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Changes in Snake Abundance After 21 Years in Southwest Florida, USA

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***Abstract*.—Global population declines in herpetofauna have been documented extensively. Southern Florida, USA, is an especially vulnerable region because of high impacts from land development, associated hydrological alterations, and invasive exotic species. To ask whether certain snake species have decreased in abundance over recent decades, we performed a baseline road survey in 1993–1994 in a rural area of southwest Florida (Lee County) and repeated it 21 y later (2014–2015). We sampled a road survey route (17.5 km) for snakes by bicycle an average of 1.3 times a week (n = 45 surveys) from June 1993 through January 1994 and 1.7 times a week from June 2014 through January 2015 (n = 61 surveys). Snake mortality increased significantly after 21 y, but this result may be due to increased road traffic rather than expanding snake populations. The snake samples were highly dissimilar in the two periods, suggesting changes in species composition. For example, one species showed a highly significant decrease in abundance (Rough Greensnake, *Opheodrys aestivus*) while another showed substantial increases (Ring-necked Snake, *Diadophis punctatus*). Because of uncertain differences in traffic volume between 1993 and 2015, other species offered ambiguous results in their abundance trends. Nevertheless, four additional species contributed at least 12.1% dissimilarity (North American Racer, *Coluber constrictor*; Red Cornsnake, *Pantherophis guttatus*; Eastern Ribbonsnake, *Thamnophis saurita*; and Southern Watersnake, *Nerodia fasciata*). Increases in human land-use due to development and agriculture along with associated loss of wetlands and native habitats may have contributed to the changes we documented. Future work should seek to understand fully these causes and the conservation needs of declining species.**

Key Words.—change in abundance; conservation; ecology; reptile; road mortality; road survey; traffic; wildlife

Introduction

The massive influence of human populations over the status and trajectory of life has prompted scientists to name the current geologic epoch the Anthropocene (Steffen et al. 2007). Unfortunately, the Anthropocene may be historically remarkable because of associated increases in rates of biodiversity loss, and many scientists now recognize this as the sixth great global extinction event (Barnosky et al. 2011). Most taxonomic groups have been affected, but among vertebrates, amphibians have received extra attention over the years (Beebee and Griffiths 2005; Wake and Vredenburg 2008). More recently, reptiles have been recognized as experiencing considerable declines (Gibbons et al. 2000) and snakes in particular are under threat in many regions (Sullivan 2000; Brodman et al. 2002; Hanson and McElroy 2015). Herpetologists have called for increased monitoring and vigilance regarding worldwide snake populations (Filippi and Luiselli 2006; Reading et al. 2010).

Roads are an anthropogenic factor that can contribute to declines of herpetofauna (Forman and Alexander 1998; Trombulak and Frissell 2000) and have such important and widespread effects on natural ecosystems that a new ecological sub-discipline in road ecology has emerged (Forman et al. 2003). An estimated 22% of land in the United States is affected ecologically by roads (Forman 2000). In addition to immediate mortality from vehicle strikes (Hels and Buchwald 2001; Lode 2000), roads cause habitat fragmentation that inhibits natural animal movements (Clark et al. 2010; Herrmann et al. 2017; Marsh et al. 2005; Shepard et al. 2008b), increase environmental pollution (Karraker et al. 2008; Reeves et al. 2008; Sanzo and Hecnar 2006), and facilitate the spread of exotic species (Urban et al. 2008). Most studies show a negative impact of roads on animal populations (Fahrig and Rytwinski 2009). Amphibians and reptiles are especially susceptible, with a majority of studies showing a negative effect of roads on species richness (Findlay and Houlahan 1997; Houlahan and Findlay 2003) and individual populations (Fahrig and Rytwinski 2009). In fact, several studies documenting the impact of roads on animal populations found that amphibians and reptiles represent the majority of all observed mortality, sometimes > 90% (Colino-Rabanal and Lizana 2012; Glista et al. 2008). Road mortality is sometimes exceedingly high with as many as 10,000 or more frogs per km killed each year (Goldingay and

Taylor 2006), and this alone can compromise population viability (Beebee 2013). Snakes, because of their use of roads for behavioral thermoregulation, are often impacted by road traffic (Evans et al. 2011, Rosen and Lowe 1994). Enge and Wood (2002) estimated conservatively that as many as 1.4 million snakes are killed each year on rural Florida, USA, highways.

