible conservation strategies for this newly elevated species. During 1997–2009, we conducted a snake coverboard study at the University of Tennessee Forestry Resource Research and Education Center in conjunction with CRESO. This paper compares data on size and growth between these two nearby but distinct populations of Black Kingsnakes in Anderson County, TN (Fig. 1A; Jenkins et al. 2001). While superficially similar, these two sites possess microhabitat differences in soil, prey abundance, and land-use histories. Our study sought to (1) provide data on snake size (SVL and mass) and growth in the wild, (2) analyze differences in size and growth between two nearby populations, (3) analyze long-term, temporal changes in body condition between sites, and, when possible, (4) explore potential mechanistic reasons for differences between the two populations.

Study Area

Anderson County Wildlife Sanctuary (ACWS)

During 1990–1996, research was conducted at the Anderson County Wildlife Sanctuary (ACWS), situated along the Clinch River in East Tennessee (36°3'N, 84°11'W; Fig 1C). This 60-ha site was used as a county dump from 1962–1972 and was then upgraded to a landfill which was closed in May 1982. In 1988, this area became ACWS and was managed by CRESO up until 1996. During the time of research, the site consisted of forest (≈40 ha), old recovering landfill and other old-field habitat (≈15 ha), pine plantation (≈3 ha), and limestone bluffs (≈2 ha), with our study focusing on the woodland-field ecotone and old-field habitats (Jenkins et al. 2001). See Jenkins et al. (2001) for a full description of ACWS study area.

Figure 1 (opposite page). (A) The two study sites in relation to each other showing the Clinch River barrier that separates each site. (B) Aerial view of the University of Tennessee Forest Resources Research and Education Center (FES). (C) Aerial view of Anderson County Wildlife Sanctuary (ACWS). The highlighted sections of each aerial image show the fields that were sampled with coverboards, with the approximate study area boundaries for each site being identified by a black polygon.


A
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University of Tennessee Forest Resources Research and Education Center (FES)

During 1997–2009, research was conducted by CRESO at the University of Tennessee Forest Resources Research and Education Center: Oak Ridge Forest and Arboretum (FES, as it was formerly known as the University of Tennessee's Forestry Experimental Station) located in the Ridge and Valley physiographic province of Anderson County, TN (35°60'N, 84°13'W, about 6 km SW of the ACWS on the opposite side of the Clinch River; Fig. 1B). The site is about 915 ha and since 1962 has been protected from uncontrolled fire with limited timber harvest.

The FES is a highly fragmented area characterized by regenerating upland hardwood and mixed pine-hardwood stands. Deciduous forest stands are comprised principally of duel-aged oak-hickory groups. The site is transected by a utility corridor containing two parallel electric transmission line right-of-ways, approximately 1.4 km in length. Our study focused on the open field and woodland-field ecotone (including the right-of-ways) habitats of 7 distinct fields (mean field size = ≈1.4 ha, SD = ≈1.9 ha). Distances between fields were not standardized and ranged from 0.2–2.5 km. The majority of the FES consists of upland hardwood and mixed pine-hardwood forest that separates each of the relatively small fields (Fig. 1).

Though the ACWS and the FES sites are in close proximity to one another, we consider each population to be separate and distinct for two primary reasons. Firstly, the largest reported cumulative move upon release for a Black Kingsnake is approximately 1.5 km (Jenkins et al. 2001). Closely related Eastern Kingsnakes show a maximum range length of approximately 1.6 km (Wund et al. 2007), and *Lampropeltis holbrooki* Stejneger (Speckled Kingsnake) showed an average maximum range length of 1012 m (SE = 120 m) for males (Plummer 2010). All of these movement distances are much shorter than the ≈6 km straight-line distance between sites. Secondly, the sites are separated by the Clinch River (width = 0.16–0.51 km), which serves as a geographical barrier to snake movement (Fig. 1A). The area between the sites also contains man-made barriers, including roads, residential areas, and an active quarry site, which may further inhibit snake movements.

