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CORRELATES OF MOVEMENTS ACROSS ROADS IN AN EVERGLADES SNAKE ASSEMBLAGE

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ABSTRACT: Data associated with a 46-month road survey in Everglades National Park, U.S.A., were used to examine selected life history traits of 19 snake species in a hydrologically fluctuating system subject to droughts and floods. A distance of 314.8 km was driven beginning at dusk for each of 204 visits during March 2008–December 2011. Habitats encompassed uplands of Long Pine Key, freshwater glades of Pahayokee, and interface with saline glades at Mahogany Hammock. The Florida Cottonmouth, *Agkistrodon conanti*, Florida Watersnake, *Nerodia fasciata pictiventris*, Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, and Eastern Gartersnake, *T. sirtalis sirtalis*, accounted for 68.6% of 1,312 individuals during three calendar years of surveys of 2009–2011. Our study included one native and one exotic species undetected in an earlier road survey conducted on Long Pine Key in the mid-1980s. Species overlap among the three distinct habitats of our study was extensive, but dominant species and relative abundances varied among them. Comparison of relative abundance on Long Pine Key with an earlier study indicated a recent shift towards more aquatic species but fewer species and total individuals. Adult body sizes and reproductive traits of selected species of this study did not differ from those of other samples from Everglades National Park. However, among species for which comparisons were possible, seasonal activity patterns were not unanimously similar. Incidence of roadkill was highest during months of least snake movements on the roads. Snakes moved in association with air temperatures and rainfall, but not water table level. However, overall numbers of snakes dropped significantly during 2011 when the water table was at its lowest. Aquatic and semi-aquatic species of short-hydroperiod freshwater wetlands were negatively affected by low water events. Abundance of the Red Cornsnake, *Pantherophis guttatus*, a semi-arboreal species, responded negatively to low water. Abundances of deep-water aquatic snakes were unaffected by the low water table of 2011. Among the species negatively affected in abundance by low water, recruitment increased in three species and decreased in three species. Recruitment increased in deep-water snakes. If current climate change trajectories hold, the Everglades will experience a series of anthropogenic successional seres of predictable ever-diminishing habitat for most and ultimately all of the snake species presently inhabiting the southern Everglades.

INTRODUCTION

The Florida Everglades is designated as a Wetland of International Importance through the Rasmar Convention in 1987 of the United Nations Scientific and Cultural Organization (UNESCO), International Biosphere Reserve in 1976, and an UNESCO World Heritage Site in 1979. The Everglades is one of 44 global sites and one of two US sites in the UNESCO list of world heritage that are in danger.

The Everglades is a large and youthful system comprising 47,000 km^2 that was formed within the last 5,000 years. The elevation gradient of this broad shallow "River of Grass" is 5 cm per km^{-1} from the headwaters of the upper Kissimmee chain of lakes to Florida Bay (Gleason and Stone, 1994). Water from the southern Everglades empties into the Southeast Gulf of Mexico, Florida Bay, and some into Biscayne Bay (Aumen et al., 2015). Everglades National Park, established in 1947, constitutes a 6,106.61 km^2 subset of this system in three south Florida counties. Except for a large 6.1 m high shell mound, elevation ranges 0–2.4 m above sea level. During 1952–2010, marsh water level in Everglades National Park increased linearly at a rate of 2.61 mm yr (Stabenau et al., 2011). This rate of increase within Everglades National Park is similar to the 2.36 mm per yr linear rate of sea level rise at Key West over the past 110 years, totaling a rise in sea level of 0.26 m (Stabenau et al., 2011). In a 50-yr window for the Florida Everglades, the combination of a 1.5 °C increase in air temperature, 10% change in rainfall (decrease being the more likely direction), and 0.46 m rise in sea level will result in severe droughts, more wildfire, loss of slough, and the restructuring of plant and animal communities (Nungesser et al., 2015). In this scenario, the greater Everglades will dry out by 2060, the ecosystem and its water supply forever altered (Obeysekera et al., 2015).

Facing human-mediated changes in climate in Everglades National Park are 55 species of native non-marine amphibians and reptiles, which comprise 40.4% of the entire native non-marine herpetofauna of Florida (Meshaka et al., 2000). The snake assemblage of Everglades National Park is comprised of 25 species, not including subspecies, of which 23 are native (Meshaka et al., 2000). In Everglades National Park, snakes occur in a wide range of upland and wetland habitats, the latter of which include short- and long-hydroperiod freshwater wetlands and brackish systems (Meshaka et al., 2000). Most of these snake species are recent colonizers from northern latitudes and have shown remarkable changes in their biology for so short a time (Meshaka and Layne, 2015).

Ecological work on Everglades National Park snakes at the level of the assemblage with attention to habitat and seasonal activity are few but comprehensive. A road survey was conducted in the long-hydroperiod wetlands of Pahayokee during 1986–1989 to assess seasonal activity and road mortality (Bernardino and Dalrymple, 1992). On the driest section of the park, Long Pine Key, a road survey was conducted during 1984–1986 that focused on seasonal activity of individual species (Dalrymple et al., 1991a). A drift fence survey of the herpetofauna of four habitats on Long Pine Key during 1984–1986 yielded 17 species of snakes from a total of 27 herpetofaunal species (Dalrymple, 1988). Snake diversity and evenness were higher on Long Pine Key than in the Pahayokee region of the park (Dalrymple et al., 1991a,b).

The goals of our study were two-fold. First, we sought to quantify ecological and demographic responses of the snake assemblage to climatic variables in the Everglades system. Second, we relate short-term responses by members of this assemblage to plausible successional seres to which the southern Everglades will be subjected under projected trajectories associated with human-mediated climate change.

STUDY SITE AND METHODS

Two hundred and four road surveys were conducted in Everglades National Park (Miami-Dade County, Monroe County, and Collier County) during March 2008–2011. Each survey began at the toll booth near Coe Visitor Center at the Homestead Entrance. The vehicle was driven down the Main Park Road, to Nike missile site on Research Road, and back to Main Park Road. The survey route continued to the Pahayokee parking lot, back to Main Park Road, to Mahogany Hammock parking lot, and back to Main Park Road. From that point, the survey route continued to the northern base of the Buttonwood Canal Bridge on Main Park Road. A direct return along Main Park Road to the toll booth near the Coe Visitor Center marked the endpoint of the survey route. Total distance associated with each survey was 97.3 km. Distributional maps along the routes are provided in the species accounts.

Three ecologically distinct regions were recognized within the study site. The first site was Long Pine Key. Consisting of pinelands, tropical hardwood hammocks and interdigitating finger glades, Long Pine Key was also the driest of the sites. Ending at Rock Reef Pass (Hog back) (12.5 km) and having included the road to the missile site (5.75 km), it ranged 18.25 km (36.5 km roundtrip per visit) to 25.433, -80.749 that constituted 37.5% of the entire roundtrip survey. The second site was Pahayokee. A freshwater long hydroperiod marsh, it was the wettest site dotted with tropical hardwood hammocks and cypress domes. Beginning at Rock Reef Pass (9.25 km) and having included roads to both Pahayokee and Mahogany Hammock (6.15 km), it ranged 15.4 km (30.8 km roundtrip per visit) that constituted 31.7% of the entire roundtrip survey. The third site was the saline glades. Consisting of tropical hardwood hammocks, mangrove and wetlands of fluctuating salinity it extended southward from near Mahogany Hammock to Florida Bay. It ranged 15.0 km (30.0 km roundtrip per visit) from the end of Pahayokee (25.293, -80.798) that constituted 30.8% of the entire roundtrip survey. Surveys took 62 minutes in Long Pine Key, 53 minutes in Pahayokee, and 51 minutes in the saline glades. Nine individuals for which exact capture locality could not be determined were not included in this breakdown.

Surveys were conducted multiple times each month during March 2008–December 2011 (**Table 1**). Surveys began at approximately sundown. Surveys began as early as 30 minutes before sunset during the colder months and up to 30 minutes after sunset during the hotter months. No surveys were conducted during heavy rainfall. The high beams of the Ford F-150, F-250, Jeep Liberty, or Chevrolet Tahoe, truck were used to increase detectability of snakes on the road. All surveys were conducted by at least two people, the driver (primary observer), and assistant (secondary observer).

Table 1. Numbers of surveys for each month in Everglades National Park during 2008–2011.

Month	2008	2009	2010	2011	Total
Jan	0	3	3	5	11
Feb	0	4	3	5	12
Mar	4	4	4	7	19
Apr	4	5	3	5	17
May	4	3	4	5	16
Jun	4	4	9	7	24
Jul	3	4	7	5	19
Aug	2	4	6	5	17
Sep	4	4	7	5	20
Oct	5	5	4	4	18
Nov	4	3	4	4	15
Dec	4	4	3	5	16
Total	38	47	57	62	204

The following data were recorded during each survey, beginning with date, start time, end time, and the names of the observers. Wind speed (mph) was measured as an average of 1.0 min. readings from a Kestrel 2000 Weather Meter. Percent (%) cloud cover was visually estimated within six categories (0, 20, 40, 60, 80, 100). Visibility of the moon was categorized as ¼, ½, ¾, none, covered by clouds. General comments were those relating to potentially relevant information not covered by the data template. Park gauges provided nightly data and monthly mean data for marsh water stage (cm) (NP62), maximum and minimum air temperature (°C) (RPL), and total precipitation (cm) (RPL). To compare with Dalrymple et al. (1991a) on Long Pine Key, we used station TSB, near Long Pine Key for water stage (cm).

Waypoints and corresponding UTMs of each snake were recorded with a Garmin GPS in WGS 84 and used to produce distribution maps for each species. Separate waypoints were not recorded for snakes within 10 m of one another. Ambient air temperature at the time of encounter with each live-captured snake was recorded with a probe thermometer. Snakes were determined to be alive on the road or dead on the road (DOR), which included mortally-wounded individuals. Snout-vent length (SVL) and total length (TL) of harmless snakes were measured to 0.1 cm using a flexible measuring tape. Snakes were sexed using lubricated probes of appropriate size. To measure body size and determine sex of venomous snakes, a "hot box" with a plexiglass shield was used into which the anterior portion was restrained gently. A Pesola scale was used to weigh (g or kg) dead snakes or live snakes with the subtracted weight of the snake bag for large individuals or that of a plastic Ziploc® bag for small individuals. Snakes were reported to have been new or recaptured. Snakes were marked using a set of small scissors to remove the third ventral scale anterior to the anal plate. A final examination was made of each snake for evidence of fresh or old wounds, ectoparasites, shedding, a recent meal, or of being gravid or spent. Individuals too mangled to categorize or those that escaped without capture and whose sex could not be determined comprised snakes of unknown status.

The data were entered into an Excel 2010 spreadsheet. In 2008, data were collected during March–December, whereas the 2009–2011 dataset encompassed three entire calendar years. March–December captures for each year of 2008–2011 were used to assess changes in total number of species, individual snakes, and number of captures for each species among years. For individual species, the 2008–2011 dataset, uncorrected for search effort, was used for sample statistics of adult body sizes, monthly distribution of weight-length relationships, estimated age at sexual maturity using presumed cohorts found in monthly distributions of body sizes, and for presentation of miscellaneous life history information concerning each species.

January–December captures for each year of 2009–2011 were used to assess changes in total number of species and individual snakes, number of live captures and DOR individuals for each species among years, and to measure relationships between monthly captures of each species and monthly values of gauged data from Everglades National Park. Captures during 2009–2011 were also used to determine population structure, monthly movements by one or more segments of the population, and ambient temperatures associated with nightly activity of live captures on the road. To compare numbers of snakes from each of the three regions during 2009–2011, raw numbers were divided by the product of total number of visits and distance in km of each site. Using Google Earth, we drew a map to show the locations of individuals encountered along the survey route of our study with the goal in mind to visualize habitat associations of these species that were quantified by calculating number of encounters per km. Appendices 1 and 2 provide raw data for the two time periods analyzed in this study.

A direct comparison of Long Pine Key results was possible between our study and that of Dalrymple et al. (1991a) who surveyed that region by vehicle during 1984–1986 (2–3 days per week, 50 hrs per mo.). Because we do not know if surveys of Dalrymple et al. (1991a) were one-way or roundtrip, we restrict our comparisons to number of snakes per hour searched. Our sampling was conducted from dusk onwards, whereas that of Dalrymple et al. (1991a) was conducted during the day throughout the cool months of the year and at night during the hot wet summer months. Therefore, by restricting counts to June–August for both studies, we could confidently compare numbers of snakes captured per hour of search time from dusk through dark and with attention paid to those species apt to move at night in the summer. Numbers of snakes during June–August from Dalrymple et al. (1991a) were divided by 150 hrs. June–August snake totals of our study during 2008–2011 were divided by 62 hrs. Dalrymple et al. (1991a) surveyed 9.6 km of road 2–3 days each week during their study. Because we could not be certain how many days were surveyed during June–August, we did not compare our results by number of snakes per km.

Road surveys during February–March 1986 and February 1987–January 1989 resulted in detecting 16 species in Pahayokee (Bernardino and Dalrymple, 1992). However, we are not certain that their surveys were conducted at night as were ours. In fact, it is more likely that they were conducted primarily, if not exclusively, during the daytime in winter like those of Dalrymple et al. (1991a). Therefore, we did not calculate quantitative comparisons. Statistics were calculated on Excel 2010. T-tests were two-tailed, Chi square tests were weighted, and statistical significance was recognized at p-values ≤ 0.05.

RESULTS

Assemblage structure- Our study, conducted at night from Long Pine Key to Florida Bay, collectively, detected a species-rich, even if highly uneven, snake assemblage of 24 species as measured during January 2009–December 2011 (**Table 2**) or March–December 2008–2011 (**Table 3**). Collectively, the snake assemblage was dominated by the Florida Cottonmouth, Florida Watersnake, Peninsula Ribbonsnake, and Eastern Gartersnake, respectively (**Table 2 and 3**). The Florida Scarletsnake, the Red Cornsnake, *Pantherophis guttatus*, and Everglades Racer were most frequently encountered among the terrestrial and terrestrial-arboreal species (**Table 2 and 3**).

Table 2. Numbers of live and dead snakes per visit encountered on the road at night in Everglades National Park during January 2009–December 2011. Weighted Chi Squares tested for differences in number of snakes encountered among years. Assessments in encounter rate among years were not conducted where precluded by sample sizes.

Species	2009	2010	2011	2009–2011	Chi Square
Agkistrodon conanti	2.70	2.28	1.05	1.94	42.89, $P < 0.001$
Cemophora coccinea coccinea	0.19	0.56	0.31	0.36	10.56, P < 0.01
Coluber constrictor paludicola	0.21	0.16	0.05	0.13	5.99, $P < 0.05$
Crotalus adamanteus	0.04	0.12	0.08	0.08	
Diadophis punctatus punctatus	0.09	0.02	0	0.03	6.91, $P < 0.05$
Drymarchon couperi	0	0.02	0	0.01	
Farancia abacura abacura	0	0.05	0.02	0.02	
Lampropeltis elapsoides	0	0	0.02	0.01	
Lampropeltis getula getula X *L. g. floridana*	0	0	0.02	0.01	
Liodytes alleni	0.15	0.12	0.05	0.1	
Liodytes pygaea cyclas	0.02	0	0	0.01	
Micrurus fulvius barbouri	0.02	0	0	0.01	
Nerodia clarkii compressicauda X *N. fasciata pictiventris*	0.66	0.61	0.05	0.42	32.22, $P < 0.001$
Nerodia fasciata pictiventris	2	1.32	0.82	1.33	27.88, $P < 0.001$
Nerodia floridana	0.4	0.35	0.35	0.37	
Nerodia taxispilota	0.26	0.09	0.23	0.19	
Opheodrys aestivus carinatus	0.06	0.02	0	0.02	
Pantherophis guttatus	0.4	0.47	0.08	0.31	16.79, $P < 0.001$
Pantherophis alleghaniensis quadrivittatus X *P. a. rossalleni*	0.21	0.14	0.16	0.17	
Python bivittatus	0.19	0.11	0.08	0.12	
Sistrurus miliarius barbouri	0.19	0.12	0.03	0.11	6.44, $P < 0.05$
Storeria victa	0.02	0.04	0	0.02	
Thamnophis saurita sackenii	1.62	1.4	0.48	1.12	36.86, $P < 0.001$
Thamnophis sirtalis sirtalis	2.17	0.74	0.44	1.03	85.34, $P < 0.001$
Total no. individuals	11.6	8.74	4.31	7.9	188.60, $P < 0.001$
Total no. species	20	20	18	24	

Table 3. Numbers of live and dead snakes per visit encountered on the road at night in Everglades National Park during March–December 2008–2011. Weighted Chi Squares tested for differences in number of snakes encountered among years. Assessments in encounter rate among years were not conducted where precluded by sample sizes.

Species	2008	2009	2010	2011	2008–2011	Chi Square
Agkistrodon conanti	1.55	3.08	2.5	1.08	2.02	55.10, $P < 0.001$
Cemophora coccinea coccinea	0.16	0.23	0.63	0.35	0.36	16.54, $P < 0.001$
Coluber constrictor paludicola	0.26	0.23	0.18	0.06	0.17	16.54, $P < 0.001$
Crotalus adamanteus	0.05	0.05	0.14	0.06	0.078	
Diadophis punctatus punctatus	0.03	0.10	0.02	0.00	0.03	NS, but nearly so. Chi value = 7.49 v. 7.82.
Drymarchon couperi	0.00	0.00	0.02	0.00	0.01	
Farancia abacura abacura	0.03	0.00	0.06	0.02	0.03	
Lampropeltis elapsoides	0.03	0.00	0.00	0.02	0.01	
Lampropeltis getula	0.08	0.00	0.00	0.00	0.02	
Liodytes alleni	0.08	0.18	0.14	0.04	0.11	
Liodytes pygaea cyclas	0.00	0.03	0.00	0.00	0.01	
Micrurus fulvius barbouri	0.00	0.03	0.00	0.00	0.01	
Nerodia c. compressicauda X *N. f. pictiventris*	0.58	0.75	0.69	0.02	0.49	33.93, $P < 0.001$
Nerodia fasciata pictiventris	0.79	1.70	1.45	0.73	1.16	26.53, $P < 0.001$
Nerodia floridana	0.32	0.33	0.37	0.19	0.30	
Nerodia taxispilota	0.18	0.25	0.10	0.23	0.19	
Opheodrys aestivus carinatus	0.00	0.08	0.02	0.00	0.02	
Pantherophis guttatus	0.29	0.45	0.47	0.10	0.32	13.98, $P < 0.001$
Pantherophis a. quadrivittatus X *P. a. rossalleni*	0.21	0.23	0.16	0.17	0.19	
Python bivittatus	0.34	0.23	0.12	0.10	0.18	9.03, $P < 0.05$
Sistrurus miliarius barbouri	0.05	0.23	0.14	0.04	0.11	8.63, $P < 0.05$
Storeria victa	0.03	0.03	0.04	0.00	0.02	
Thamnophis saurita sackenii	0.37	1.78	1.53	0.42	1.02	69.31, $P < 0.001$
Thamnophis sirtalis sirtalis	1.08	2.13	0.78	0.38	1.03	71.37, $P < 0.001$
Total no. individuals	6.50	12.10	9.55	4.00	7.89	215.37, $P < 0.001$
Total no. species	20	20	20	17	24	

Across three regions of Long Pine Key, Pahayokee, and the saline glades, numbers of species did not vary and overlapped with 14 species among them (**Table 4**). The three sites shared an unevenness in species composition, especially the former two sites, where the Florida Cottonmouth was the dominant form (**Table 4**). Both *Thamnophis* species and the Florida Watersnake were common on Long Pine Key, and the Florida Watersnake was the most abundant natricine in Pahayokee. Approaching Mahogany Hammock in the saline glades, hybrids between the Mangrove Saltmarsh Watersnake, *Nerodia clarkii compressicauda*, and Florida Watersnake were the most frequently encountered snake, but the Florida Cottonmouth, both *Thamnophis* species, the Florida Scarletsnake, and Red Cornsnake were also common (**Table 4**).

During the entirety of this study encounter rates varied significantly among the three regions (**Table 3**), with most snakes having been encountered at Pahayokee and followed by the saline glades and Long Pine Key, respectively (**Table 3**). The extremely high numbers of the Florida Cottonmouth at Pahayokee best explains the high productivity of Pahayokee relative to the other two regions. On the other hand, encounter rates were higher for more species in the saline glades than on Long Pine Key (**Table 3**). Numbers of both individual snakes and species encountered on Long Pine Key were higher than those reported during June–August sampling of Long Pine Key in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Table 4. Assemblage structure of snakes expressed in number of individuals per total km from each of the three regions of Everglades National Park during March–December 2008–2011.

Species	Long Pine Key	Pahayokee	Saline	Chi Square
Agkistrodon conanti	0.02	0.04	0.007	133.12, $P < 0.001$
Cemophora coccinea coccinea	0.0001	0.001	0.01	104.65, $P < 0.001$
Coluber constrictor paludicola	0.003	0.0006	0.001	14.15, $P < 0.001$
Crotalus adamanteus	0.001	0.0003	0.0008	NS
Diadophis punctatus punctatus	0.0005	0.0002	0.0002	NS
Drymarchon couperi	0	0	0.0002	NS
Farancia abacura abacura	0.0003	0.0002	0.0003	NS
Lampropeltis elapsoides	0	0	0.0003	NS
Lampropeltis getula getula X L. g. floridana	0.0001	0.0005	0	NS
Liodytes alleni	0.0008	0.002	0	14.15, $P < 0.001$
Liodytes pygaea cyclas	0	0.0002	0	NS
Micrurus fulvius barbouri	0.0001	0	0	NS
Nerodia clarkii compressicauda X N. fasciata pictiventris	0	0.0005	0.01	185.32, $P < 0.001$
Nerodia fasciata pictiventris	0.007	0.027	0.004	166.56, $P < 0.001$
Nerodia floridana	0.0005	0.007	0.004	35.19, $P < 0.001$
Nerodia taxispilota	0.0007	0.005	0.0005	35.46, $P < 0.001$
Opheodrys aestivus carinatus	0.0004	0	0.0002	NS
Pantherophis alleghaneinsis quadrivittatus X P. a. rossalleni	0.0019	0.0008	0.003	6.74, $P < 0.05$
Pantherophis guttatus	0.002	0.002	0.007	30.08, $P < 0.001$
Python bivittatus	0.001	0.0006	0.004	19.93, $P < 0.001$
Sistrurus miliarius barbouri	0	0.0002	0.003	30.08, $P < 0.001$
Storeria victa	0.0001	0.0005	0	NS
Thamnophis sauritus sackenii	0.008	0.02	0.007	39.30, $P < 0.001$
Thamnophis sirtalis sirtalis	0.01	0.008	0.01	8.61, $P < 0.02$
Total no. individuals	0.06	0.11	0.08	114.47, $P < 0.001$
Total no. species	19	20	19	NS

Table 5. A comparison between our study and that of Dalrymple (1991a) of number of snakes encountered per hr at night on Long Pine Key, Everglades National Park, during June–August.

Species	This study	Dalrymple et al. (1991a)	X^2
Agkistrodon conanti	0.53	0.05	122.37, P < 0.001
Cemophora coccinea coccinea	0	0.01	ns
Coluber constrictor paludicola	0.1	0.17	ns
Crotalus adamanteus	0.05	0.02	ns
Diadophis punctatus punctatus	0.02	0.1	4.51, P < 0.05
Drymarchon couperi	0	0.004	ns
Farancia abacura abacura	0.02	0	7.09, P < 0.01
Lampropeltis elapsoides	0	0	ns
Lampropeltis getula getula X L. g. floridana	0.02	0.01	ns
Liodytes alleni	0.03	0.002	8.20, P < 0.01
Liodytes pygaea cyclas	0	0	ns
Micrurus fulvius barbouri	0	0.004	ns
Nerodia clarkii compressicauda X N. fasciata pictiventris	0	0	ns
Nerodia fasciata pictiventris	0.33	0.02	95.08, P < 0.000
Nerodia floridana	0.03	0	14.18, P < 0.000
Nerodia taxispilota	0.03	0.002	8.20, P < 0.01
Opheodrys aestivus carinatus	0	0.12	7.61 P < 0.01
Pantherophis alleghaneinsis quadrivittatus X P. a. rossalleni	0.13	0.07	ns
Pantherophis guttatus	0.11	0.05	ns
Python bivittatus	0.02	0	7.09, P < 0.01
Sistrurus miliarius barbouri	0	0.14	8.35, P < 0.01
Storeria victa	0.02	0.13	6.24, P < 0.02
Thamnophis sauritus sackenii	0.32	0.22	ns
Thamnophis sirtalis sirtalis	0.34	0.17	8.27, P < 0.01
Total no. individuals	2.1	1.4	26.00, P < 0.001
Total no. species	0.26	0.04	37.11, P < 0.001
No. hrs search	62	450	

Within-study differences in assemblage structure and abundance among years– We never encountered all 24 snake species within a single given year of our study. During March–December 2008–2011, we encountered 19, 20, 20, and 17 species each year, respectively. During January 2009–December 2011, we encountered 18–20 species in any given year (**Table 2**). Individual encounter rates across species varied among years with lowest numbers in 2011 associated with a very low water table (average water stage from 2009–2011 was 82.5 cm, with each year measuring 86.8 cm, 90.2 cm, and 70.4 cm, respectively). Total number of individual snake encounters differed significantly across years, both during 2009–2011 (X^2 = 188.60, df = 2, P < 0.001) and during 2008–2011 (X^2 = 215.37, df = 3, P < 0.001) (**Table 2**).

Monthly activity for all years combined– During 2009–2011, snakes were most active in March and during July–November (**Figure 1).** Number of all snakes per visit per month was positively correlated to mean monthly high air temperatures (r = 0.67, P = 0.02), mean monthly low temperatures (r = 0.67, P = 0.02), but not rainfall volume(r = 0.49, P = 0.11) or water level (r = 0.07, P = 0.84).

Ambient temperatures associated with nightly activity- Among species with more than one record, the range of mean ambient temperatures was 24.0–26.5 °C. No significant difference was detected in temperatures among the 22 of 24 species for which we had data (ANOVA; F = 0.8877, df = 21; P = 0.61).

Road mortality– For the 2009–2011 combined sample, encounter rate per visit was 7.904 for all snakes and 2.964 for DOR snakes. Highest monthly encounter rates of DORs were during February, March, and November with no significant relationship (P > 0.05) to the numbers of all snakes encountered across months (**Figure 1**). Thus, snakes were not differentially killed on the road from monthly numbers of snakes encountered on the road. Looking at combined sample sizes for 2009–2011, 492/1312 snakes (37.5%) were DOR, and a significant negative correlation existed between all numbers of DOR as a percent of all snakes (**Figure 2**). In turn, the monthly percent of DOR was negatively associated with total numbers of snakes over the 12-month period (**Figure 3**).

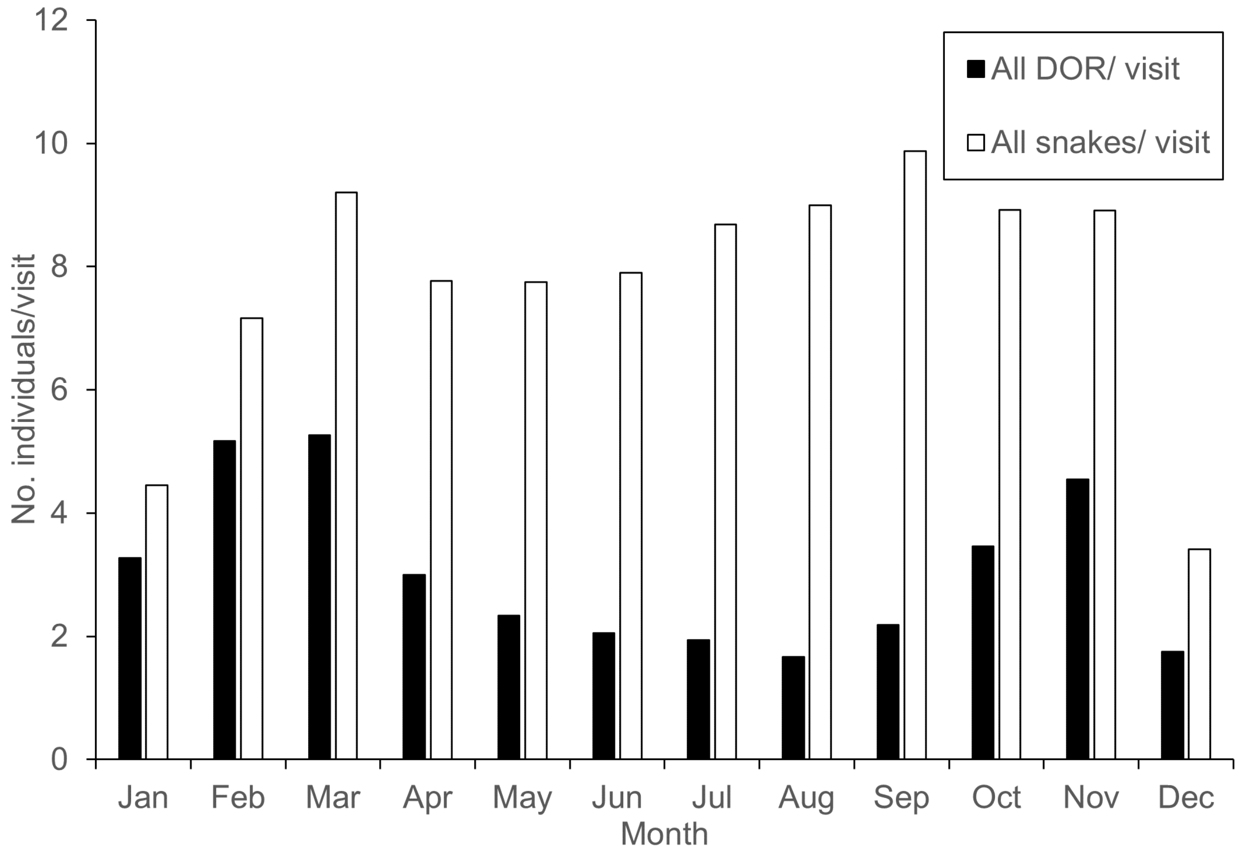

Figure 1. Number of live and dead (DOR) snakes per visit encountered on the road at night in Everglades National Park during January 2009–December 2011.

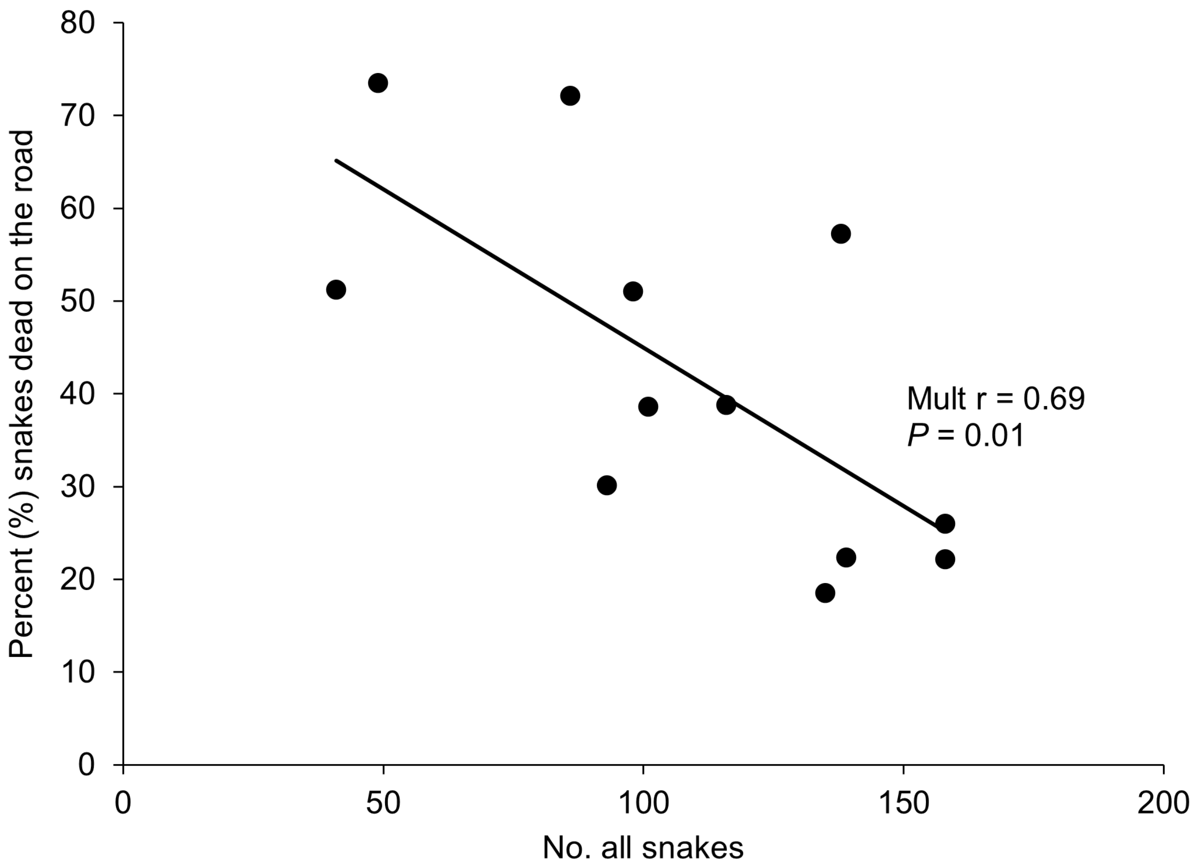

Figure 2. The relationship between the percent of dead snakes and the number of all snakes encountered on the road at night in Everglades National Park during January–December 2009–2011.

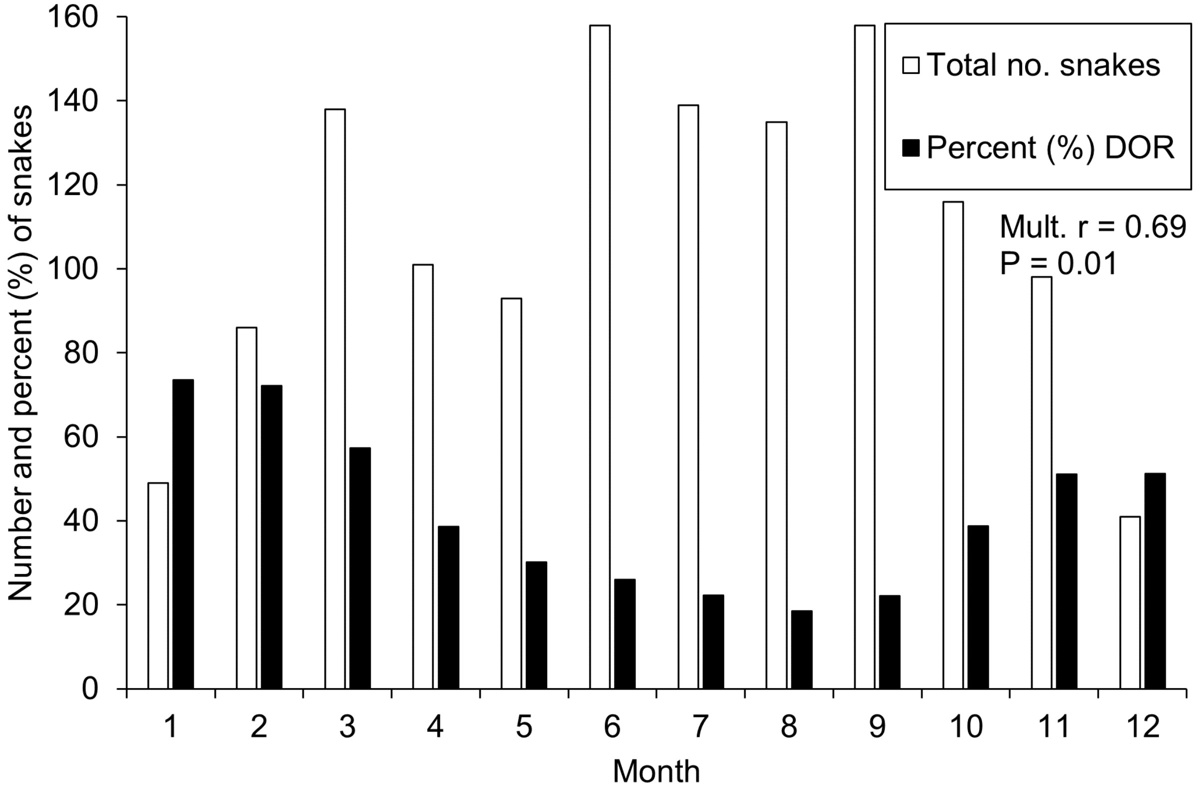

Figure 3. The relationship between monthly values of percent of dead snakes and the number of all snakes encountered on the road at night in Everglades National Park during January–December 2009–2011.