Despite their negative ecological consequences, roads can be effective as incidental sampling transects for snakes and other herpetofauna. Use of roads to collect data has a long history in herpetology (e.g., Fitch 1949; Campbell 1953) and can be employed to sample live and dead snakes by car, bicycle, or on foot (Bonnet et al. 1999; McDonald 2012). Such road surveys are often part of efforts to characterize a local fauna (Coleman et al. 2008; Desroches et al. 2010; Enge and Wood 2002). This method is a convenient, but underused, approach for long-term monitoring of threatened amphibian and reptile communities, and it can allow researchers to perform retrospective comparative studies to document change (Sullivan 2000). It is also a useful way to assess the need for and success of ongoing mitigation efforts to reduce animal mortality on roads (Aresco 2005; Shepard et al. 2008a; Shwiff et al. 2007). However, as with any sampling method, there are important limitations and biases inherent to road surveys (discussed in Steen and Smith 2006). For example, small, cryptic, arboreal, and fossorial individuals and species are likely not observed as readily. Moreover, roads have the potential to attract or repel animals, and crossing behavior may differ due to sex, life stage, or condition of the animal (Jochimsen 2006).

In Florida, declines of snakes and other herpetofauna have been documented (e.g., Godley and Moler 2013) and retrospective studies suggest that shifts in community composition have occurred (Dodd et al. 2007; Cassani et al. 2015). Although the causes are complex, multifactorial, and sometimes enigmatic (as in Winne et al. 2007), they likely consist of a combination of habitat loss (Enge and Marion 1986), habitat degradation (Delis et al. 1996), habitat fragmentation (Pike and Roznik 2009), invasive exotic species (Forys and Allen 1999; Smith 2006), altered hydrology (Greenberg et al. 2015), and climate change (Catano et al. 2015). We know that such changes in animal populations will continue, but it is difficult to predict them in a way that can inform important decisions related to conservation and management. Understanding these changes on a local and regional scale will require the collection of baseline inventory data. Resampling years later with the same field methods can offer clues about the response of animal communities to habitat change (Brodman et al. 2002; Hossack et al. 2005; Dodd et al. 2007; Measey et al. 2009; Cassani et al. 2015).

Here, we aim to document possible differences in snake relative abundance between two time periods separated by 21 y in a rural area of southwest Florida, USA, while simultaneously providing baseline inventory data for future retrospective analyses. We collected snake road survey data in 1993–1994 and 2014–2015. A comparison of the two sampling periods allowed us to determine if the relative abundance of snake species has changed during these two decades and, if so, which species show evidence of abundance increases and decreases.

Materials and Methods

We established a road survey route (17.5 km) in Buckingham, Lee County, Florida, USA (Fig. 1) in the summer of 1993. This area offers a mixture of upland and wetland habitats, the former being used mainly in small agricultural operations and rural residential. We conducted 45 surveys by bicycle from June 1993 to January 1994 (mean = 1.29 ± 1.07 SD surveys per week) and 61 surveys from June 2014 to January 2015 (mean = 1.74 ± 0.70 surveys per week). We conducted surveys without seasonal bias as shown by an analysis of their days of the year, with 1 January as 1, 2 January as 2, and so on (t = 0.01, df = 104, P = 0.990; 1993–1994 mean = 224.9 ± 79.36 SD, 2014–2015 mean = 224.7 ± 102.5). We positively identified species and recorded GPS coordinates of all encountered snakes (living or dead) before removing them from the roadway to ensure they were not counted in subsequent surveys.

