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Enigmatic Decline of a Protected Population of Eastern Kingsnakes, *Lampropeltis getula,* in South Carolina

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Although recent reports of global amphibian declines have received considerable attention, reptile declines have gone largely unreported. Among reptiles, snakes are particularly difficult to quantitatively sample, and thus, most reports of snake declines are based on qualitative or anecdotal evidence. Recently, several sources have suggested that Eastern Kingsnakes (*Lampropeltis getula*) have declined over a substantial portion of their range in the southeastern United States, particularly in Florida. However, published evidence for *L. getula* declines or their potential causes are limited. We monitored the status of a population of *L. getula* on the U.S. Department of Energy's Savannah River Site (SRS) in Aiken, South Carolina, USA, from 1975 to 2006. Herpetofaunal populations on the Savannah River Site have been protected from the pressures of collecting and development since 1951 due to site access restrictions. Here, we document a decline in both abundance and body condition of *L. getula* inhabiting the vicinity of a large isolated wetland over the past three decades. Because this *L. getula* population was protected from anthropogenic habitat degradation, collection, and road mortality, we are able to exclude these factors as possible causes of the documented decline. Although the definitive cause of the decline remains enigmatic, natural succession of the surrounding uplands, periodic extreme droughts, shifts in community composition (e.g., increased *Agkistrodon piscivorus* abundance), introduced fire ants, or disease are all potential contributors to the decline.

RECENT global declines in animal populations have prompted the need to monitor populations and species distributions among a diversity of taxa (Alford and Richards, 1999; Gibbons et al., 2000; Sekercioglu et al., 2004). Monitoring the status of populations and documenting species declines is a prerequisite for any conservation or management plan. Additionally, conservation actions to remediate a population decline will only be successful if the cause of the decline has been identified. Among herpetofauna, amphibian declines have received considerable attention (Alford and Richards, 1999; Houlahan et al., 2000; Collins and Storfer, 2003; Semlitsch, 2003), whereas reptile declines have not been widely publicized (Gibbons et al., 2000). While the documentation of amphibian and reptile population dynamics is generally challenging due to the covert nature of many species (Lovich and Gibbons, 1997), many snakes are particularly cryptic, have low or sporadic activity patterns, and are not easily collected using standardized sampling techniques, thereby complicating the assessment of their population status over time (Parker and Plummer, 1987; Gibbons et al., 2000). Consequently, perceived snake declines are often based on qualitative or anecdotal evidence rather than on quantitative, long-term field studies (Dodd, 1993; Krysko, 2001).

Eastern Kingsnakes (*Lampropeltis getula*) are found throughout the southern half of the United States and northern Mexico (Ernst and Ernst, 2003). Historically, *L. getula* were common throughout their range (Kauffeld, 1957; Wilson and Porras, 1983). Anecdotal evidence suggests that in recent years, *L. getula* may have suffered precipitous declines in some parts of their range, particularly in Florida (Dodd, 1993; Means, 2000; Krysko and Smith, 2005). Some of the suspected agents of decline include collection for the pet trade, unsustainable road mortality, habitat destruction and alteration, predation by invasive fire ants (*Solenopsis invicta*), and disease (Wilson and Porras, 1983; Dodd, 1993; Krysko, 2001, 2002; Wojcik et al., 2001; Allen et al., 2004). One or more of these factors have been proposed or documented as causing declines in other snake species. For example, habitat destruction and collection for the pet trade are both considered culprits for the decline of Australia's most endangered snake, the Broad-headed Snake (*Hoplocephalus bungaroides*, Webb et al., 2002). Similarly, road mortality is suspected to have resulted in the removal of at least 50% of Timber Rattlesnakes (*Crotalus horridus*) within 450 m of roads in eastern Texas (Rudolph et al., 1999) and to have caused a decline in a population of Mexican Rosy Boas (*Lichanura trivirgata trivirgata*, Rosen and Lowe, 1994). Also, habitat destruction and introduced fire ants (*Solenopsis invicta*) are suggested as potential contributors to the perceived decline of Southern Hognose Snakes (*Heterodon simus*, Tuberville et al., 2000). Nevertheless, quantitative evidence has not been published for *L. getula* population declines or their causes.

We have monitored the status of a population of *L. getula* on the U.S. Department of Energy's (DOE) 770-km^2 Savannah River Site (SRS) in Aiken, South Carolina since 1975. The SRS is a National Environmental Research Park with restricted access (Shearer and Frazer, 1997) and provides a rare opportunity to study herpetofaunal populations isolated from anthropogenic impacts frequently associated with species declines. Here, we document a decline in both abundance and body condition of *L. getula* inhabiting the vicinity of a large isolated wetland, Ellenton Bay, over the past three decades. Because this *L. getula* population has been protected from anthropogenic habitat degradation, collection, and road mortality (Shearer and Frazer, 1997), we are able to exclude these factors as possible causes of the decline.

Materials and Methods

Study site.—Our focal study site, Ellenton Bay, is a large (10-ha) isolated wetland surrounded by upland habitat and, since 1968, has been the focus of numerous long-term studies on the ecology of reptiles and amphibians (Gibbons, 1990; Willson et al., 2006; Winne et al., 2006a). Most wetlands on the SRS have been protected since 1951 from environmental perturbations that typically result from agricultural, urban, and industrial development in the southeastern United States. In particular, Ellenton Bay and the surrounding uplands have received special protection as part of the DOE Set-Aside Program (Davis and Janecek, 1997) that was established to protect habitats and facilitate long-term research. Seventy-four species of reptiles and amphibians have been captured at the wetland and surrounding uplands over the years. Previous studies have described the high abundances of turtles (Gibbons, 1990) and amphibians (Gibbons et al., 2006) at this wetland. Additionally, Ellenton Bay and the surrounding area support high abundances of semi-aquatic (Seigel et al., 1995; Winne et al., 2005) and terrestrial snakes (Todd et al., in press).