SPECIES ACCOUNTS

Cemophora coccinea coccinea (Blumenbach, 1788)- Florida Scarletsnake (**Figure 4**).

Habitat association- The Florida Scarletsnake occurred in all three regions of Everglades National Park (**Table 4; Figure 5**). Fewer encounters occurred on Long Pine Key and Pahayokee compared to the saline glades, where it was the second most frequently encountered snake (**Table 4**).

Population structure- During the three full calendar years of 2009–2011, 31 males, 13 females, seven juveniles, and nine individuals of unknown status comprised the 60 total Florida Scarlet Snakes, live and dead, encountered on the road at night. Additional counterparts recorded during March–December 2008 were one male, four females, one juvenile, and zero individuals of unknown status comprising a total of six individuals.

The Florida Scarletsnake was uncommonly encountered during our study. The total number of sightings comprised 4.58% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 4.57% of all snakes seen during March–December of 2008–2011 (**Table 3**). Encounter rates were higher in 2009 and 2011 than in 2010, with the lowest encounter rate occurring during a non-drought year.

The male:female sex ratio among adult Florida Scarletsnakes was 2.39:1.00 during 2009–2011, 6.00:1.00 in 2010, 2.13:1.00 in 2010, and 2.00:1.00 in 2011. Adults were encountered more often than juveniles. Recruitment was highest in 2011. Excluding individuals of unknown category, juveniles comprised 13.73% of observations during 2009–2011, 12.50% in 2009, 7.41% in 2010, and 25.00% in 2011. When individuals of unknown category were included, respective percentages of young were 11.67% in 2009–2011, 11.11% in 2009, 6.25% in 2010, and 21.05% in 2011.

Monthly movements- The Florida Scarletsnake was active in all months but January in Everglades National Park. Collectively, this species was most active during May–August (**Figure 6**). Males were most active during June–July (**Figure 6**). Females were active during April–December, and juveniles were active during February–November. Too few individuals of both categories were encountered to identify any monthly peaks in activity (**Figure 5**). Relationships between monthly movements by the Florida Scarletsnake and environmental factors were significant from pooled data, the strongest of which was with rainfall volume **(Table 6)**. Water table level did not affect movements of this species **(Table 6).**

Ambient temperatures associated with nightly activity- Temperatures associated with activity of the Florida Scarletsnake ranged 23.2–30.5 °C (**Figure 7**). Mean ambient temperatures did not significantly differ (ANOVA; F = 0.0279, *P* = 0.98) among males (25.9 ± 2.0 °C; range = 23.2–30.5; n = 26), females (25.8 ± 1.6 °C; range = 23.9–28.0; n = 10), and juveniles (25.7 ± 1.5 °C; range = 24.0–28.0; n = 7). Temperatures for all categories combined averaged 25.8 °C (± 1.8 °C; range = 23.2–30.5).

Roadkill dynamics- Florida Scarletsnakes were killed by vehicles on the road. DOR Florida Scarletsnakes comprised 1.83% of all DOR snakes and 15.0% of all conspecifics recorded during 2009–2011. Dead Florida Scarletsnakes were found during April–November, with the highest incidence of DOR individuals in April, May, and November (**Figure 8**). No significant association (Multiple R = 0.03, *P* = 0.94) existed between %DOR and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 38.9 ± 7.2 cm SVL; range = 29.5–53.3; n = 32) did not differ significantly than that of females (Mean = 41.2 ± 5.7 cm SVL; range = 34.3–52.1; n = 17) with respect to variance (F = 1.608, *P* = 0.16) or mean (t = -1.195, df = 47, *P* = 0.27). Male:female sexual size dimorphism of this sample was 1.07:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, up to 2000, for comparison with those of this study. The body sizes of three females (mean = 37.5 ± 4.1 cm SVL) were available from those data: 32.8, 39.7, 40.0 cm SVL. Monthly distribution of body sizes **(Figure 9)** suggests that minimum body size at sexual maturity for both sexes could be reached by 1.5 years of age.

Table 6. Relationship of environmental conditions to monthly movements of the Florida Scarletnake, *Cemophora coccinea coccinea*, in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.80, *P* = 0.002
Mean monthly minimum air temperature	r = 0.78, *P* = 0.003
Total monthly rainfall volume	r = 0.84, *P* < 0.007
Mean monthly water level	r = 0.24, *P* = 0.46

Figure 4. A Florida Scarletsnake, *Cemophora coccinea coccinea*, from Everglades National Park. (A) Photographed by M. Rochford. (B, C) Photographed by Arik Hartmann.

Figure 5. Distribution of the Florida Scarletsnake, *Cemophora coccinea coccinea*, in Everglades National Park.

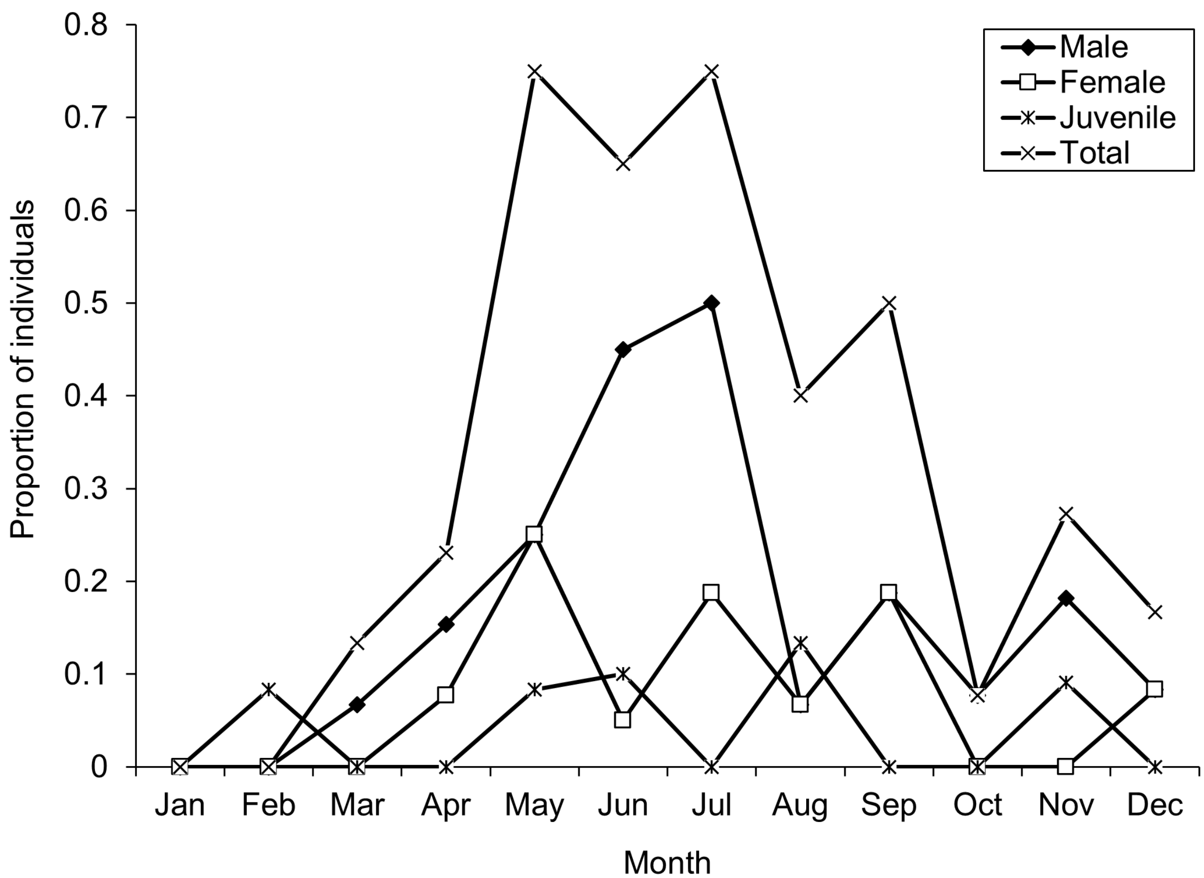

Figure 6. Monthly distribution of the Florida Scarletsnake, *Cemophora coccinea coccinea*, crossing roads at night in Everglades National Park during 2009–2011.

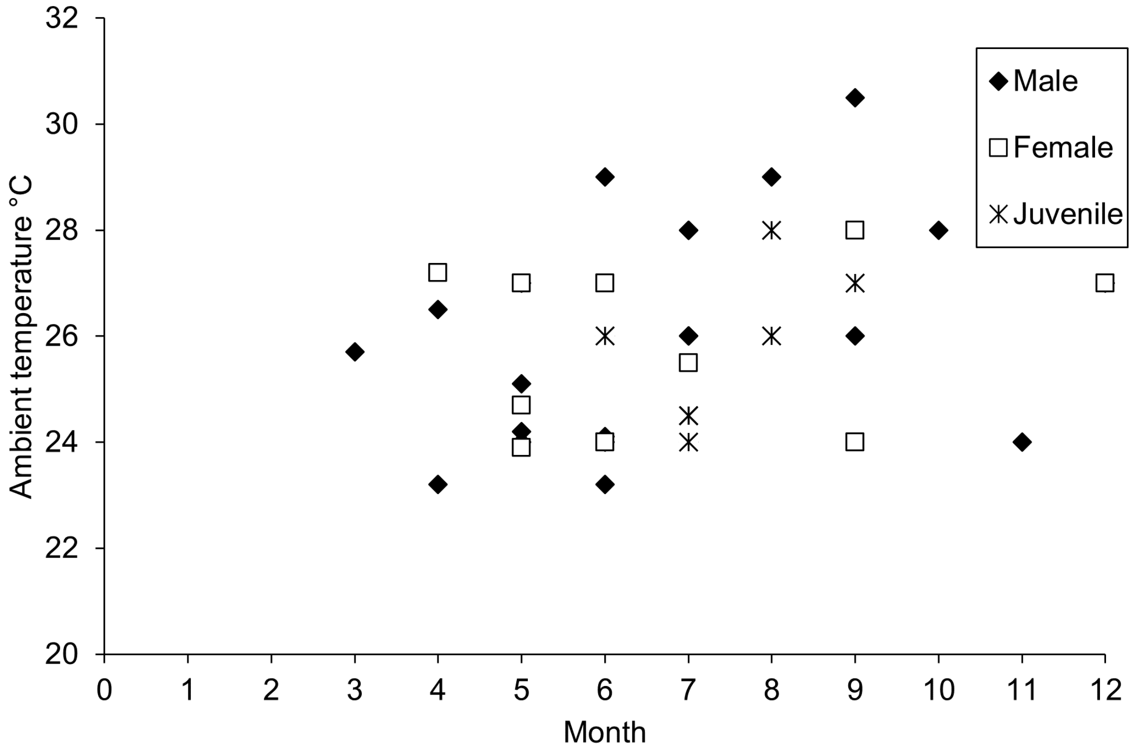

Figure 7. Ambient temperatures associated with activity of the Florida Scarletsnake, *Cemophora coccinea coccinea*, crossing roads at night in Everglades National Park during 2009 –2011.

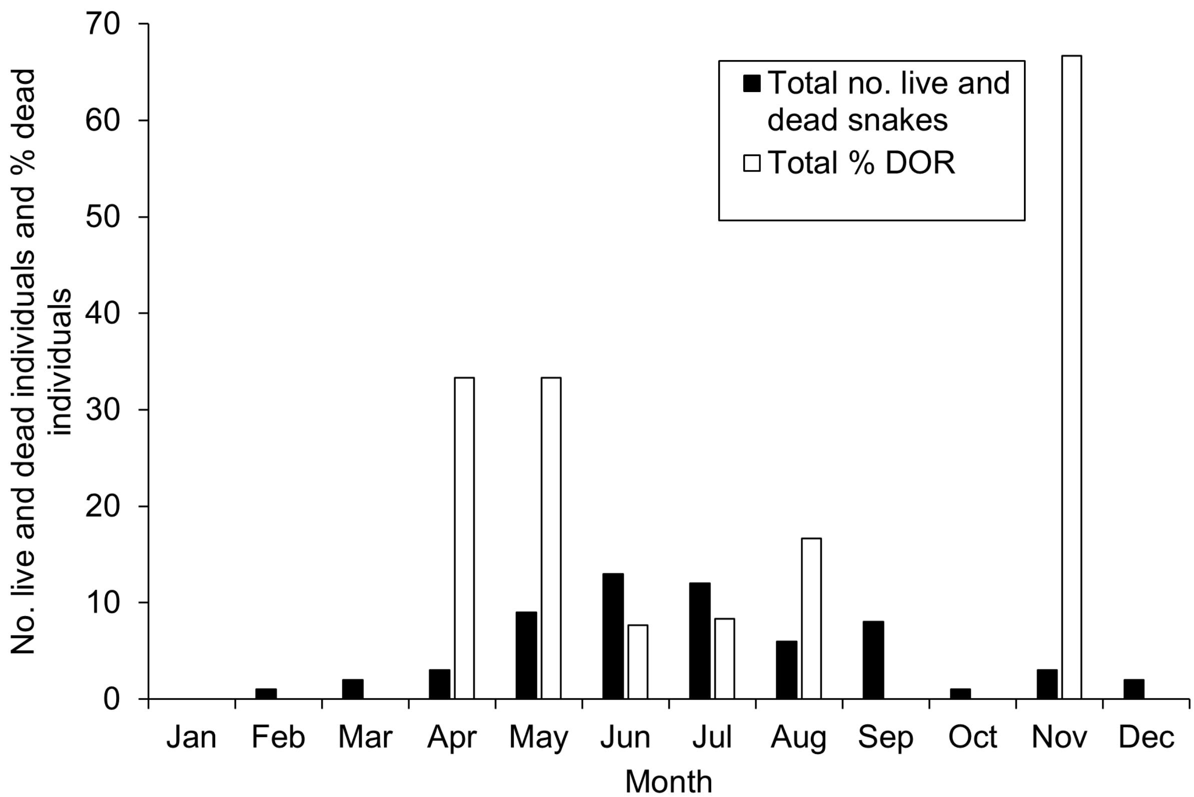

Figure 8. Monthly distribution of all and percent dead individuals of the Florida Scarletsnake, *Cemophora coccinea coccinea*, on roads at night in Everglades National Park during 2009–2011.

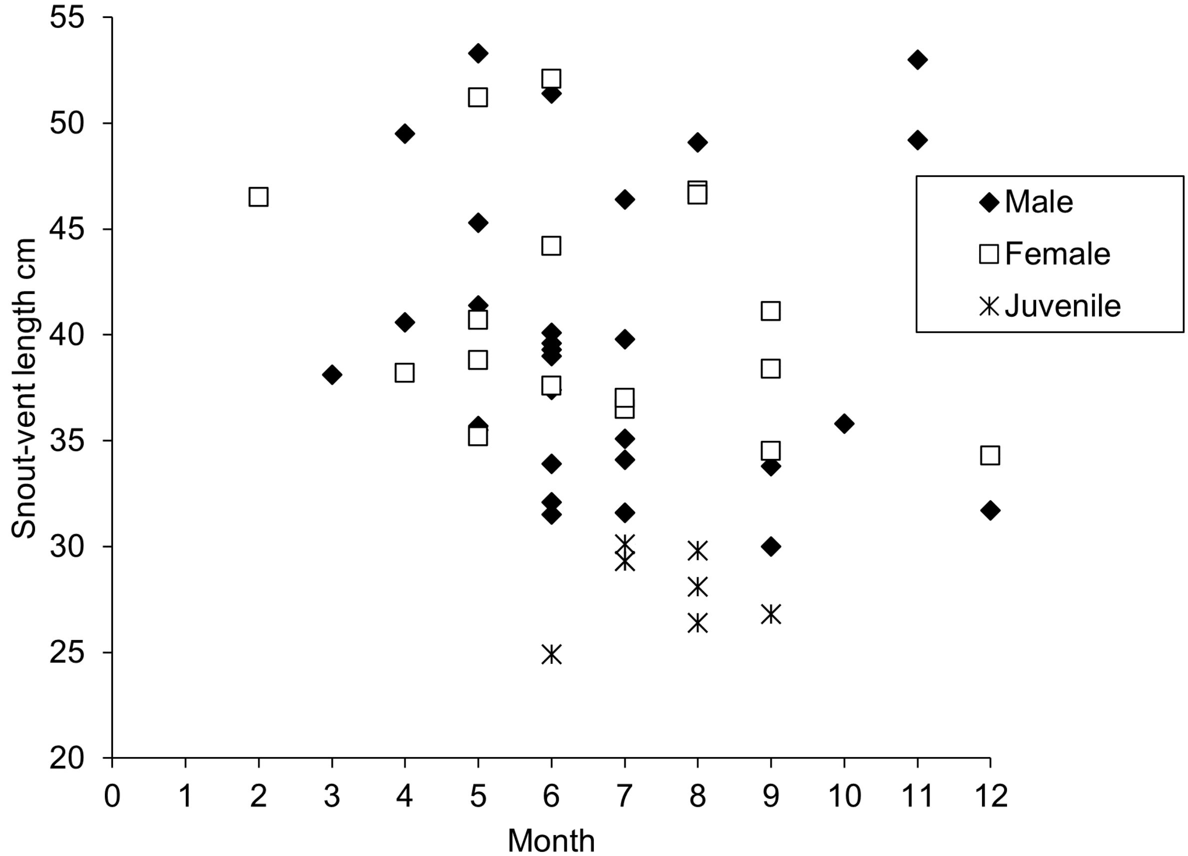

Figure 9. Monthly distribution of body sizes of the Florida Scarletsnake, *Cemophora coccinea coccinea*, from Everglades National Park during 2008–2011.

Coluber constrictor paludicola Auffenberg and Babbitt, 1955- Everglades Racer (**Figure 10**).

Habitat association- Despite strongly diurnal habits, the Everglades Racer was encountered in all three regions of Everglades National Park and its placement in respective assemblages was reflective of its stronger association with short hydroperiod and terrestrial conditions of Long Pine Key (**Table 4; Figure 11**). Its encounter rates mirrored that association with a slightly higher rate of encounter on Long Pine Key (X^2 = 10.41, df = 2, *P* < 0.01).

Population structure- During the three full calendar years of 2009–2011, five males, two females, one juveniles, and 14 individuals of unknown status comprised the 22 total Everglades Racers, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were one male, three females, zero juveniles, and six individuals of unknown status comprising a total of 10 individuals.

The Everglades Racer, a diurnal species, was uncommonly encountered during our study. The total number of sightings comprised 1.67% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 2.18% of all snakes seen during March–December of 2008–2011 (**Table 3**). The Everglades racer was seen in each year but least often so in 2011. The Everglades Racer was consistently more numerous in 2009 and 2010. However, differences in abundance among years did not differ significantly during 2009–2011.

The ratio of male: females among adult Everglades Racers was 2.50:1.00 during 2009–2011. Among the few racers encountered, most were adults. Excluding individuals of unknown category, juveniles comprised 12.52% of observations during 2009–2011. When individuals of unknown category were included, percentage of young 4.6**0**% in 2009–2011.

Monthly movements- The Everglades Racer was absent from the road survey in January, March and November. Collectively, this species was most active during April–October (**Figure 12**). Unimodal in its seasonal movements, numbers of individuals on the road peaked in September (**Figure 12**). examination of movement data from Long Pine Key corroborated a peak in September with many fewer individuals in October. Both examinations point to a great deal of summer activity, peaking in September. The apparent unimodal trend in its seasonal movements differs from that of Dalrymple et al. (1991a) who found a single strong peak in May for the species generally on Long Pine Key. Juveniles were not identified.

Relationships between monthly movements by the Everglades Racer and environmental factors were evident during the combined period of 2009–2011 (**Table 7**). Collectively, monthly movements were most strongly related to average air temperature maxima and minima, and marginally so by rainfall volume (**Table 7**). A primarily terrestrial species, the Everglades Racer was unaffected in its movements by water table (**Table 7**).

Ambient temperatures associated with nightly activity- An ambient temperature of 27.0 °C was recorded for a 101.5 cm SVL male encountered on 15 September 2009. An ambient temperature of 26.0 °C was recorded for a 85.2 cm SVL female encountered on 15 July 2009.

Roadkill dynamics- Everglades Racers were killed by vehicles on the road. DOR Everglades Racers comprised 3.25% of all DOR snakes and 72.70% of all conspecifics recorded during 2009–2011. Individuals were killed throughout the year, most often being the only records of the snakes for the month's survey (**Figure 13a)**. No significant relationship (Multiple R = 0.35 = P = 0.25) was detected between monthly percent DORs and total number of individuals per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 84.1 $\pm$ 9.7 cm SVL; range = 75.0–101.5; n = 6) did not differ significantly than that of females (Mean = 91.3 $\pm$ 8.0 cm SVL; range = 85.0–104.5; n = 5) with respect to variance mean (F = 1.468, *P* = 0.37) or mean (t = -1.324, df = 9, *P* = 0.22). Male:female sexual size dimorphism of this sample was 0.92:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Mean body size of adult males (mean = 86.6 $\pm$ 8.8 cm SVL; range = 70.2–99.0; N = 15) did not differ significantly (F = 0.48, P = 0.09) from that of females (mean = 90.3 $\pm$ 12.7 cm SVL; range = 70.0–120.0; N = 15), and male:female sexual size dimorphism (1.00:1.00). Between samples, no significant differences existed in adult body sizes among males (F = 0.825, P = 0.36; t = 0.520, df = 19, P = 0.61) or females (F = 0.396, P = 0.19; t = 0.158, df = 18, P = 0.88) Combined, adult males averaged 85.7 cm SVL ($\pm$ 8.8 cm SVL), adult females averaged 90.5 cm SVL ($\pm$ 11.5 cm SVL), and sexual size dimorphism for the sample 0.95:1.00. In a monthly distribution of body sizes **(Figure 13b),** the smallest individual was 47.5 cm SVL and found in February. In southern Florida generally (Meshaka and Layne, 2015), YOY individuals were found during June–December.

Injury- From individuals encountered on the road during 2008–2011, a 98.0 cm SVL individual of undetermined sex was found to have an incomplete tail, comprising 3.13% of the sampled population.

Table 7. Relationship of environmental conditions to monthly movements of the Everglades Racer, *Coluber constrictor paludicola*, in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.66, *P* = 0.02
Mean monthly minimum air temperature	r = 0.67, *P* = 0.02
Total monthly rainfall volume	r = 0.52, *P* = 0.08
Mean monthly water level	r = 0.212, *P* = 0.51

Figure 10. An Everglades Racer, *Coluber constrictor paludicola*, from Everglades National Park. Photographed by M. Rochford.

Figure 11. Distribution of the Everglades Racer, *Coluber constrictor paludicola*, in Everglades National Park.

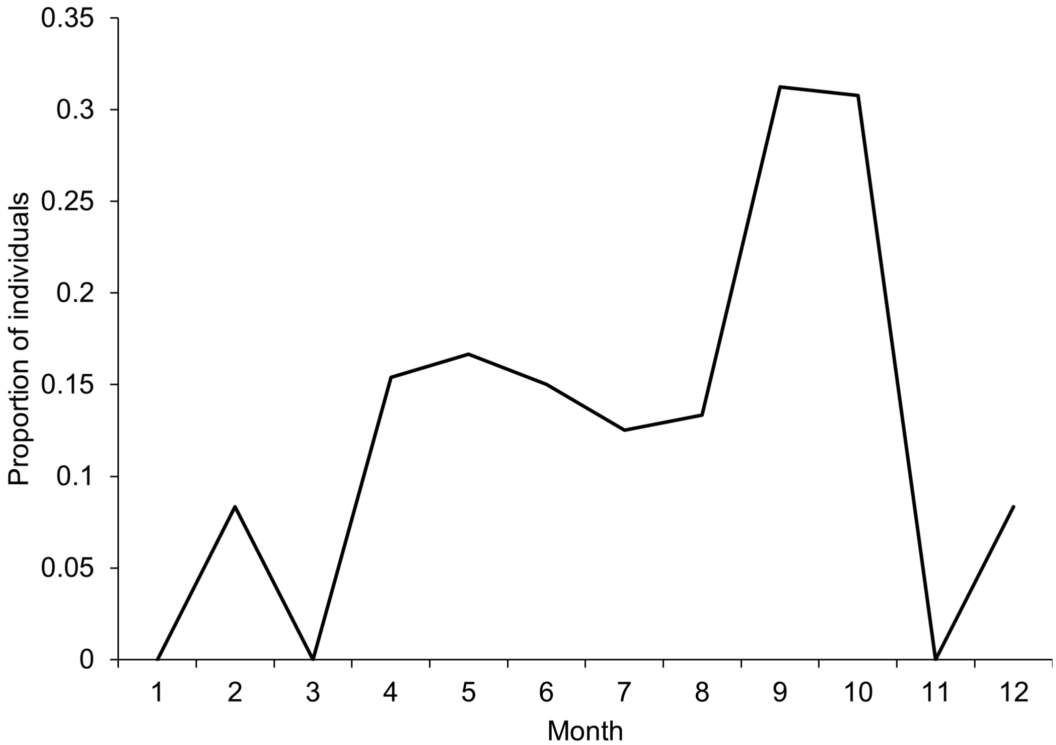

Figure 12. Monthly distribution of the Everglades Racer, *Coluber constrictor paludicola*, crossing roads in Everglades National Park during 2009–2011.

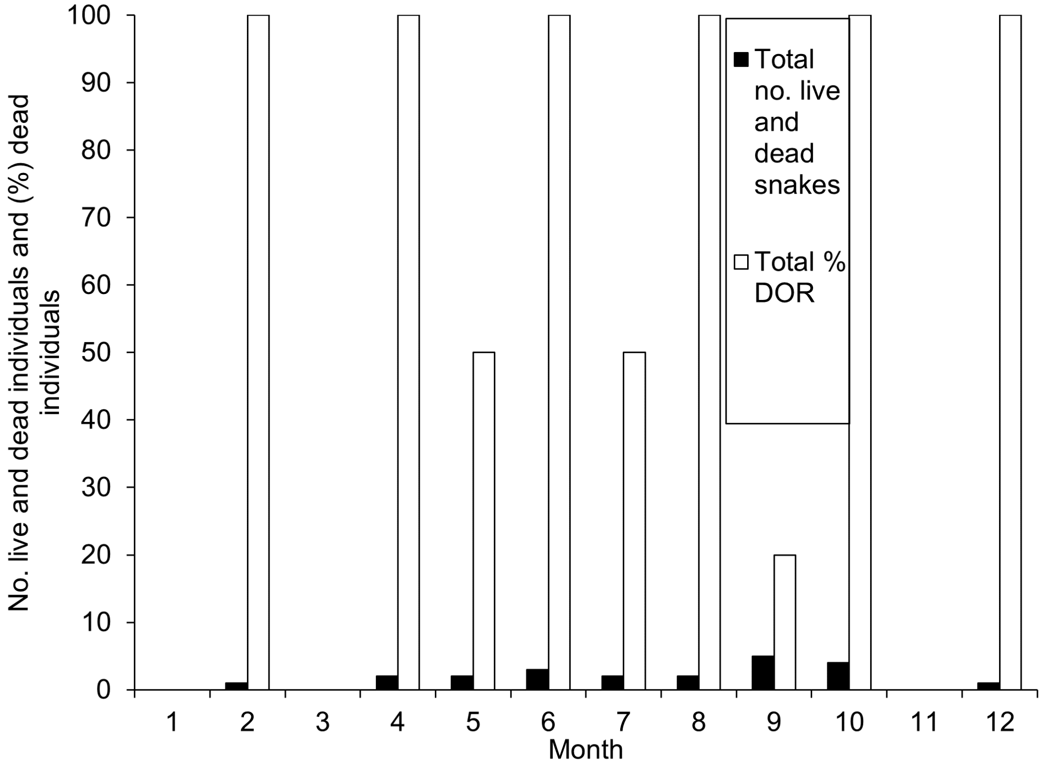

Figure 13a. Monthly distribution of all and percent dead individuals of the Everglades Racer, *Coluber constrictor paludicola*, on roads at night in Everglades National Park during 2009–2011.

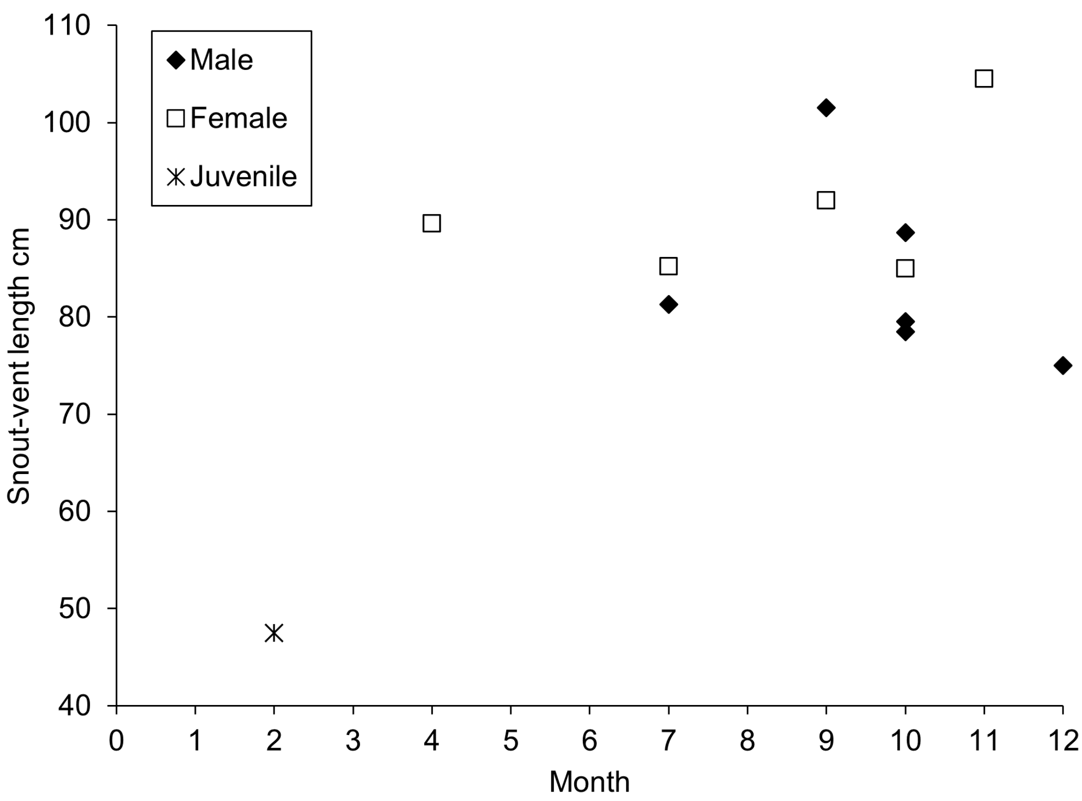

Figure 13b. Monthly distribution of body sizes of the Everglades Racer, *Coluber constrictor paludicola*, in Everglades National Park during 2008–2011.

Diadophis punctatus punctatus (Linnaeus, 1766)- Southern Ring-necked Snake (**Figure 14**).

Habitat association- the Southern Ring-necked Snake occurred in all three regions of Everglades National Park (**Table 4; Figure 15**). A minor component of any of the assemblages, it was most often seen on Long Pine Key but not significantly so. On Long Pine Key, this species was significantly less abundant (X^2 = 4.51, df = 1, P < 0.05) than it was during 1984–1986 (Dalrymple et al., 1991a) (**Table 4**). On Long Pine Key, this species was much less abundant during June–August at the time of our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, one male, four females, zero juveniles, and zero of unknown status comprised the five total Southern Ring-necked Snakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were zero males, one female, zero juveniles, and zero individuals of unknown status comprising a total of one individual.

The Southern Ring-necked Snake was uncommonly encountered during our study. The total number of sightings comprised 0.38% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 0.42% of all snakes seen during March–December of 2008–2011 (**Table 3**). Numbers of individuals differed significantly during 2009–2011 in association with a very low water table in 2011.

The male:female ratio among adult Southern Ring-necked Snakes was 0.25:1.00 during 2009–2011. Excluding individuals of unknown category, juveniles comprised 0.00% during 2009–2011. Likewise, recruitment was 0.00% when individuals of unknown category were included.

Monthly movements- The Southern Ring-necked Snake was encountered in April (n = 1), May (n = 2), June (n = 1), and August (n = 1) during 2009–2011. The single male was encountered in May. Consequently, we could not compare our findings with those of Dalrymple et al. (1991a) on Long Pine Key, where it was abundant.

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity ranged 25.0–30.0 °C. Ambient temperature associated with activity of a single male was 24.0 °C. Mean temperatures associated with female activity was 26.3 °C ($\pm$ 2.6 °C; range = 24.0–30.0; n = 4), Ambient temperatures for all five individuals averaged 25.8 °C ($\pm$ 2.5 °C; range = 24.0–30.0).

Roadkill dynamics- No DOR Southern Ring-necked Snakes were encountered during 2009–2011, thus comprised 0.00% of all DOR snakes and 0.00% of all conspecifics recorded during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size was available for one male, 16.2 cm SVL, and five females (Mean = 23.7 cm SVL $\pm$ 3.1 cm SVL; range = 20.4–28.0; n = 5). Male:female sexual size dimorphism of this sample was 0.68:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. From a small sample size, we combined samples from Meshaka and Layne (2015) with those of this study and calculated a mean value of adult body size from males (mean = 19.5 $\pm$ 3.0 cm SVL; range = 16.2–22.2; N = 4) and females (mean = 22.9 $\pm$ 2.7 cm SVL; range = 20.4–28.0; N = 8), which did not differ significantly from one another (F = 1.312, P = 0.34; t = 1.958, df = 10, P = 0.08). The male:female sexual size dimorphism ratio for this combined sample was 0.86:1.00.

Reproduction- A 23.9 cm SVL female was found to be gravid when caught on 16 June 2010.

Injury- From individuals encountered on the road during 2008–2011, a 20.4 cm SVL female captured on 29 April 2009 was found with an injured tail, comprising 16.67% of the sampled population.

Figure 14. A Southern Ring-necked Snake, *Diadophis punctatus punctatus*, Aerojet Road (just outside Everglades National Park near Coe Visitor Center at park entrance). Photographed by Jake Scott.

Figure 15. Distribution of the Southern Ring-necked Snake, *Diadophis punctatus punctatus*, in Everglades National Park.

Drymarchon couperi (Holbrook, 1842)- Eastern Indigo Snake (**Figure 16**).

Habitat association- The Eastern Indigo Snake was found only in the saline glades; however, this association was not significant (**Table 4; Figure 17**). A minor component of its assemblage, its encounter rate was among the lowest of that region. Its diurnal habits could in part explain overall low encounter rates.

Population structure- During the three full calendar years of 2009–2011, a single adult of unknown sex comprised the one total of Eastern Indigo Snakes, live and dead, encountered on the road at night (**Table 2**). No counterparts were recorded during March–December 2008 (**Table 3**) comprising a total of zero individuals. The Eastern Indigo Snake was one of the five fewest species encountered during our study. The total number of sightings comprised 0.08% of all snakes seen during January–December of 2009–2011. The distribution of this species did not differ significantly during 2009–2011.

Monthly movements- The Eastern Indigo Snake was encountered once during our study. A mostly skeletonized individual of unknown sex was found on 20 October 2010.

Roadkill dynamics- Eastern Indigo Snakes were killed by vehicles on the road. DOR Eastern Indigo Snakes comprised 0.20% of all DOR snakes and 100.00% of all conspecifics recorded during 2009–2011. The single Eastern Indigo Snake encountered was a mostly skeletonized adult of unknown sex found in October.

Adult body size and age at sexual maturity- the single adult female we found measured 185.6 cm TL.

Figure 16. An Eastern Indigo Snake, *Drymarchon couperi*, from Highlands County, Florida. Photographed by M. Rochford.

Figure 17. The Distribution of the Eastern Indigo Snake, *Drymarchon couperi*, in Everglades National Park.

Figure 18. An Eastern Mudsnake, *Farancia abacura abacura*, from Everglades National Park. (A) Photographed by M. Rochford. (B) Photographed by Arik Hartmann.