We analyzed snake observation data to ask whether there were differences between the two sampling periods (1993–1994 and 2014–2015). Because our counts are not distributed normally, we used the nonparametric Wilcoxon signed-rank test for paired samples in the NPAR1WAY procedure in SAS (SAS Institute 2003) to test for differences between sampling periods in the mean number of individuals recorded during each sampling run for all species. We set the threshold for statistical significance *a priori* to 0.05. Traffic volume often correlates positively with animal mortality (Mazerolle 2004; Fahrig et al. 2005; Coleman et al. 2008), although the precise nature of the relationship is poorly understood and likely species-specific (Grilo et al. 2015). To account for expected differences in traffic volume over the 21-y study period, we adjusted the 1993–1994 abundance data with a conversion factor of 2.94 for all species, assuming a positive linear relationship between traffic and mortality for simplicity. To estimate this conversion factor, we gathered traffic volume data from the Lee County Traffic Count Database (http://lee.ms2soft.com/tcds/tsearch.asp?loc=Lee&mod=) along Buckingham Road, the most traveled and lengthiest of

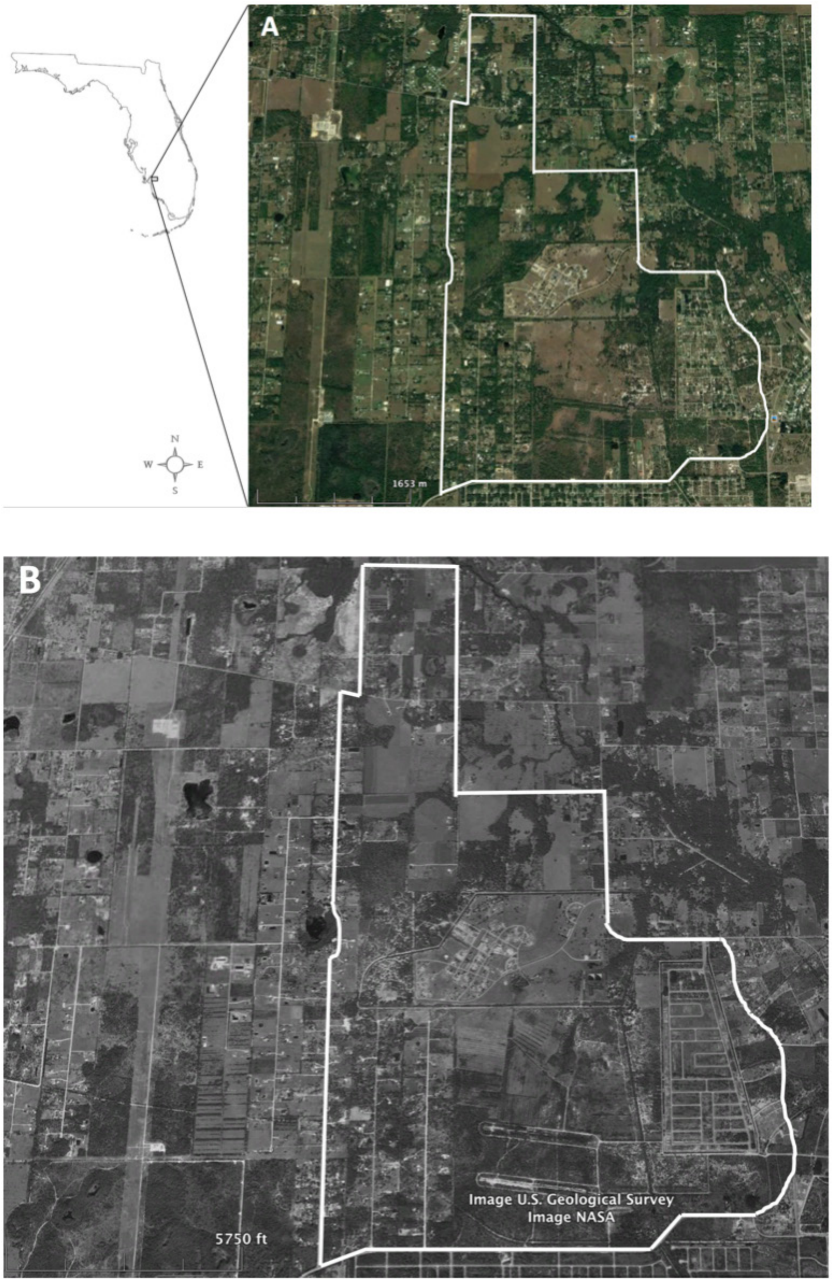

Figure 1. Satellite images of the study area and road survey route (17.5 km, highlighted in white, 26°38–41'N 81°43–45'W) in Buckingham, Lee County, Florida, USA. Photographs were taken at (A) the end of the study in 2015 and (B) near the beginning of the study in 1994. (Images from Google Earth 2015, U.S. Geological Survey, and National Atmospheric and Space Administration 1994).