Today, the upland habitat surrounding Ellenton Bay is forested with mixed hardwoods and loblolly and slash pines (*Pinus taeda* and *P. elliottii*). However, in 1951, forested habitat comprised <20% of the area within 1 km of Ellenton Bay due to agriculture that occurred in the area from the 1800s until 1951 (Gibbons et al., 2006). In 1957, pine trees were planted within 80 m of the south end of the wetland, and natural establishment of pines adjacent to the bay began to occur by the mid-1960s. Since that time, Ellenton Bay and most of the surrounding fields have undergone natural vegetative succession with forest coverage within 1 km of the bay increasing to 60–75% by 2001 (Gibbons et al., 2006). Further details of the study site can be found in Gibbons (1990) and Gibbons et al. (2006).

Snake captures.—Research priorities and sampling effort at Ellenton Bay have fluctuated over the past 39 years (1968–2006), but several large peaks of snake sampling have occurred at Ellenton Bay since 1975. Over the years, three standard sampling methods have been used extensively to capture snakes at Ellenton Bay: terrestrial drift fences with funnel and pitfall traps (Gibbons and Semlitsch, 1982), artificial coverboard arrays (Grant et al., 1992), and aquatic funnel traps (Willson et al., 2005). In 1968, a terrestrial drift fence was installed to completely encircle Ellenton Bay and allow reptiles and amphibians to be captured as they migrated between the wetland and surrounding upland habitats. The drift fence was equipped with pitfall and funnel traps and used for all or part of 19 of the 28 years from 1968 to 1994 (Gibbons, 1990; Seigel et al., 1995), for all of 2003 (Gibbons et al., 2006), and parts of 2004, 2005, and 2006. Additionally, in some years (1984–1986) a series of drift fences with funnel traps were used to capture snakes in upland habitat surrounding the wetland. Since 1984, coverboards (Grant et al., 1992) have been used to sample the terrestrial and aquatic snake fauna at Ellenton Bay. Coverboards were constructed of metal, wood, or roofing material and placed in both upland and aquatic habitats to serve as artificial refugia for snakes. Commercially available aquatic funnel traps (Willson et al., 2005) have been used since 1975 to capture snakes along the shallow margins of the wetland.

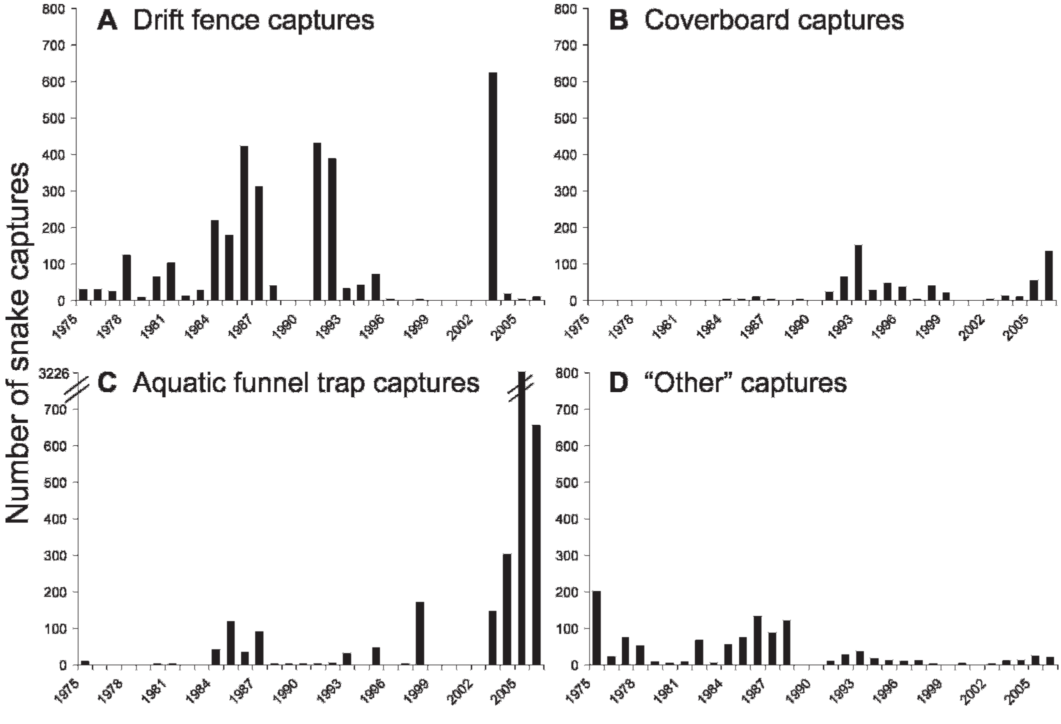

Fig. 1. Number of snake captures at Ellenton Bay on the Savannah River Site, SC, USA, from 1975–2006 by capture method for (A) drift fence captures, (B) artificial coverboard captures, (C) aquatic funnel trap captures, and (D) ''other'' captures (opportunistic hand captures and captures of unknown method).

Further details of the capture methods can be found in Seigel et al. (1995), Winne et al. (2005, 2006a), and Gibbons et al. (2006).

In addition to snakes collected at Ellenton Bay, we also provide data on the body condition of *L. getula* captured from other populations on the Savannah River Site. Snakes from non-Ellenton Bay populations were collected primarily while road cruising or incidentally during other field research. We do not report abundance data for *L. getula* across the entire SRS because we do not have a reliable measure of sampling effort.