Farancia abacura abacura (Holbrook, 1836)-Eastern Mudsnake. (**Figure 18**).

Habitat association- The Eastern Mudsnake occurred in all three regions of Everglades National Park where its otherwise low compositions were highest in the saline glades but not significantly so (**Table 4; Figure 19**). On Long Pine Key, this species was much more abundant during June–August during our study than it was in the 1980s Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, one male, two females, two juveniles, and zero individuals of unknown status comprised the five total Eastern Mudsnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were one male, zero females, zero juveniles, and zero individuals of unknown status comprising a total of one individual.

The Eastern Mudsnake was uncommonly encountered during our study. The total number of sightings comprised 0.31% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 0.35% of all snakes seen during March–December of 2008–2011 (**Table 3**). Stable in assemblage composition among sampling periods, the Eastern Mudsnake did not differ significantly during 2009–2011. The male:female ratio among adults was 0.50:1.00 during 2009–2011. Excluding individuals of unknown category, juveniles comprised 40.00% of observations during 2009–2011.

Monthly movements- The Eastern Mudsnake was represented by one male in April, a female in August, and a juvenile each in April and September.

Ambient temperatures associated with nightly activity- Ambient temperatures associated with activity of the Eastern Mudsnake ranged 21.2–29.0 °C. Associated temperatures for all four individuals combined averaged 25.0 °C ($\pm$ 3.5 °C; range = 21.2–29.0).

Roadkill dynamics- The Eastern Mudsnake was not encountered as DORs during 2009–2011. Consequently, DORs comprised 0.00% of all snakes encountered and of conspecifics.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size measurements were available for two males (67.8 and 90.3 cm SVL) and one female (109.2 cm SVL). Male:female sexual size dimorphism of this sample was 0.72:1.00. From a small sample size, we combined samples from Meshaka and Layne (2015) with those of this study and calculated a mean value of adult body size from males (mean = 84.0 $\pm$ 13.4 cm SVL; range = 67.8–106.0; N = 8) and females (mean = 119.1 $\pm$ 14.0 cm SVL; range = 109.2–129.0; N = 2). The male:female sexual size dimorphism ratio for this combined sample was 0.71:1.00. The smallest individuals encountered were two juveniles, 21.6 cm SVL in September and 28.7 cm SVL in April.

Figure 19. Distribution of the Eastern Mudsnake, *Farancia abacura abacura*, in Everglades National Park.

Lampropeltis elapsoides (Holbrook, 1838)- Scarlet Kingsnake (**Figure 20**).

Habitat association- The Scarlet Kingsnake occurred only in the saline glades (**Table 4; Figure 21)** where it comprised a small portion of the snake assemblage. Its presence, however, was nonrandom among the three regions.

Population structure- During the three full calendar years of 2009–2011, zero males, one female, zero juveniles, and zero individuals of unknown status comprised the one total Scarlet Kingsnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were zero males, one female, zero juveniles, and zero individuals of unknown status comprising a total of one individual.

The Scarlet Kingsnake was one of the five fewest species encountered during our study. The total number of sightings comprised 0.08% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 0.14% of all snakes seen during March–December of 2008–2011 (**Table 3**). The distribution of this species did not differ significantly during 2009–2011.

Monthly movements- The Scarlet Kingsnake was encountered once during 2009–2011. A live adult female was found on 13 August 2009.

Roadkill dynamics- **The** Scarlet Kingsnake comprised 0.00% of all DOR snakes and 0.00% of all conspecifics recorded during 2009–2011.

Ambient temperatures associated with nightly activity- Ambient temperature associated with the activity of an adult female encountered on 20 April 2011 was 24.1 °C.

Adult body size and age at sexual maturity-, Two adult females, 43.2 and 36.0 cm SVL were encountered on the road during 2008–2011.

Reproduction- A gravid 36 cm SVL individual was encountered on 27 August 2008.

Figure 20. A Scarlet Kingsnake, *Lampropeltis elapsoides*, St. George Island, Franklin County, Florida. Photographed by M. Rochford.

Figure 21. Distribution of the Scarlet Kingsnake, *Lampropeltis elapsoides*, in Everglades National Park.

Lampropeltis getula floridana Blanchard, 1919- Florida Kingsnake and intergrades of ***L. g. floridana*** X ***L. g. getula*** (Linnaeus, 1766)- Eastern Kingsnake (**Figure 22**).

Habitat association- This snake was a minor component of Long Pine Key and Pahayokee, the only regions in which it was seen (**Table 4; Figure 23**). Its encounter rate was likewise low at both regions, the higher of which was Pahayokee, but not significantly so.

Population structure- During the three full calendar years of 2009–2011, zero males, zero females, one Juvenile, and zero individuals of unknown status comprised the one total Florida Kingsnake and its intergrades, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were two males, zero females, one juvenile, and zero individuals of unknown status comprising a total of three individuals.

The Florida Kingsnake and its intergrades were one of the five fewest species encountered during our study. The total number of sightings comprised 0.08% of all snakes seen during January–December of 2009–2011 **(Table 1)** and 0.21% of all snakes seen during March–December of 2008–2011 **(Table 2)**. Uncommon and variably present between sampling periods, it was stable in assemblage composition among sampling periods, not having differed significantly during 2009–2011 (Chi Square = $X^2 = 2.00$, df = 2, $p > 0.05$) or during 2008–2011 (Chi Square = $X^2 = 9.00$, df = 3, $p > 0.05$).

The male:female ratio among adult Florida Kingsnakes and intergrades during 2009–2011 could not be calculated as all captures were of juveniles. Excluding individuals of unknown category, juveniles comprised 100.00% of observations during 2009–2011. When individuals of unknown category were included, percentage of young was 100.00% in 2009–2011.

Monthly movements- The Florida Kingsnake and its intergrades were represented by one juvenile on 24 February 2011 during 2009–2011.

Roadkill dynamics- Florida Kingsnakes and intergrades comprised 0.20% of all DOR snakes and 100.00% (n = 1) of all conspecifics recorded during 2009–2011.

Ambient temperatures associated with nightly activity- Ambient temperature associated with activity of a single juvenile encountered on 24 February 2011 was 19.5 °C.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of two males were 98.0 and 88.7 cm SVL. Juveniles were encountered in February 2011 (48.6 cm SVL) and October 2008 (41.3 cm SVL).

Figure 22. (A) A Florida Kingsnake, *Lampropeltis getula floridana*, X Eastern Kingsnake, *L. g. getula,* from Bird Drive Basin (near Krome Avenue and US-41). Photographed by M. Rochford. (B) An adult on the road and (C) a juvenile in Everglades National Park. (B, C) Photographed by Arik Hartmann. Note variation between adults of this intergrade.

Figure 23. Distribution of the Florida Kingsnake, *Lampropeltis getula floridana*, X Eastern Kingsnake, *L. g. getula,* in Everglades National Park.

Liodytes alleni (Garman, 1874)- Striped Swampsnake (**Figure 24**).

Habitat association- The Striped Swampsnake occurred on Long Pine Key and at Pahayokee as a small component of the respective regions (**Table 4; Figure 25**). The encounter rates of this highly aquatic species differed significantly among the sites (X^2 = 12.89, df = 2, *P* < 0.01). On Long Pine Key, this species was much more abundant during June–August at the time of our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, five males, 11 females, zero juveniles, and one individual of unknown status comprised the 17 total Striped Swampsnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were one male, two females, zero juveniles, and zero individuals of unknown status comprising a total of three individuals.

The Striped Swampsnake was uncommonly encountered during our study. The total number of sightings comprised 1.30% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 1.33% of all snakes seen during March–December of 2008–2011 (**Table 3**). Stable in assemblage composition among sampling periods, the Striped Swampsnake did not differ significantly during 2009–2011. The male:female ratio among adult Striped Swampsnakes was 0.46:1.00 during 2009–2011. Adults comprised all actively moving individuals. This was true when excluded or included individuals of unknown category.

Monthly movements- The Striped Swampsnake was encountered in months exclusive of February, June, and December (**Figure 25**). Collectively, activity was bimodal in seasonal distribution, peaking in April and during October–November (**Figure 25)**. The few males encountered were seen in April and October, and the bimodal peak in seasonal activity of females was April and November (**Figure 25**). Juveniles were absent from our surveys (**Figure 25**). No significant relationships existed between monthly movements by the Striped Swampsnake and environmental factors (**Table 8**). On Long Pine Key, this species was much more abundant during June–August during our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with the Striped Swampsnake ranged 25.0–29.0 °C (**Figure 26**). Ambient temperatures were available for two males (25.0, 26.0 °C) and six females (mean = 26.2 ± 2.5 °C; range =23.0–29.0). Ambient temperatures for all eight individuals combined averaged 26.0 °C (± 2.1 °C; range = 23.0–29.0).

Roadkill dynamics- Striped Swampsnakes were killed by vehicles on the road. DOR Striped Swampsnakes comprised 1.83% of all DOR snakes and 52.94% of all conspecifics recorded during 2009–2011. Striped Swampsnakes were killed primarily during winter–spring (**Figure 27**). No significant relationship (Multiple R = 0.45, P = 0.14) existed between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 37.3 ± 0.8 cm SVL; range = 35.9–38.2; n = 5) differed significantly than that of females (Mean = 39.9 ± 5.6 cm SVL; range = 32.0–50.3; n = 13) with respect to variance (F = 0.022, *P* = 0.0003) but not mean (t = -1.650, df = 13, P = 0.13). Male:female sexual size dimorphism of this sample was 0.94:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. One male (35.3 cm SVL) and 14 females (mean = 41.8 ± 6.2 cm SVL; range = 30.4–51.3) were available. Male:female sexual size dimorphism of this sample was 0.85:1.00. No significant difference in body sizes (F = 1.223, P = 0.37; t = 0.837, df = 25, P = 0.41) was detected between females of the two samples. Combining the samples provided averages for males (mean = 37.0 ± 1.1 cm SVL; range = 35.3–38.2; N = 7) and females (mean = 40.9 ± 5.9 cm SVL; range = 30.4–51.3; N = 27), which differed significantly from one another (F = 0.033, P = 0.0002; t = -3.240, df = 31, P = 0.003). Male:female sexual size dimorphism of this combined sample was 0.91:1.00.

Reproduction- A gravid 48.6 cm SVL female was encountered on 18 August 2010. A subset of data from Meshaka and Layne (2015) provided clutch sizes based on enlarged follicles from three females in May (40.2 cm SVL females with 20 young), August (49.8 cm SVL females with 28 young), and September (32.6 cm SVL female with 23 young) for Everglades National Park.

Injury- Water blisters were evident on a 36.8 cm SVL male captured on 20 April 2009. A 35.9 cm SVL male was found with a bobbed tail. Consequently, 20.00% males and 5.00% of the sample were missing a portion of their tail.

Table 8. Relationship of environmental conditions to monthly movements of the Striped Swampsnake, *Liodytes alleni*, in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.04, P = 0.90
Mean monthly minimum air temperature	r = 0.04, P = 0.90
Total monthly rainfall volume	r = 0.36, P = 0.25
Mean monthly water level	r = 0.06, P = 0.87

Figure 24. A Striped Swampsnake, *Liodytes alleni*, on the road in Everglades National Park. (A) Photographed by M. Rochford. (B) Photographed by Arik Hartmann.

Figure 25. The distribution of the Striped Swampsnake, *Liodytes alleni*, in Everglades National Park.

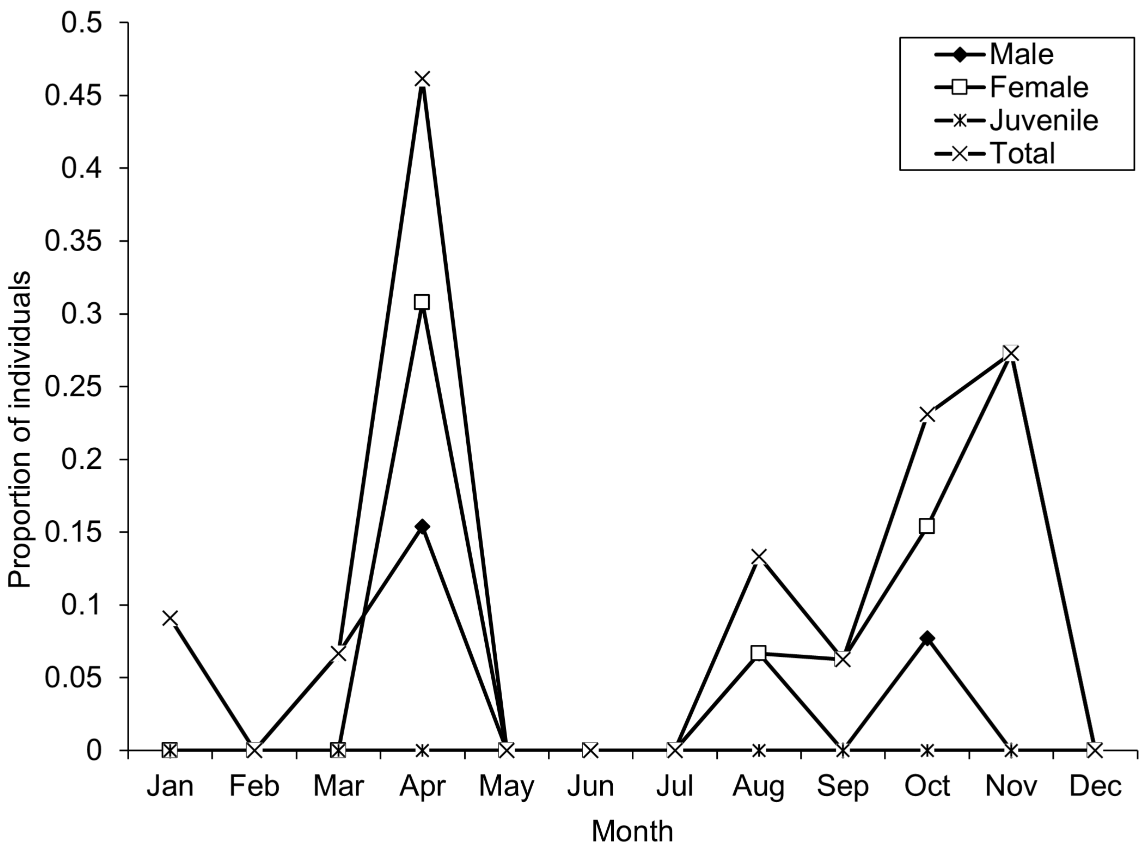

Figure 26. Monthly distribution of the Striped Swampsnake, *Liodytes alleni*, crossing roads in Everglades National Park during 2009–2011.

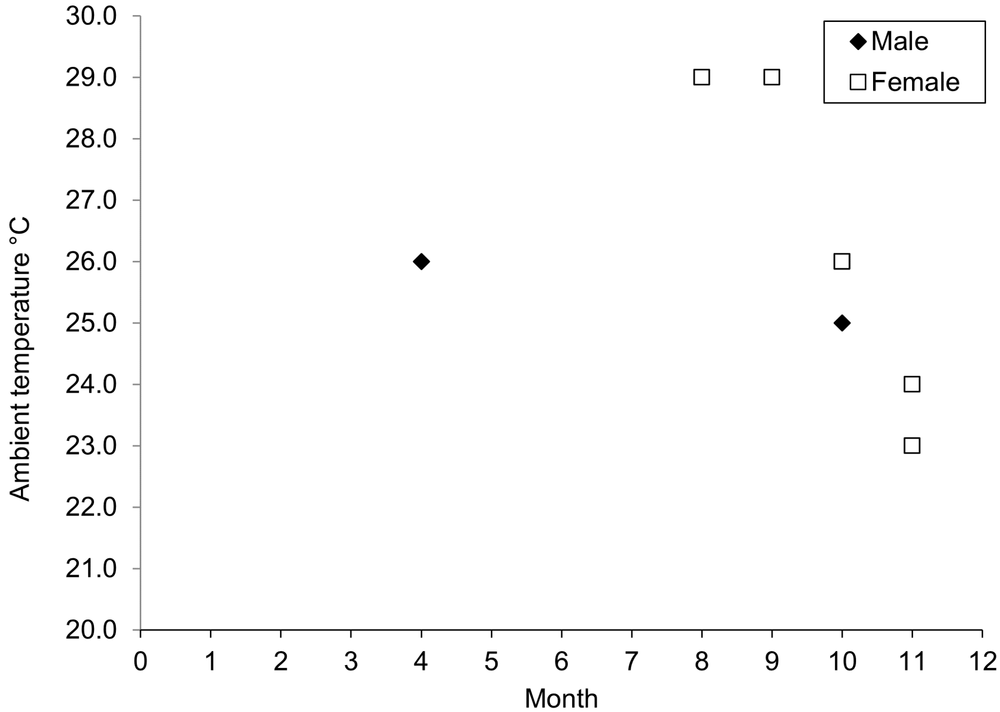

Figure 27. Ambient temperatures associated with the Striped Swampsnake, *Liodytes alleni*, crossing roads at night in Everglades National Park during 2009–2011.

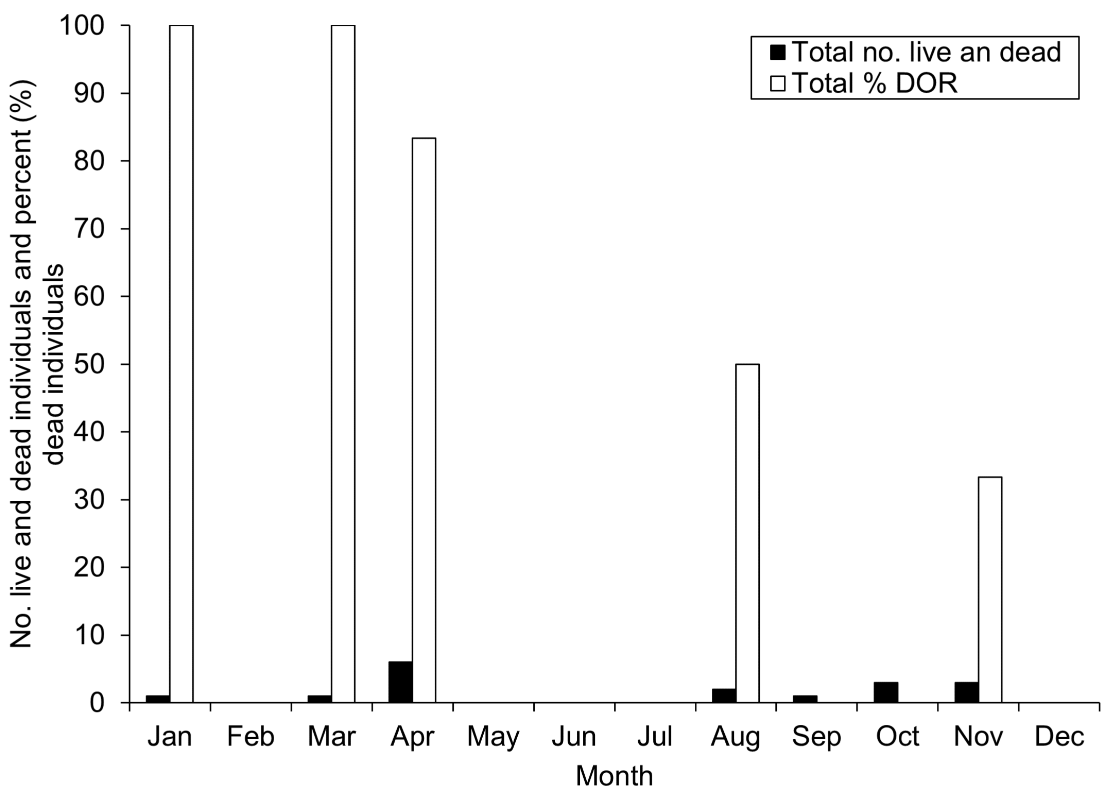

Figure 28. Monthly distribution of all and percent dead individuals of the Striped Swampsnake, *Liodytes alleni*, on roads at night in Everglades National Park during 2009–2011.

Liodytes pygaea cyclas Dowling, 1950- Southern Florida Swampsnake (**Figure 29**).

Habitat association- The Southern Florida Swampsnake was detected only at Pahayokee, where it was an uncommon snake of the assemblage (**Table 4; Figure 30)**.

Population structure- During the three full calendar years of 2009–2011, a single female comprised the total Southern Florida Swampsnakes, live and dead, encountered on the road at night. No counterparts were encountered during March–December 2008. The Southern Florida Swampsnake was one of the three fewest species encountered during our study. The total number of sightings comprised 0.08% of all snakes seen during January–December of 2009–2011 **(Table 2)** and 0.07% of all snakes seen during March–December of 2008–2011 **(Table 3)**. The distribution of this species did not differ significantly during 2009–2011 (Chi Square = X^2 = 2.00, df = 2, $P > 0.05$) or during 2008–2011 (Chi Square = X^2 = 3.00, df = 3, $p > 0.05$).

Monthly movements- The Southern Florida Swampsnake was encountered once during our study. A live adult female was found on 13 August 2009.

Ambient temperatures associated with nightly activity- Ambient temperature associated with activity of a single adult gravid female was 26.0 °C.

Adult body size and age at sexual maturity- the single adult female we found measured 25.3 cm SVL._

Reproduction- A gravid female that measured 25.3 cm SVL and weighed 26 g was captured alive on 13 August 2009.

Figure 29. A Southern Florida Swampsnake, *Liodytes pygaea cyclas,* from Everglades National Park. Photographed by M. Rochford.

Figure 30. Distribution of the Southern Florida Swampsnake, *Liodytes pygaea cyclas,* in Everglades National Park.

Nerodia clarkii compressicauda Kennicott, 1860- Mangrove Saltmarsh Watersnake X ***N. fasciata pictiventris*** (Cope, 1895)- Florida Watersnake hybrid. (**Figure 31**).

Mangrove-Florida Watersnake hybrid

Habitat association- This snake was absent from Long Pine Key, present in Pahayokee, and most numerous in the saline glades (X^2 = 191.02, df = 2, $P < 0.001$) where it was the dominant form (**Table 4; Figure 32**. In turn, it was replaced in Pahayokee by larger numbers of the Florida Watersnake.

Population structure- During the three full calendar years of 2009–2011, 16 males, 33 females, eight Juveniles, and 12 individuals of unknown status comprised the 69 total Mangrove-Florida Watersnake hybrids, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were seven males, eight females, three juveniles, and four individuals of unknown status comprising a total of 22 individuals.

The Mangrove-Florida Watersnake hybrid was the second most commonly encountered watersnake during our study. The total number of sightings comprised 5.26% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 6.18% of all snakes seen during March–December of 2008–2011 (**Table 3**). Numbers of individuals differed significantly during 2009–2011 in association with a very low water table in 2011.

The male:female ratio among adult Mangrove-Florida Watersnake hybrids was 0.49:1.00 during 2009–2011. Sex ratios were even in each of the years of this study: 0.47:1.00 in 2009, 0.56:1.00 in 2010. Only two females were captured in 2011. Adults comprised the majority of actively moving individuals. Excluding individuals of unknown category, juveniles comprised 14.04% of observations during 2009–2011. Recruitment was at 18.52% in 2009, 10.71% in 2010, and 0.00% in 2011. When individuals of unknown category were included, respective percentages of young were lower: 11.59% in 2009–2011, 16.13% in 2009, 8.57% in 2010, and 0.00% in 2011.

Monthly movements- The Mangrove-Florida Watersnake hybrid was active year-round in Everglades National Park. Collectively, it was most active in June and November (**Figure 5**). Males were most active during June-July and in November (**Figure 33**). Females were most active in June and September. (**Figure 33**). Juveniles may have had a bimodal pattern to seasonal movements with peaks in June and October (**Figure 30**).

Relationships between monthly movements by the Mangrove-Florida Watersnake hybrid and environmental factors were not significant (**Table 9**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Mangrove-Florida Watersnake hybrid ranged 25.0–29.0 °C (**Figure 34**). Mean temperatures did not significantly differ among males (25.4 $\pm$ 1.9 °C; range =22.0–28.0; n = 9), females (25.6 $\pm$ 1.6°C; range = 22.0–29.0; n = 22), and juveniles (25.4 $\pm$ 1.8 °C; range = 24.0–29.0; n = 7) (one-way ANOVA; F = 0.045, *P* = 0.96). Ambient temperatures associated with activity for all 38 snakes combined averaged 25.5 °C ($\pm$ 1.7 °C; range = 22.0–29.0; n = 38).

Roadkill dynamics- Mangrove-Florida Watersnake hybrids were killed by vehicles on the road. DOR Mangrove-Florida Watersnake hybrids comprised 4.68% of all DOR snakes and 33.33% of all conspecifics recorded during 2009–2011. Mangrove-Florida Watersnake hybrids were killed throughout the year, with peak incidences of DOR individuals at the beginning and end of the wet season (**Figure 35**). No significant relationship (Multiple R = 0.17, *P* = 0.59) existed between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 43.5 $\pm$ 5.5 cm SVL; range = 33.5–55.3; n = 23) differed significantly than that of females (Mean = 53.3 $\pm$ 7.8 cm SVL; range = 41.5–73.8; n = 41) with respect to variance (F = 0.4950, df = 22, p = 0.04) and mean (t = -5.885, df = 59, p < 0.000). Male:female sexual size dimorphism of this sample was 0.82:1.00. In Everglades National Park, mean adult body sizes were similar between males (mean = 42.8 cm SVL) and females (mean = 48.2 cm SVL) (Mealey et al., 2005). Body sizes of two males (44, 47 cm SVL) and a mean body size of females (mean = 51.3 cm SVL) are also available from Everglades National Park (Meshaka and Layne, 2015). Respective sexual size dimorphism values were both 0.89:1.00. The smallest individuals in our sample, 21.3 and 22.2 cm SVL were encountered in June **(Figure 36)**. The monthly distribution of body sizes indicates that sexual maturity may have been reached before one year of life **(Figure 36**).

Reproduction- A gravid female (48.7 cm SVL) was encountered on 19 September 2008, and another gravid female (52.4 cm SVL) was encountered on 21 May 2010. In Everglades National Park, a very gravid female was encountered in July (Meshaka and Layne, 2015).

Injury- A 64.2 cm SVL female appeared to have been thin. The smaller of the two gravid females had a kinked tail, and the larger counterpart was found with a bobbed tail. A male (33.5 cm SVL) and two females (44.6, 58.0 cm SVL) were found with bobbed tails. Consequently, bobbed tails occurred in 4.35% of males, 4.88% of females, and 4.40% of the population. However, bobbed tails occurred 3.30% of all individuals.

Miscellany- One male (39.0 cm SVL) and four females 47.9, 52.1, 54.7, 60.5 cm SVL) were of the red morph. Consequently, this morph occurred in 4.35% of males, 9.76% of females, and 5.50% of the population. However, the red morph occurred in 7.81% of adults.

Table 9. Relationship of environmental conditions to monthly movements of the Mangrove-Florida Watersnake hybrid, *Nerodia clarkii compressicauda* X *N. fasciata pictiventris,* in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.29, *P* = 0.36
Mean monthly minimum air temperature	r = 0.31, *P* = 0.33
Total monthly rainfall volume	r = 0.14, *P* = 0.66
Mean monthly water level	r = 0.16, *P* = 0.62

Figure 31. Two phases (A, B) of the Mangrove Saltmarsh Snake, *Nerodia clarkii compressicauda*, a species known to hybridize extensively with the Florida Watersnake, *N. fasciata pictiventris*, from Everglades National Park. Photographed by Arik Hartmann.

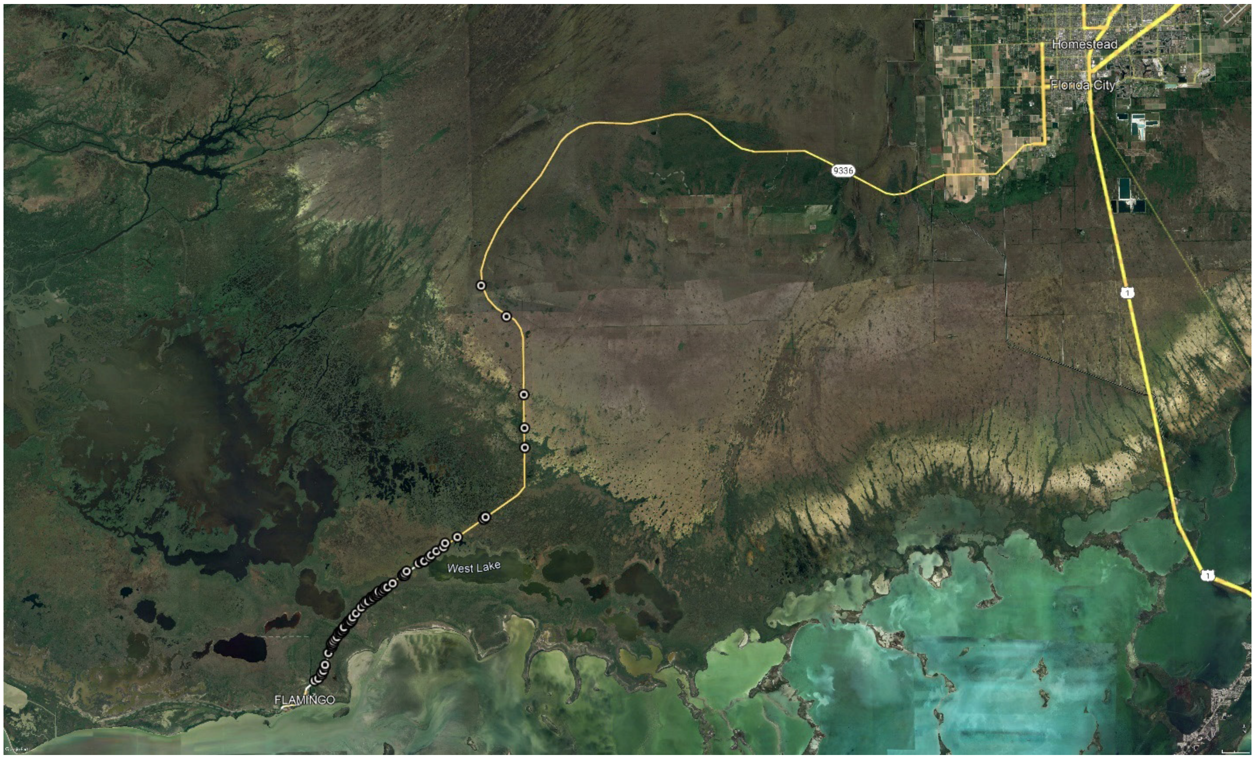

Figure 32. Distribution of the Mangrove-Florida Watersnake hybrid, *Nerodia clarkii compressicauda* X *N. fasciata pictiventris*, in Everglades National Park.

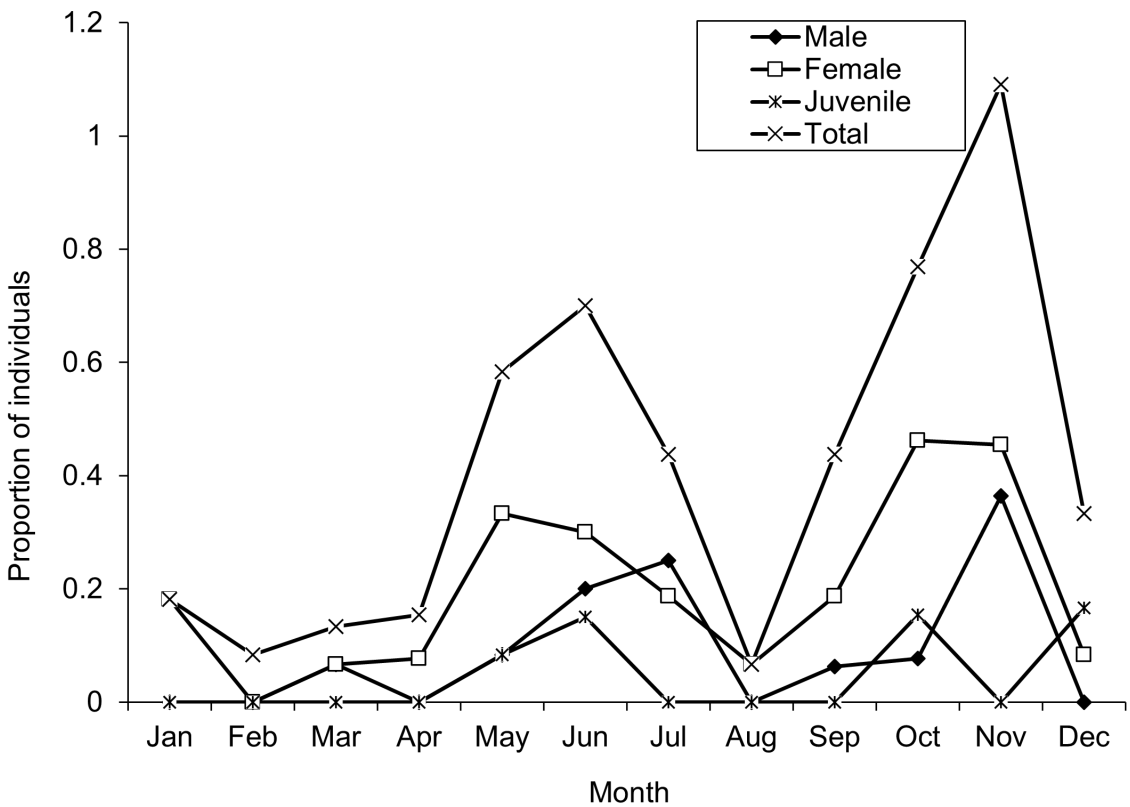

Figure 33. Monthly distribution of the Mangrove-Florida Watersnake hybrid, *Nerodia clarkii compressicauda* X *N. fasciata pictiventris*, crossing roads in Everglades National Park during 2009–2011.

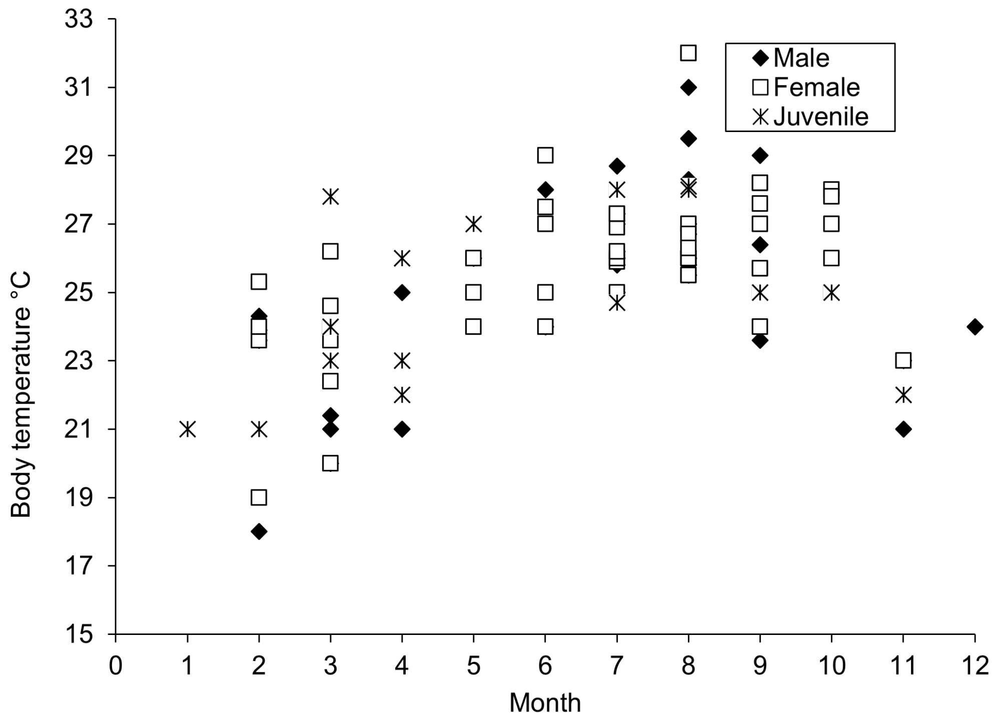

Figure 34. Ambient temperatures associated with the Mangrove-Florida Watersnake hybrid, *Nerodia clarkii compressicauda* X *N. fasciata pictiventris*, crossing roads at night in Everglades National Park during 2009–2011.