Species richness was similar between the two sites; however, species abundance was often vastly different. We captured 180 Black Kingsnakes a total of 400 times at ACWS and 85 Black Kingsnakes a total of 156 times at FES; these captures made up 54.8% and 7.2% of all snake encounters including recaptures, respectively (Jenkins et al. 2001; T. Faust, unpubl. data).

Methods

Sampling methods

We placed coverboards along the woodland-field ecotone of fields and utility company right-of-ways. Coverboards were wood (ACWS: n = 50, FES: n = 110; mean size = 1.5 m^2, range = 0.4–4.4 m^2) and metal (ACWS: n = 99, FES: n = 110; mean size = 1.7 m^2, range = 0.4–4.4 m^2). Coverboards were generally placed as coverboard units (each unit = one wood and one metal coverboard

<5 m apart), but 49 metal coverboards were placed singly at the ACWS. At FES, 25 coverboard units were placed along P field in 1997, with the addition of 6 more coverboard units in April 2001. In May 2001, 79 coverboard units were added to 7 new fields at FES (Fig. 1B). Black Kingsnakes showed no preference for wood or metal coverboards at either site (Jenkins et al. 2001). Other studies that utilized coverboards have shown an absence of size-related biases in snakes (Willson et al. 2008) and produced capture rates for kingsnakes that varied greatly from FES and ACWS rates (e.g., Johnson [1964] for Black Kingsnakes and Grant et al. [1992] for Eastern Kingsnakes). This research suggests that the use of coverboards resulted in small to negligent sampling bias for the kingsnakes in our studies. Coverboard units were placed 6.5–124 m (SD = 22.6 m) apart. On average, searches were conducted 6.4 (SD = 3.7) times per month from April–September and 1.0 (SD = 0.8) times per month in March, October, and November. Our standard protocol consisted of 30-second visual searches of the coverboard substrate, usually by two or more individuals (Jenkins et al. 2001).

Snout-to-vent length (SVL, ± 0.1 cm) and vent-to-tail length (VTL, ± 0.1 cm) were recorded by straightening snakes along a 100-cm measuring stick (Fitch 1987). Usually two independent length measurements were taken for each snake to ensure accuracy. Independent measurements were usually within 1 cm, and means were used when independent measurements differed. Rarely, only one researcher was present and measurements were taken only once. An Ohaus digital scale was used to record mass (± 0.1 g). Snakes were released under the original capture site coverboard within 24 h after capture, and individuals recaptured within 14 days of previous capture were not remeasured. At ACWS, individuals were marked by clipping caudal scales (Blanchard and Finster 1933), and photocopies of ventral patterns were used as an additional identification technique during the last four years of the study (Jenkins et al. 2001). At FES, passive integrated transponder tags (PIT-tags) were injected into snakes in order to identify individuals (Gibbons and Andrews 2004). Cloacal probing was used to determine sex at both sites (Blanchard and Finster 1933, Schaefer 1934).

Analyses

Mass and SVL were analyzed based on one corresponding data point from each individual. Some individuals were captured multiple times over multiple years resulting in a large range of measurements for these individuals. For individuals that were captured more than once during the study, a representative mass and SVL data point was selected randomly. Points were randomly selected to meet the statistical assumption of independent data points. Kingsnakes that were not PIT-tagged (n = 16) were treated as the same individual unless date, location, and size of the snake made it obvious that the unmarked snake was a separate individual. We identified 8 individuals during the study that were not PIT-tagged. These methods yielded a full dataset of 252 individuals (n = 170 at ACWS; n = 82 at FES) for mass and SVL analyses, and all statistical analyses were performed in SAS (version 9.1, SAS Institute, Cary, NC). We investigated if the SVL and mass of snakes varied among the two sites and sexes (including unsexed animals as a third category) using two-way multivariate analysis of variance (MANOVA statement in PROC GLM). We tested the effect of site, sex, and the interaction of these two factors, and used Tukey's post-hoc pairwise comparisons to examine differences within each factor. Following Jenkins et al. (2001), we used simple linear regression to test if an exponential function ($y = ax^b$) described the relationship between mass and SVL (PROC REG). We used one-way analysis of covariance (ANCOVA, PROC GLM) with site as a factor in the model and mass as a covariate to examine if the slopes of the regression line describing the relationship between mass and SVL varied from the relationship reported by Jenkins et al. (2001) where mass = 0.0005 $SVL^{2.95}$.