During all years, captured snakes were identified to species. In most years, snakes were returned to the laboratory where snout-to-vent length (SVL) and mass were measured, and sex was determined by probing. Palpation was used to determine if a snake contained food items or follicles. Several snakes that contained food items were manually forced to regurgitate their meal (Fitch, 1987), enabling identification of prey items from 23 snakes captured across the SRS. Snakes that were returned to the lab were scale-clipped (Fitch, 1987), PIT-tagged (Gibbons and Andrews, 2004), or heat-branded (Winne et al., 2006b) with a unique code to allow individuals to be recognized upon recapture. All *L. getula* were returned to their original capture location, except for three individuals from Ellenton Bay and 11 from other locations on the Savannah River Site, which were deposited in the collection at the University of Georgia Museum of Natural History. After thousands of snake captures and recaptures over the years, we have seen no evidence that our capture or processing methods negatively affect snake populations or animal health.

Relative abundance.—Trapping effort was not always recorded, especially in earlier years. Therefore, we used the total number of snake captures at Ellenton Bay as a proxy for sampling effort over the years. Since capture methods were similar across years, changes in relative abundance among species should predominantly reflect changes in population size. Additionally, we provide plots of capture data by trapping method (Fig. 1) to demonstrate that our sampling effort during the final years, when *L. getula* disappeared from Ellenton Bay, was of equal or greater intensity than sampling effort during previous years. During some years, method of capture was not recorded for all individuals; thus, captures from unknown methods and incidental hand captures were combined into the ''other'' category. For the purposes of this study, all snakes captured along a drift fence, including hand captures, were recorded as drift-fence captures.

Body condition analyses.—To examine changes in body condition over time, we calculated a body condition index (BCI) as:

$$\mathrm{BCI} = \left(\text{Body mass}/\mathrm{SVL}^3\right) \times 10^5,$$

modifying the methods of Romero and Wikelski (2001). For all body condition analyses, we eliminated gravid females and snakes that contained discernable food items but were not forced to regurgitate. To ensure that the BCI was an appropriate measure of body condition and was not affected by body length (SVL), we conducted a regression of BCI on SVL irrespective of sex using all *L. getula* captured on the SRS. We used 211 snakes of known sex and 22 snakes of unknown sex for a total of 237 snakes in the analysis. The results indicated that the BCI was relatively constant across all SVLs ($P = 0.56$), suggesting that our BCI was free from size-related bias and was therefore appropriate for evaluating body condition in *L. getula* from the SRS.

To test whether the body condition of *L. getula* changed over time, we conducted a regression of BCI on the year of capture, irrespective of sex, for two groups of interest: (1) Ellenton Bay and (2) all other *L. getula* captured on the SRS, excluding Ellenton Bay. Only the first capture of an individual in a year was included in the analyses, leaving a total of 132 records for the Ellenton Bay population and 105 records for the site-wide analysis. To determine whether males and females within a population experienced similar changes in body condition over time, we performed an ANCOVA on BCIs with year of capture as a covariate and sex as the determining factor. This allowed us to compare the slopes of the regressions of BCI on year for males and females.

Finally, to determine whether our analyses of body condition over time were susceptible to biases arising from differences in body condition between the sexes, we performed an ANCOVA on log-transformed body mass using log-transformed SVL as a covariate and sex as the determining factor (Garcia-Berthou, 2001). We included data from all *L. getula* captures on the SRS for which sex was positively identified and mass and SVL were recorded. Only the first capture of an individual in a year was included in the analysis, leaving a total of 215 records for final analysis.

We performed all statistical tests using the STATISTICA for Windows software package (StatSoft Inc., 1998, Tulsa, OK). The data were examined prior to each analysis and transformed where necessary to ensure that all statistical assumptions were met.

Results

Relative abundance.—Sampling intensity and total snake captures at Ellenton Bay varied across years (Figs. 1, 2). Snake captures were high from 1984–1988, before the drought, and from 1991–1993 after the wetland refilled (Seigel et al., 1995; Figs. 1, 2). Similarly, sampling intensity and snake captures were high from February 2003 to May 2006, after the conclusion of the second major drought (Fig. 2). During the final three years of the study (February 2003–May 2006) we obtained 5,253 snake captures using the same techniques (but greater sampling effort) as in previous years (Figs. 1, 2). Thus, the number of snake captures during the final three years of the study was greater than the number of snake captures (4,551) during the previous 28 years from 1975–2002. Presumably, this reflects a higher sampling intensity during the final years. Thus, if the *L. getula* population size remained unchanged over time, we should have detected similar or greater numbers of *L. getula* at Ellenton Bay from 2003–2006 than in previous years, barring any exceptional change in detectability for this species.

The annual proportion of *L. getula* captures among total snake captures at Ellenton Bay ranged from 0 to 16.47% (Fig. 2A). The percentage of *L. getula* captures, the number of individual *L. getula*, and the number of recaptured *L. getula* were relatively high from 1978–1996 (Fig. 2). However, *L. getula* were virtually absent at Ellenton Bay after 2002 (Fig. 2), despite higher numbers of snake captures. Indeed, of 792 snakes captured in 2003, only one was a *L. getula*. Moreover, during 2005, the year with the highest number of total snake captures (3,307), only a single *L. getula* individual was captured. The individual was in noticeably poor condition (Fig. 3), was captured on three occasions, and ultimately died from a presumed physiological response to prolonged starvation despite being fed a mouse in the laboratory on its third capture. It is worth noting that snakes (Willson et al., 2006; Winne et al. 2006b), turtles (J. W. Gibbons, unpubl. data), and small mammals (CTW and JDW, pers. obs.), the primary prey items of *L. getula* on the SRS (Table 1), were all abundant at Ellenton Bay during 2005.