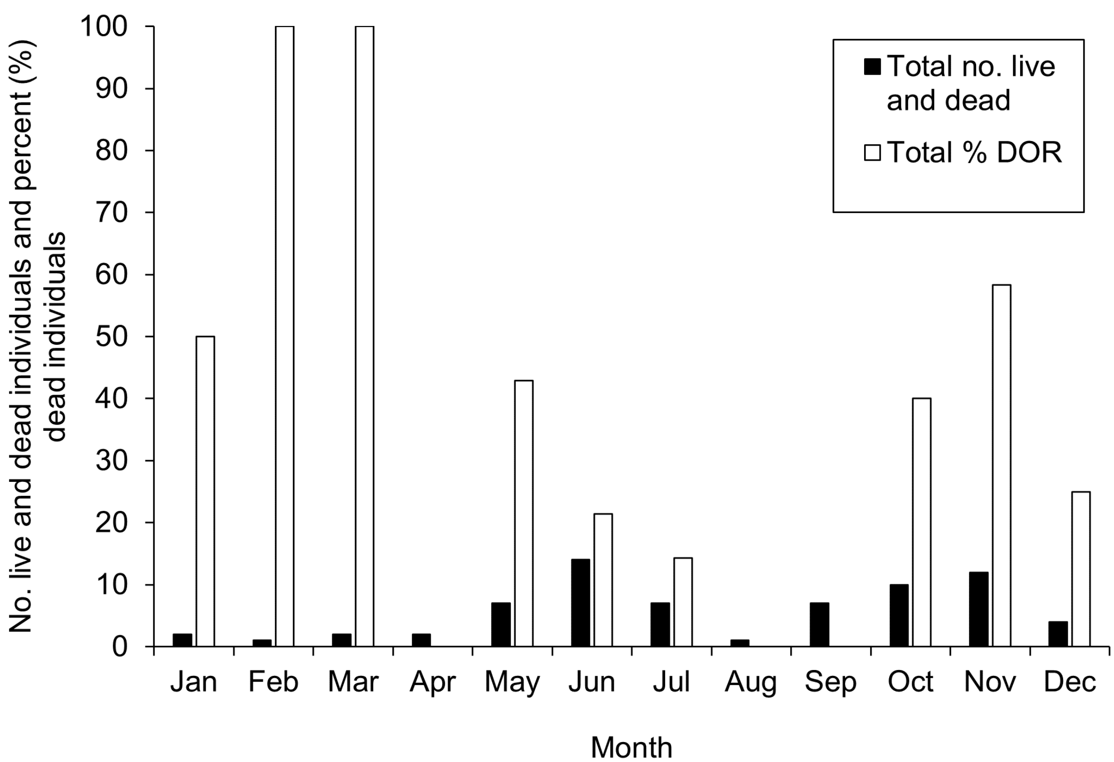

Figure 35. Monthly distribution of all and percent dead individuals of the Mangrove-Florida Watersnake hybrid, *Nerodia clarkii compressicauda* X *N. fasciata pictiventris*, on roads at night in Everglades National Park during 2009–2011.

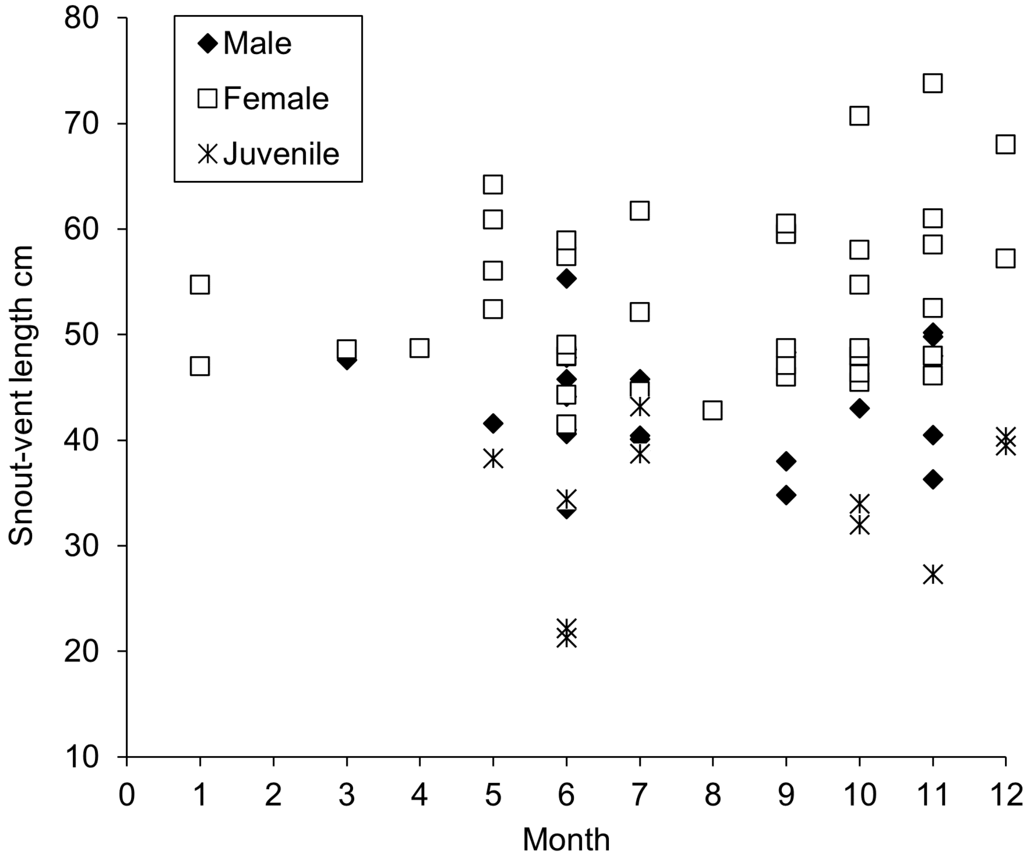

Figure 36. Monthly distribution of body sizes of the Mangrove-Florida Watersnake hybrid, *Nerodia clarkii compressicauda* X *N. fasciata pictiventris*, from Everglades National Park during 2008–2011.

Nerodia fasciata pictiventris (Cope, 1895)- Florida Watersnake. (**Figure 37**).

Habitat association- The Florida Watersnake occurred in all three regions of Everglades National Park but was the most abundant in Pahayokee (X^2 = 148.46, df = 2, P < 0.001), where it was the dominant species of that assemblage (**Table 4; Figure 38**). Its encounter rate corroborated its preference for the freshwater marsh of Pahayokee, south of which it extensively hybridized with the Mangrove Saltmarsh Watersnake. On Long Pine Key, this species was much more abundant during June–August at the time of our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, 75 males, 89 females, 26 juveniles, and 30 individuals of unknown status comprised the 220 total Florida Watersnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were eight males, 17 females, one juvenile, and four individuals of unknown status comprising a total of 30 individuals.

The Florida Watersnake was the most commonly encountered watersnake during our study. The total number of sightings comprised 16.78% of all snakes seen during January–December of 2009–2011(**Table 2**) and 14.75% of all snakes seen during March–December of 2008–2011 (**Table 3**). Encounter rates were higher in 2009 and 2011 than in 2010; however, its lowest encounter rate was during a non-drought year.

The male:female ratio among adult Florida Watersnakes was 0.84:1.00 during 2009–2011. Sex ratios varied among years of this study with the fewest males encountered in 2011:1.06:1.00 in 2009, 0.88:1.00 in 2010, and 0.52:1.00 in 2011. Adults, although evenly distributed between the sexes, generally comprised one-half of actively moving individuals. Recruitment was lowest in 2011. Excluding individuals of unknown category, juveniles comprised 13.68% of observations during 2009–2011. Recruitment was at 18.52% in 2009, 10.45% in 2010, and 9.52% in 2011. When individuals of unknown category were included, respective percentages of young were variable: 11.82% in 2009–2011, 15.96% in 2009, 9.33% in 2010, and 7.84% in 2011.

Monthly movements- The Florida Watersnake was active year-round in Everglades National Park. Collectively, this species was most active during February–March, July–August, and a possible third lesser peak in November (**Figure 39**). Monthly activity of males mirrored that of the species generally (**Figure 39**). Female activity was bimodal: February–March and again in August-October. (**Figure 39**). Monthly numbers of juveniles were stable, with the possible exception of a February–March peak in encounters (**Figure 39**). Relationships between monthly movements by the Florida Watersnake and environmental factors were not significant (**Table 10**). On Long Pine Key, this species was much more abundant during June–August during our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Florida Watersnake ranged 20.0–30.0 °C (**Figure 40**). Mean temperatures did not significantly differ among males (25.2 $\pm$ 2.8 °C; range = 18.0–31.0; n = 44), females (25.8 $\pm$ 2.3 °C; range = 19.0–32.0; n = 52), and juveniles (24.7 $\pm$ 2.6 °C; range = 21.0–28.1; n = 16) (one way ANOVA; F = 1.399, df = 2, P = 0.25). Ambient temperatures associated with all 112 individuals combined averaged 25.4 °C ($\pm$ 2.6 °C; range = 18.0–32.0; n = 112).

Roadkill dynamics- Florida Watersnakes were killed by vehicles on the road. DOR Florida Watersnakes comprised 19.11% of all DOR snakes and 42.73% of all conspecifics recorded during 2009–2011. Florida Watersnakes were killed throughout the year, with the highest incidence of DOR individuals during November– April (**Figure 41**). No significant relationship (Multiple R = 0.14, P = 0.65) existed between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 44.9 $\pm$ 5.0 cm SVL; range = 34.7–54.2; n = 83) differed significantly than that of females (Mean = 57.4 $\pm$ 10.0 cm SVL; range = 41.6–81.4; n = 106) with respect to variance (F = 0.250, P < 0.000) and mean (t = -11.247, df = 162, P < 0.000). Male:female sexual size dimorphism of this sample was 0.78:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Adult body sizes of males (Mean = 46.2 $\pm$ 5.9 cm SVL; range = 33.7–57.8; n = 45) and females (Mean = 58.0 $\pm$ 9.0 cm SVL; range = 41.1–81.8; n = 47) differed significantly (F = 0.439, P = 0.004; t = -7.390, df = 80, P < 0.0000) from one another. Male:female sexual size dimorphism of this sample was 0.78:1.00. A comparison of body sizes between the samples of this study and from Meshaka and Layne (2015) revealed no significant differences in either males (F = 0.686, P = 0.07; t = -1.325, df = 126, P = 0.19) or females (F = 1.202, P = 0.25; t = -3.778, df = 151, P = 0.71). The combined sample resulted in significant differences (F = 0.309, P < 0.0000; t = 13.364, df = 245, P < 0.0000) between males (Mean = 45.4 $\pm$ 5.4 cm SVL; range = 33.7–57.8; n = 128) and females (Mean = 57.6 $\pm$ 9.7 cm SVL; range = 41.1–81.8; n = 153). The sexual size dimorphism the combined sample was 0.79:100.

Florida Watersnakes grew quickly in Everglades National Park. The smallest individual measured 25.2 cm SVL when captured in April **(Figure 41)**. Presumed growth trajectories from the monthly distribution of body sizes (**Figure 41**) suggests that both sexes were sexually mature by one year of age.

Reproduction- A gravid 75.2 cm SVL female was encountered on 27 August 2008. A spent 63.7 cm SVL female was encountered on 13 August 2009. From a subset of data of Meshaka and Layne (2015), clutch sizes were available from four females in Everglades National Park (Mean = 17.3 $\pm$ 4.0 young; range = 11–22).

Injury- A male (43.5 cm SVL) and female (57.7 cm SVL) each had an injured eye. A 60.7 cm SVL female was found to have a scar along her dorsum, and a 37.0 cm SVL juvenile female was found alive with a fresh slice wound on its neck. An adult of undetermined SVL was found to have an injury near its vent.

Five males (35.0, 38.3, 45.5, 46.8, 51.0 cm SVL), four females (51.6, 64.6, 65.4, 79.4 cm SVL), and one juvenile (37.2 cm SVL) were found to have bobbed tails. Consequently, bobbed tails occurred in 6.02% of males, 3.80% of females, 3.70% of juveniles, and 4.90% of the population.

Miscellany- A 42.1 cm SVL female encountered on 9 March 2011 had retained an eye scale on her left eye from past ecdysis. A 44.0 cm SVL female, upon capture by its tail, spun vigorously and detached its tail.

Figure 37. A Florida Watersnake, *Nerodia fasciata pictiventris*, from Everglades National Park. (A) Photographed by M. Rochford. (B) A juvenile from Everglades National Park. Photographed by Arik Hartmann.

Table 10. Relationship of environmental conditions to monthly movements of the Florida Watersnake, *Nerodia fasciata pictiventris*, in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.07, P = 0.83
Mean monthly minimum air temperature	r = 0.07, P = 0.84
Total monthly rainfall volume	r = 0.12, P = 0.71
Mean monthly water level	r = 0.28, P = 0.39

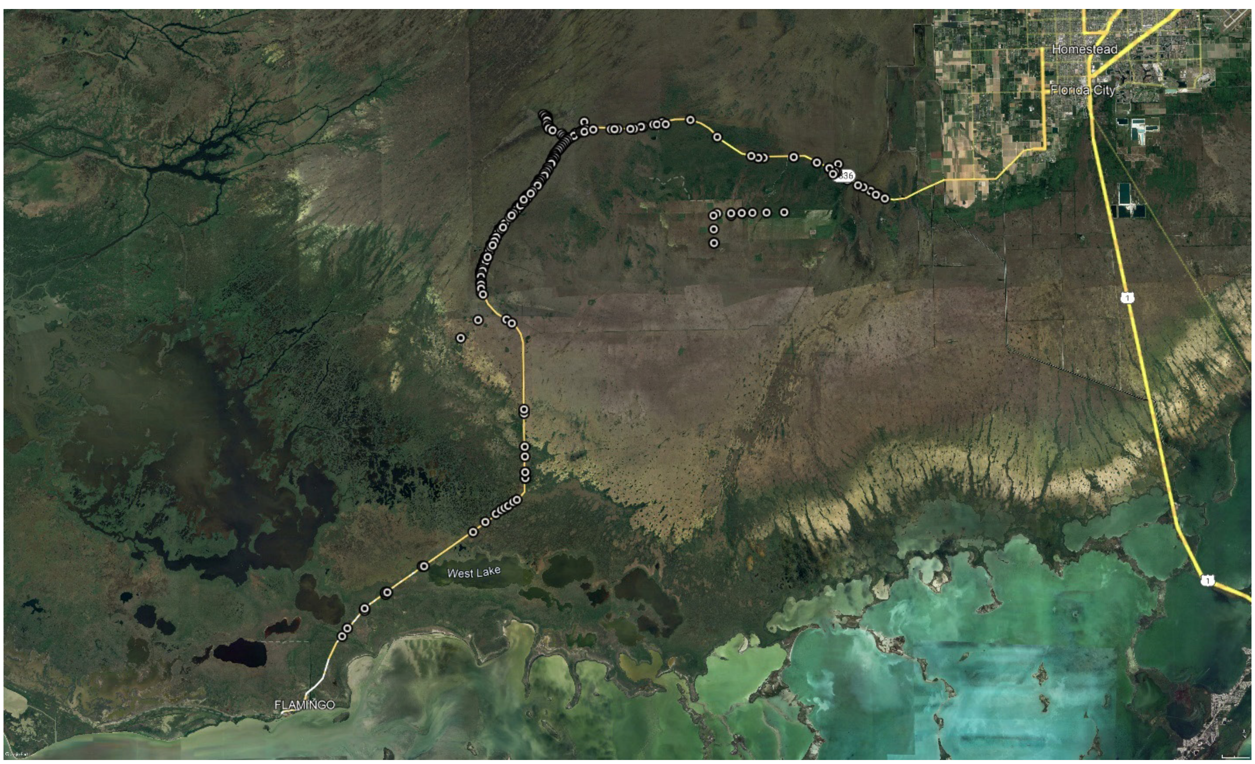

Figure 38. Distribution of the Florida Watersnake, *Nerodia fasciata pictiventris*, in Everglades National Park.

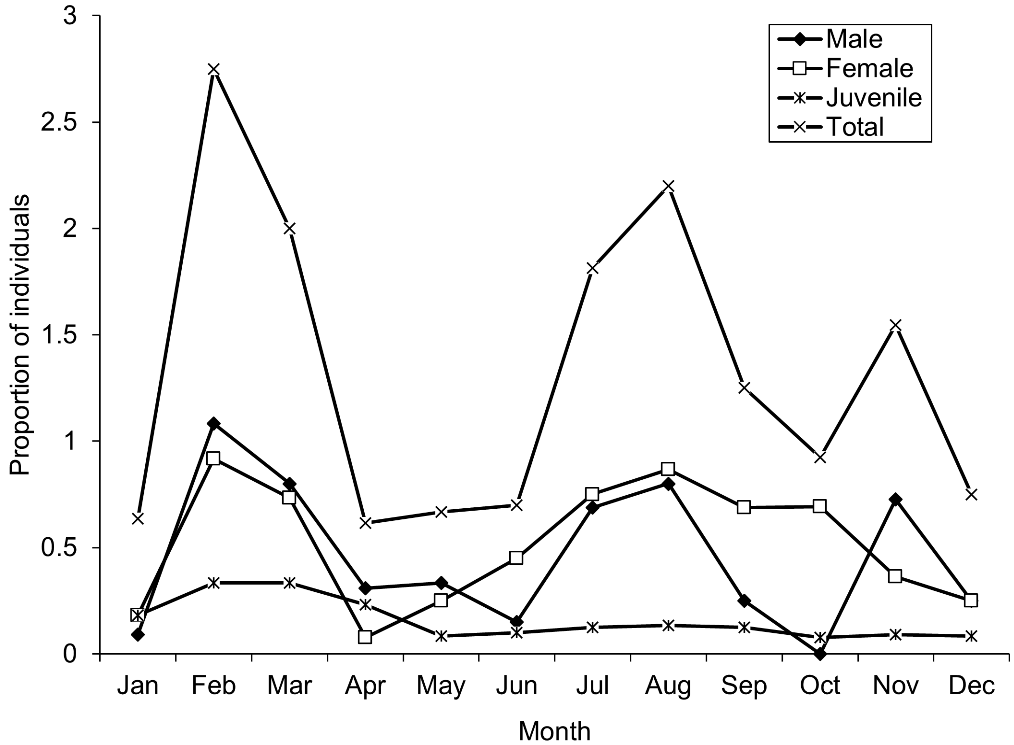

Figure 39. Monthly distribution of the Florida Watersnake, *Nerodia fasciata pictiventris*, crossing roads in Everglades National Park during 2009–2011.

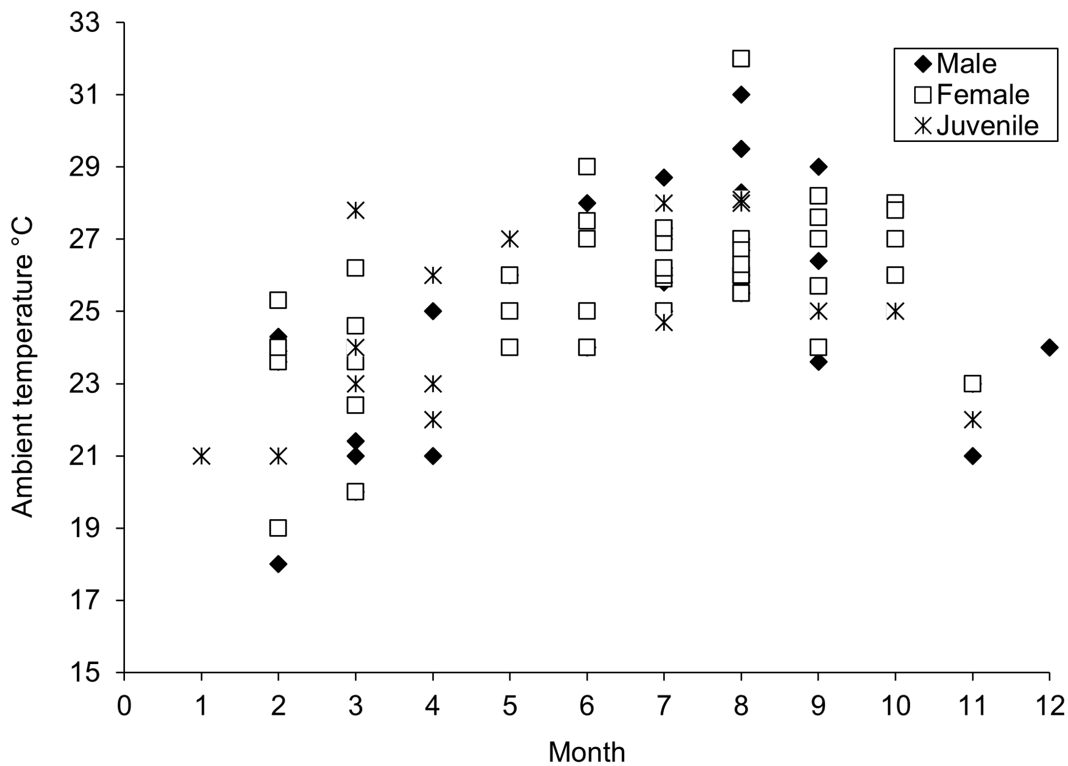

Figure 40. Ambient temperatures associated with the Florida Watersnake, *Nerodia fasciata pictiventris*, crossing roads at night in Everglades National Park during 2009–2011.

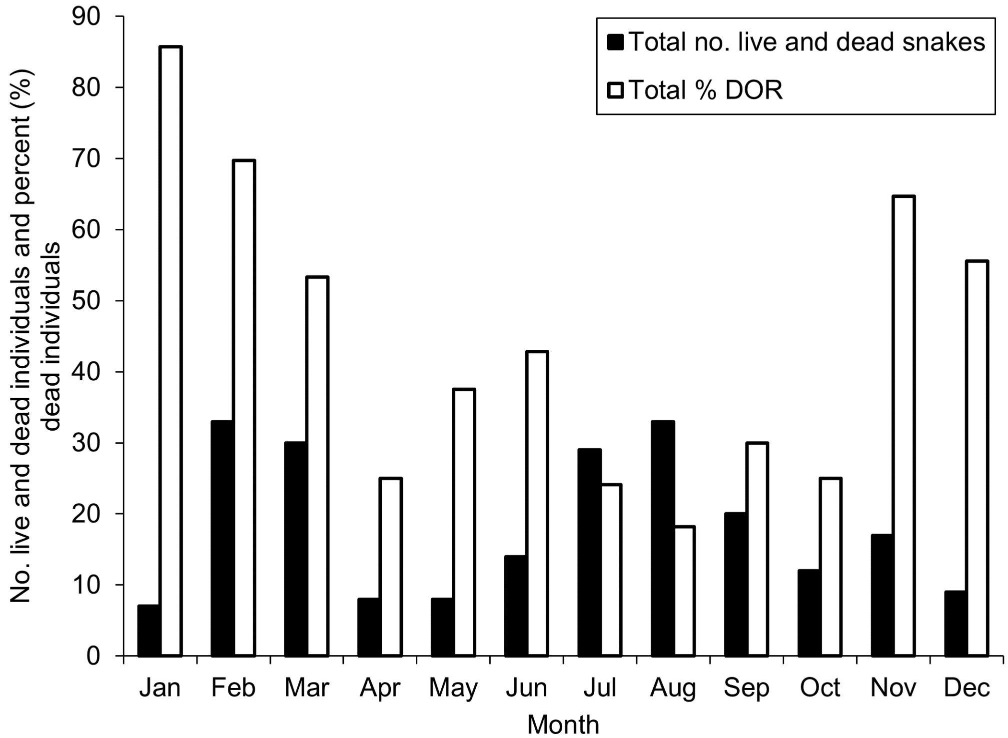

Figure 41. Monthly distribution of all and percent dead individuals of the Florida Watersnake, *Nerodia fasciata pictiventris*, on roads at night in Everglades National Park during 2009–2011.

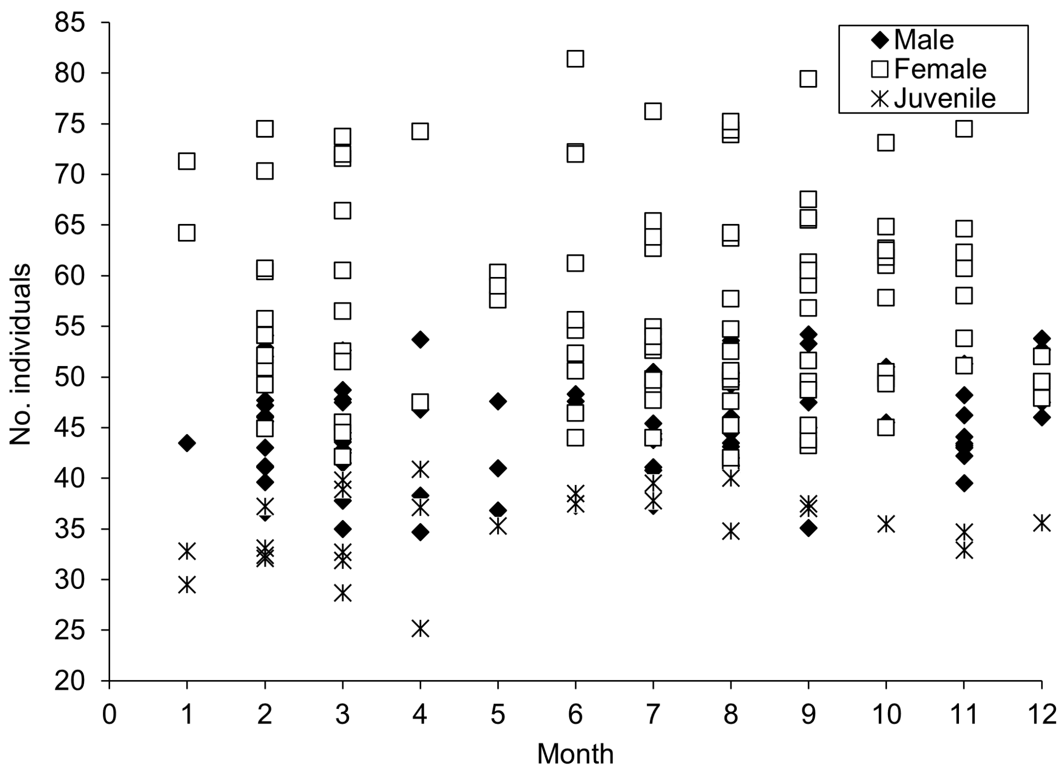

Figure 42. Monthly distribution of body sizes of the Florida Watersnake, *Nerodia fasciata pictiventris*, from Everglades National Park during 2008–2011.

Nerodia floridana (Goff, 1936)- Florida Green Watersnake (**Figure 43**).

Habitat association- The Florida Green Watersnake occurred in all three regions of Everglades National Park (**Table 4; Figure 44)**. Its encounter rates in the three regions were nonrandom (X^2 = 32.17, df = 2, *P* < 0.001), the fewest of which was on Long Pine Key, the driest of the three systems. On Long Pine Key, this species was much more abundant during June–August at the time our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, 14 males, 25 females, 15 juveniles, and seven individuals of unknown status comprised the 61 total Florida Green Watersnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were four males, six females, one juvenile, and one individual of unknown status comprising a total of 12 individuals.

The Florida Green Watersnake was the third most commonly encountered watersnake during our study. The total number of sightings comprised 4.65% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 3.79% of all snakes seen during March–December of 2008–2011 (**Table 3**). Numbers of encounters varied little among years such that numbers of individuals did not differ significantly during 2009–2011.

The male:female ratio among adult Florida Green Watersnakes was 0.56:1.00 during 2009–2011, and most males were encountered in 2011: 0.63:1.00 in 2009, 0.33:1.00 in 2010, 1.00:1.00 in 2011. Adults comprised more than one-half of actively moving individuals. Recruitment was highest in 2011. Excluding individuals of unknown category, juveniles comprised 27.78% of observations during 2009–2011, 27.78% in 2009, 15.79% in 2010, 41.18% in 2011. When individuals of unknown category were included, percentages of young comprised 24.59% of observations during 2009–2011, 26.32% in 2009, 15.00% in 2010, 31.82% in 2011.

Monthly movements- The Florida Green Watersnake was active year-round in Everglades National Park. Collectively, this species was most active in February, July, and November (**Figure 45**). Males were most active During November–February (**Figure 45**). Females were most active during February–March, July–August, and November (**Figure 45**). Juvenile activity peaked in February and June. (**Figure 45**).

Relationships between monthly movements by the Florida Green Watersnake and environmental factors were not significant (**Table 11**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Florida Green Watersnake ranged 24.0–30.0 °C (**Figure 46**). Mean temperatures did not significantly differ (t-test, p > 0.05) among males (23.5 ± 2.4°C; range = 21.0–26.0; n = 5), females (25.9 ± 3.6 °C; range = 20.0–30.8; n = 13), and juveniles (25.7 ± 2.5 °C; range = 22.0–30.0; n = 7). Ambient temperatures associated with all 25 individuals combined averaged 25.4 °C (± 3.1 °C; range = 20.0–30.8).

Roadkill dynamics- Florida Green Watersnakes were killed by vehicles on the road. DOR Florida Green Watersnakes comprised 6.91% of all DOR snakes and 55.74% of all conspecifics recorded during 2009–2011. Florida Green Watersnakes were killed throughout the year, with the highest incidence of DOR individuals in February (**Figure 47**). No significant relationship (Multiple R = 0.23, *P* = 0.47) existed between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 53.7 ± 8.1 cm SVL; range = 40.7–66.7; n = 18) differed significantly than that of females (Mean = 66.8 ± 12.7 cm SVL; range = 46.6–94.0; n = 31) with respect to variance (F = 0.412, df = 17, *P* = 0.03) and mean (T= -4.384, df = 46, *P* < 0.000). Male:female sexual size dimorphism of this sample was 0.80:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Six males averaged 50.8 cm SVL (± 5.7 cm SVL; range = 44.2–60.4), and 18 females averaged 72.0 cm SVL (± 14.2 cm SVL; range = 50.9–98.2). Sexual size dimorphism of this Everglades National Park sample was 0.71:1.00. No significant differences (F = 0.796, P = 0.28; t = -1.342, df = 47, P = 0.19) were detected in adult female body sizes between the two samples. The combined sample resulted in significant differences (F = 0.323, P = 0.002; t = -6.395, df = 69, P = < 0.0000) in body sizes of males (Mean = 53.0 ± 7.6 cm SVL; range = 40.7–66.7; n = 24) and females (Mean = 68.7 ± 13.4 cm SVL; range = 46.6–98.2; n = 49). The male:female sexual size dimorphism of the combined sample was 0.77:1.00. Florida Green Watersnakes grew quickly in Everglades National Park. Monthly distribution of body sizes **(Figure 48)** suggests that minimum body size at sexual maturity for both sexes could be reached by one year of life or shortly thereafter.

Reproduction- A 71.7 cm SVL female captured alive on 18 August 2009 appeared to be spent. From a subset of data of Meshaka and Layne (2015) form Everglades National Park, a clutch size of 12 was estimated in a 60.4 cm SVL female.

Injury- Bobbed tails were detected on a 53.8 cm SVL female and a 41.8 cm SVL juvenile. Consequently, 3.20% of females, 6.30% of juveniles, and 2.70**%** of all individuals were missing part of their tails.

Table 11. Relationship of environmental conditions to monthly movements of the Florida Green Watersnake, *Nerodia floridana*, in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.52, *P* = 0.08
Mean monthly minimum air temperature	r = 0.52, *P* = 0.08
Total monthly rainfall volume	r = 0.25, *P* = 0.43
Mean monthly water level	r = 0.07, *P* = 0.83

Figure 43. A Florida Green Watersnake, *Nerodia floridana*, from Everglades National Park. Photographed by M. Rochford.

Figure 44. Distribution of the Florida Green Watersnake, *Nerodia floridana*, in Everglades National Park.

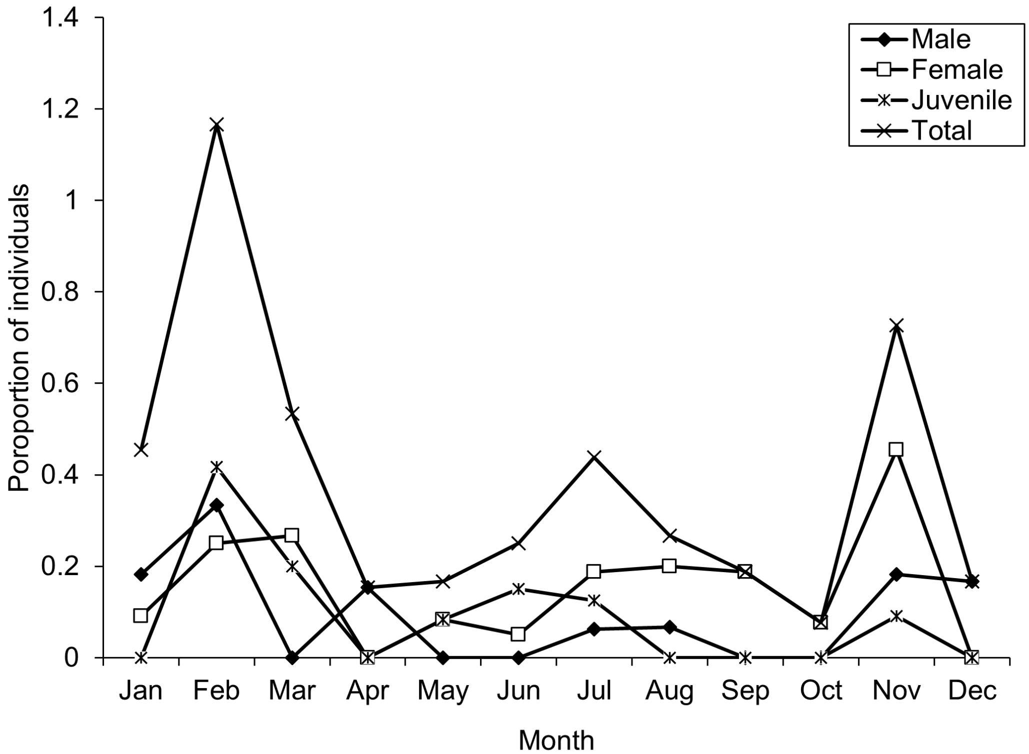

Figure 45. Monthly distribution of the Florida Green Watersnake, *Nerodia floridana*, crossing roads in Everglades National Park during 2009–2011.

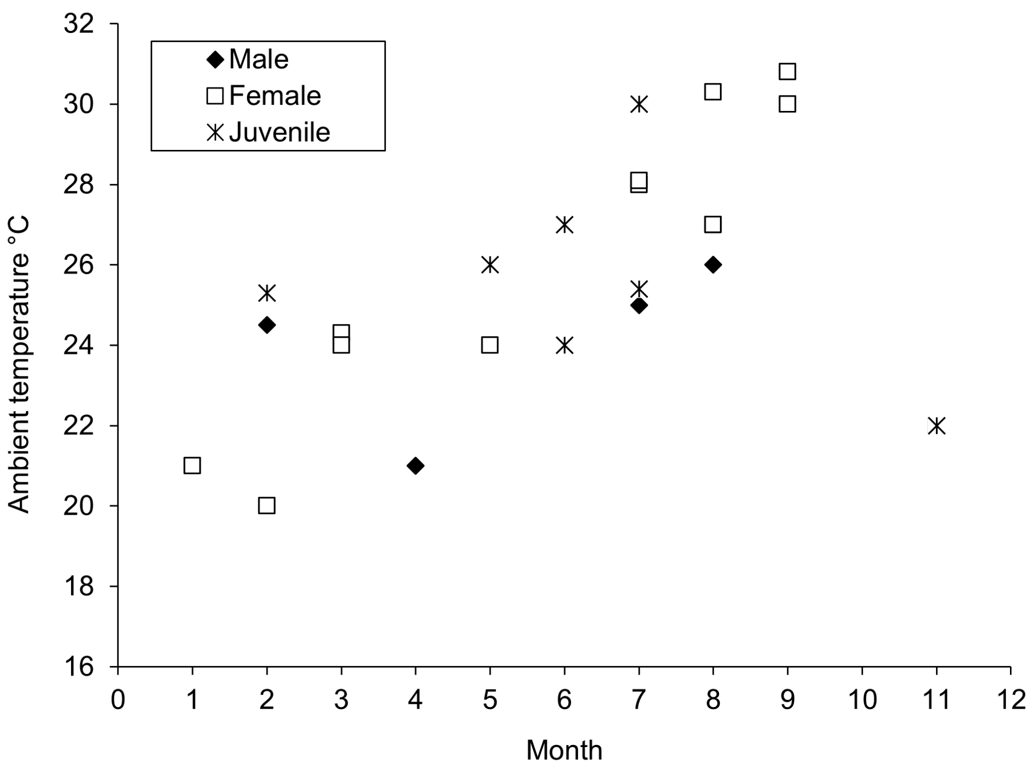

Figure 46. Ambient temperatures associated with the Florida Green Watersnake, *Nerodia floridana*, crossing roads at night in Everglades National Park during 2009–2011.