We used a subset of 44 (27 at ACWS, 17 at FES) individuals that were recaptured at least once during the study to investigate differences in growth rate. Growth rates were calculated by taking the initial capture SVL and the final capture SVL and dividing the change in SVL by the total months of growth. Using a 30-day month, we eliminated snakes with fewer than two months of growth and calculated change in SVL based on a six-month growing season (April–September) for individuals that were captured in more than one year (Jenkins et al. 2001). Size at maturity (60 cm SVL) was based on previous reports for Black Kingsnakes (Jenkins et al. 2001, Mitchell 1994) and on field observations at our two study sites. We calculated growth rates for snakes based on the SVL at initial capture for juvenile (≤60 cm SVL) and adult snakes (>60 cm SVL). To investigate if the growth rate of snakes varied among the two sites and by sexual maturity, we used two-way analysis of variance (ANOVA, PROC GLM). We tested the effect of site, maturity, and the interaction of these two factors, and used Tukey's post-hoc pairwise comparisons to examine differences within each factor. Furthermore, we tested the assumption that maturity influenced growth rate over the course of an individual's life by using simple linear regression to determine if growth rate was related to size at initial capture.

To evaluate changes in the body condition of snakes over the study period, we calculated a body condition index (BCI) based on the relationship for Eastern Kingsnakes: BCI = ($mass/SVL^3$) x 10^5 (Winne et al. 2007). Following Winne et al. (2007), only the first capture record for each individual was used in analysis; additionally, we also removed gravid females and snakes that were known to have recently fed due to evident bulges or regurgitations. This procedue resulted in 5 individuals from ACWS and 3 from FES being removed from the full 252-snake dataset, and a total of 244 individuals (n = 165 at ACWS, n = 79 at FES) being used for BCI analyses. We investigated if BCI varied over time and if the change in BCI varied among the sites and sexes. Although comparison of sites is not a direct comparison because of the temporal differences in the studies, we compared sites to examine if widespread changes were occurring at both sites. We used simple linear regression to determine if BCI changed across years with site and sex. We used one-way ANCOVA with either site or sex as a factor in the model and year as a covariate to examine if the slopes of the regression line describing the relationship between BCI and year varied.

The data were primarily normal based on histograms, skewness, and kurtosis of each variable. For regression analyses, we visually examined residuals to assess variance homogeneity; all regression analyses met this assumption. Means ± standard deviation are reported unless otherwise specified, and $\alpha = 0.05$ was used to evaluate all tests.

Results

Size

Kingsnakes ranged from 25.0–86.5 cm SVL, 29.2–95.6 cm TL, and 6.6–250.0 g at FES (n = 82) and from 25.0–112.0 cm SVL, 28.5–129.2 cm TL, and 4.6–521.0 g at ACWS (n = 170) (Table 1; Jenkins et al. 2001). Snakes at the FES were on average 11.1 cm shorter (partial-$F_{1,246} = 6.06$, $P = 0.015$) and 82.1 g lighter (partial-$F_{1,246} = 6.81$, $P = 0.001$) than snakes at the ACWS (two-way MANOVA: Wilks' $\lambda = 0.97$, $F_{2,245} = 3.42$, $P = 0.034$). Snout-to-vent length and mass of males and females were not significantly different (two-way MANOVA: Wilks' λ= 0.99, $F_{4,490} = 0.82$, $P = 0.516$), and the effects of site and sex were independent (two-way MANOVA: Wilks' $\lambda = 0.98$, $F_{4,490} = 1.19$, $P = 0.314$). Tail length-to-total length ratios of sexually mature males and females (SVL > 60 cm) ranged from 12.3–15.4% (n = 20) and 10.3–13.6% (n = 15), respectively, at the FES, which is within the range reported by other studies on this species (e.g., Kaufman and Gibbons 1975). An exponential curve (mass [g] = 0.0004 SVL [cm]$^{2.98}$) described the relationship between mass and SVL at the FES ($r^2 = 0.95$, $F_{1,81} = 1449.58$, $P < 0.001$; Fig. 2). This relationship was not significantly different than that described by Jenkins et al. (2001) for the ACWS (mass [g] = 0.0005 SVL [cm]$^{2.95}$; ANCOVA site factor partial-$F_{1,251} = 1.01$, $P = 0.316$).