four roads that comprise our study route. Because no data are available before the year 2001, we assumed that the people to traffic ratio did not change between 1993 and 2001. We used the ratio of population to average traffic count (vehicles/day) in 2001 (142.5 people:traffic count) and U.S. Census population data for Lee County in 1993 (368,938 people) to estimate a 1993 traffic count of 2,589.1 vehicles/day. The ratio of 2014 traffic count (7,624.7 vehicles/day) to that estimated for 1993 is 2.94:

$$\frac{2014\ traffic\ volume}{1993\ traffic\ volume} = \frac{7{,}624.7\ vehicles/day}{2{,}589.1\ vehicles/day} = 2.94\,,$$

which is the factor we used to scale 1993 traffic to that of 2014. Although this number is likely inaccurate because of simplifying assumptions, and traffic volume was probably variable over the different roads of our route, we believe it to be a conservative underestimate because of extreme population growth in this part of

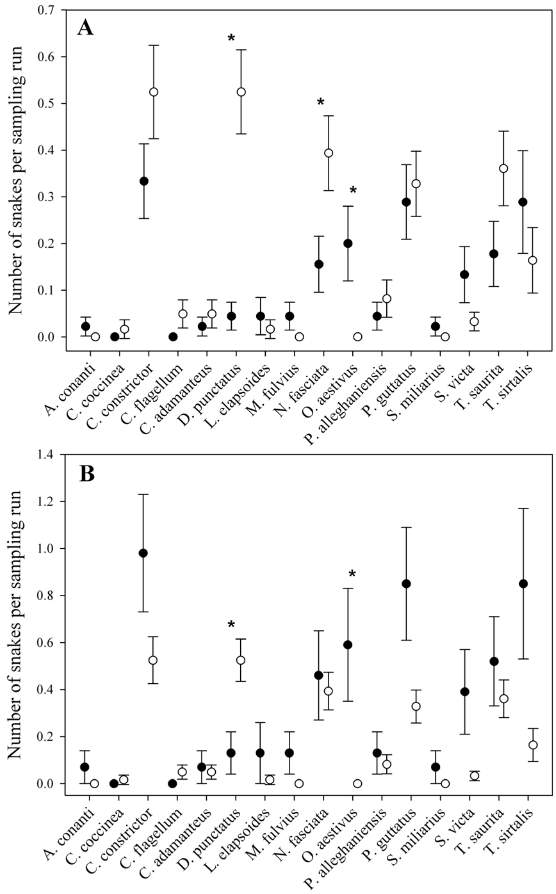

Figure 2. Mean (± standard error) numbers of each snake species recorded per sampling run in the two sampling periods (1993–1994 and 2014–2015) at a study site in Buckingham, Lee County, Florida, USA. Data depicted are raw unadjusted numbers (A) and with a conversion factor to account for increases in traffic volume over the 21-y study period (B, see Materials and Methods).

southwest Florida. Data from the U.S. Census indicate that Lee County grew by 32% during the 1990s and then another 40% during the 2000s (https://florida.reaproject.org/analysis/comparative-trends-analysis/population/tools/120071/120000/).

We also used observation data from the two sampling periods to assess possible evidence for changes in snake species community composition and relative abundance. We used the software package Primer, Version 6 (Clarke and Gorley 2006) to calculate Margalef and Shannon diversity indices. We normalized count data based on sampling effort (i.e., number of surveys) and fourth-root transformed to down-weigh the importance of extremely abundant species (Clarke and Warwick 2001). We then used a Bray-Curtis similarity matrix (Bray and Curtis 1957; Bloom 1981) and the Similarity Percentage Test (SIMPER) to identify the contributions of individual species in forming the dissimilarity between sampling periods.