Body condition.—The BCI of *L. getula* at Ellenton Bay declined an average of 25.7% from 1970 to 2005 ($P = 0.01$; Fig. 3A). The decline in body

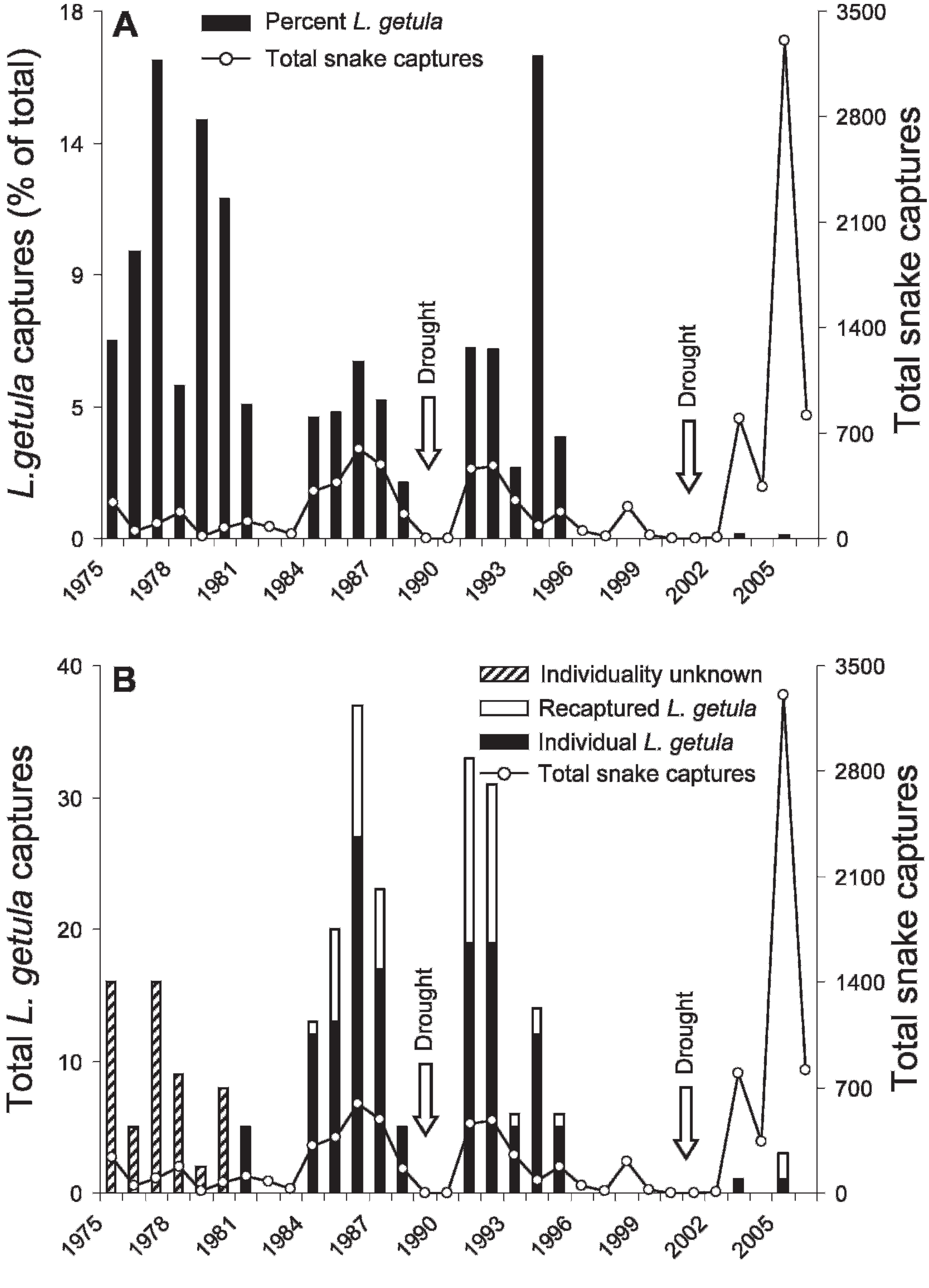

Fig. 2. Abundance of Eastern Kingsnakes (*Lampropeltis getula*) and total number of snake captures at Ellenton Bay from 1975–2006. (A) Percent of snake captures that were *L. getula*. (B) Total number of *L. getula* captured. Cross-hatched bars represent the total number of *L.getula* captures during years when individuals were not marked and, therefore, the number of individuals could not be determined; solid black bars represent the number of individual *L. getula* captured in a given year; unfilled bars represent the number of *L. getula* recaptures in a given year. The two most severe droughts that have occurred in the past three decades are indicated with arrows.