Table 1. Mean mass (g), snout-to-vent length (SVL; cm), vent-to-tail length (VTL; cm), and total length (TL; cm) in two populations of Black Kingsnakes in Anderson County, TN (FES = University of Tennessee Forest Resources Research and Education Center; ACWS = Anderson County Wildlife Sanctuary).

	n	SVL (SD)	VTL (SD)	TL (SD)	Mass (SD)
FES					
Females	38	55.3 (19)	7.4 (2.8)	62.6 (21)	85.2 (71)
Males	43	56.7 (15)	8.8 (2.6)	65.5 (18)	78.0 (50)
Unknown sex	1	33.5	4.6	38.1	12.0
All	82	55.8 (17)	8.1 (2.7)	63.8 (19)	80.5 (61)
ACWS					
Females	60	63.2 (22)	8.4 (2.9)	71.6 (25)	126.6 (116)
Males	62	63.9 (25)	9.6 (3.7)	73.5 (28)	138.9 (143)
Unknown sex	48	75.3 (26)	10.9 (4.3)	86.2 (30)	237.8 (159)
All	170	66.9 (25)	9.5 (3.7)	76.4 (28)	162.4 (146)
Overall					
Females	98	60.1 (21)	8.0 (2.9)	68.1 (24)	110.5 (103)
Males	105	61.0 (21)	9.3 (3.3)	70.2 (25)	113.9 (118)
Unknown sex	49	74.4 (26)	10.8 (4.3)	85.2 (30)	233.1 (160)
All	252	63.3 (23)	9.1 (3.5)	72.3 (26)	135.8 (131)

Growth

Based on recaptures of 44 individuals (27 at ACWS, 17 at FES) with a minimum of 2 (mean = 9.2) growing months between first and last capture of each individual, growth rates varied from 0.0–4.2 cm/mo (Table 2). Across both sites, we found that juvenile kingsnakes grew at a 1.1-cm/mo-faster rate than adult individuals (two-way ANOVA: $F_{3,43} = 5.77$, $P = 0.002$; maturity factor partial-$F_{1,43} = 12.84$, $P < 0.001$). Further, growth rates declined with increasing SVL at initial capture at the FES ($r^2 = 0.26$, $F_{1,16} = 5.16$, $P = 0.038$), which is similar to the pattern described by Jenkins et al. (2001) for the ACWS site. Additionally, snakes at