Although Lee County's population grew significantly during the study period, development to support this growth occurred principally along the gulf coast, west of the study area. Limited development occurred along some roads within the study area. Development throughout the county has impacted upland habitats compared to protected wetlands. Wetland protection focuses on function. However, wetlands created for mitigation often fail to meet wildlife habitat requirements, and mitigation may be met outside of watershed boundaries. In addition, altered storm water drainage can result in changes of downstream wetland areas, effectively changing their land use designation. Overall, native habitats, both upland and wetland, declined in the study area, but not to the degree of other parts of the county. To evaluate land-use change quantitatively over the study period at our road route, we used the Esri (Redlands, California, USA) GIS software ArcMap, Version 10.5.1, for the nearest available years, 1991 and 2012, using Florida Land Use Cover and Forms Classification System (FLUCCS) maps (Florida Department of Transportation 1999). We calculated land-use as a percentage of area relative to the total within a 500-m buffer surrounding the road route on either side using the following categories: Human Use (including both development and agriculture), Wetland, and Other Native Habitats based on FLUCCS code designations.

Results

We recorded 14 snake species during 1993–1994 and 12 species in 2014–2015 (Table 1), for a total of 16 species throughout the study. Among these, we encountered 10 species in both sampling periods. We did not record the Rough Greensnake (*Opheodrys aestivus*), a relatively abundant species in 1993–1994 (fourth most abundant), during 2014–2015 (Fig. 2). Species that were relatively uncommonly encountered in 1993–1994 (one to three observations) and absent in 2014–2015 included Florida Cottonmouth (*Agkistrodon conanti*), Harlequin Coralsnake (*Micrurus fulvius*), and Pygmy Rattlesnake (*Sistrurus miliarius*). We encountered the Florida Brownsnake (*Storeria victa*) and Common Gartersnake (*Thamnophis sirtalis*) relatively often in 1993–1994 but rarely in 2014–2015. Species that were absent in 1993–1994 and that we recorded rarely in 2014–2015 were Scarletsnake (*Cemophora coccinea*) and Coachwhip (*Coluber flagellum*). Observations of three species increased considerably in the 2014–2015 sampling period (Ring-necked Snake, *Diadophis punctatus*; Southern Watersnake, *Nerodia fasciata*; and Eastern Ribbonsnake, *Thamnophis saurita*).

Raw observation count data yielded just one species that showed a statistically significant decrease in abundance (*O. aestivus*, Table 1) and two species with significant increases (*D. punctatus* and *N. fasciata*) over the 21-y study period. After we adjusted 1993–

Table 1. Numbers of each snake species documented during the two sampling periods (n = 46 surveys in 1993–1994 and n = 61 surveys in 2014–2015) at a study site in Buckingham, Lee County, Florida, USA. Results of two Wilcoxon signed-rank statistical tests for differences in the mean observations of a species (number of individuals per survey) between the two periods are shown. The adjusted test calibrated 1993–1994 data by a factor that estimates traffic increases over the 21-y study period (2.94, see Materials and Methods). Unidentified specimens are included in the total numbers.

			Mean Observations Test (Raw)			Mean Observations Test (Adjusted)		
Species	1993–1994	2014–2015	*Z*	*P*	Change	*Z*	*P*	Change
Agkistrodon conanti	1	0	1.15	0.25		1.15	0.25	
Cemophora coccinea	0	1	-0.84	0.40		-0.84	0.40	
Coluber constrictor	15	32	-1.17	0.24		-0.07	0.95	
Coluber flagellum	0	3	-1.49	0.14		-1.49	0.14	
Crotalus adamanteus	1	3	-0.71	0.48		-0.68	0.50	
Diadophis punctatus	2	32	-4.39	< 0.001	Increase	-4.14	< 0.001	Increase
Lampropeltis elapsoides	2	1	0.22	0.83		0.22	0.83	
Micrurus fulvius	2	0	1.64	0.10		1.64	0.10	
Nerodia fasciata	7	24	-1.99	0.05	Increase	-1.46	0.14	
Opheodrys aestivus	9	0	3.16	0.002	Decrease	3.16	0.002	Decrease
Pantherophis alleghaniensis	2	5	-0.76	0.45		-0.68	0.49	
Pantherophis guttatus	13	20	-0.51	0.61		0.24	0.81	
Sistrurus miliarius	1	0	1.15	0.25		1.15	0.25	
Storeria victa	6	2	1.60	0.11		1.66	0.10	
Thamnophis saurita	8	22	-1.56	0.12		-0.95	0.34	
Thamnophis sirtalis	13	10	1.44	0.15		1.60	0.11	
Total	89	179	-1.72	0.09		2.78	0.005	Decrease