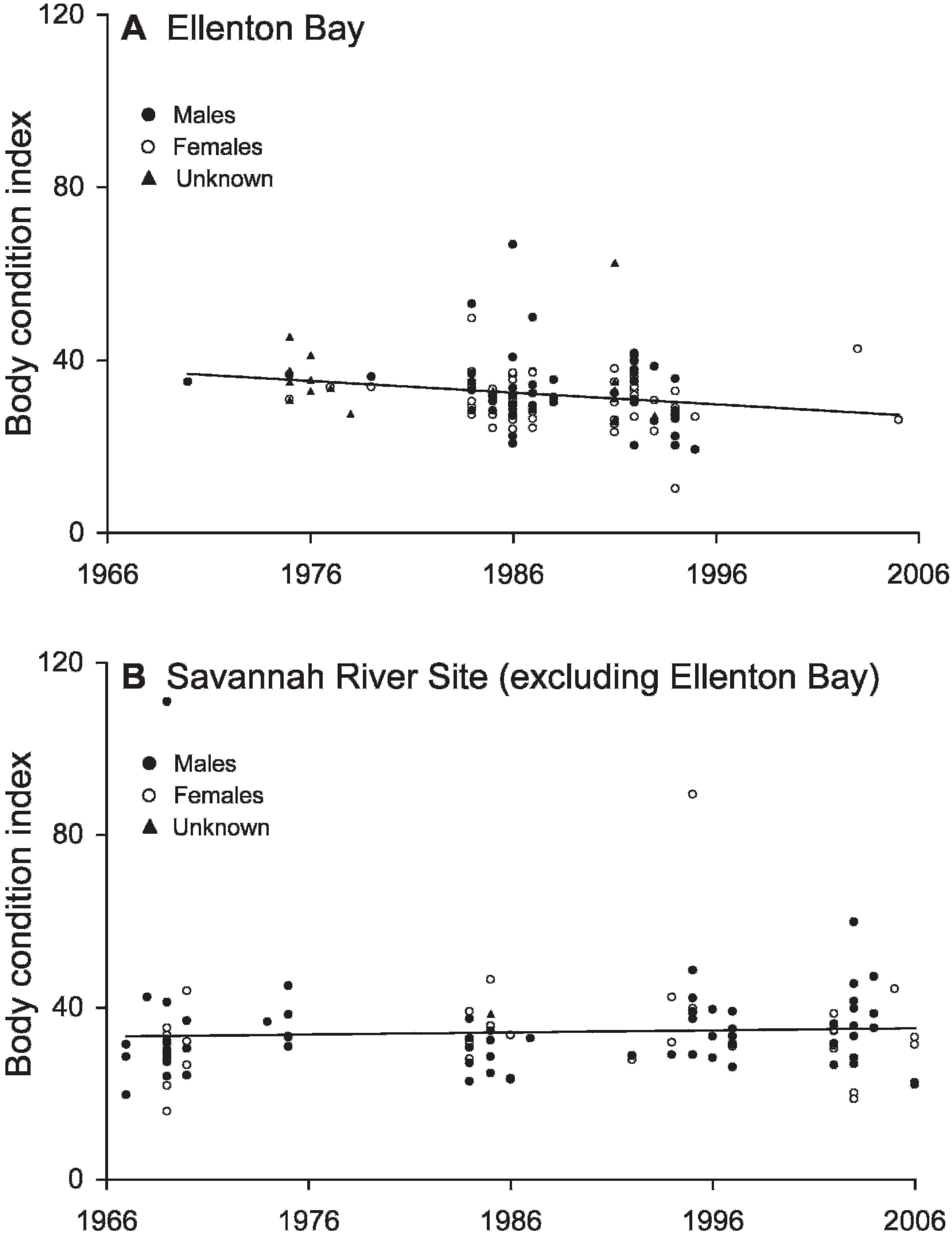

Fig. 3. Body condition of Eastern Kingsnakes (*Lampropeltis getula*) declined over time at (A) Ellenton Bay (P = 0.01) but remained constant across years (B) on the rest of the Savannah River Site, excluding Ellenton Bay (P = 0.589). The line in each figure represents the best fit linear regression of body condition on year, irrespective of sex.

condition occurred in both males and females, and the slopes of the declines did not differ significantly between the sexes ($F_{1,108} = 1.35$; $P =$ 0.247). Moreover, the decline in body condition is not likely due to artifacts of the data collection. For example, given that sex was not always recorded for *L. getula* in earlier years, it is difficult to know if sex ratios of captured animals

TABLE 1. FOOD ITEMS IDENTIFIED FROM EASTERN KINGSNAKES (*Lampropeltis getula*) FROM THE SAVANNAH RIVER SITE (SRS) AND SURROUNDING AREAS IN AIKEN AND BARNWELL CO., SOUTH CAROLINA, BETWEEN 1975 AND 2005.

	Lampropeltis getula				
Food items	Sex	SVL (cm)	Comments	Location	Date
Turtle eggs (*n*)					
Trachemys scripta	F	114	Found excavating nest	Ellenton Bay	11 July 1992
Sternotherus odoratus	F	74	Found eating eggs	SRS	4 May 2005
Kinosternon subrubrum (3)	F	72		Ellenton Bay	5 May 1992
Chelydra serpentina (9)	M	102		Ellenton Bay	26 May 1992
C. serpentina or *Apalone spinifera* (2)	F	100		SRS	18 July 2002
C. serpentina (1), kinosternid (1), emydid (7)	F	112	Knight and Loraine, 1986	Ellenton Bay	27 May 1984
S. odoratus (3), kinosternid (14)	F	124	Knight and Loraine, 1986	SRS	22 June 1984
Species unknown	F	74	Found eating eggs	Ellenton Bay	25 May 1991
Species unknown	F	100	Found eating eggs	Ellenton Bay	28 June 1993
Snakes					
Thamnophis sirtalis	M	102		SRS	28 May 2004
T. sirtalis	F	92		Ellenton Bay	15 June 1992
Seminatrix pygaea (2)	—	74		Ellenton Bay	9 June 1991
S. pygaea (2)	M	—		Ellenton Bay	2 June 1994
S. pygaea	M	100		Ellenton Bay	19 June 1993
Nerodia floridana	—	115	Found eating snake	Ellenton Bay	25 April 1975
N. fasciata	M	92		Ellenton Bay	25 April 1994
N. fasciata	M	88		Ellenton Bay	3 Nov. 1994
N. fasciata	—	—	Eaten in trap	SRS	Oct. 2005
Lampropeltis getula	—	—	Tony Mills, pers. comm.	Aiken Co., SC	May 1992
Coluber constrictor	F	62	Found eating snake	Ellenton Bay	10 Aug. 1992
Crotalus horridus	—	—		SRS	14 May 1988
Mammals					
Blarina carolinensis	F	59		Ellenton Bay	28 May 2005
Small mammal (probably *Sigmodon hispidus*)	F	141		Ellenton Bay	28 April 1986