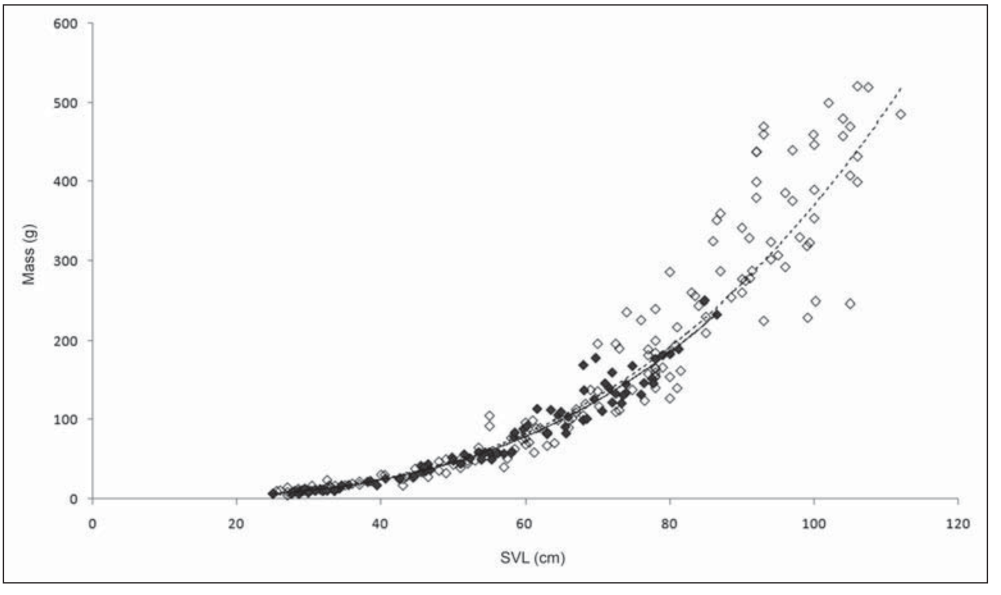

Figure 2. Relationship between mass and snout-to-vent length in two populations of Black Kingsnakes in Anderson County, TN. Mass and snout-to-vent length of snakes from the University of Tennessee Forest Resources Research and Education Center (filled diamonds, solid line) and Anderson County Wildlife Sanctuary (open diamonds, dashed line) showed the same pattern within each population.

Table 2. Monthly growth (cm/mo) in two populations of Black Kingsnakes in Anderson County, TN (FES = University of Tennessee Forest Resources Research and Education Center; ACWS = Anderson County Wildlife Sanctuary).

	Female			Male			Overall		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
FES									
Monthly growth (cm/mo)	2.0	1.2	11	1.9	1.3	6	2.0	1.2	17
Juvenile monthly growth (cm/mo)	2.2	0.7	8	2.7	2.1	2	2.3	0.9	10
Adult monthly growth (cm/mo)	1.5	2.1	3	1.4	0.8	4	1.4	1.3	7
ACWS									
Monthly growth (cm/mo)	0.9	0.7	11	1.6	1.1	16	1.4	1.0	27
Juvenile monthly growth (cm/mo)	1.2	0.9	4	2.7	0.9	6	2.1	1.1	10
Adult monthly growth (cm/mo)	0.8	0.7	7	1.0	0.7	10	0.9	0.6	17

FES had 0.6-cm/mo-higher growth rates than at ACWS (two-way ANOVA: site factor partial-$F_{1,43}$ = 4.27, P = 0.045). We found no evidence that there was an interaction between site and growth rate of juvenile and adult individuals (two-way ANOVA: interaction partial-$F_{1,43}$ = 0.19, P = 0.665).

Body condition

The body condition index of Black Kingsnakes declined by 0.191 units annually (r^2 = 0.02, $F_{1,243}$ = 5.21, P = 0.023; Fig. 3) from 1990 to 2009 across sites. During 1990–1996 at the ACWS site, BCI declined by 0.960 units annually (r^2 = 0.04, $F_{1,164}$ = 7.35, P = 0.007), and BCI declined by 0.981 annually during 1997–2009 at the FES site (r^2 = 0.18, $F_{1,78}$ = 16.39, P = 0.001; Fig 3). The BCI ranged from 21.3–71.6 across both study sites (n = 244), and mean BCI was 37.5 ± 6.4 at FES (n = 79) and 38.4 ± 8.7 at ACWS (n = 165). Mean BCI was 37.6 ± 7.2 for males (n = 43) and 37.4 ± 5.3 for females (n = 36) at FES, and mean BCI was 37.5 ± 8.1 for males (n = 61), 36.0 ± 8.1 (n = 55) for females, and 42.3 ± 9.0 for unsexed snakes (n = 49) at ACWS. Body condition did not vary between the two sites (ANCOVA: $F_{2,243}$ = 9.46, P < 0.001; site partial-$F_{1,243}$ = 0.75, P = 0.386), but the change in BCI showed the same increasing then decreasing pattern across each of the two studies (year partial-$F_{1,243}$ = 18.17, P < 0.001; Fig. 3). The BCI values of unsexed snakes were 5.1 points higher than males and females (ANCOVA: $F_{3,243}$ = 6.01, P < 0.001; Sex