1994 numbers to account for lower traffic volume, the significant increase in abundance of *D. punctatus* and decrease of *O. aestivus* remained; however, the increased abundance of *N. fasciata* did not remain. Species diversity was similar in the two sampling periods, with richness decreasing by two in 2014–2015 (from 14 to 12). The diversity indices also decreased, but the magnitude was negligible (from 4.55 to 4.10 and from 2.68 to 2.60, respectively). SIMPER analysis indicated an average dissimilarity between 1993–1994 and 2014–2015 of 86.8%, suggesting a substantial shift in snake community composition. Three of the top eight species contributing to that temporal dissimilarity showed some evidence for changes in abundance after the 21 y (Table 2). Most notably among these, *D. punctatus* (strong abundance increase) and *O. aestivus* (strong decrease) contributed 13.9% and 5.4% of the dissimilarity, respectively. Two additional species in the top eight showed marginal evidence of declining abundance (*S. victa* and *T. sirtalis*).

Table 2. SIMPER results comparing species contributions to the dissimilarity between the 1993–1994 and 2014–2015 sampling periods (total average dissimilarity = 86.76%) for a site in Buckingham, Lee County, Florida, USA.

Species	Contribution %	Cumulative %
Coluber constrictor	18.04	18.04
Pantherophis guttatus	14.93	32.98
Diadophis punctatus	13.90	46.87
Thamnophis saurita	13.14	60.02
Nerodia fasciata	12.11	72.13
Thamnophis sirtalis	7.74	79.87
Opheodrys aestivus	5.42	85.29
Storeria victa	3.98	89.27
Pantherophis alleghaniensis	3.43	92.70

Human land-use (combined development and agriculture) increased modestly from 1991 to 2012, with about a 7.4% increase in overall land coverage over the 21 y (Table 3). This may have been a greater increase if the map coverage of roads had not been changed from polygons in 1991 to a linear feature in 2012. Wetlands and Other Native Habitats designations experienced substantial decreases with loss of 30.8 and 24.3% of the original cover, respectively.

Table 3. Land-use changes at our study site in Buckingham, Lee County, Florida, USA, between 1991 and 2012 using a 500-m buffer around the Buckingham survey route.

Land-Use	1991	2012
Human Use (Development and Agriculture)	72.4%	79.8% (+7.4)
Wetland	10.7%	7.4% (-3.3)
Other Native Habitat	16.9%	12.8% (-4.1)

Discussion

This study shows clear differences in the relative abundance of snake species on our road survey route in Buckingham, Florida, after 21 y. The extremely high average dissimilarity of nearly 90% reflects likely changes in the relative abundance of snake species over that study period. Most notable were significant increases in abundance of *Diadophis punctatus* and significant decreases in abundance of *Opheodrys aestivus*. These striking results for individual snake species were also evident in another more comprehensive study in the same region (Cassani et al. 2015), offering enhanced support for the idea that our observed differences reflect true population changes. In that study, *D. punctatus* observations increased from zero to 17 and *O. aestivus* was completely absent from drift fence samples taken in 1996–1997 and 2010–2011 at Corkscrew Regional Ecosystem Watershed, the largest tract of preserved land in southwest Florida. Thus, increased abundance of *D. punctatus* and decreased abundance of *O. aestivus* have now been shown over multiple studies in southwest Florida, suggesting an important regional trend.

Although we cannot identify the definitive causes of snake abundance change, there was an association with land cover change over the study period. Human land-use coverage increased about 7% from 1991 to 2012. Much of the difference in human land-use was due to enhanced agriculture in this rural part of Lee County. Although human development per se did not increase, wetland and native habitat experienced considerable losses that were likely due, in part, to enhanced agricultural use near our survey route. These changes could have contributed to changes in snake abundance.