have changed over time and, thus, may have affected our results. However, male and female *L. getula* did not have significantly different body conditions on the SRS ($F_{1,212} = 2.54$; $P = 0.11$), suggesting that our results are robust to such possibilities. Furthermore, in contrast to the Ellenton Bay population, the body condition of site-wide *L. getula* (excluding Ellenton Bay) did not change significantly over time ($P = 0.589$; Fig. 3B). Additionally, males and females from these site-wide captures had similar body conditions across time and the slopes of their regressions did not differ significantly ($F_{1,100} = 0.489$; $P = 0.486$).

Although a cursory examination of Figures 3A and B would suggest the presence of at least seven outliers, we carefully reviewed these data points to locate any processing or recording errors and we did not find any substantive reasons for removal of these animals. These particular individuals appeared only to be very heavy-bodied or light-bodied snakes. Furthermore, removal of these outliers from the statistical analyses did not affect the results or interpretation of these results. In fact, in the case of the declining body condition of Ellenton Bay *L. getula*, removal of three apparent outliers strengthened the downward trajectory of the decline. Given the lack of a substantive reason to remove these heavy-bodied individuals, we have kept all data points in the figures and analyses to present the most comprehensive analysis possible.

Food records.—The majority of prey items eaten by *L. getula* on the SRS, and at Ellenton Bay in particular, were aquatic snakes and turtle eggs (Table 1). Of the 23 *L. getula* captured containing or eating food items, 52% consumed one or more snakes, 39% consumed eggs of various turtle species, and 9% consumed small mammals. Aquatic and semi-aquatic snakes (*Nerodia fasciata*, *N. floridana*, *Seminatrix pygaea*, *Thamnophis sirtalis*) constituted 79% of the snakes consumed, whereas only 11% of the prey snakes were terrestrial species (*Coluber constrictor*, *Crotalus horridus*, *L. getula*).

Discussion

Over the past 31 years we have monitored snake populations at Ellenton Bay with varying intensities. During this time, the wetland was protected from typical anthropogenic threats such as habitat alteration, snake removal, and environmental contamination. During the first two decades of study, *L. getula* were a relatively common component of the Ellenton Bay snake community, comprising 2.5–16.5% of snake captures during years with high sampling intensity. However, sometime after 1996, *L. getula* virtually disappeared from Ellenton Bay, with only two individuals captured (one individual was captured three times) out of a total of 5,253 snakes captured during 2003–2006. In addition to a decline in *L. getula* abundance, we also observed a decline in the body condition of *L. getula* at Ellenton Bay.

Proposed agents of reptile declines include environmental pollution, unsustainable removal (collection and road mortality), habitat loss and degradation (natural or anthropogenic), global climate change, introduced invasive species, and disease (Gibbons et al., 2000). Of these factors, environmental pollution and unsustainable removal are unlikely to be responsible for the *L. getula* decline we observed because Ellenton Bay has been protected from these factors since 1951, when it became part of a U.S. defense facility, and later, as part of a National Environmental Research Park (Shearer and Frazer, 1997). Nonetheless, the other aforementioned factors may have contributed to the decline of the Ellenton Bay *L. getula* population, and we will discuss all of the proposed agents in more detail below.

Environmental pollution.—The potential for contaminants to cause population-level effects remains largely unknown, both for reptiles and amphibians (Gibbons et al., 2000). However, environmental monitoring of contaminants in wetlands on the SRS has revealed that Ellenton Bay does not contain elevated levels of metals, with the exception of an elevated concentration of lead, which must have been introduced to Ellenton Bay prior to 1951 (Roe et al., 2005). Additionally, pesticides have been shown to negatively affect reptiles, including snakes (Hopkins et al., 2005; Hopkins and Winne, 2006). However, given the prevalence of *L. getula* during the first two decades of study and the lack of pesticide use and agriculture since 1951, it is unlikely that contaminants could have caused the decline of *L. getula* that we observed.

Unsustainable removal.—Unsustainable removal of reptiles from the wild includes harvest for consumption and commercial or recreational collection for the pet and skin trades, all of which have been implicated in the decline of reptiles (Gibbons et al., 2000; Schlaepfer et al., 2005). In particular, collection for the pet trade has received considerable attention as a potential cause of snake declines or extirpations for a number of species (Dodd, 1987, 1993; Brown, 1993; Webb et al., 2002; Boback, 2005), including *L. getula* in Florida (Krysko, 2002). In contrast, collection pressure has been non-existent at Ellenton Bay, at least since 1951. Ellenton Bay is located on federally protected land, where the general public is prohibited from entering the site without an escort. Moreover, only three *L. getula* from Ellenton Bay were ''harvested'' by researchers (i.e., deposited in a museum) over the years. Likewise, all captured *L. getula* were handled identically to other snake species, and there is no evidence that our handling of snakes negatively affected their populations or led to the *L. getula* decline. Thus, snake collection and snake handling are both implausible causes for the decline that we document here.