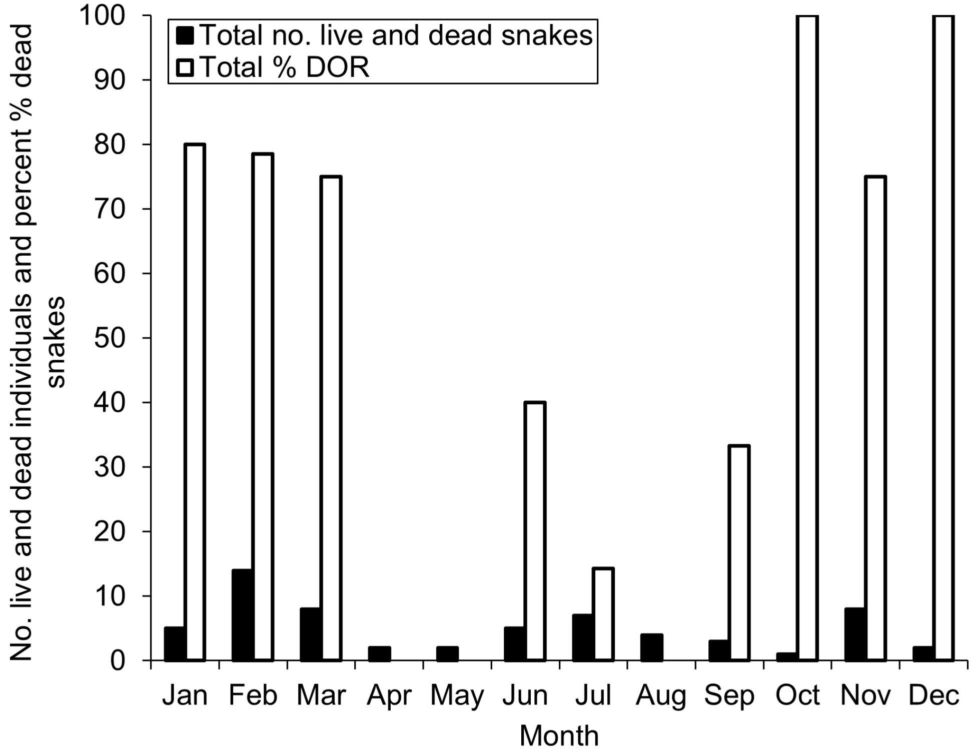

Figure 47. Monthly distribution of all and percent dead individuals of the Florida Green Watersnake, *Nerodia floridana*, on roads at night in Everglades National Park during 2009–2011.

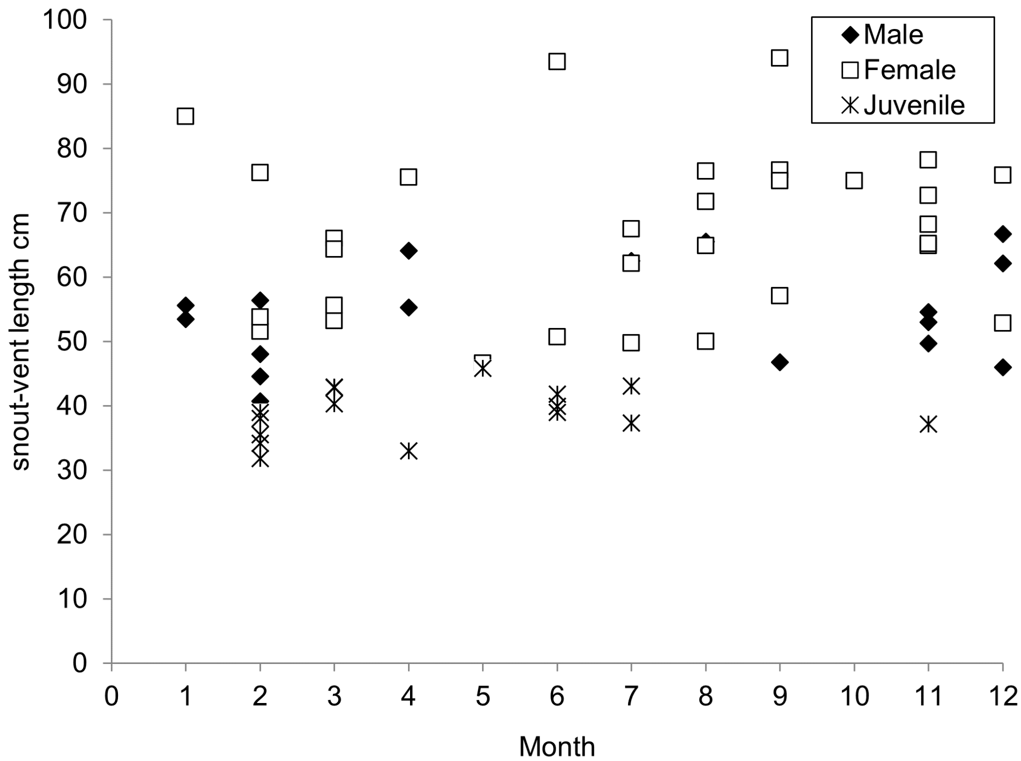

Figure 48. Monthly distribution of body sizes of the Florida Green Watersnake, *Nerodia floridana*, from Everglades National Park during 2008–2011.

Nerodia taxispilota (Holbrook, 1838)- Brown Watersnake (**Figure 49**).

Habitat association- The Brown Watersnake was present in all three regions of Everglades National Park (**Table 4; Figure 50**). Its preference of deep water could explain its highest encounter rate (X^2 = 32.07, df = 2, *P* < 0.001) in Pahayokee.

Population structure- During the three full calendar years of 2009–2011, 14 males, 11 females, four Juveniles, and two individuals of unknown status comprised the 31 total Brown Watersnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were four males, two females, zero juveniles, and one individual of unknown status comprising a total of seven individuals.

The Brown Watersnake was the least encountered watersnake during our study. The total number of sightings comprised 2.37% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 2.39% of all snakes seen during March–December of 2008–2011 (**Table 3**). Encounter rates were higher in 2009 and 2011 than in 2010; however, its lowest encounter rate was during a non-drought year.

The male:female ratio among adult Brown Watersnakes was 1.27:1.00 during 2009–2011 and varied among years: 1.50:1.00 in 2009, 0.40:1.00 in 2010, and 1.33:1.00 in 2011. Adults comprised the majority of encounters. Recruitment was highest in 2011. Excluding individuals of unknown category, juveniles comprised 23.08% of observations during 2009–2011, 9.09% in 2009, 0.00% in 2010, and 23.08% in 2011. When individuals of unknown category were included, percentage of young was 12.9% during 2009–2011, 8.33% in 2009, 0.00% in 2010, and 21.43% in 2011.

Monthly movements- The Brown Watersnake was encountered in all months except October in Everglades National Park. Collectively, seasonal activity may have been bimodal with a primary pulse of activity in April, followed by a possible secondary pulse in August (**Figure 51**). Males were most active in April (**Figure 51**). The seasonal pattern of females was suggestive of a unimodal spring pulse of activity (**Figure 51**). The few juveniles were encountered in equal numbers in February and July (**Figure 51**). Relationships between monthly movements by the Brown Watersnake and environmental factors were significant only in monthly water table stages (**Table 12**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Brown Watersnake ranged 21.0–28.0 °C (**Figure 52**). Mean temperatures were not significantly different (t = - 2.078, df = 12, *P* = 0.59) between that of males (22.7 $\pm$ 3.0 °C; range = 16.0–26.3; n = 9) and females (25.7 $\pm$ 1.5 °C; range = 24.0–27.0; n = 5). Temperatures were available for two juveniles: 25.0 and 27.5 °C. Ambient temperatures associated with all 16 individuals combined averaged 24.0 °C ($\pm$ 2.9 °C; range = 16.0–27.5).

Roadkill dynamics- Brown Watersnakes were killed by vehicles on the road. DOR Brown Watersnakes comprised 3.05% of all DOR snakes and 48.39% of all conspecifics recorded during 2009–2011. Brown Watersnakes were killed in high numbers and in most but not all months in which individuals were encountered (**Figure 53**). The highest incidences were in February and November but included a steady monthly rise from May to July (**Figure 53**). No significant relationship (Multiple R = 0.32, *P* = 0.30) was detected between %DORs and total individuals per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, mean adult body size of males (Mean = 52.8 $\pm$ 11.3 cm SVL; range = 39.6–85.0; n = 18) did not differ significantly from that of females (Mean = 60.4 $\pm$ 13.0 cm SVL; range = 41.5–89.5; n = 13) with respect to variance (F = 0.762, *P* = 0.30) and mean (t = -1.726, df = 29, P = 0.10). Male:female sexual size dimorphism of this sample was 0.88:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. From that sample, mean adult body sizes were available for seven males (Mean = 44.3 $\pm$ 5.9 cm SVL; range = 37.2–53.0) and four females (Mean = 56.2 $\pm$ 19.9 cm SVL; range = 39.1–77.0). Male:female sexual size dimorphism for this sample was 0.79:1.00. The combination of Everglades National Park samples of Meshaka and Layne (2015) and this study resulted in significant differences (F = 0.565, P = 0.10; t = -2.330, df = 40, P = 0.03) in body sizes between males (Mean = 50.4 $\pm$ 10.7 cm SVL; range = 37,2–85.0; N = 25) and females (Mean = 59.4 $\pm$ 14.3 cm SVL; range = 39.1–89.5; N = 17). The male:female sexual size dimorphism value for this sample was 0.85:1.00. Brown Watersnakes grew quickly in Everglades National Park. Monthly distribution of body sizes **(Figure 54)** suggests that minimum body size at sexual maturity for both sexes could be reached by one year of life or shortly thereafter.

Injury- Bobbed tail was observed on a 43.0 cm SVL male and 45.0 cm SVL female. Consequently, 5.56% of males, 7.69% of females and 5.26% of the population were missing a portion of their tail.

Table 12. Relationship of environmental conditions to monthly movements of the Brown Watersnake, *Nerodia taxispilota*, in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.03, *P* = 0.94
Mean monthly minimum air temperature	r = 0.06, *P* = 0.86
Total monthly rainfall volume	r = 0.18, *P* = 0.57
Mean monthly water level	r = 0.59, *P* = 0.05

Figure 49. A Brown Watersnake, *Nerodia taxispilota*, on the road in Everglades National Park. Photographed by M. Rochford.

Figure 50. Distribution of the Brown Watersnake, *Nerodia taxispilota*, in Everglades National Park.

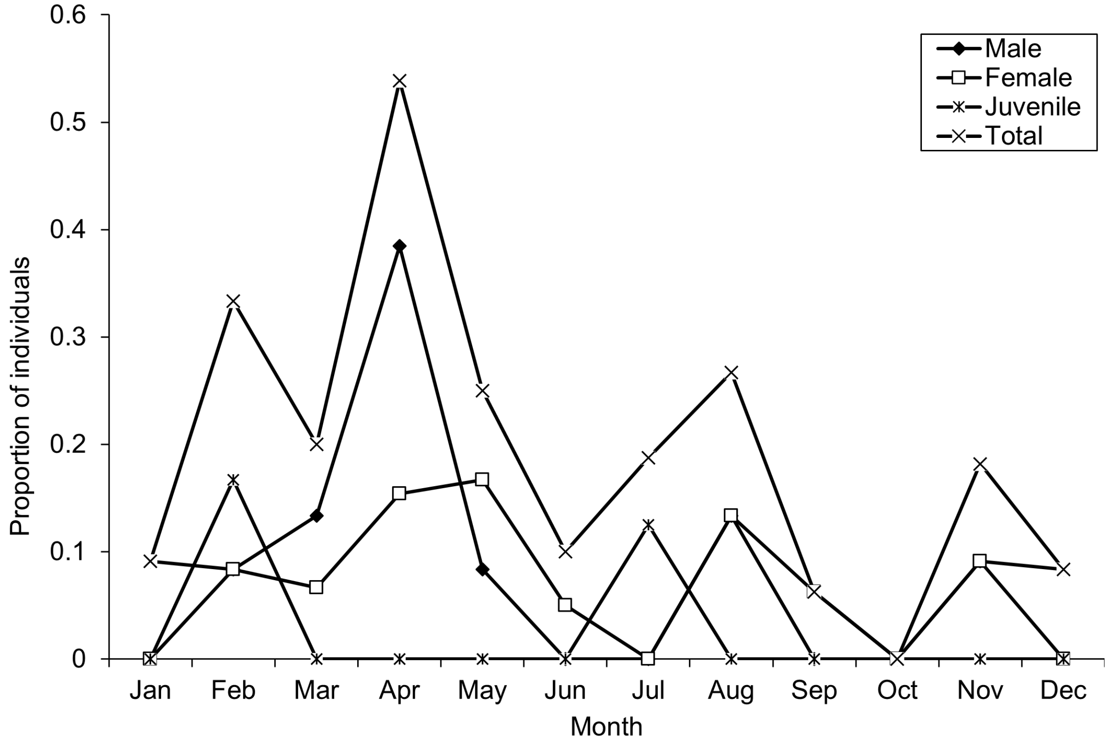

Figure 51. Monthly distribution of the Brown Watersnake, *Nerodia taxispilota*, crossing roads in Everglades National Park during 2009–2011.

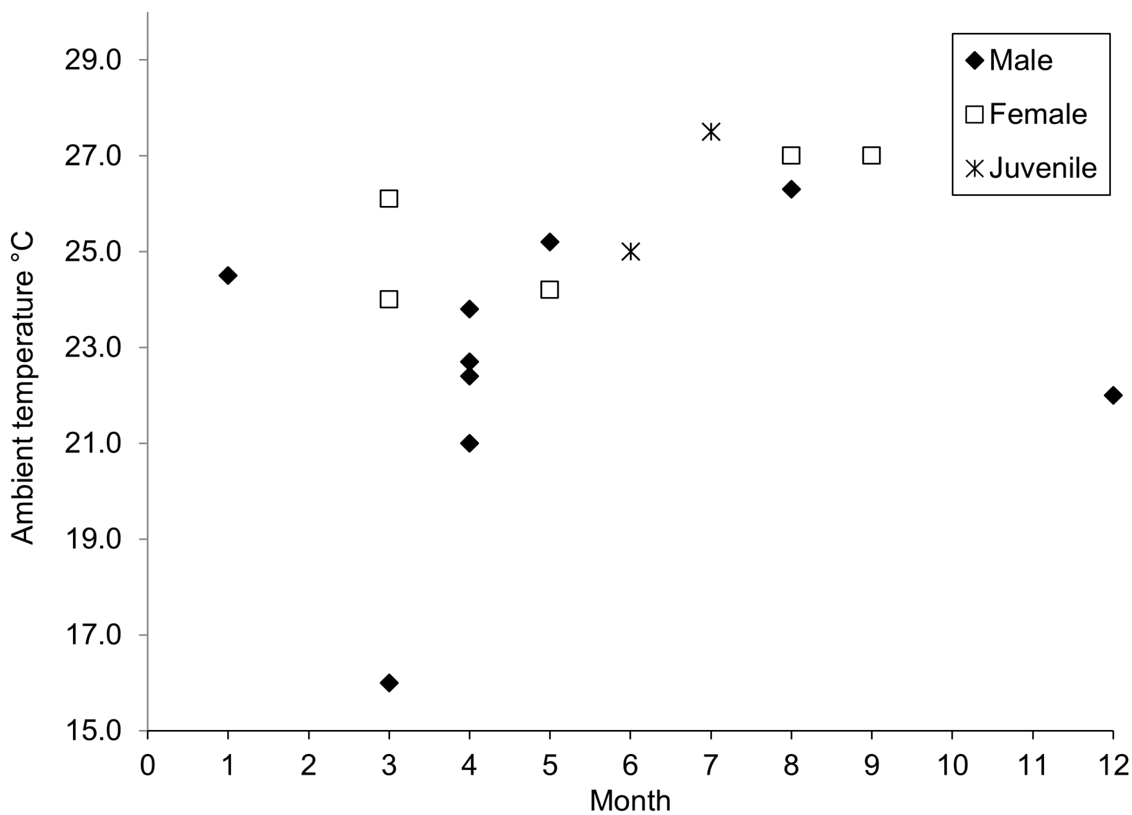

Figure 52. Ambient temperatures associated with the Brown Watersnake, *Nerodia taxispilota*, crossing roads at night in Everglades National Park during 2009–2011.

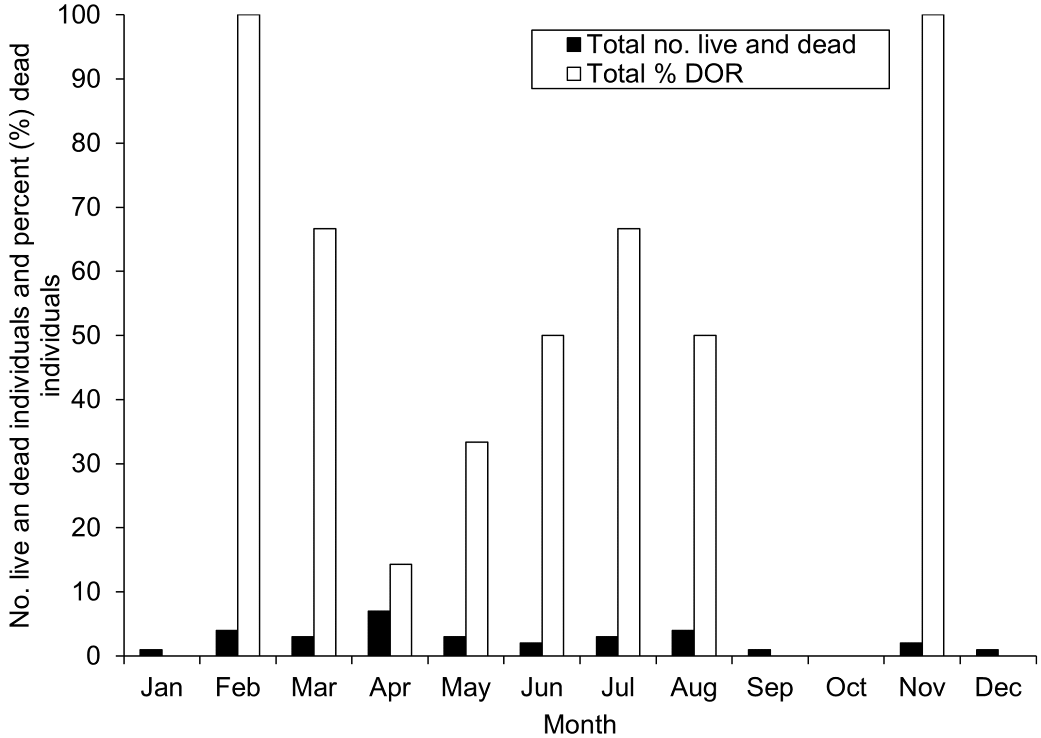

Figure 53. Monthly distribution of all and percent dead individuals of the Brown Watersnake, *Nerodia taxispilota*, on roads at night in Everglades National Park during 2009–2011.

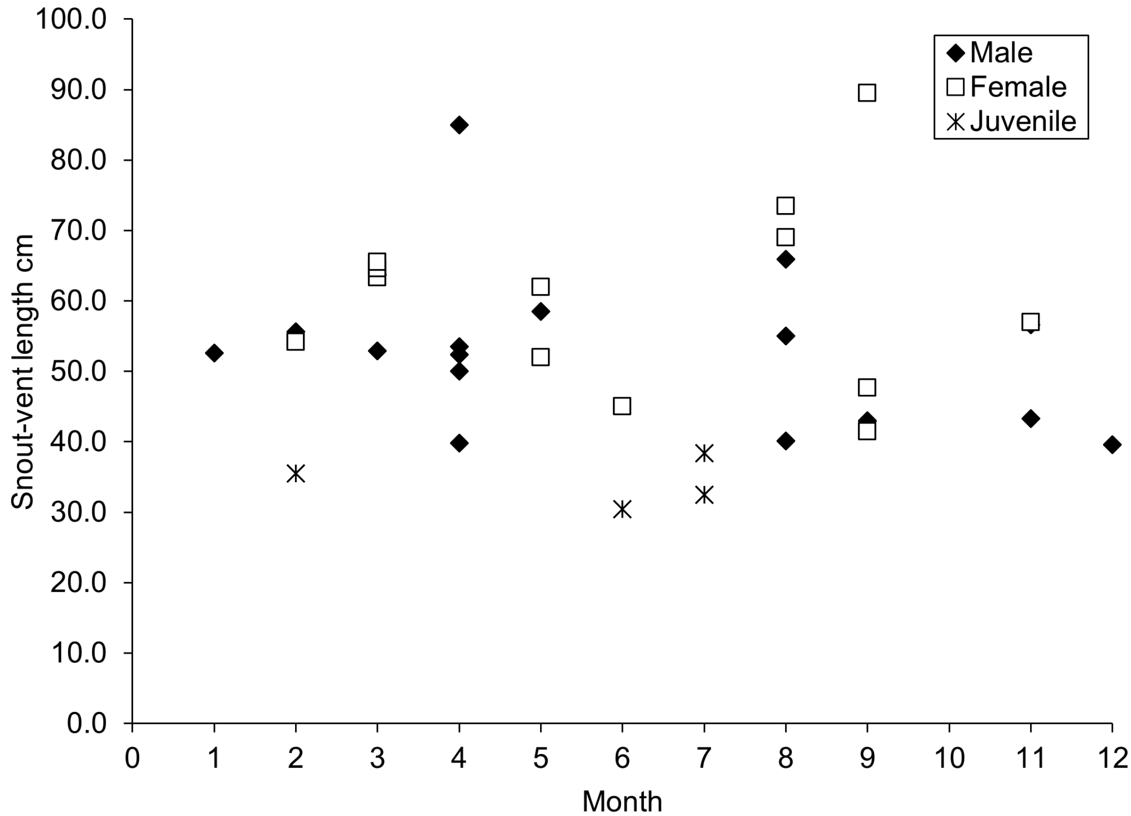

Figure 54. Monthly distribution of body sizes of the Brown Watersnake, *Nerodia taxispilota*, in Everglades National Park during 2008–2011.

Opheodrys aestivus carinatus Grobman, 1984- Florida Rough Greensnake (**Figure 55**).

Habitat association- Primarily diurnal in habits and strongly arboreal, especially near water, the Florida Rough Greensnake was doubtlessly under-represented in encounters. Nonetheless, as expected, this species was detected in Long Pine Key and saline glade assemblages but not significantly so (**Table 4; Figure 55)**. On Long Pine Key, this species was much less abundant during June–August at the time of our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, one male, one female, two juveniles, and zero individuals of unknown status comprised the four total Florida Rough Greensnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were zero males, zero females, zero juveniles, and zero individuals of unknown status comprising a total of zero individuals.

The Florida Rough Greensnake was uncommonly encountered during our study. The total number of sightings comprised 0.31% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 0.28% of all snakes seen during March–December of 2008–2011 (**Table 3**). Stable in assemblage composition among sampling periods, the Florida Rough Greensnake did not differ significantly during 2009–2011. The male:female ratio among adult Florida Rough Greensnakes was 1.00:1.00 during 2009–2011. Excluding individuals of unknown category, juveniles comprised 50.00% of observations during 2009–2011. When individuals of unknown category were included, respective percentage of young was also 50.00%.

Monthly movements- The Florida Rough Greensnake was comprised of one male in May 2010, a female in September 2009, and two juveniles in March 2009.

Ambient temperatures associated with nightly activity- Ambient temperatures associated with all four combined individuals averaged 24.5 °C ($\pm$ 2.9 °C; range = 22.0–27.0; n = 4).

Roadkill dynamics- Florida Rough Greensnakes were not represented by DORs during 2009–2011 and so comprised 0.00% DORs for the species and for all DOR snakes encountered.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body sizes are available for a male, 36.6 cm SVL, and female, 38.5 cm SVL. Male:female sexual size dimorphism of this sample was 0.95:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. From this sample, body sizes were available for three males (42.0 $\pm$ 2.0 cm SVL; range = 40.3–44.7) and five females (48.5 $\pm$ 5.2 cm SVL; range = 40.7–56.3). The male:female sexual size dimorphism value was 0.87:1.00. Combining both samples resulted in an average body size of 40.6 cm SVL ($\pm$ 3.3 cm SVL; range = 36.6–44.7) for males and 46.8 cm SVL ($\pm$ 6.6 cm SVL; range = 38.5–56.3) for females. The male:female sexual size dimorphism value was 0.87:1.00. Two juveniles, 28.4 and 32.7 cm SVL, were encountered on 4 March 2009.

Figure 55. A Florida Rough Greensnake, *Opheodrys aestivus carinatus*, on the road in Everglades National Park. Photographed by M. Rochford.

Figure 56. Distribution of the Florida Rough Greensnake, *Opheodrys aestivus carinatus*, in Everglades National Park.

Pantherophis alleghaniensis rossalleni (Neill, 1949)- Everglades Ratsnake, ***P. a. quadrivittatus*** (Holbrook, 1836)- Yellow Ratsnake, and intergrades (**Figure 57**).

Habitat association- This ratsnake was found in all three regions of Everglades National Park (**Table 4; Figure 58**). Owing to its strongly arboreal habits, this ratsnake was found to have comprised a greater percentage of the snake assemblages of Long Pine Key and the saline glades than that of Pahayokee ($X^2 = 7.59$, df = 2, $P < 0.05$). Still, its presence in Pahayokee wetlands is not surprising in light of the facility with which it will traverse wetlands to reach hammocks.

Population structure- During the three full calendar years of 2009–2011, eight males, zero females, 16 Juveniles, and four individuals of unknown status comprised the 28 total ratsnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were one male, three females, two juveniles, and two individuals of unknown status comprising a total of eight individuals.

The ratsnake was uncommonly encountered snake during our study. The total number of sightings comprised 2.14% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 2.39% of all snakes seen during March–December of 2008–2011 (**Table 3**). This species was stable in its composition of the assemblage and also stable in assemblage composition among sampling periods, not differing significantly during 2009–2011 ($X^2 = 0.29$, df = 2, $p > 0.05$) or during 2008–2011 ($X^2 = 0.12$, df = 3, $p > 0.05$). The male:female ratio among adult ratsnakes was 8.02:0.00 during 2009–2011. Excluding individuals of unknown category, juveniles comprised 66.67% of observations during 2009–2011. When individuals of unknown category were included, the percentage of young was 57.14% during 2009–2011.

Monthly movements- The ratsnake was active year-round in Everglades National Park. Collectively, this species may have exhibited a multimodal seasonal activity pattern, with peak numbers in March, May–June, and October (**Figure 59**). Few males were encountered, mostly in March, and no females were seen during the survey (**Figure 59**). Juveniles were seen intermittently through the year, with most encounters during May–June and in October (**Figure 59**). Dalrymple et al. (1991a) found a bimodal annual activity cycle on Long Pine Key. Juveniles were not identified. Relationships between monthly movements by the ratsnake and environmental factors were not significant (**Table 3**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of this species ranged 21.0–29.0 °C (**Figure 60**). Ambient temperatures with male activity averaged 27.1 °C ($\pm$ 3.6°C; range = 23.5 –32.0; n = 4) and were available for activity of two females (26.9, 27.1 °C). Ambient temperatures associated with juveniles averaged 25.8 °C ($\pm$ 2.1 °C; range = 21.0 –29.0; n = 14) and for all 20 individuals combined averaged 26.2 °C ($\pm$ 2.4 °C; range = 21.0–32.0).

Roadkill dynamics- Ratsnakes were killed by vehicles on the road. DOR ratsnakes comprised 1.22% of all DOR snakes and 21.43% of all conspecifics recorded during 2009–2011. Ratsnakes were killed primarily in the months of January and March. Others were killed in June and October (**Figure 61**). No significant relationship (Multiple R = 0.13, $P = 0.69$) existed between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size is available for adults of males (Mean = 106.6 $\pm$ 21.7 cm SVL; range = 82.4–138.1; n = 9) and females (Mean = 102.4 $\pm$ 20.4 cm SVL; range = 87.2–125.6; n = 3). Male:female sexual size dimorphism of this sample was 1.04:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Inclusion of those data provided mean values for three males (Mean = 109.3 $\pm$ 17.6 cm SVL; range = 85.0–126.0) and five females (Mean = 109.2 $\pm$ 13.3 cm SVL; range = 91.1–122.0) with a male:female sexual size dimorphism value of 1.00:1.00. Combining samples of Meshaka and Layne (2015) and this study resulted in average body sizes of 107.3 cm SVL ($\pm$ 20.7 cm SVL; range = 82.4–138.1) among males and 106.7 cm SVL ($\pm$ 16.1 cm SVL; range = 87.2–125.6) among females with a male:female sexual size dimorphism value of 1.00:1.01. Monthly distribution of body sizes **(Figure 62)** revealed YOY individuals in August and October and was suggestive of sexual maturity in three years.

Injury- Bobbed tails were present in two males (93.0, 130.5 cm SVL), one female (94.3 cm SVL) and two juveniles (57.8, 62.6 cm SVL). Consequently, 22.2% of males, 33.3% of females, 11.1% of juveniles, and 13.9% of the sampled population of this species was missing a portion of their tail.

Table 13. Relationship of environmental conditions to monthly movements of the Everglades Ratsnake, *Pantherophis alleghaniensis rossalleni*, Yellow Ratsnake, *S. a. quadrivittatus*, and intergrade in Everglades National Park during 2009–2011.

Environmental factors	correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.39, $P = 0.21$
Mean monthly minimum air temperature	r = 0.38, $P = 0.22$
Total monthly rainfall volume	r = 0.16, $P = 0.61$
Mean monthly water level	r = 0.38, $P = 0.22$

Figure 57. Everglades Ratsnakes, *Pantherophis alleghaniensis rossalleni*, from Frog Pond (just outside Everglades National Park) (A) and Aerojet Road (just outside Everglades National Park near Coe Visitor Center at park entrance) (B). (A, B) Photographed by M. Rochford. (C) An individual on the road. (D) An intergrade of the Everglades Ratsnake and the Yellow Ratsnake, *P. a. quadrivittatus*. (C, D) Photographed by Arik Hartmann.

Figure 58. Distribution of the Everglades Ratsnake, *Pantherophis alleghaniensis rossalleni*, Yellow Ratsnake, *P. a. quadrivittatus*, and intergrade in Everglades National Park.

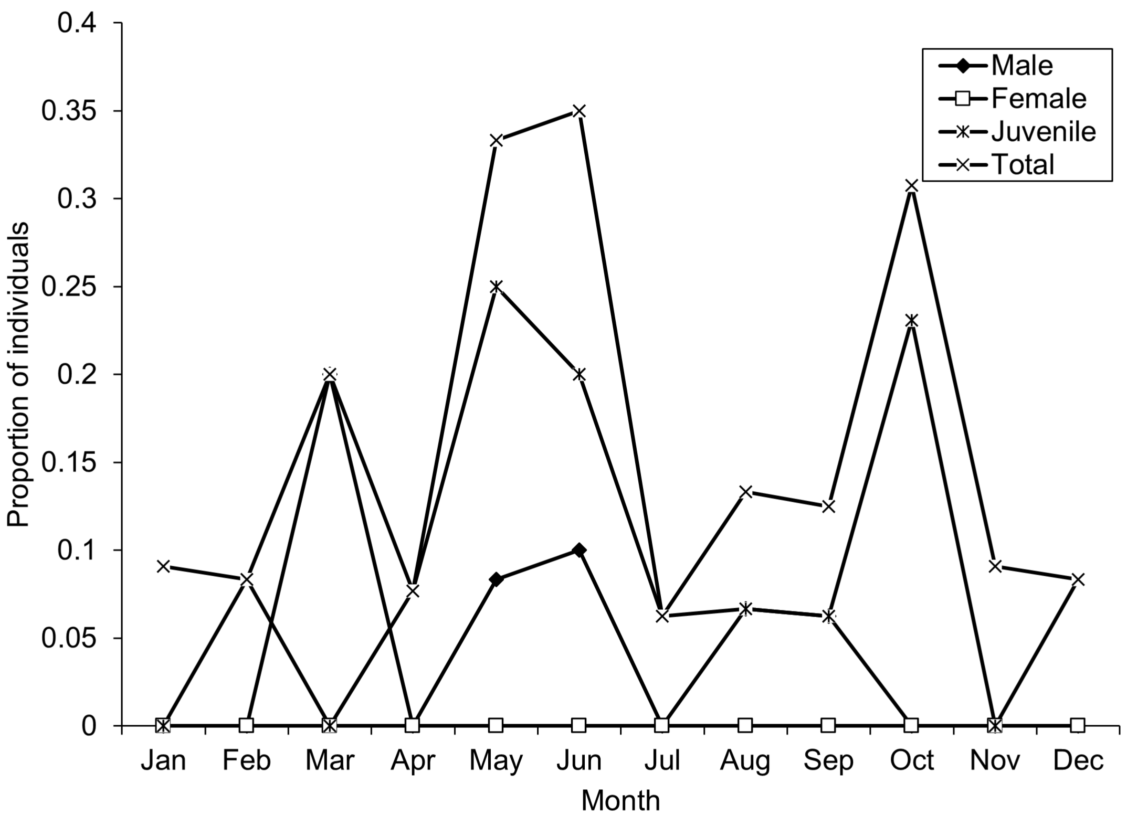

Figure 59. Monthly distribution of the Everglades Ratsnake, *Pantherophis alleghaniensis rossalleni*, Yellow Ratsnake, *P. a. quadrivittatus*, and intergrade crossing roads at night in Everglades National Park during 2009–2011.

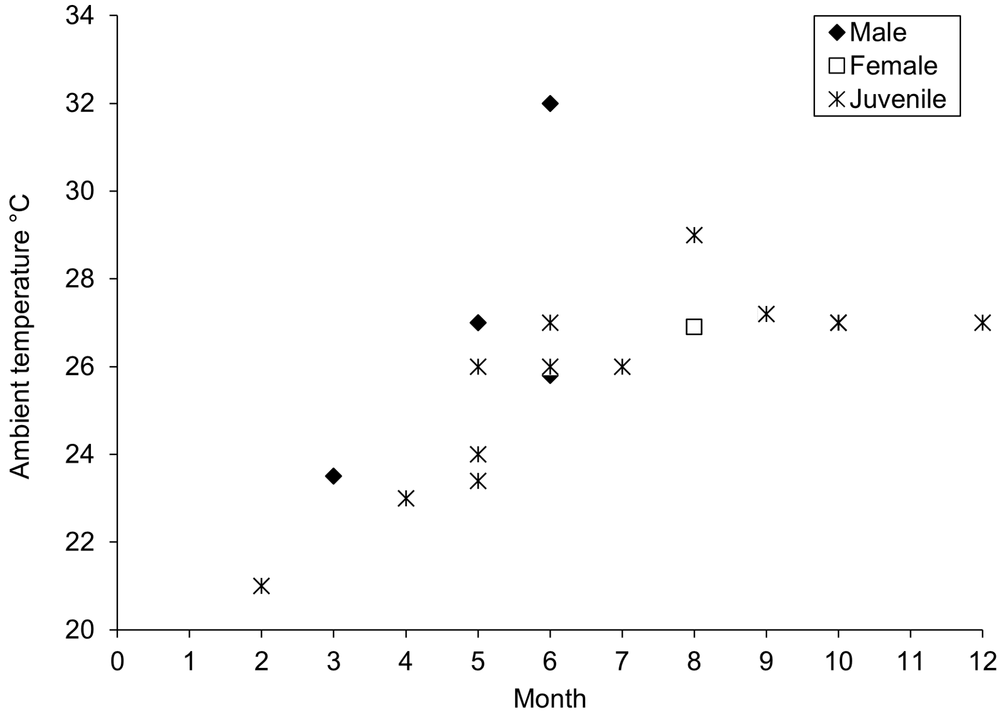

Figure 60. Ambient temperatures associated with the Everglades Ratsnake, *Pantherophis alleghaniensis rossalleni*, Yellow Ratsnake, *P. a. quadrivittatus*, and intergrade crossing roads at night in Everglades National Park during 2009–2011.