Uncertain differences in traffic volume between the two sampling periods may create a confounding variable that weakens conclusions from quantitative tests of abundance change. We have strong data showing a 2.45-fold increase in traffic between 2001 and 2014 and an estimated increase of 2.94-fold from 1993, but this is only from one locality along our survey route. Despite the real nature of this effect, higher traffic volume is likely to increase snake mortality (Oxley et al. 1974; Coleman et al. 2008; Jones et al. 2011), biasing our unadjusted results toward abundance increases. Nevertheless, our analyses of raw data showed a highly significant abundance decrease in *Opheodrys aestivus*, substantiated by community analysis of relative abundance data that does not suffer from traffic biases (Cassani et al. 2015). The one species (*Diadophis punctatus*) that showed a highly significant abundance increase from the raw data was not affected by traffic volume adjustment. Raw data indicated a marginally significant abundance increase in *Nerodia fasciata* that disappeared after traffic adjustment and two commonly observed species that showed marginal decreases in both analyses (*Storeria victa* and *Thamnophis sirtalis*). These results may not reflect true changes because of uncertain effects of differences in traffic volume and other variables. Nevertheless, the fact that they contributed rather high dissimilarity to the two sampling periods underscores the need for continued monitoring of these species.

As with any field sampling method, road surveys have inherent limitations and biases. For example, smaller species are less likely to attempt a road crossing and venomous species cross more slowly (Andrews and Gibbons 2005). Such variation almost certainly caused among-species differences in detection probability for our road survey method in Buckingham, but it likely does not affect our comparisons between the two sampling periods. Nevertheless, we cannot rule out the possibility that observed differences reflect mere population fluctuations or behavioral alterations rather than true changes in the snake community. Moreover, our study reflects just two snapshots in time (1993–1994 and 2014–2015), although the sampling methods were robust and consistent over multiple seasons of the year (wet, dry, summer, fall, and winter). A comprehensive study using drift fence and other sampling methods may offer a more thorough understanding of this snake community.

Behavioral road avoidance by snakes is a factor that could have varied between the two sampling periods due to traffic increases. Road mortality often increases with traffic (Fahrig et al. 1995; Jones et al. 2011) but some have suggested a threshold traffic volume above which mortality decreases because animals reduce crossing attempts (Clarke et al. 1998). However, the nature of this threshold effect likely differs considerably amongst animal groups and species, some species do not exhibit it, the magnitude of potential traffic thresholds is unknown, and it is unclear how snakes respond to traffic variation (Grilo et al. 2015). Still, it could be argued that this type of avoidance behavior may account for the decreased abundance of *O. aestivus* found in this study. Although we do not know how this species responds to traffic, several lines of evidence suggest the idea to be unlikely. First, of seven frequently observed species, it was the only one to show considerable decreases, suggesting that road avoidance was not excessive in this study. Second, we documented a large increase in abundance of a species (*D. punctatus*) that has been shown to avoid crossing roads (Andrews and Gibbons 2005). Third, Oxley et al. (1974) found that reptile mortality continually increased with traffic up to 10,000 vehicles/day, and Buckingham Road did not increase above an average of 7,032 vehicles/day. Therefore, we believe avoidance effects were not a major factor confounding differences between our two sampling periods. More likely is that mortality increased in the 2014–2015 sampling period because of higher traffic.

Our results showed a highly significant decline in abundance of *Opheodrys aestivus*, a species that also was absent in another recent retrospective resampling study in the region (Cassani et al. 2015). Because of the abundance decrease of that species in each of these two studies, we suggest that it is likely to be in severe local decline. We know of only a few specimens collected in the region over recent years and therefore highlight the urgent need for further studies to explore the status of this population. There was no definitive evidence for decline in abundance of other snake species in this study, but some offered marginal statistical support for that hypothesis. Probably the most likely additional candidate to be under threat is Storeria victa, which decreased in abundance from six individuals in 1993–1994 to two in 2014–2015. Three venomous species (*Agkistrodon conanti*, *Micrurus fulvius*, and *Sistrurus miliarius*) were absent in the latter sampling. Clearly, however, much more data are needed before we can offer a robust statement about the trajectory of these local populations. We hope that our work will stimulate such studies.

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