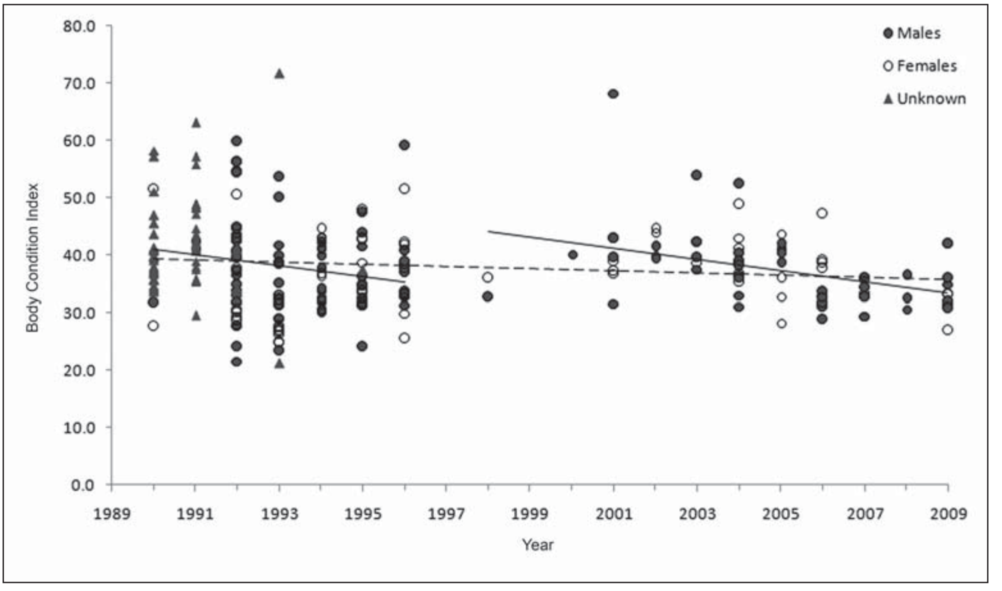

Figure 3. Body condition index for two populations of Black Kingsnakes in Anderson County, TN. Body condition of snakes declined by approximately 1.0 BCI unit per year at both the Anderson County Wildlife Sanctuary study site during 1990–1996 (y = -0.960x + 1951; r^2 = 0.04) and at University of Tennessee Forest Resources Research and Education Center study site during 1997–2009 (y = -0.981x + 2004; r^2 = 0.18). Across both studies during 1990–2009, snake body condition declined by approximately 0.2 BCI units per year (y = -0.191x + 419.8; r^2 = 0.02). The lines represent the linear regression of body condition irrespective of sex for each site separately (solid lines) and together (dashed line).

partial-$F_{2,243}$ = 6.30, P = 0.002), but BCI did not co-vary with sex from 1990–2009 (year partial-$F_{1,299}$ = 0.16, P = 0.694).

Discussion

Black Kingsnakes may show local and rangewide geographic variation in body size. The mass and SVL of our two populations are the smallest reported for this species. Despite obvious size differences between populations, the mass-SVL relationships and growth rate similarities between geographically distinct kingsnake populations suggest that growth patterns may be consistent across the Black Kingsnake's and Eastern Kingsnake's ranges regardless of maximal size. Differences due to land-use histories in soil, prey compositions, and other microhabitat aspects may have a significant effect on SVL and mass, even between nearby populations.