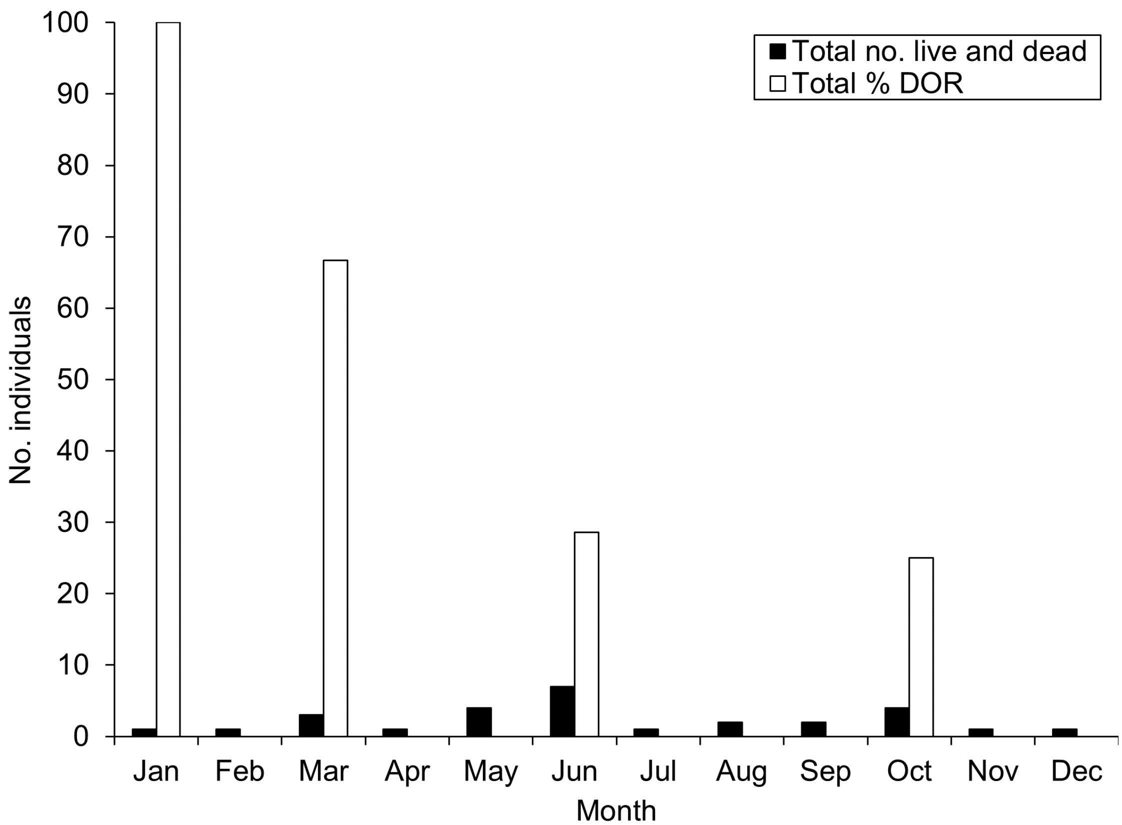

Figure 61. Monthly distribution of all and percent dead individuals of the Everglades Ratsnake, *Pantherophis alleghaniensis rossalleni*, Yellow Ratsnake, *P. a. quadrivittatus*, and intergrade form on roads at night in Everglades National Park during 2009–2011.

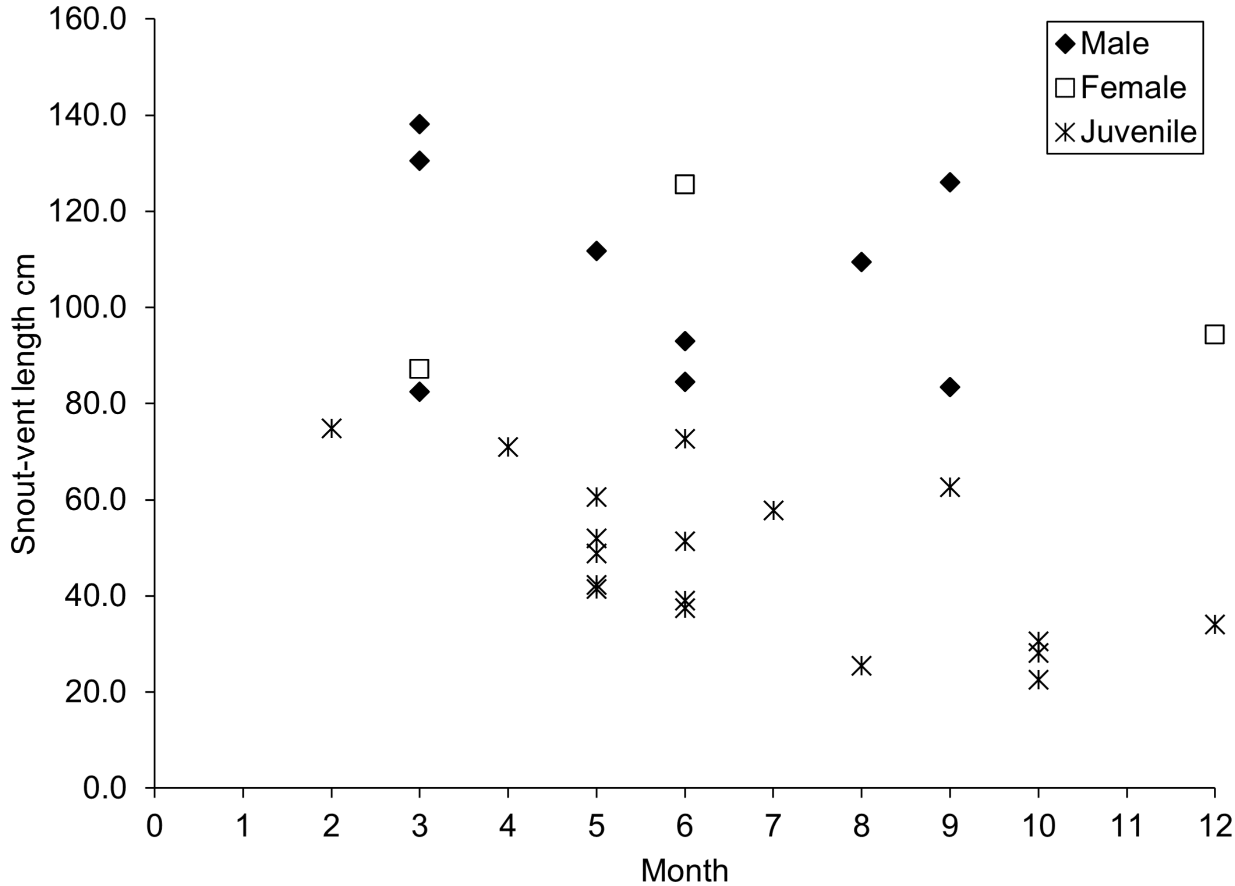

Figure 62. Monthly distribution of body sizes of the Everglades Ratsnake, *Pantherophis alleghaniensis rossalleni*, Yellow Ratsnake, *P. a. quadrivittatus*, and intergrade in Everglades National Park during 2008–2011.

Pantherophis guttatus (Linnaeus, 1766)- Red Cornsnake. (**Figure 63**).

Habitat association- The Red Cornsnake was present in all three regions of Everglades National Park (**Table 4; Figure 64**). Its encounter rate was highest in the saline glades ($X^2 = 31.96$, df = 2, $P < 0.001$) and distantly followed by Long Pine Key and Pahayokee (**Table 4**).

Population structure- During the three full calendar years of 2009–2011, 18 males, 12 females, 16 juveniles, and five individuals of unknown status comprised the 51 total Red Cornsnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were six males, three females, one juvenile, and one individual of unknown status comprising a total of 11 individuals.

The Red Cornsnake was uncommonly encountered during our study. The total number of sightings comprised 3.89% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 4.07% of all snakes seen during March–December of 2008–2011 (**Table 3**). Numbers of individuals differed significantly during 2009–2011 in association with a very low water table in 2011. The male:female ratio among adult Red Cornsnakes was 1.50:1.00 during 2009–2011. Sex ratios varied among years of this study: 1.80:1.00 in 2009, 3.00:1.00 in 2010, and no males in 2011.

Adults generally comprised approximately two-thirds of actively moving individuals. Recruitment was highest in 2011. Excluding individuals of unknown category, juveniles comprised 34.78% of observations during 2009–2011, 26.32% in 2009, 47.83% in 2010, and 00.00% in 2011. When individuals of unknown category were included, respective percentages of young were 31.37% in 2009–2011, 26.32% in 2009, 40.74% in 2010, and 00.00% in 2011.

Monthly movements- The Red Cornsnake was encountered in all months except March in Everglades National Park. Collectively, this species was distinctly most active in June (**Figure 65**). Males were also most active in June (**Figure 65**). Females exhibited no discernible pattern to monthly movements, whereas monthly movements of juveniles peaked in July (**Figure 65**). On Long Pine Key (Dalrymple et al., 1991a), annual activity of the species generally and males was multimodal (May, July, October), and females were most often encountered in July. Juveniles were not identified.

Relationships between monthly movements by the Red Cornsnake and environmental factors were strongly significant where evident (**Table 14**). Collectively, monthly movements were strongly related to average air temperature maxima and minima and by rainfall volume (**Table 14**). Water table was not associated significantly with movements of the Red Cornsnake (**Table 14**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Red Cornsnake ranged 21.0–29.0 °C (**Figure 66**). Mean ambient temperatures did not significantly differ (t-test, p > 0.05) among males (25.6 $\pm$ 3.0 °C; range = 17.0–29.0; n = 19), females (25.6 $\pm$ 1.4°C; range = 23.0–28.0; n = 12), and juveniles (26.6 $\pm$ 1.5 °C; range = 24.0–29.0; n = 16). Ambient temperatures associated with all 47 individuals combined averaged 25.9 °C ($\pm$ 2.2 °C; range = 17.0–29.0).

Roadkill dynamics- Red Cornsnakes were killed by vehicles on the road. DOR Red Cornsnakes comprised 1.83% of all DOR snakes and 17.65% of all conspecifics recorded during 2009–2011. Red Cornsnakes were killed during six months of the year, with the highest incidence of DOR individuals in January, May, and December (**Figure 67**). No significant relationship (Multiple R = 0.07, *P* = 0.67) existed between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 68.3 cm SVL $\pm$ 14.2 cm SVL; range = 50.4–102.8; n = 24) did not differ significantly than that of females (Mean = 74.8 cm SVL $\pm$ 9.9 cm SVL; range = 62.4–89.1; n = 15) with respect to variance (F = 2.074, *P* = 0.08) and mean (t = -1.553, df = 37, *P* = 0.13). Male:female sexual size dimorphism of this sample was 0.91:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Data from that sample provided mean values of 63.3 cm SVL ($\pm$ 8.9; range = 57.0–78.6; N = 4) for males and 66.6 cm SVL ($\pm$ 4.0; range = 62.5–72.0; N = 3) and a male:female sexual size dimorphism value of 0.95:1.00. No significant differences (F = 2.011, P = 0.06; t = -1.581, df = 44, P = 0.12) were detected between body sizes of adult males (67.6 $\pm$ 13.7; range = 50.4–103.0; N = 28) and females (73.5 $\pm$ 9.7; range = 62.4–89.1; N = 18) from the combined samples, the values resulted in a male:female sexual size dimorphism value of 0.92:1.00.

Monthly distribution of body sizes **(Figure 68)** suggests that minimum body size at sexual maturity for both sexes could be reached by one year of life or shortly thereafter. The smallest individual encountered was a YOY measuring 23.7 cm SVL in October (**Figure 68**).

Reproduction- A gravid 65.2 cm SVL female was found alive on 30 July 2008. On Long Pine Key, gravid females were detected in July, and a clutch hatched in September (Dalrymple et al., 1991a).

Injury- From individuals encountered on the road during 2008–2011, a 66.8 cm SVL male was found with a bobbed tail. Consequently, 4.17% of males and 1.61% of the population were missing a portion of their tail. The same gravid female found 30 July 2008 also had an injury on her cloaca.

Table 14. Relationship of environmental conditions to monthly movements of the Red Cornsnake, *Pantherophis guttatus*, in Everglades National Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.64, *P* = 0.02
Mean monthly minimum air temperature	r = 0.66, *P* = 0.02
Total monthly rainfall volume	r = 0.71, *P* = 0.01
Mean monthly water level	r = 0.25, P = 0.42

Figure 63. A Red Cornsnake, *Pantherophis guttatus*, from Everglades National Park, Florida. (A) Photographed by M. Rochford. (B) On road and (C) close-up of another individual (B, C) Photographed by Arik Hartmann.

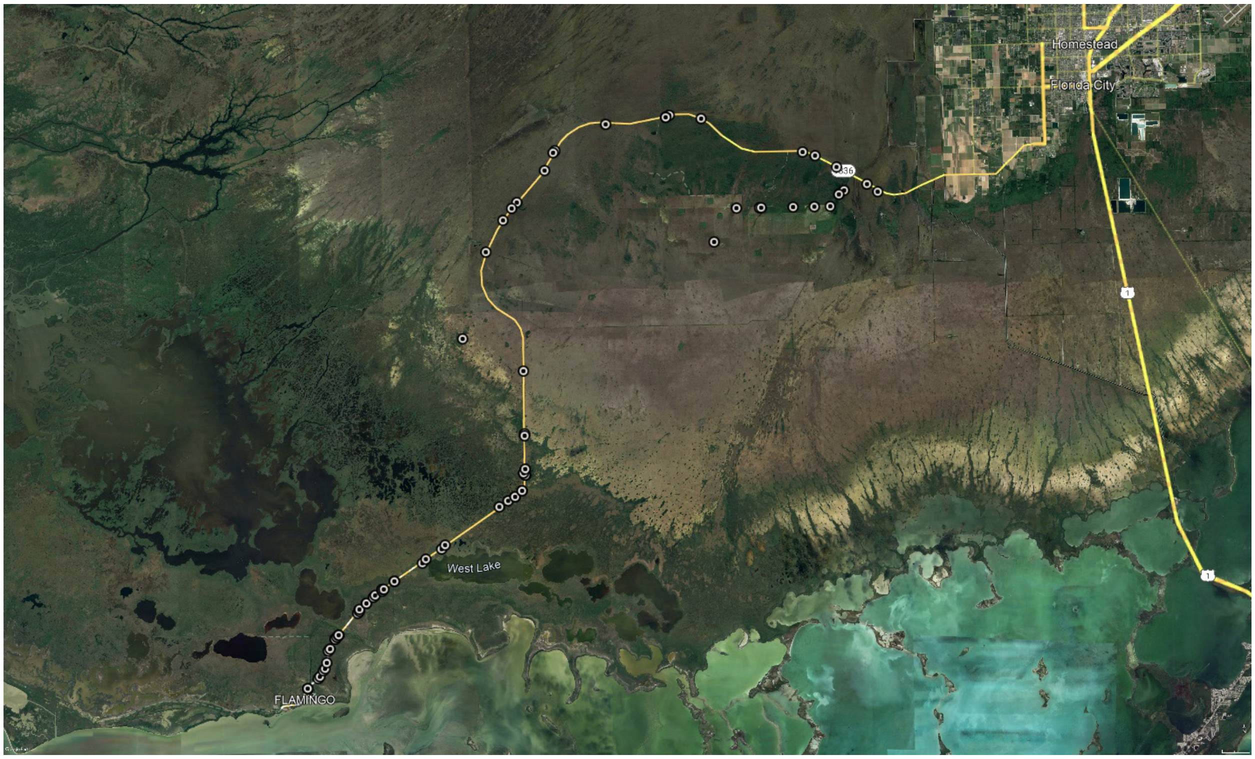

Figure 64. Distribution of the Red Cornsnake, *Pantherophis guttatus*, in Everglades National Park.

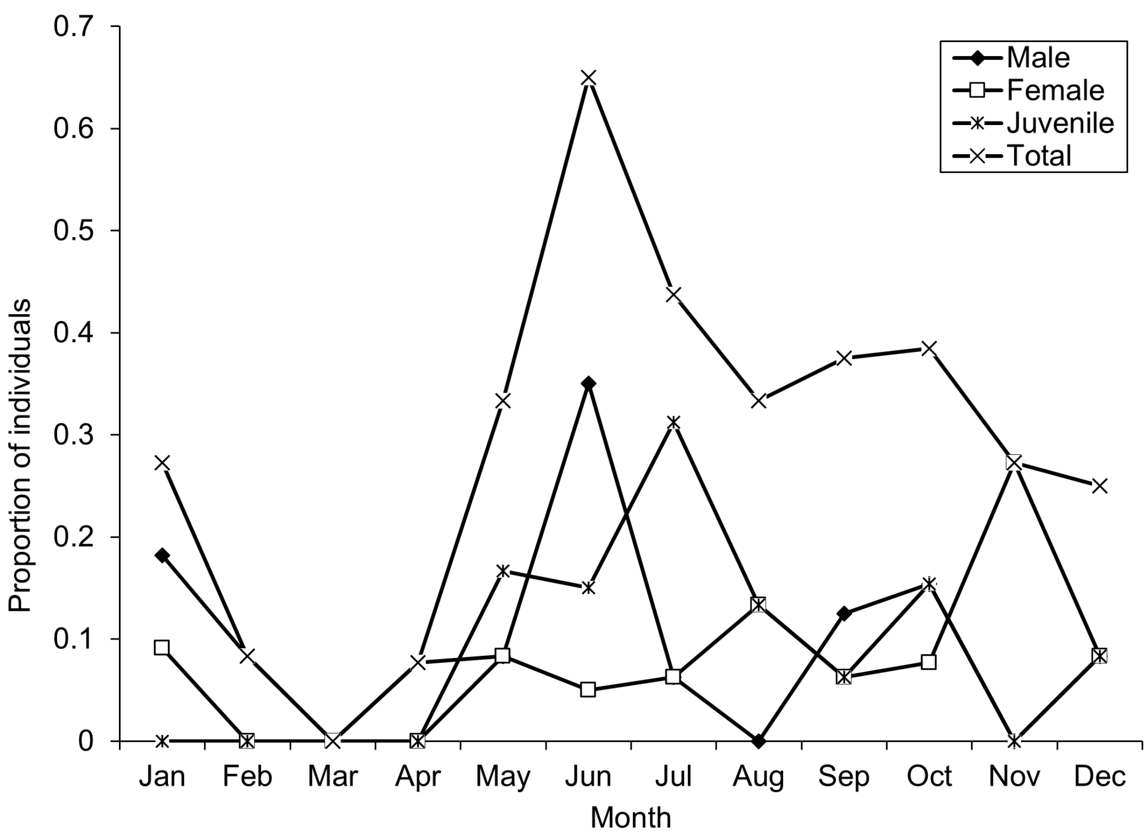

Figure 65. Monthly distribution of the Red Cornsnake, *Pantherophis guttatus*, crossing roads in Everglades National Park during 2009–2011.

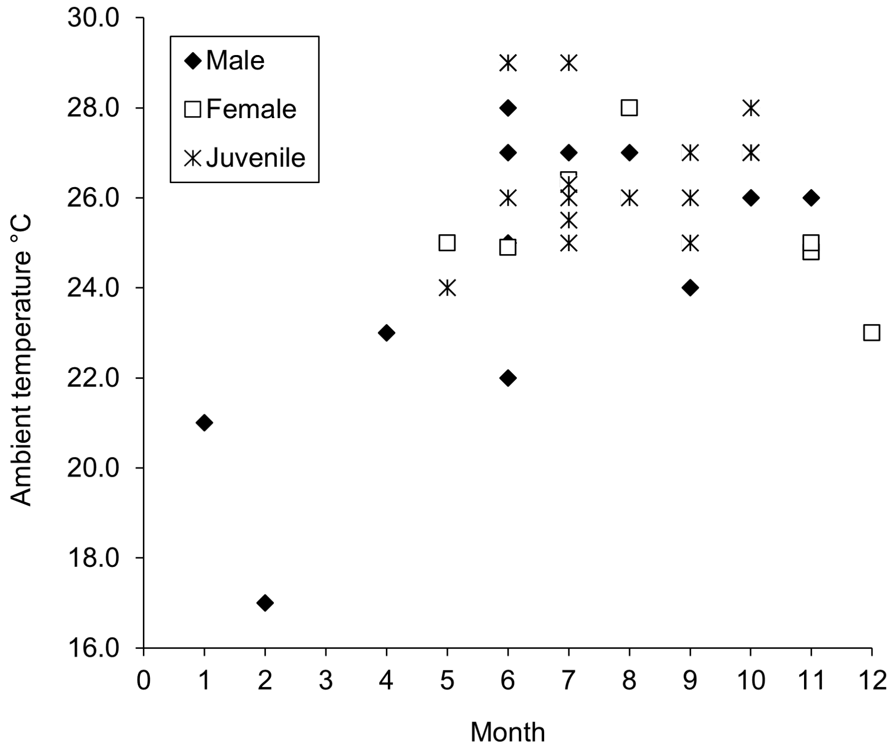

Figure 66. Ambient temperatures associated with the Red Cornsnake, *Pantherophis guttatus*, crossing roads at night in Everglades National Park during 2009–2011.

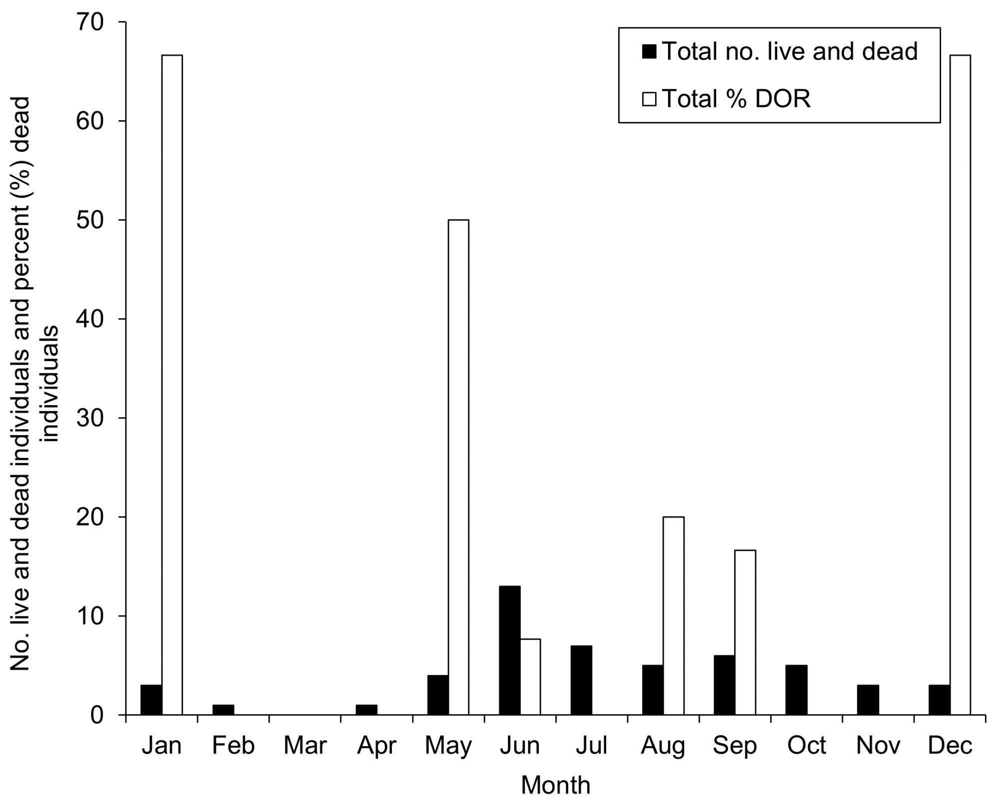

Figure 67. Monthly distribution of all and percent DOR Red Cornsnakes, *Pantherophis guttatus*, crossing roads at night in Everglades National Park during 2009–2011.

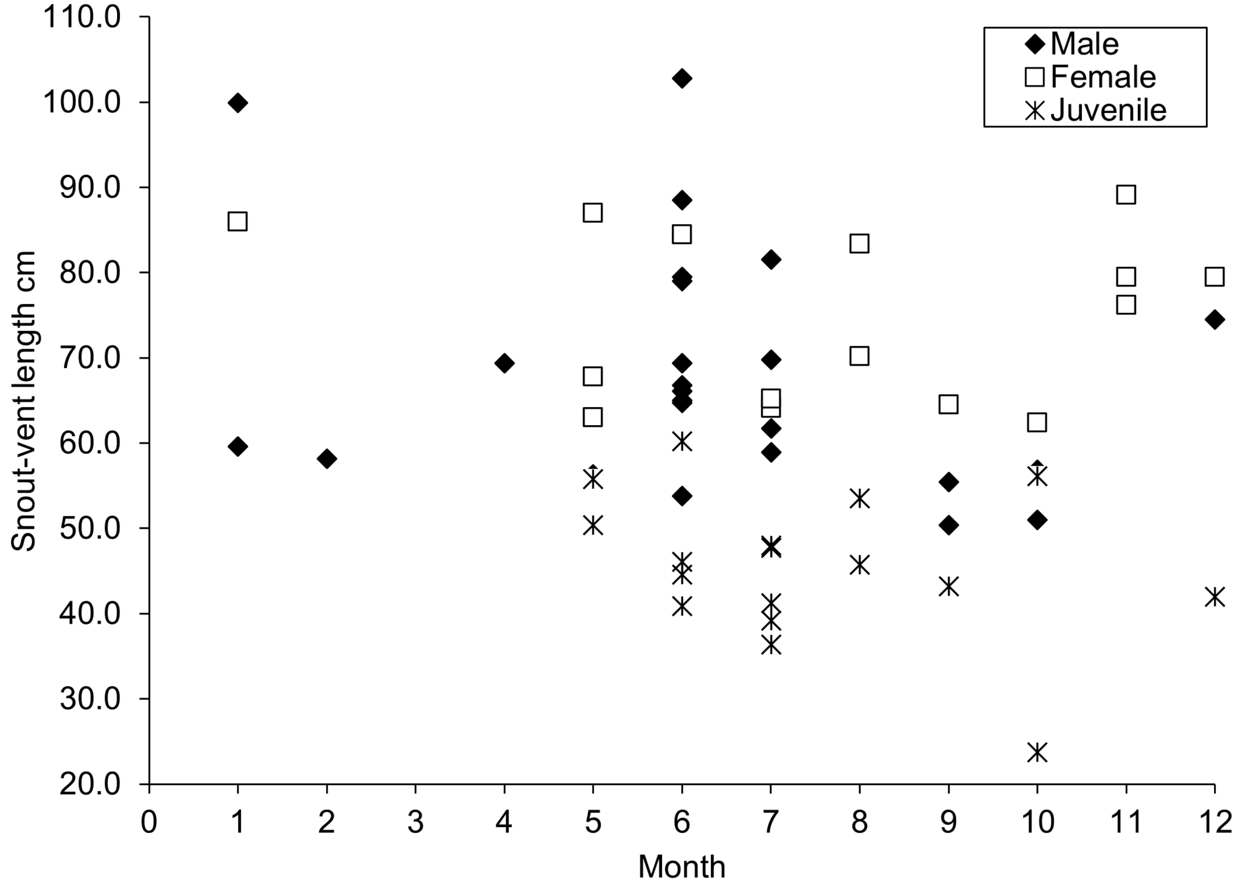

Figure 68. Monthly distribution of body sizes of the Red Cornsnake, *Pantherophis guttatus*, from Everglades National Park during 2008–2011.

Storeria victa Hay, 1892- Florida Brownsnake. (**Figure 69**).

Habitat association- The Florida Brownsnake occurred on Long Pine Key and at Pahayokee (**Table 4; Figure 70**). On Long Pine Key, this species was much less abundant during June–August at the time of our study than it was in the 1980s Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, zero males, three females, zero juveniles, and zero individuals of unknown status comprised the three total Florida Brownsnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were one male, zero females, zero juveniles, and zero individuals of unknown status comprising a total of one individual.

The Florida Brownsnake was uncommonly encountered during our study. The total number of sightings comprised 0.23% of all snakes seen during January–December of 2009–2011 **(Table 2)** and 0.28% of all snakes seen during March–December of 2008–2011 **(Table 3)**. Stable in assemblage composition among sampling periods, the Florida Brownsnake did not differ significantly during 2009–2011 ($X^2 = 2.00$, df = 2, $p > 0.05$) or during 2008–2011 ($X^2 = 2.00$, df = 3, $p > 0.05$). With only three adult females, having the male:female ratio among adult Florida Brownsnakes was 0.00:3.00 during 2009–2011. On Long Pine Key, the sex ratio was 0.54:1.00 (Dalrymple et al., 1991a). With only three adults in our sample, recruitment was 0.00%.

Monthly movements- Three individuals were encountered singly in March, August, and October. Consequently, we could not compare our findings with those of Dalrymple et al. (1991a) on Long Pine Key, where it was abundant. Too few individuals were encountered to examine relationships between monthly movements and environmental factors.

Ambient temperatures associated with nightly activity- One female (24.8 cm SVL) was captured at an ambient temperature 29.0 °C.

Roadkill dynamics- Florida Brownsnakes were killed by vehicles on the road. DOR Florida Brownsnakes comprised 0.41% of all DOR snakes and 66.67% of all conspecifics recorded during 2009–2011. Two of the three females encountered were DORs, one in March, the other in October. Too few individuals were encountered to examine the relationship between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, one adult male measured 20.7 cm SVL. Body sizes were available for three females (20.7, 20.7, 24.8 cm SVL). Male:female sexual size dimorphism of this sample was 0.94:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. From this sample, sexual size dimorphism of two males (Mean = 22.1 $\pm$ 4.8 cm SVL; range = 18.7–25.5) and seven females (Mean = 26.3 $\pm$ 2.2 cm SVL; range = 23.0–29.5) was 0.84:1.00. The combined samples of Meshaka and Layne (2015) and this study resulted in mean body sizes 21.6 cm SVL in males ($\pm$ 3.5 cm SVL; range = 18.7–25.5) and 25.0 cm SVL ($\pm$ 2.9 cm SVL; range = 20.7–29.5) in females with a male:female sexual size dimorphism value of 0.87:1.00 for Everglades National Park.

Figure 69. A Florida Brownsnake, *Storeria victa*, on the road in Everglades National Park. Photographed by Arik Hartmann.

Figure 70. Distribution of the Florida Brownsnake, *Storeria victa*, in Everglades National Park.

Thamnophis saurita sackenii (Kennicott, 1859)-Peninsula Ribbonsnake. (**Figure 71**).

Habitat association- The Peninsula Ribbonsnake occurred in all three regions of Everglades National Park (**Table 4; Figure 72**). However, reflecting a preference for long hydroperiod wetlands, encounter rates were highest at Pahayokee (X^2 = 32.96, *P* < 0.001), and equally low for Long Pine Key and the saline glades.

Population structure- During the three full calendar years of 2009–2011, 53 males, 68 females, 13 juveniles, and 52 individuals of unknown status comprised the 186 total Peninsula Ribbonsnakes, live and dead, encountered on the road at night. The male:female sex ratio did not differ from unity (X^2 = 1.860, df = 1, p > 0.05) in this sample. Counterparts recorded during March–December 2008 were zero males, 10 females, two juveniles, and two individuals of unknown status comprising a total of 14 individuals.

The Peninsula Ribbonsnake was the third commonly encountered snake during our study. The total number of sightings comprised 14.19% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 12.99% of all snakes seen during March–December of 2008–2011 (**Table 3**). Numbers of individuals differed significantly during 2009–2011 in association with a very low water table in 2011.

The male:female ratio among adults was 0.78:1.00 during 2009–2011 and did not vary from unity (X^2 = 1.860, df = 1, P > 0.05). Males were most common in 2011: 0.71:1.00, in 2009, 0.83:1.00 in 2010, and 0.88:1.00 in 2011. On Long Pine Key, the sex ratio was 0.96:1.00 (Dalrymple et al., 1991a) and did not vary from unity (X^2 = 0.044, df = 1, p > 0.05). Adults comprised approximately two-thirds of actively moving individuals. Excluding individuals of unknown category, juveniles comprised 9.70% of observations during 2009–2011. Recruitment was highest in 2011: 10.17% in 2009, 7.02% in 2010, and 16.67% in 2011. When individuals of unknown category were included, respective percentages of young were lower: 6.99% in 2009–2011; 7.90% in 2009, 5.00% in 2010, and 10.00% in 2011.

Monthly movements- The Peninsula Ribbonsnake was active year-round in Everglades National Park. Collectively, this species was most active in March and October (**Figure 67**). Males were most active in April (**Figure 73**). Female and juvenile movements were greatest in March and October. (**Figure 73**). In an earlier study on Long Pine Key (Dalrymple et al., 1991a), annual activity peaked during June–July, followed by a lesser peak in October. In that same study, males were most active during June–August, and females during May–July. Relationships between monthly movements by the Peninsula Ribbonsnake and environmental factors approached significance with air temperatures (**Table 15**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Peninsula Ribbonsnake ranged 22.0–29.0 °C (**Figure 74**). Mean ambient temperatures did not significantly differ (t-test, p > 0.05) among males (24.7 $\pm$ 2.8 °C; range = 17.0–28.0; n = 16), females (25.8 $\pm$ 1.8 °C; range = 22.4–29.0; n = 37), and juveniles (25.1 $\pm$ 2.6 °C; range = 22.0–29.0; n = 8). Ambient temperatures associated with all 61 individuals combined averaged 25.4 °C ($\pm$ 2.2 °C; range = 17.0–29.0).

Roadkill dynamics- Peninsula Ribbonsnakes were killed by vehicles on the road. DOR individuals comprised 19.11% of all DOR snakes and 50.54% of all conspecifics recorded during 2009–2011. Peninsula Ribbonsnakes were killed throughout the year, with the highest incidence of DOR individuals during January–March (**Figure 75**). No significant relationship (Multiple R = 0.56, *P* = 0.059) was detected between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 40.7 $\pm$ 4.1 cm SVL; range = 32.0–51.7; n = 53) differed significantly than that of females (Mean = 43.6 $\pm$ 5.7 cm SVL; range = 33.3–71.2; n = 78) with respect to variance (F = 0.5085, *P* = 0.005) and mean (t = -3.339, df = 129, *P* = 0.001). Male:female sexual size dimorphism of this sample was 0.93:1.00.

A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Mean body size of males (Mean = 40.1 $\pm$ 5.9 cm SVL; range = 32.0–52.4; n = 22) and females (Mean = 45.4 $\pm$ 6.3 cm SVL; range = 33.4–67.1; n = 59) differed significantly (F = 0.614, P = 0.11; t = -3.571, df = 79, P < 0.0006) from one another. Male:female sexual size dimorphism of this sample was 0.89:1.00. A comparison of body sizes between the samples of this study and from Meshaka and Layne (2015) revealed no significant difference in body size of males (F = 1.474, P = 0.13; t = 0.549, df = 73, P = 0.59) or females (F = 1.220, P = 0.21; t = 1.817, df = 135, P = 0.07). The combined sample resulted in significant differences (F = 0.514, P = 0.001; t = -5.354, df = 195, P < 0.0000) between body sizes of males (Mean = 40.5 $\pm$ 4.3 cm SVL; range = 32.0–52.4; n = 75) and females (Mean = 44.4 $\pm$ 6.0 cm SVL; range = 33.3–71.2; n = 137). The sexual size dimorphism of the combined sample was 0.91:100. Monthly distribution of body sizes **(Figure 76)** suggests that the Peninsula Ribbonsnake is a fast-growing species in Everglades National Park. Minimum body size at sexual maturity for both sexes could be reached before one year of life.

Reproduction- Gravid females were found as DORs on 20 June 2009 (44.0 cm SVL) and on 7 July 2010 (55.9 cm SVL). Twelve embryos were palped from the latter female. On Long Pine Key, females were gravid in June and August–October, and one female gave birth in July (Dalrymple et al., 1991a). From the Everglades National Park sample of Meshaka and Layne (2015), near-term females were evident during May–October. Estimates of clutch size based on enlarged follicles (Mean = 8.6 $\pm$ 3.8 young; range = 4–17; n = 11) and near-term young (Mean = 8.2 $\pm$ 1.9 young; range = 5–10 n = 6) did not differ significantly from one another (F = 3.731, P = 0.08; t = -0.284, df = 15, P = 0.78). Combined clutch size for 17 Peninsula Ribbonsnakes (46.7 $\pm$ 6.5 cm SVL; range = 35.8–56.4) averaged 8.5 young ($\pm$ 3.2 young; range = 4–17). A strong causative relationship existed between clutch size and female body size (r^2 = 0.47, P = 0.002; Y = 0.3323X – 7.0368) in this combined sample from Everglades National Park.