Road mortality can be considered a form of harvest because it permanently removes otherwise healthy animals from the population (Wilson and Porras, 1983; Krysko and Smith, 2005; Smith et al., 2005). In fact, road mortality is a growing concern for the conservation of reptiles (Dodd et al., 1989; Gibbs and Steen, 2005; Andrews et al., in press). Although several studies have reported high levels of road mortality in snakes (Smith and Dodd, 2003) and some authors have explicitly labeled road mortality as a causative factor in snake declines (Klauber, 1939), few studies have provided data on the effects of road mortality on snake populations (but see Rosen and Lowe, 1994; Rudolph et al., 1999). At Ellenton Bay, only a few, infrequently-traveled roads are located within the vicinity of the study site. Compared to other SRS roads and public access roads in particular, road mortality of all species is drastically reduced on these roads, and no road mortality has been recorded for *L. getula* within 5 km of Ellenton Bay during the past 39 years. Thus, it is highly unlikely that road mortality has contributed to the decline of *L. getula* at Ellenton Bay.

Habitat loss and degradation.—Habitat loss and degradation are considered to be the leading threats to reptile populations worldwide (Dodd, 1987; Mittermeier et al., 1992; Dodd, 1993; Gibbons et al., 2000) and are the greatest catalysts for federal endangered species listings

(Wilcove et al., 1998). Habitat alteration, whether natural (e.g., succession or drought) or anthropogenic, may make regions unsuitable for individuals and, on a large scale, can lead to decline or extinction of species. Habitat degradation can take many forms and render areas unsuitable to snakes in a variety of ways, including loss of prey, insufficient shelter or winter hibernacula, inadequate thermal environments, and loss of suitable nesting habitats.

We observed a gradual decline in *L. getula* body condition at Ellenton Bay, suggesting that some component of the habitat may have become increasingly unsuitable for this species in recent years. Yet, anthropogenic habitat alteration *per se* is unlikely to be responsible for the decline of *L. getula* at Ellenton Bay because of the protection it has received from the presence of a large U.S. Department of Energy (formerly, the Atomic Energy Commission) nuclear facility (Gibbons, 1990). However, over the past 55 years, the uplands surrounding the wetland have undergone natural succession from abandoned agricultural fields, through old-field and early-successional forests, to a closed-canopy mixed pine–hardwood forest (Gibbons et al., 2006). McLeod and Gates (1998) found that *L. getula* were more abundant in burned pine forests compared to unburned pine forests. The burned forests contained reduced density and basal areas of standing trees, more open canopies, and reduced litter depth (McLeod and Gates, 1998). If *L. getula*, or their prey, prefer more open habitats, then the increased forest cover and lack of prescribed burns in recent years immediately surrounding Ellenton Bay may be at least partially responsible for the observed decline. However, the aquatic portion of the wetland itself has always had an open canopy and has not undergone substantial changes in recent decades (JWG, pers. obs.). Moreover, a 5–6 m-wide dike that bisects Ellenton Bay has consistently provided habitat similar to canal banks in Florida that contained large numbers of *L. getula* in the past (Godley, 1982; Krysko, 2002).

Few long-term studies of snake communities exist (Parker and Plummer, 1987; Vitt, 1987; Fitch, 1999), but natural habitat changes are known to alter species composition in some ecosystems (e.g., vegetational succession, Mendelson and Jennings, 1992; Fitch, 1999; flooding, Seigel et al., 1998). Local declines or extirpations of Glossy Snakes (*Arizona elegans*), Massasauga Rattlesnakes (*Sistrurus catenatus*), and Western Rattlesnakes (*Crotalus viridis*) have been associated with the reduction of grassland habitats in the Chihuahuan Desert, while more generalist species (*L. getula*; Gopher Snakes, *Pituophis catenifer*) have shown little change in abundance (Mendelson and Jennings, 1992). In the same study, Checkered Garter Snakes (*Thamnophis marcianus*) and Western Diamond-backed Rattlesnakes (*C. atrox*) increased in relative abundance over a 30-yr period, whereas the relative abundance of Mojave Rattlesnakes (*C. scutulatus*) decreased (Mendelson and Jennings, 1992). Interestingly, cottonmouths (*Agkistrodon piscivorus*) have increased in abundance at Ellenton Bay (Willson et al., 2006; Glaudas et al., 2007) concomitant with the decline of *L. getula*. Whether *A. piscivorus* and *L. getula* are responding differently to natural habitat change or are directly influencing each other's abundance is unresolved. The increase in *A. piscivorus*, for example, could be due to the decline in *L. getula* (e.g., a release from direct predation by *L. getula* or a release from competition with *L. getula* for prey) or the increase in *A. piscivorus* may have caused the decline in *L. getula* (e.g., through competition for prey or direct predation on *L. getula* by *A. piscivorus*). Interestingly, a similar shift in relative abundance of the two species has been described at Paynes Prairie in Florida (Dodd, 1993; Krysko, 2001).