The limited published literature on Black Kingsnakes indicates there may be some geographic variation in body size among populations (Johnson 1964, Meade and Palmer-Ball 2003, Pyron and Burbrink 2009a), and the mean mass and SVL of Black Kingsnakes at our two study sites were the smallest reported for this species. At both sites, most Black Kingsnakes fell below the reported range (mean TL = 90–122 cm; Pyron and Burbrink 2009a). The only other noteworthy report on the size of Black Kingsnakes indicates geographic variation among populations; Meade and Palmer-Ball (2003) report the size range of 28 adult males of 73.6–148.0 cm TL and 65.4–130.9 cm SVL in Kentucky and southern Indiana, with the largest individual found in southern Indiana. The closely related Eastern Kingsnake and Speckled Kingsnake have maximum lengths of 208 cm TL (Ernst and Barbour 1989) and 183 cm TL (Pyron and Burbrink 2009a), respectively, indicating further geographic variation within this complex. For example, 2 Eastern Kingsnake and 1 Speckled Kingsnake radio-telemetry studies reported mean SVLs and masses (reported in 2 studies only) that were larger than either of our site's means (Plummer 2010, Steen et al. 2010, Wund et al. 2007). These researchers likely selected larger individuals for radio-telemetry, thus likely skewing the means towards the high end. However, maximum SVL and mass were substantially higher for Eastern Kingsnakes (Steen et al. 2010, Wund et al. 2007) and approximately equal for Speckled Kingsnakes (Plummer 2010) when compared to our study. Krysko (2002) reported a majority of individuals near 90 cm SVL, with a maximum SVL of 160 cm in southern Florida. Variation among these studies suggests that the *Lampropeltis getula* complex likely has both intra- and inter-specific body size variation in the 3 species discussed (Black Kingsnakes, Eastern Kingsnakes, and Speckled Kingsnakes), with Speckled Kingsnakes falling the closest to our reported size ranges (Plummer 2010).

The *Lampropeltis getula* complex also appears to exhibit geographic variation in size at maturity. Krysko (2002) reported an SVL of 80 cm for maturity in Eastern Kingsnakes which has been used to define maturity in other kingsnake studies (e.g., Plummer 2010). Speckled Kingsnake females are known to mature at <70 cm SVL (Trauth et al. 1994). Our reported value for maturity (60 cm SVL) was, in part, based on a gravid female (SVL = 66.5 cm, mass = 101.8 g) found with 9 eggs at ACWS. Additionally, a male (SVL = 72.5 cm, mass = 133 g) and a female (SVL = 71.0 cm, mass = 146 g) were found in copulation at FES in early 2009.

Geographic variation was even evident between sites; Black Kingsnakes at FES were significantly smaller in both SVL and mass than those at ACWS (Jenkins et al. 2001). Although some size differences can be expected between geographically distant populations (Beaupre 1995, Grant and Dunham 1990), it is less intuitive that populations <6 km apart would show such distinct differences as found between FES and ACWS. However, Hill and Beaupre (2008) showed significant size differences between populations of *Agkistrodon piscivorus leucostoma* Troost (Western Cottonmouth) located <50 km apart.

The Black Kingsnake mass-SVL relationship (mass = 0.0006 $(SVL)^{2.98}$) at FES is similar to what Jenkins et al. (2001) reported at ACWS (mass = 0.0005 $(SVL)^{2.95}$) and Kaufman and Gibbons (1975) reported (mass = 0.0004 $(SVL)^{2.94}$) in a South Carolina population of Eastern Kingsnakes. Jenkins et al. (2001) suggested that this metric can be used to monitor the health of an individual or a population. These similar body-size relationships among different populations of kingsnakes provide a useful range for comparison among populations and indicate that these two species may have similar growth patterns.