Diet- From individuals encountered on the road during 2008–2011, an individual of unrecorded body size or sex was encountered on 26 October 2010 as it was eating a Southern Leopard Frog. A 40.6 cm SVL was encountered on 9 September 2009 as it was eating a Southern Leopard Frog. An individual of unrecorded body size or sex was encountered on 21 April 2010 as a DOR having been in the process of eating a fish. A 40.9 cm SVL male with a food bulge was encountered on 21 March 2010.

Injury- From individuals encountered on the road during 2008–2011, a 46.7 cm SVL male was encountered having a scar half-way down its body. Bobbed tails were present on one male (38.2 cm SVL), three females (41.3, 48.6, 71.2 cm SVL), and one individual of unknown sex or body size. Consequently, bobbed tails were present on 1.89% of males, 3.85% of females, and 2.50% of the population.

Table 15. Relationship of environmental conditions to monthly movements of the Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, in Everglades national Park during 2009–2011.

Environmental factors	Correlation coefficient, *P* value
Mean monthly maximum air temperature	r = 0.42, *P* = 0.18
Mean monthly minimum air temperature	r = 0.41, *P* = 0.19
Total monthly rainfall volume	r = 0.26, *P* = 0.42
Mean monthly water level	r = 0.10, *P* = 0.75

Figure 71. A Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, from Everglades National Park. (A) Photographed by M. Rochford. (B) Close-up of a bluish-patterned individual. Photographed by Arik Hartmann.

Figure 72. Distribution of the Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, in Everglades National Park.

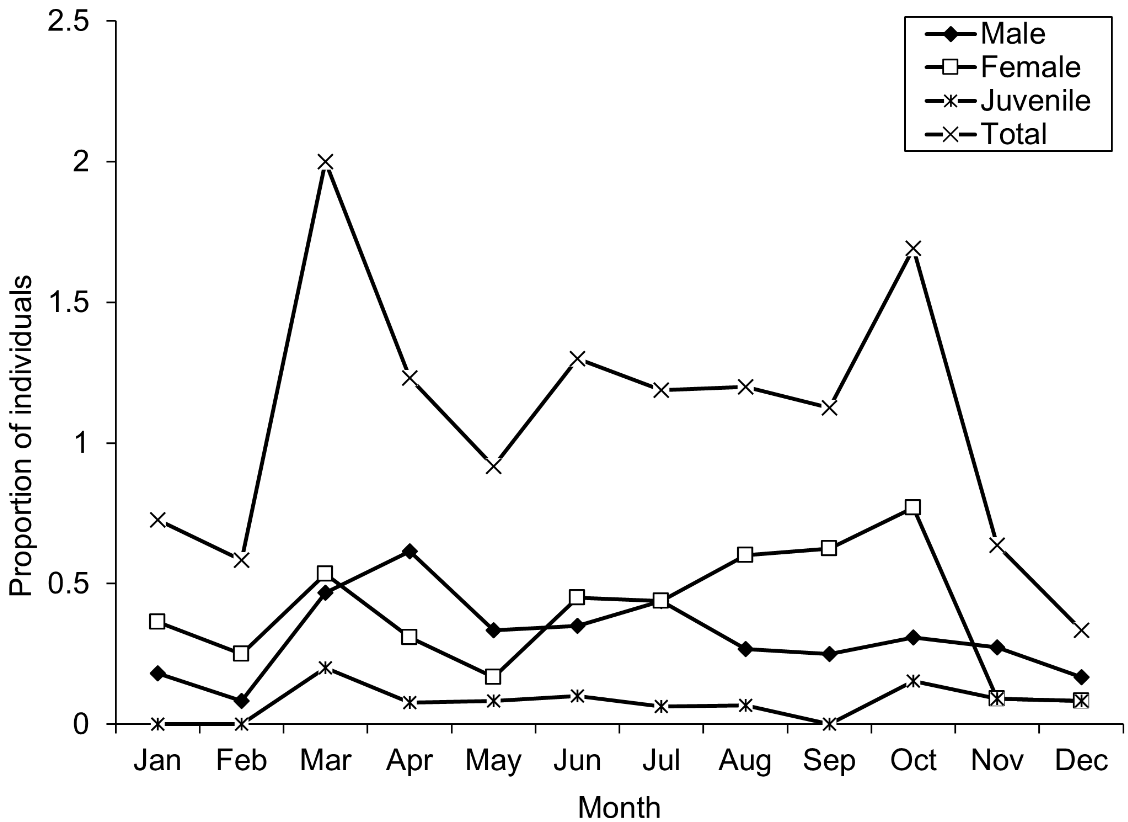

Figure 73. Monthly distribution of the Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, crossing roads in Everglades National Park. A = Males, females, and juveniles during 2009–2011. B = All individuals during 2009–2011.

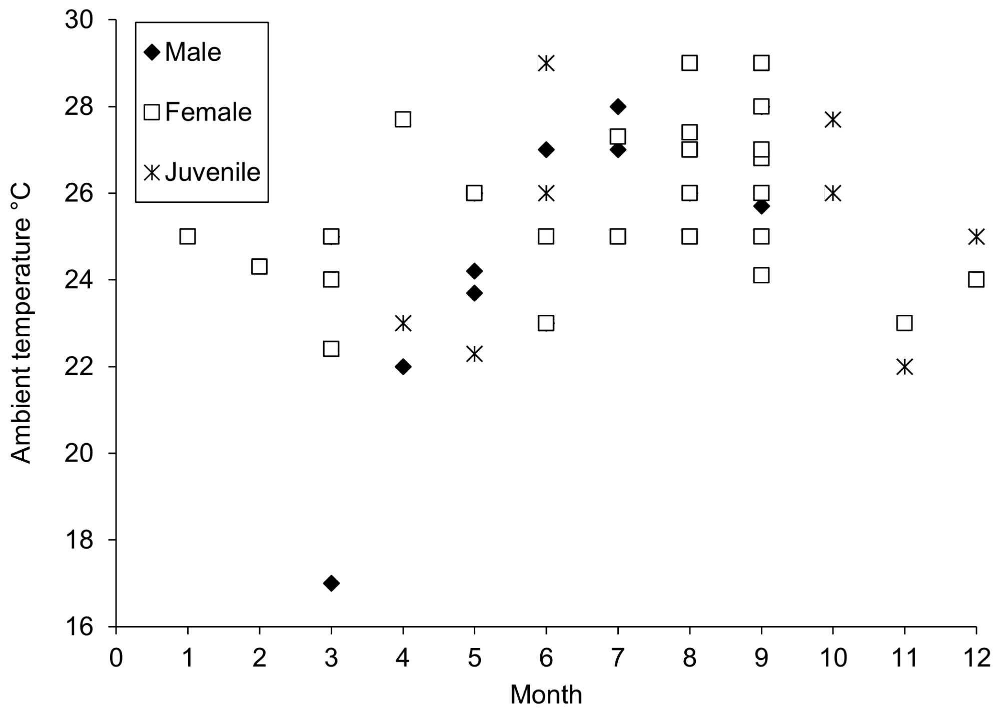

Figure 74. Ambient temperatures associated with the Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, crossing roads at night in Everglades National Park during 2009–2011.

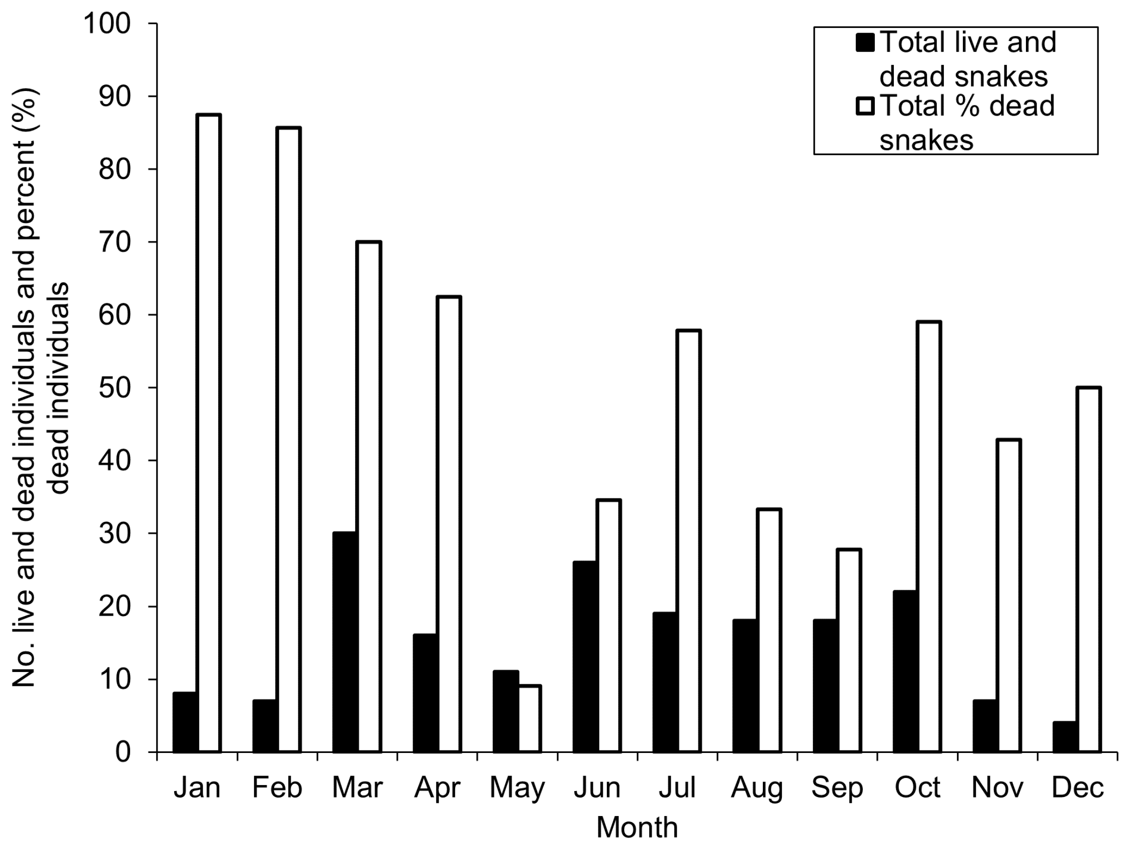

Figure 75. Monthly distribution of all and percent dead individuals of the Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, on roads at night in Everglades National Park during 2009–2011.

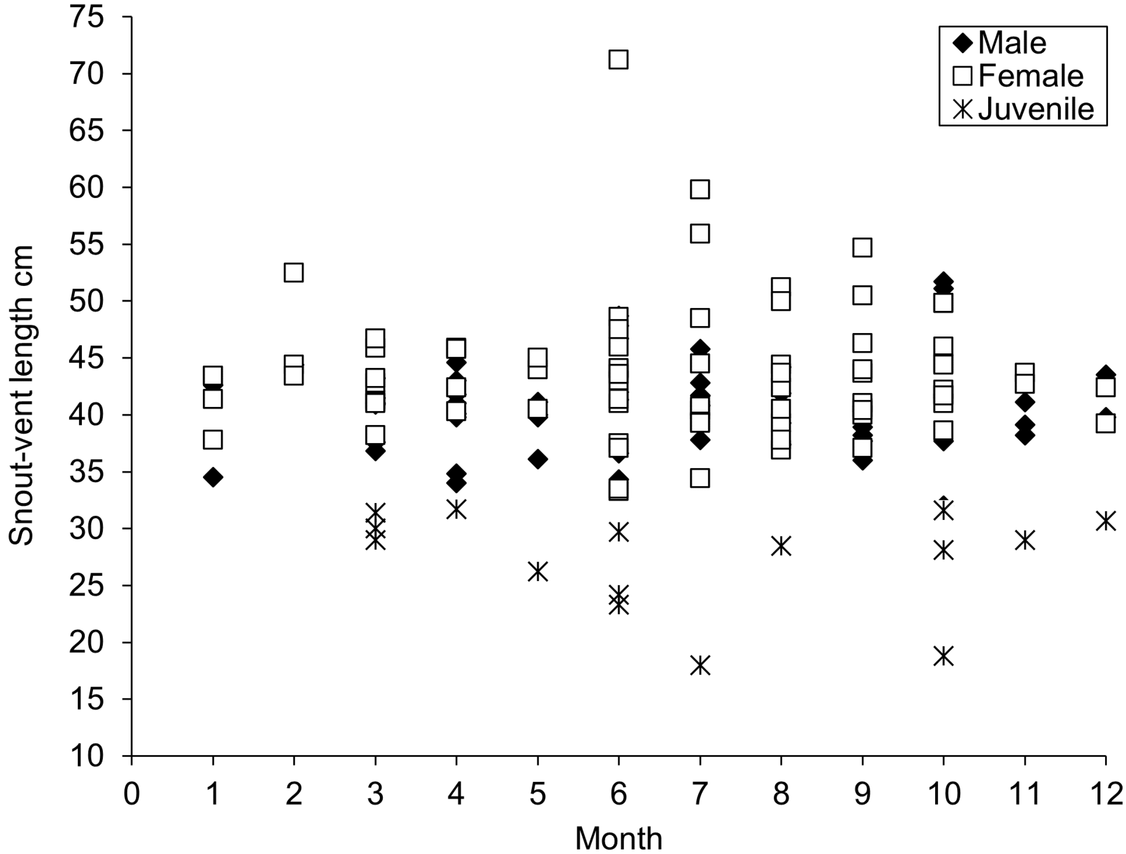

Figure 76. Monthly distribution of body sizes of the Peninsula Ribbonsnake, *Thamnophis saurita sackenii*, from Everglades National Park during 2008–2011.

Thamnophis sirtalis sirtalis (Linnaeus, 1858)- Eastern Gartersnake (**Figure 77**).

Habitat association- The Eastern Gartersnake occurred in all three regions of Everglades National Park (**Table 4; Figure 78**). Its encounter rates, highest on Long Pine Key and lowest at Pahayokee, were nonrandom among the three regions (X^2 = 12.65, df = 2, *P* < 0.001). On Long Pine Key, this species was much more abundant during June–August at the time of our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, 50 males, 72 females, 10 juveniles, and 39 individuals of unknown status comprised the 171 total number of Eastern Gartersnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were eight males, 22 females, two juveniles, and nine individuals of unknown status comprising a total of 41 individuals. The male:female sex ratio did not differ from unity (X^2 = 3.97, df = 1, P < 0.05) in this sample nor in that from Long Pine Key (Dalrymple et al., 1991a) (X^2 = 9.830, df = 1, P < 0.01).

The Eastern Gartersnake was the fourth most commonly encountered snake during our study. The total number of sightings comprised 13.04% during 2009–2011 (**Table 2**) and 13.06% of all snakes seen during 2008–2011 (**Table 3**). Numbers of individuals differed significantly during 2009–2011 in association with a very low water table in 2011.

The male:female ratio among adult Eastern Gartersnakes was 0.69:1.00 during 2009–2011. Males were most common in 2011: 0.70:1.00 in 2009, 0.65:1.00 in 2010, and 0.78:1.00 in 2011. The sex ratio of Eastern Gartersnakes on Long Pine Key was 0.61:1.00 (Dalrymple et al., 1991a). Adults comprised the overwhelming number of records of actively moving individuals. Recruitment was highest in 2011. Excluding individuals of unknown category, juveniles comprised 7.58% of observations during 2009–2011. Recruitment was at 7.60% in 2009, 2.94% in 2010 and 15.79% in 2011. When individuals of unknown category were included, respective percentages of young were also low: 5.85% in 2009–2011; 5.89% in 2009, 2.38% in 2010 and 11.1% in 2011.

Monthly movements- The Eastern Gartersnake was active year-round in Everglades National Park. Collectively, seasonal overland movements were unimodal, with the fewest individuals seen in December and most in November. (**Figure 79**). Male movements peaked in November, and those of females peaked in June and November (**Figure 79**). Juveniles were encountered intermittently and found during March–April and September–October (**Figure 79**). On Long Pine Key, annual activity of the species generally was bimodal; increasing gradually until July, crashing and peaking almost twice that of the earlier peak in October (Dalrymple et al., 1991a). Males and females of that study shared the same bimodality of the species. No environmental factors that we measured were significantly associated with monthly movements in this species (**Table 16**). However, water table level approached most closely to statistical significance in the movements of this semi-aquatic species.

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Eastern Gartersnake ranged 21.0–29.0 °C (**Figure 80**). Mean ambient temperatures did not significantly differ (ANOVA F = 2.000, p = 0.14) among males (23.8 $\pm$ 2.9 °C; range = 17.0–29.1; n = 21), females (25.3 $\pm$ 3.1 °C; range = 13.0–30.0; n = 46), and juveniles (25.2 $\pm$ 1.1 °C; range = 23.5–26.0; n = 5). Ambient temperatures associated with all 72 individuals combined averaged 24.9 °C ($\pm$ 3.0 °C; range = 13.0–20.0).

Roadkill dynamics- The Eastern Gartersnake was subject to being roadkilled in Everglades National Park. DOR Eastern Gartersnakes comprised 16.06% of all DOR snakes but 46.20% of all conspecifics recorded during 2009–2011. The highest incidence of roadkill occurred during the coolest months **(Figure 81)**. No significant relationship existed (Multiple R = 0.47, *P* = 0.12) between %DORs and total number of individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (mean = 49.2 $\pm$ 8.2 cm SVL; range = 32.5–62.0; n = 58) differed significantly than that of females (mean = 55.7 $\pm$ 11.1 cm SVL; range = 35.1–81.5; n = 94) with respect to variance (F = 0.551, df = 57, *P* = 0.008) and mean (T = -3.905, df = 150, *P* = 0.0001). Male:female sexual size dimorphism of this sample was 0.88:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Adult body sizes of males (Mean = 49.9 $\pm$ 7.9 cm SVL; range = 33.3–63.2; n = 21) and females (Mean = 53.2 $\pm$ 9.6 cm SVL; range = 35.1–71.4; n = 40) did not differ significantly (F = 0.674, P = 0.17; t = -1.349, df = 59, P = 0.18) from one another. Male:female sexual size dimorphism of this sample was 0.90:1.00. A comparison of body sizes between the samples of this study and from Meshaka and Layne (2015) revealed no significant differences in either males (F = 0.921, P = 0.44; t = 0.344, df = 77, P = 0.73) or females (F = 0.754, P = 0.16; t = -1.276, df = 132, P = 0.20). The combined sample resulted in significant differences (F = 0.573, P = 0.004; t = -4.334, df = 198, P < 0.0000) in body sizes between males (Mean = 49.4 $\pm$ 8.1 cm SVL; range = 32.5–63.2; n = 79) and females (Mean = 55.0 $\pm$ 10.1 cm SVL; range = 35.1–81.5; n = 134). The sexual size dimorphism of the combined sample was 0.90:100. Smallest individuals (25.3, 25.7 cm SVL) were found in September (**Figure 82**). This species grows quickly in Everglades National Park. Monthly distribution of body sizes **(Figure 82)** suggests that minimum body size at sexual maturity for both sexes could be reached by one year of life or shortly thereafter.

Reproduction- Gravid females were found on 19 September 2008 (61.7 cm SVL) and on 3 June 2009 (74.0 cm SVL). Females from Long Pine Key gave birth in May, July, and November (Dalrymple et al., 1991). The subset of Everglades National Park data from Meshaka and Layne (2015) contained one record of clutch size: A 60.2 cm SVL female contained eight fully formed young in July. The relative clutch mass (clutch mass/clutch mass + body mass X 100) was 35.6%.

Diet- A 44.9 cm SVL female and 25.3 cm juvenile both captured on 15 September 2009 were encountered as each of them was eating a Southern Leopard Frog. An individual of unrecorded body size or sex was encountered on 12 September 2008 as it was eating a Southern Leopard Frog. An individual of unrecorded body size or sex was encountered on 4 November 2009 as it was eating a *Lithobates* species. A 32.6 cm SVL juvenile captured on 29 September 2010 voided live earthworms from its cloaca. An individual of unrecorded body size or sex was encountered on 13 August 2009 as it was eating a Southern Toad, *Anaxyrus terrestris*. A juvenile of 29.6 cm SVL captured on 11 June 2008 regurgitated a freshly-ingested Southern Toad.

Injury- Bobbed tails were found on four males (mean = 52.3 ± 3.7 cm SVL; range = 47.8–55.7) and 10 females (mean = 54.5 ± 11.8 cm AVL; range = 40.6–74.0). Consequently, 6.90% of males, 14.89% of females, and 6.60% of the population were missing a portion of their tail.

Table 16. Relationship of environmental conditions to monthly movements of the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, in Everglades National Park during 2009–2011.

Environmental factors	2009	2009–2011
Mean monthly maximum air temperature	r = 0.14, *P* = 0.68	r = 0.06, *P* = 0.85
Mean monthly minimum air temperature	r = 0.11, *P* = 0.74	r = 0.04, *P* = 0.91
Total monthly rainfall volume	r = 0.07, *P* = 0.84	r = 0.10, *P* = 0.77
Mean monthly water level	r = 0.39, *P* = 0.21	r = 0.43, *P* = 0.17

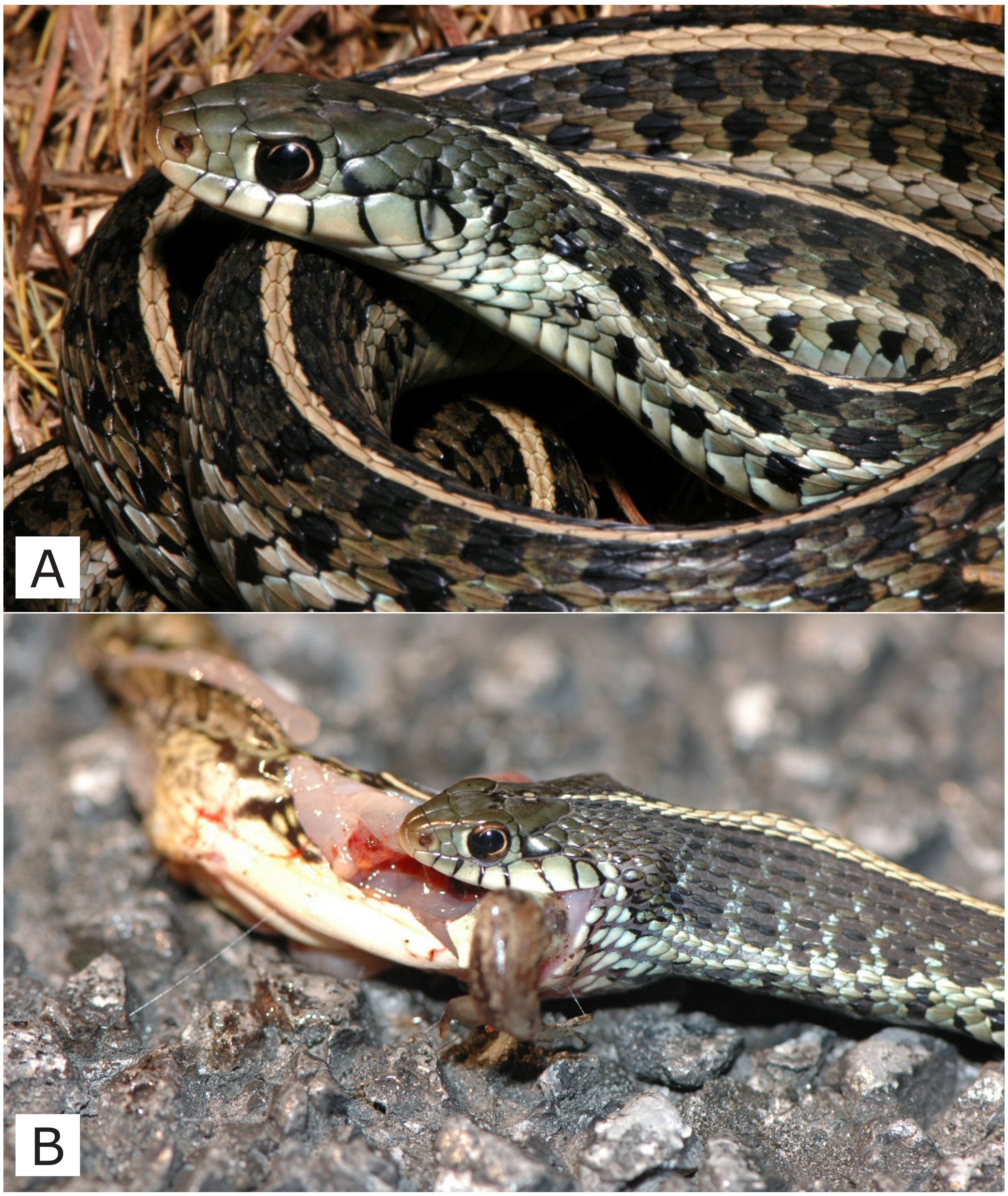

Figure 77. An Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, at rest (A) and foraging on a road-killed Southern Leopard Frog, *Lithobates sphenocephalus*, on the road (B) in Everglades National Park. Photographed by M. Rochford.

Figure 78. Distribution of the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, in Everglades National Park.

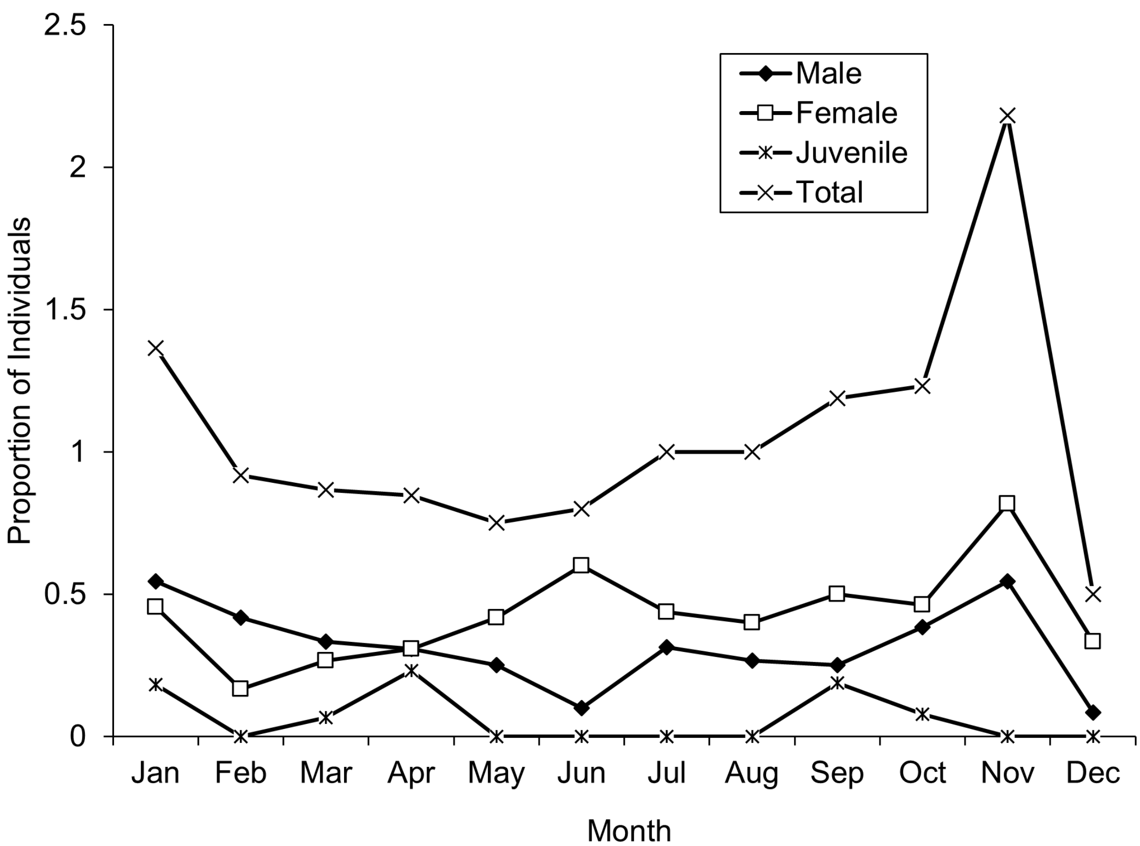

Figure 79. Monthly distribution of Eastern Gartersnakes, *Thamnophis sirtalis sirtalis,* crossing roads in Everglades National Park during 2009–2011.

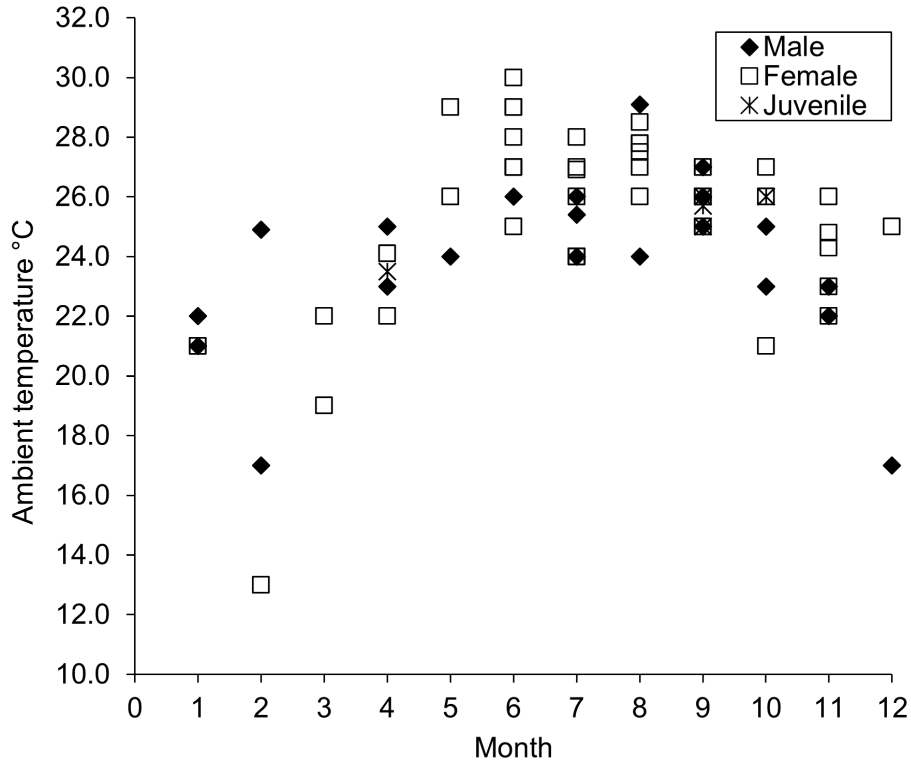

Figure 80. Ambient temperatures associated with the Eastern Gartersnake, *Thamnophis sirtalis sirtalis,* crossing roads at night in Everglades National Park during 2009–2011.

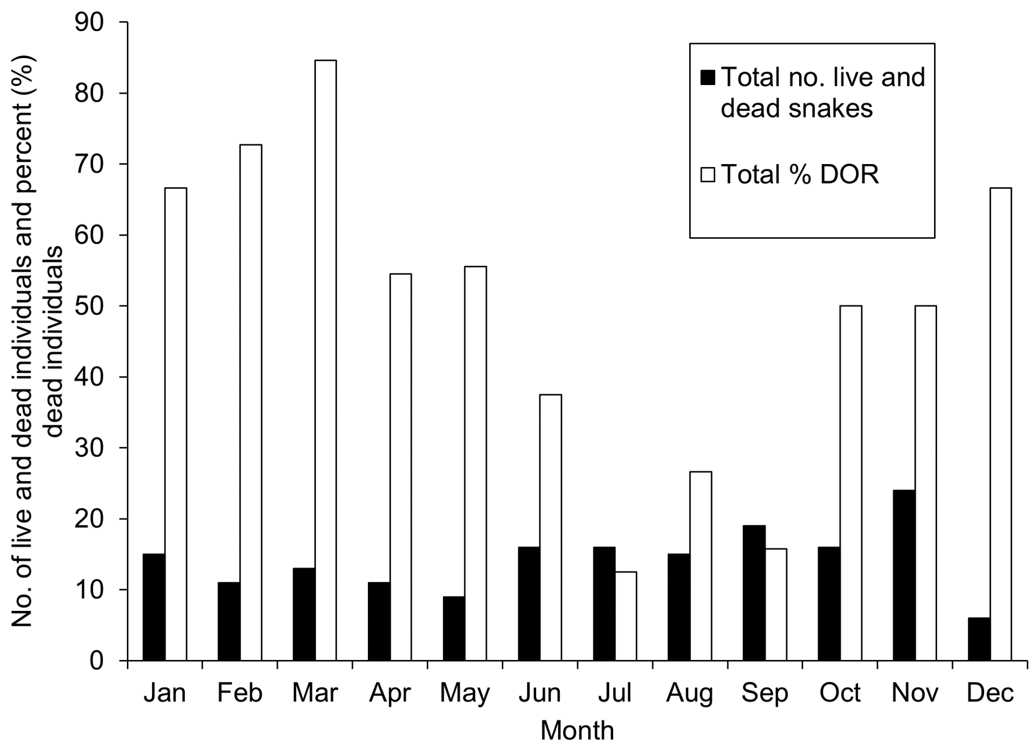

Figure 81. Monthly distribution of all and percent dead individuals of the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, on roads at night in Everglades National Park during 2009–2011.

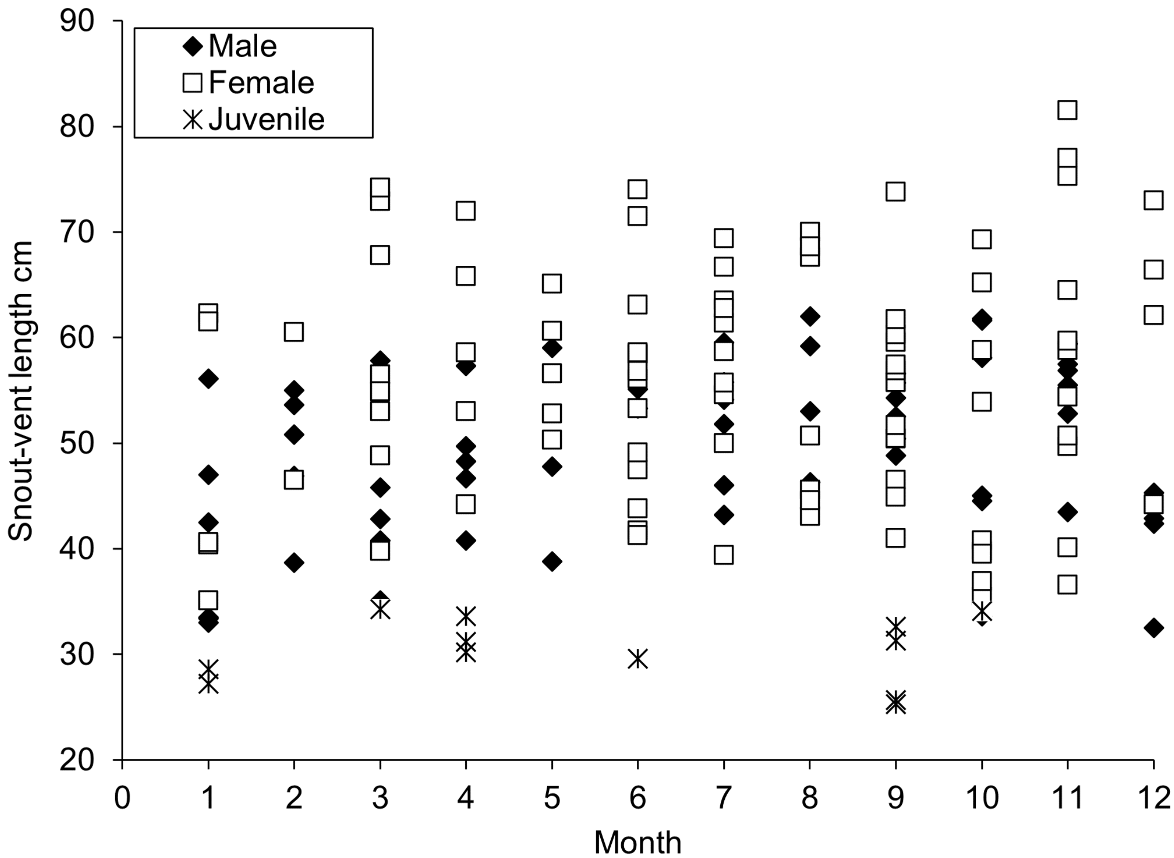

Figure 82. Monthly distribution of body sizes of the Eastern Gartersnake, *Thamnophis sirtalis sirtalis,* from Everglades National Park during 2008–2011.