On the SRS and at Ellenton Bay, *L. getula* are generalist predators with a preference for aquatic snakes and turtle eggs. This diet is consistent with that of *L. getula* across the United States (Ernst and Ernst, 2003). The continued general abundance of snakes (Willson et al., 2006; Winne et al., 2006a), turtles (J. W. Gibbons, unpubl. data), and small mammals (CTW and JDW, pers. obs.) at Ellenton Bay suggests that lack of appropriate prey has not played a major role in the decline of this population of *L. getula*. Alternatively, although the habitat and prey availability at Ellenton Bay is suitable for *L. getula* in most years, periodic extreme droughts may have rendered the habitat inhospitable long enough to reduce *L. getula* populations. In the past three decades, Ellenton Bay has experienced two extreme droughts that rendered the wetland completely dry for two or more years (Fig. 2; Willson et al., 2006; Winne et al., 2006a). Sharp declines in the abundance of aquatic snakes (particularly *Nerodia* spp.) occurred at Ellenton Bay during both of these droughts (Seigel et al., 1995; Willson et al., 2006). Also, egg production and nesting by at least three turtle species (Common Snapping Turtle, *Chelydra serpentina*; Yellow-bellied Slider, *Trachemys scripta*; and Common Musk Turtle, *Sternotherus odoratus*), the eggs of which are commonly eaten by *L. getula* at Ellenton Bay (Knight and Lorraine, 1986; Table 1), were likely reduced during the droughts (Gibbons et al., 1983). Thus, although prey has generally remained abundant at Ellenton Bay over the years, short-term food shortages during drought, or the associated lack of aquatic habitat, could be responsible for the decline of *L. getula* at Ellenton Bay. However, the *L. getula* population was notably robust from 1991–1995 (Fig. 2), following the first extreme drought. Their presence after the first drought suggests that drought alone may not be the ultimate cause of decline. Further, Ellenton Bay has one of the longest hydroperiods of non-permanent wetlands on the SRS, suggesting that *L. getula* dependent upon aquatic habitats should be less affected by drought at this site than at others. Importantly, *L. getula* is not restricted to wetland habitats on the SRS. Many of the non-Ellenton Bay *L. getula* were captured away from wetlands and, thus, may not have been as negatively affected by drought. Regardless, if droughts do cause declines in *L. getula*, recent global climate change models that predict an increase in the frequency and severity of droughts (National Assessment Synthesis Team, 2001) may foreshadow declines in this species in some parts of its range.

Introduced invasive species.—Introduced species are a growing concern in snake conservation and have been demonstrated to have both positive (e.g., Round Gobies, *Neogobius melanostomus*, King et al., 2006) and negative (e.g., Cane Toads, *Bufo marinus*, Phillips et al., 2003) impacts on snake species. Introduced fire ants (*Solenopsis invicta*) have been proposed as a potential threat to egg laying reptiles (Donaldson et al., 1994; Tuberville et al., 2000; Buhlmann and Coffman, 2001), including *L. getula* (Wojcik et al., 2001; Allen et al., 2004). Fire ants have been present at Ellenton Bay since the mid-1980s (Buhlmann and Coffman, 2001), but there is no direct evidence that they have negatively affected *L. getula* or other egg-laying snake species that remain common at Ellenton Bay (e.g., *Heterodon platirhinos*, *C. constrictor*, *Elaphe guttata*). Nonetheless, fire ants possibly have had a negative impact on *L. getula* directly (e.g., predation on *L. getula* eggs) or indirectly (e.g., through competitive predation on turtle eggs; Buhlmann and Coffman, 2001), and we encourage experimental investigations of this topic.

Disease and parasites.—A final potential cause for the decline of *L. getula* at Ellenton Bay is disease or parasitism. Parasitism has been shown to reduce growth rates and negatively affect body condition in snakes (Madsen et al., 2005). Although we observed a decline in body condition among *L. getula* at Ellenton Bay, we do not have any direct evidence of diseased individuals or data on parasite infection rates of *L. getula* on the SRS. Given the important impact that diseases have on many species of amphibians (Daszak et al., 1999) and for reptiles such as the Gopher Tortoise (*Gopherus polyphemus*, Seigel et al., 2003), disease and parasitism warrant further investigation. The value of preserving incidentally killed snakes for future dissection, or of collecting non-destructive pathogenic samples from living animals (blood samples or oral and cloacal swabs), should not be underestimated. Data such as these can add greatly to our understanding of the baseline health of snake populations as well as the prevalence, distribution, and impact of diseases.

Conclusions.—Documenting snake population declines can be an onerous task that requires intensive, long-term field studies with records of sampling effort and/or estimates of population size (Gibbons et al., 2000; Webb et al., 2002), and researchers can benefit from marking animals individually in their study populations. Furthermore, the causes of population declines are often unclear and can result from multiple, interactive factors. Studies conducted on protected populations, such as those at Ellenton Bay, can be valuable tools for decoupling the effects of anthropogenic and natural stressors on population persistence. Over the past 31 years, we were able to unambiguously document the decline of a *L. getula* population in South Carolina. Although *L. getula* continue to be observed incidentally in other areas of the SRS, the cause of the *L. getula* decline at Ellenton Bay remains enigmatic. Natural succession of the surrounding uplands, periodic droughts, shifts in species composition (e.g., increased *A. piscivorus* density), introduced fire ants, or disease are all possible causes of the decline. Although we can eliminate over-collection and road mortality, two of the most commonly proposed causes of snake population declines (Krysko, 2002; Andrews et al., in press), as causative agents of the *L. getula* decline at our study site, these factors may be important for other populations in the southeastern United States. Interestingly, our observations at Ellenton Bay bear a striking resemblance to anecdotal reports of *L. getula* declines at Paynes Prairie, Florida (Dodd, 1993; Krysko, 2001).

Many populations exhibit natural fluctuations over years or decades that remain inexplicable and yet may vary geographically (Smith and Davis, 1981; Pechmann et al., 1991). Thus, focused studies on defined populations such as those carried out at Ellenton Bay provide an empirical base for addressing potential causes of decline and for comparisons with populations in other regions. Continued studies at Ellenton Bay and on the Savannah River Site will establish whether the decline we observed in *L. getula* was an isolated occurrence and part of natural population fluctuations, or a permanent localized extirpation of this species. Additional long-term studies on *L. getula* are needed to verify if the species is declining throughout the SRS or over an appreciable part of its range. Further, we encourage additional studies of habitat associations and population characteristics of *L. getula* in locations where they are still common to aid in identification of factors that may contribute to their putative widespread decline. Ultimately, it is only through long-term, quantitative population studies, coupled with manipulative or correlative studies of behavior and physiology, that we can begin to understand snake population dynamics and the resources and management tools necessary to ensure their continued existence.

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