Juvenile Black Kingsnakes grew faster than adult Black Kingsnakes, and growth rate declined with increasing SVL at both FES and ACWS. Both Madsen (1983) and Pearson et al. (2002) also showed that growth rates declined with increasing SVL in two other snake species; however, both of these studies show that female snakes do not slow their growth to the same extent as males. Compared to these studies, our growth data was limited, but we did not find any differences in growth between sexes. Although FES snakes grew 0.6 cm/mo faster than ACWS snakes, this may be in part due to the larger proportion of mature snakes at ACWS because the similar mass-SVL relationships between sites suggest a similar growth pattern. We hypothesize that FES kingsnakes may be lacking the resources (e.g., habitat and prey) needed to reach the larger sizes seen at ACWS. Although we cannot address this with our dataset, an analysis of size and age-specific growth and survival rates may help to clarify such observed differences among populations.

Geographic variation among populations has been explained by regional differences in elevation, habitat, temperature, and precipitation (Ernst and Barbour 1989, Grant and Dunham 1990, Hill and Beaupre 2008, Reinert 1993). Between our two sites, differences in elevation were not notable and neither were temporal temperature or precipitation differences (NOAA 2010). Consistent differences seen in SVL and mass between the two sites may suggest the habitat is of higher quality or more suitable habitat exists at ACWS. On a macrohabitat level, ACWS and FES sites were relatively similar; however, there were distinct differences between sites on a microhabitat level. The sites differ in both soil composition and prey compositions, which we hypothesize as the primary factors for size differences between the sites. Additionally, we believe that land-use histories are the primary mechanism for differences in soil and prey compositions. The FES soils are composed of a compact clay soil with abundant chert rock, and this area possesses a relatively mild history of soil disturbances (Jenkins et al. 2001). Conversely, the ACWS soils are loose and porous from many years of disturbance (e.g., intensive farming and landfill activities; Jenkins et al. 2001). Small mammals, especially *Microtus pinetorum* LeConte (Pine Voles), are much more abundant at the ACWS site (F. Holtzclaw, Webb School of Knoxville, Knoxville, TN, unpubl. data; Jenkins et al. 2001), possibly due to the soil structure, and this may be important for the snakes at that site for two reasons. First, the loose soils at ACWS allow for a high density of burrows, which are refuge sites for kingsnakes (J. Byrd, pers. comm.; Steen et al. 2010). Second, small mammals are also a food source of kingsnakes (Jenkins et al. 2001, Wilson and Friddle 1946, Winne et al. 2007). Black Kingsnakes appear to exhibit an ontogenetic shift in diet from primarily snakes as juveniles to small mammals as adults (T. Faust and J. Byrd, unpubl. data; Jenkins et al. 2001), and the combination of fewer small mammals and more compact soils at the FES might explain why few snakes grow beyond 80 cm SVL there. These mechanistic reasons for the size differences we have described in this paper are an avenue for future research.

Body condition index may be helpful in determining changes in a population's health over time. Both FES and ACWS showed significant declines in body condition over their respective study periods. Declines in BCI have been followed by declines in abundance (Winne et al. 2007), and stable BCIs have been shown in seemingly stable populations of Eastern Kingsnakes (Linehan et al. 2010, Winne et al. 2007). Currently, there is no apparent population decline in the FES Black Kingsnake population, and snakes continue to be captured at rates similar to those from previous years (J. Weber, CRESO, Clinton, TN, pers. comm.). Though a declining survival and BCI have been strongly correlated in other taxa (e.g., Reading 2007), it is unclear if survival and BCI are strongly related in Black Kingsnakes, and future research should evaluate the strength of this relationship. It is also unclear if BCI declines in our two studies were independent of sampling influence since both sampling methods and apparent declines were very similar. Though recaptures were not included, it is possible that simply lifting coverboards disrupted prey population and, in turn, affected BCI over the course of each study period.

Our study adds to the limited body of research on the growth rates within the *Lampropeltis getula* complex, and this could be a productive avenue for future research. Reports of declines in multiple Eastern Kingsnake populations (Krysko and Smith 2005, Stapleton et al. 2008, Winne et al. 2007) illustrate the need to better understand the effects that a declining yearly BCI may have on a population. Declining BCI could potentially serve as a forewarning of population decline if the relationship among vital rates (e.g., survival and population growth rate) and BCI were better understood.

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