Python bivittatus Kuhl, 1820- Burmese Python (**Figure 83**).

Habitat association- The Burmese Python was found in all three regions of Everglades National Park (**Table 4; Figure 84**). Its encounter rate was highest in the saline glades, the area from which its establishment in the park was first documented (Table 4). This species was not detected anywhere in Everglades National Park by Dalrymple et al. (1991a).

Population structure- During the three full calendar years of 2009–2011, zero males, zero females, zero juveniles, and 20 individuals of unknown status comprised the 20 total Burmese Pythons, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were zero males, zero females, four juveniles, and nine individuals of unknown status comprising a total of 13 individuals.

The Burmese Python was uncommonly encountered during our study. The total number of sightings comprised 1.53% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 2.32% of all snakes seen during March–December of 2008–2011) (**Table 3**). The numbers of individuals did not differ significantly during 2009–2011 in association with a very low water table in 2011 (**Table 3**)

The male:female ratio among adult Burmese Pythons was unknown during 2009–2011. Excluding individuals of unknown category, juveniles comprised 0.00% of observations during 2009–2011. When individuals of unknown category were included, percentage was also 0.00% during 2009–2011.

Monthly movements- The Burmese Python was active during March–December (**Figure 79**). Numbers of encounters were highest in June and November, the fewest in spring and in August (**Figure 85**). Relationships between monthly movements by the Burmese Python and environmental factors were not significant (**Table 17**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Burmese Python ranged 25.7–28.8 °C (**Figure 86**). Ambient temperatures associated with all 10 individuals combined averaged 25.8 °C ($\pm$ 2.2 °C; range =22.0–28.8).

Roadkill dynamics- One Burmese Python was killed by a vehicle on the road. DOR Burmese Pythons comprised 0.20% of all DOR snakes and 5.00% of all conspecifics recorded during 2009–2011. The single DOR Burmese Python was encountered in September.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, four juveniles measuring 47.2, 48.5, 52.0, and 53.6 cm SVL were encountered 9 July 2008.

Injury- From individuals encountered on the road during 2008–2011, one individual of undetermined sex or size was found to have a bobbed tail. Consequently, 3.03% of the sampled population was missing a portion of its tail.

Table 17. Relationship of environmental conditions to monthly movements of the Burmese Python, *Python bivittatus*, in Everglades National Park during 2009–2011.

Environmental factors	2009–2011
Mean monthly maximum air temperature	r = 0.49, P = 0.11
Mean monthly minimum air temperature	r = 0.51, P = 0.09
Total monthly rainfall volume	r = 0.47, P = 0.13
Mean monthly water level	r = 0.43, P = 0.16

Figure 83. A Burmese Python, *Python bivittatus*, (A) guarding its nest and (B) a large individual crossing the road at night, both in Everglades National Park. Photographed by M. Rochford.

Figure 84. Distribution of the Burmese Python, *Python bivittatus*, in Everglades National Park.

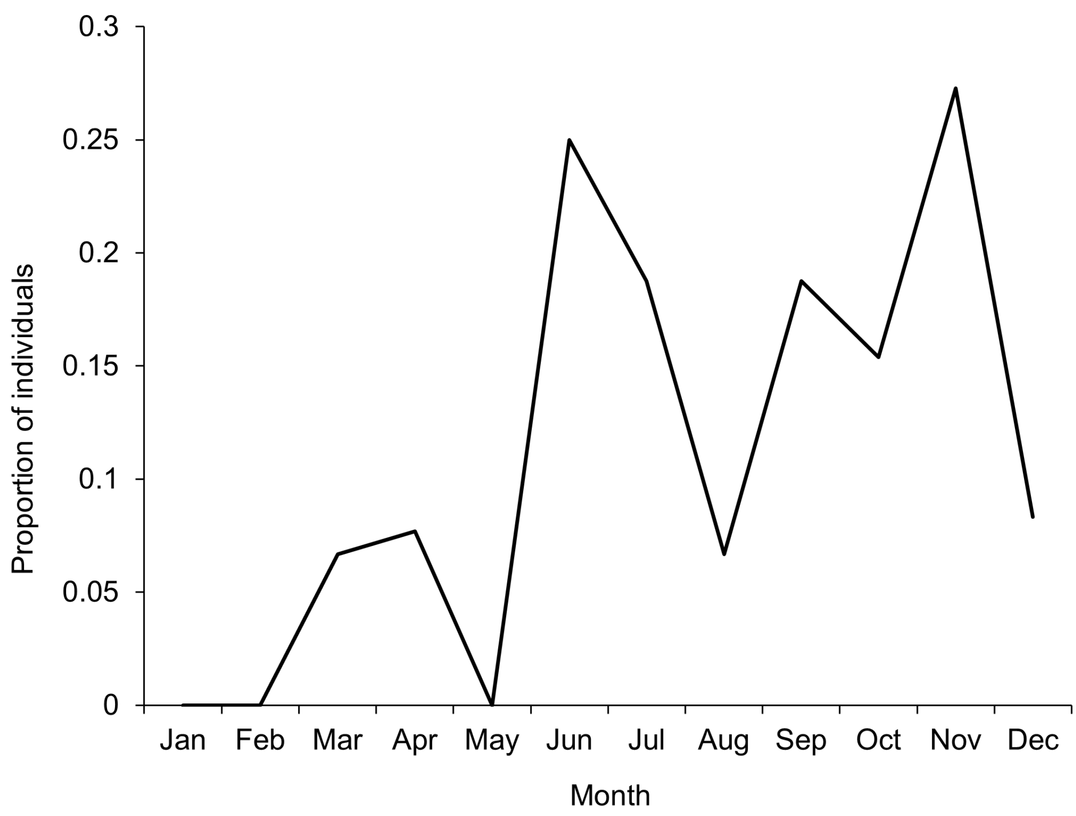

Figure 85. Monthly distribution of the Burmese Python, *Python bivittatus*, crossing roads in Everglades National Park during 2009–2011.

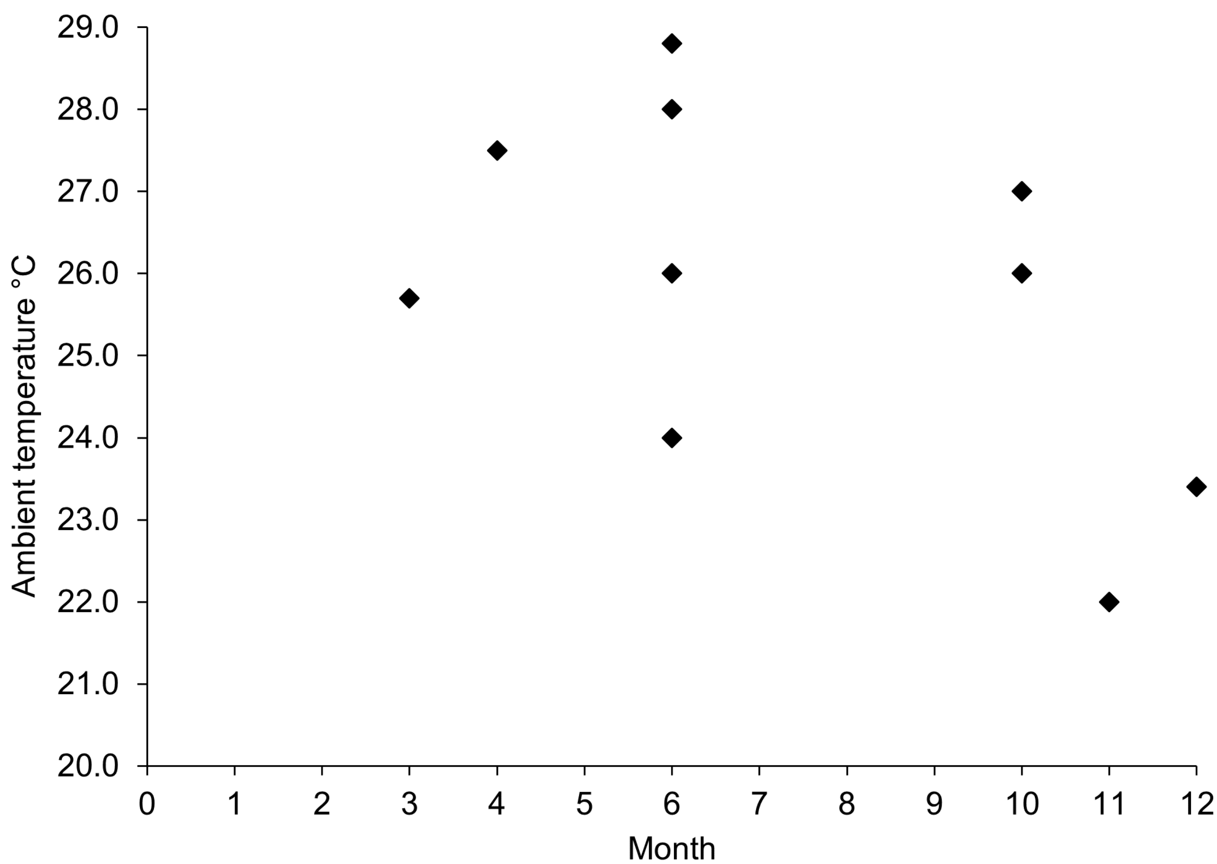

Figure 86. Ambient temperatures associated with the Burmese Python, *Python bivittatus*, crossing roads at night in Everglades National Park during 2009–2011.

Micrurus fulvius barbouri (Schmidt, 1928)- South Florida Coralsnake (**Figure 87**).

Habitat association- Strongly an upland snake, the South Florida Coralsnake was found exclusively on Long Pine Key (**Table 4; Figure 88**). Perhaps, owing to its diurnal habits, individuals were scarcely detected even in its preferred habitat.

Population structure- During the three full calendar years of 2009–2011, a single female comprised the total South Florida Coralsnakes, live and dead, encountered on the road at night. No counterparts were encountered during March–December 2008.

The South Florida Coralsnake was one of the three fewest species encountered during our study. The total number of sightings comprised 0.08% of all snakes seen during January–December of 2009–2011 **(Table 2)** and 0.07% of all snakes seen during March–December of 2008–2011 **(Table 3)**. The distribution of this species did not differ significantly during 2009–2011 ($X^2 = 2.00$, df = 2, $P > 0.05$) or during 2008–2011 ($X^2 = 3.00$, df = 3, $P > 0.05$).

Monthly movements- The South Florida Coralsnake was encountered once during our study. A live adult female was found on 20 April 2009. Consequently, we could not compare our findings with those of Dalrymple et al. (1991a) on Long Pine Key, where they encountered 22 individuals.

Ambient temperatures associated with nightly activity- Ambient temperature associated with the single adult female measured 24.0 °C.

Adult body size and age at sexual maturity- The single adult female we found measured 64.5 cm SVL. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Mean body sizes of eight males (mean = 53.5 $\pm$ 6.1 cm SVL; range = 44.0–63.2) and two females (mean = 56.7 $\pm$ 1.3 cm SVL; range = 55.7–57.6) provided a male:female sexual dimorphism value of 0.90:1.00. The combined samples of females provided an average SVL of 59.3 $\pm$ 4.6 cm SVL; range = 55.7–64.5) and a sexual size dimorphism value of 0.90:1.00.

Figure 87. A South Florida Coralsnake, *Micrurus fulvius barbouri*, from Everglades National Park. (A) Photographed by M. Rochford. (B) Dead and (C) live on the road (B, C) Photographed by Arik Hartmann.

Figure 88. The distribution of the South Florida Coralsnake, *Micrurus fulvius barbouri*, in Everglades National Park.

Agkistrodon conanti Gloyd, 1969- Florida Cottonmouth (**Figure 89**).

Habitat association- The Florida Cottonmouth occurred in all three regions of Everglades National Park (**Table 4; Figure 90**). Its habitat distribution was nonrandom (X^2 = 116.22, df = 2, *P* < 0.001) and it was the dominant snake on Long Pine Key and at Pahayokee, where it was twice as common in the freshwater wetlands than upland habitat (**Table 4**). On Long Pine Key, this species was much more abundant during June–August during our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, 57 males, 56 females, 139 Juveniles, and 70 individuals of unknown status comprised the 322 total Florida Cottonmouths, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were 14 males, eight females, 30 juveniles, and seven individuals of unknown status comprising a total of 59 individuals.

The Florida Cottonmouth was the most commonly encountered snake during our study. The total number of sightings comprised 24.56% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 25.70% of all snakes seen during March–December of 2008–2011 (**Table 3**). Numbers of individuals differed significantly during 2009–2011 in association with a very low water table in 2011.

The male:female ratio among adult Florida Cottonmouths was 1.02:1.00 during 2009–2011. The male:female sex ratio varied among years of this study with males most common in 2011: 0.89:1.00 in 2009, 1.05:1.00 in 2010, and 1.38:1.00 in 2011. Adults generally comprised one-half of actively moving individuals. Recruitment was highest in 2011. Excluding individuals of unknown category, juveniles comprised 55.16% of observations during 2009–2011. Recruitment was at 51.43% in 2009, 53.76% in 2010, and 64.82% in 2011. When individuals of unknown category were included, respective percentages of young were lower and likewise highest in 2011: 43.17% in 2009–2011, 42.52% in 2009 38.46% in 2010, and 53.85% in 2011.

Monthly movements- The Florida Cottonmouth was active year-round in Everglades National Park. Collectively, this species was most active in March and September; however, modality varied among years (**Figure 91**). Males were most active during March–June and probably October (**Figure 91**). Females were most active during March–May and again during August–September. (**Figure 91**). Juvenile movements were greatest in April and again more so in September. (**Figure 91**). June and September–October were the two peaks associated with annual activity of the species generally in an earlier study on Long Pine Key (Dalrymple et al., 1991a).

Relationships between monthly movements by the Florida Cottonmouth and environmental factors could be equivocal among years (**Table 18**). Collectively, monthly movements were most strongly related to average air temperature maxima and minima and followed by rainfall volume (**Table 18**). Water table was never associated significantly with movements of the Florida Cottonmouth (**Table 18**).

Ambient temperatures associated with nightly activity- Most ambient temperatures associated with activity of the Florida Cottonmouth ranged 20–30 °C (**Figure 92**). Mean temperatures did not significantly differ (ANOVA; F = 0.3032; *P* = 0.74) among males (25.7 ± 2.8 °C; range = 19–32; n = 38), females (25.3 ± 3.3 °C; range = 18–32; n = 36), and juveniles (25.7 ± 2.6°C; range = 18–32; n = 106). Ambient temperatures associated with all individuals combined averaged 25.6 °C (± 2.8 °C; range = 18–32; n = 180).

Roadkill dynamics- Florida Cottonmouths were killed by vehicles on the road. DOR Florida Cottonmouths comprised 17.48% of all DOR snakes and 26.71% of all conspecifics recorded during 2009–2011. Florida Cottonmouths were killed throughout the year, with the highest incidence of DOR individuals during November–March (**Figure 93**). A negative relationship (Multiple R = 0.56, *P* = 0.059) approaching significance existed between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 71.7 ± 11.3 cm SVL; range = 53.6–101.7; n = 71) differed significantly than that of females (Mean = 67.3 ± 9.1 cm SVL; range = 56.0–106.7; n = 64) with respect to variance (F = 1.526, df = 70, *P* = 0.05) and mean (t = 2.511, df = 132, *P* = 0.01). Male:female sexual size dimorphism of this sample was 1.07:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. Significant differences (F = 5.800, P = 0.0005; t = 2.932, df = 26, P = 0.007) existed between males (mean = 74.5 ± 15.2 cm SVL; range = 53.4–105.2; N = 20) and females (mean = 63.6 ± 6.4 cm SVL; range = 56.4–78.9; N = 17) and in variances between males (F = 1.806, P = 0.04; t = 0.771, df = 25, P = 0.45) and females (F = 0.483, df = 0.053; t = -1.925, df = 36, P = 0.06) of both samples. The male:female sexual size dimorphism of the Meshaka and Layne (2015) sample was 1.17:1.00. Combined, body sizes of males (mean = 72.3 ± 12.2 cm SVL; range = 53.4–105.2; N = 91) and females (mean = 66.5 ± 8.7 cm SVL; range = 56.0–106.7; N = 81) results in a male:female sexual size dimorphism of 1.09:1.00. Monthly distribution of body sizes **(Figure 94)** suggests that minimum body size at sexual maturity for both sexes could be reached by two years of age.

Diet- From individuals encountered on the road during 2008–2011, an individual of unrecorded body size or sex was encountered on 4 November 2009 as it was eating a true frog, *Lithobates* sp. A 64.5 cm SVL male was encountered on 4 June 2010 with evidence of a fresh meal. A 63.0 cm SVL female was encountered on 9 September 2009 with a Southern Leopard Frog, in its stomach. A 41.5 cm SVL juvenile was found drinking water from the road on 24 September 2008.

Injury- From individuals encountered on the road during 2008–2011, one individual, an 84.5 cm SVL female, was found with a bobbed tail, the incidence of which represented 1.56% of female Florida Cottonmouths and 0.26% of all individuals of the Florida Cottonmouth encountered.

Miscellany- From individuals encountered on the road during 2008–2011, a 66.9 cm SVL female was found alive on the road on 11 July 2010. She appeared sickly and was skinny and had a noticeable bulge in her stomach.

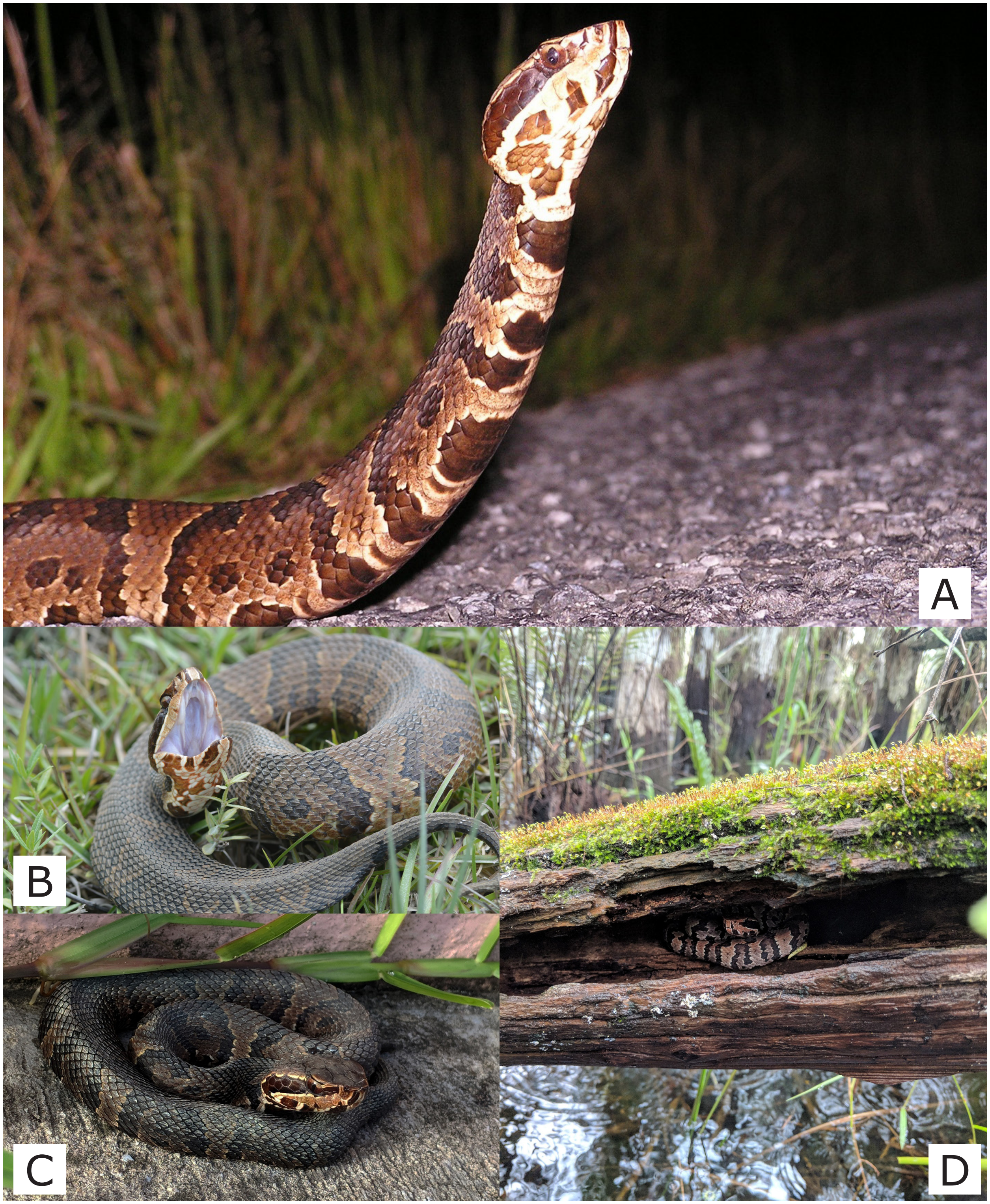

Figure 89. A Florida Cottonmouth, *Agkistrodon conanti*, along the edge of a road in Everglades National Park. (A) Photographed by M. Rochford. (B) A displaying individual and (C, D) individuals in sit-and-wait for prey. Photographed by Arik Hartmann.

Table 18. Relationship of environmental conditions to monthly movements of the Florida Cottonmouth, *Agkistrodon conanti*, in Everglades National Park during 2009–2011.

Environmental factors	2009	2010	2011	2009–2011
Mean monthly maximum air temperature	r = 0.59, *P* = 0.04	r = 0.82, *P* < 0.001	r = 0.07, *P* = 0.83	r = 0.71 *P* = 0.01
Mean monthly minimum air temperature	r = 0.58, *P* = 0.05	r = 0.81, *P* < 0.001	r = 0.09, *P* = 0.78	r = 0.70 *P* = 0.01
Total monthly rainfall volume	r = 0.44 *P* = 0.15	r = 0.50, *P* = 0.10	r = 0.03, *P* = 0.92	r = 0.70, *P* = 0.01
Mean monthly water level	r = 0.11 *P* = 0.74	r = 0.09, *P* = 0.79	r = 0.010, *P* = 0.98	r = 0.03, *P* = 0.93

Figure 90. Distribution of the Florida Cottonmouth, *Agkistrodon conanti*, in Everglades National Park.

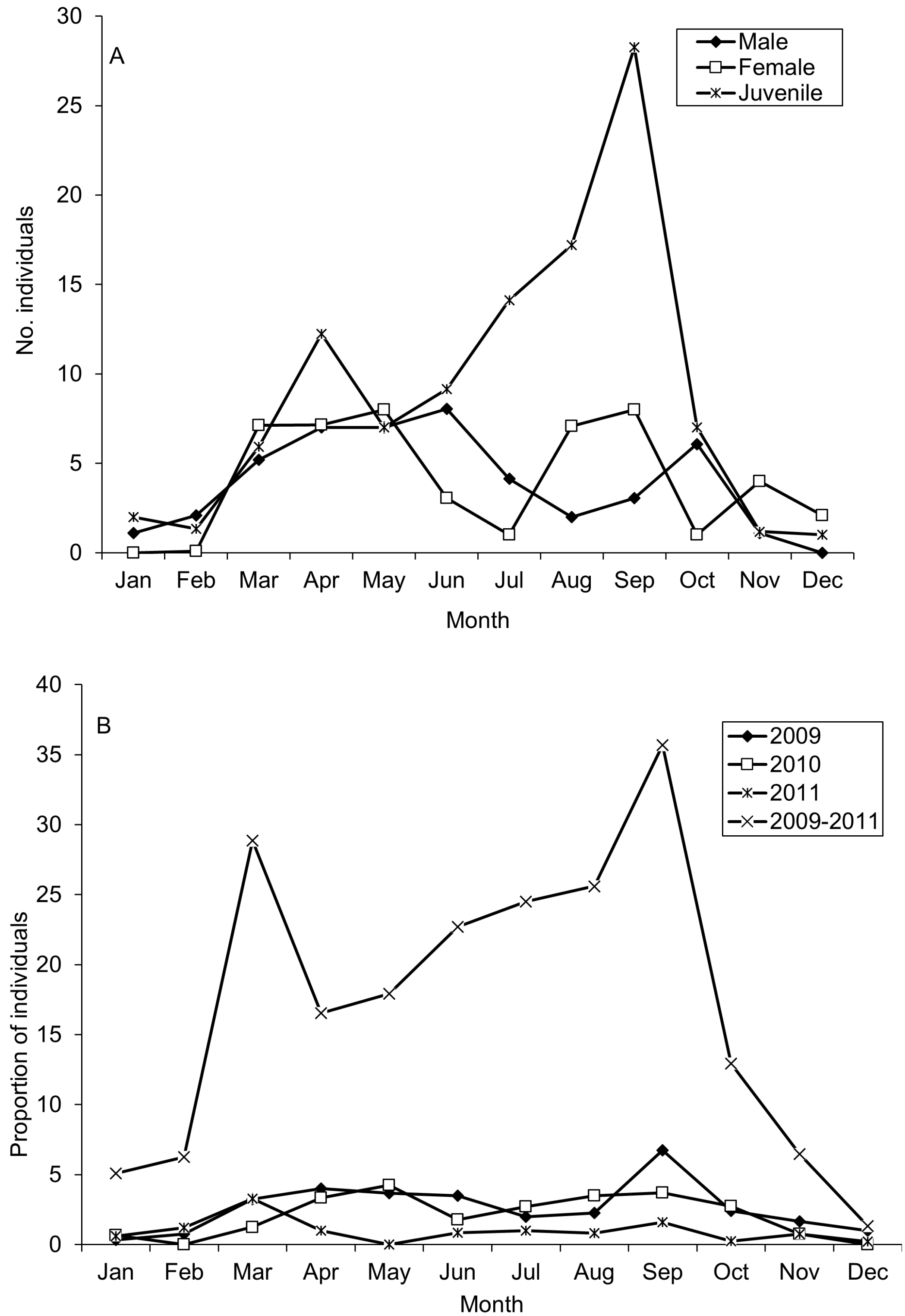

Figure 91. Monthly distribution of the Florida Cottonmouth, *Agkistrodon conanti*, crossing roads in Everglades National Park. A = Males, females, and juveniles during 2009–2011. B = All individuals during 2009–2011.

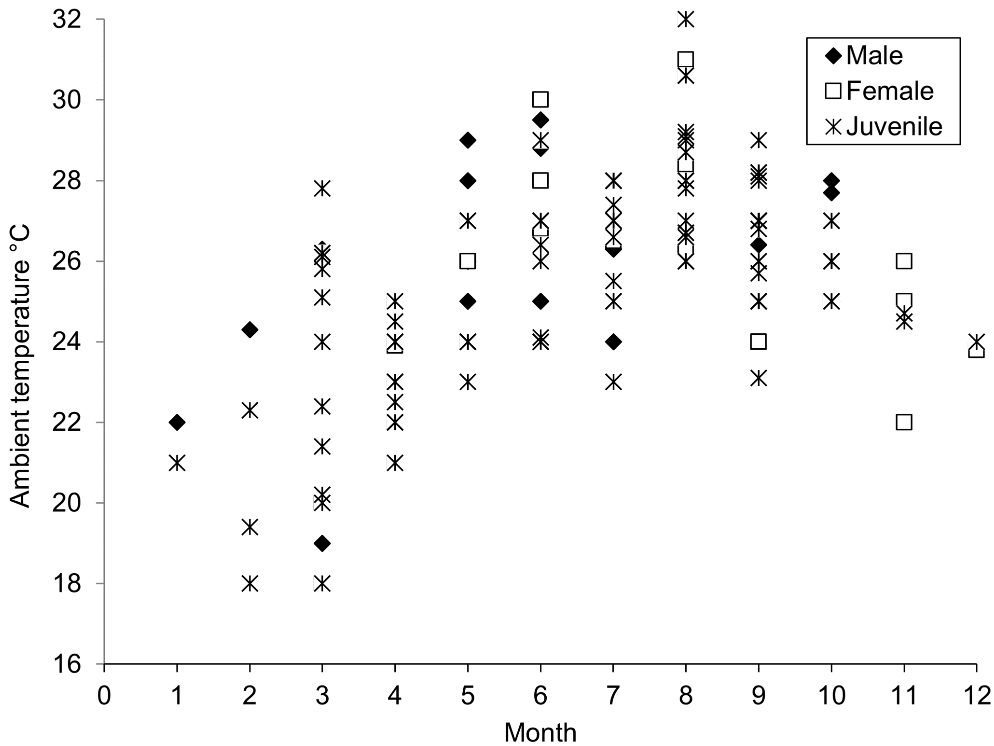

Figure 92. Ambient temperatures associated with the Florida Cottonmouth, *Agkistrodon conanti*, crossing roads at night in Everglades National Park during 2009–2011.

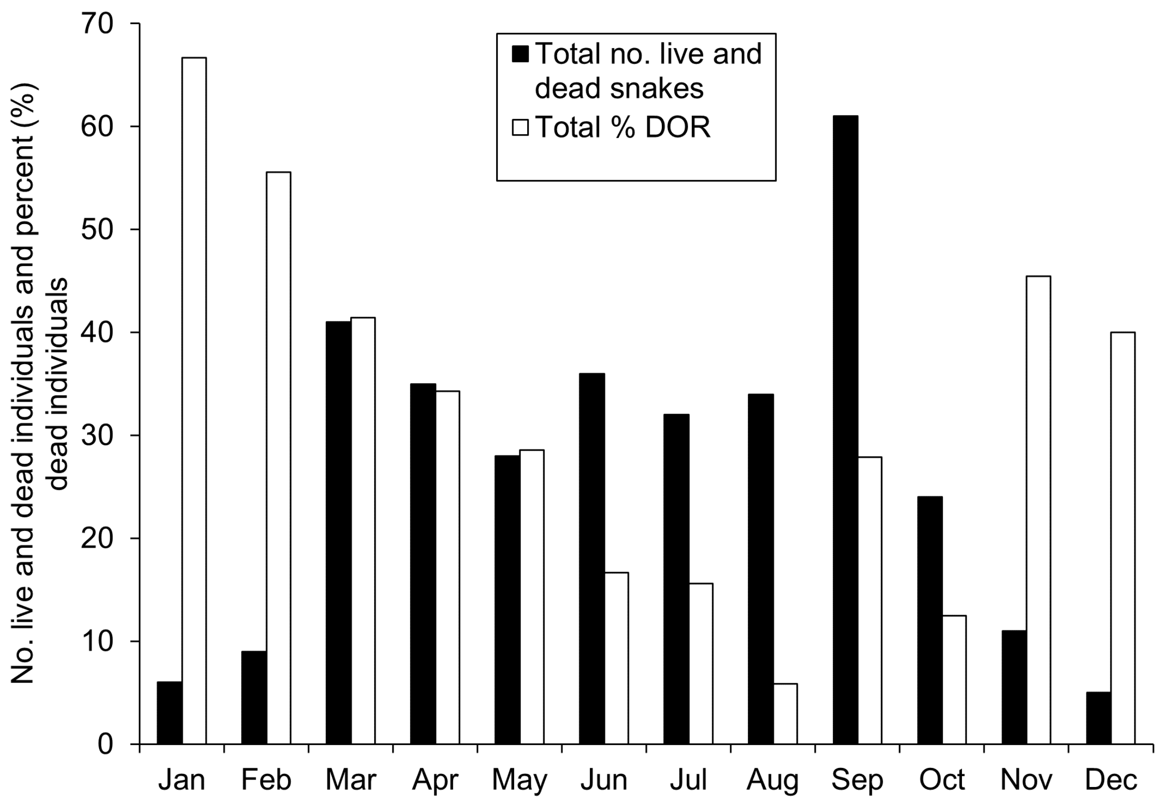

Figure 93. Monthly distribution of all and percent dead individuals of the Florida Cottonmouth, *Agkistrodon conanti*, on roads at night in Everglades National Park during 2009–2011.

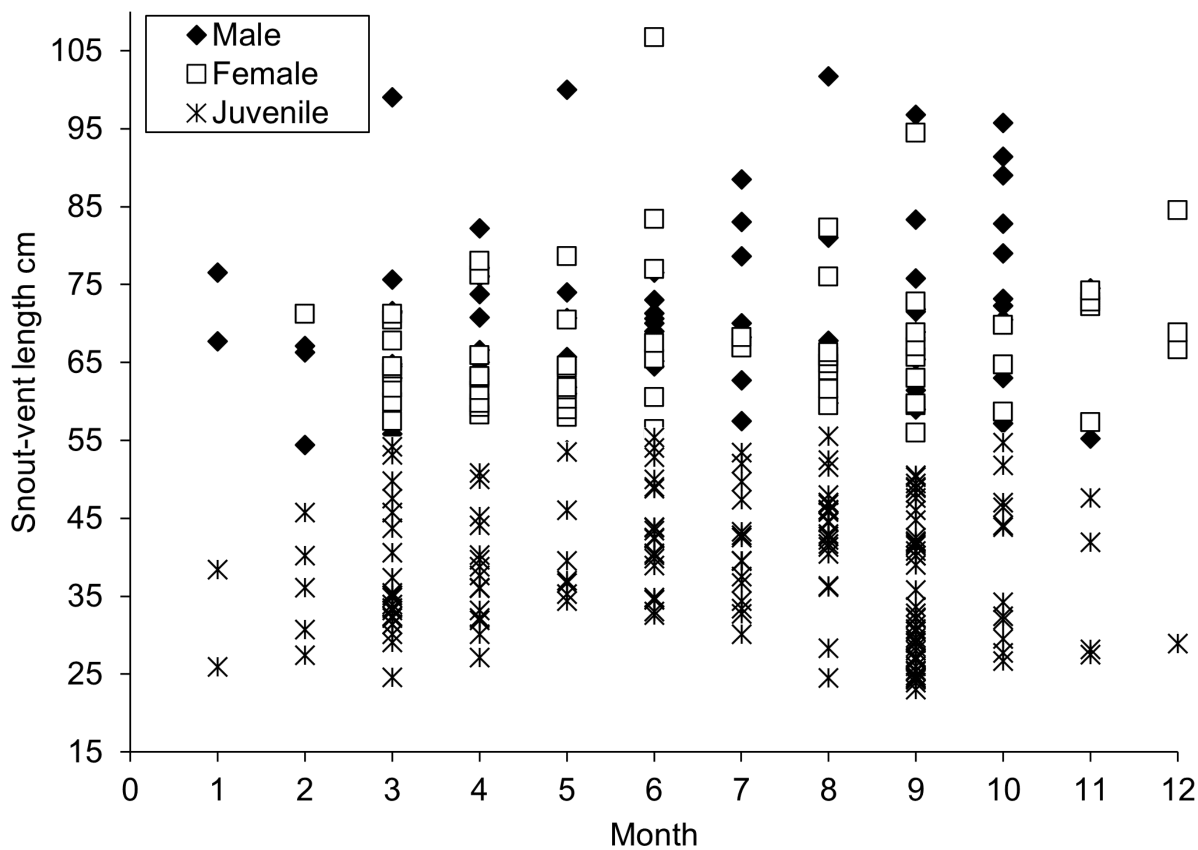

Figure 94. Monthly distribution of body sizes of the Florida Cottonmouth, *Agkistrodon conanti*, from Everglades National Park during 2008–2011.

Crotalus adamanteus Palisot de Beauvois, 1799- Eastern Diamond-backed Rattlesnake (**Figure 95**).

Habitat association- The Eastern Diamond-backed Rattlesnake occurred in all three regions of Everglades National Park (**Table 4; Figure 96**). A primarily diurnally active species, it was doubtlessly under-represented in encounters. The fewest sightings were in Pahayokee; however, its distribution among the three regions was not significantly different.

Population structure- During the three full calendar years of 2009–2011, three males, five females, four Juveniles, and two individuals of unknown status comprised the 14 total Eastern Diamond-backed Rattlesnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were zero males, zero females, two juveniles, and zero individuals of unknown status comprising a total of two individuals.

The Eastern Diamond-backed Rattlesnake was uncommonly encountered during our study. The total number of sightings comprised 1.07% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 0.98% of all snakes seen during March–December of 2008–2011 (**Table 3**). Stable in assemblage composition among sampling periods, the Eastern Diamond-backed Rattlesnake did not differ significantly during 2009–2011.

The male:female ratio among adult Eastern Diamond-backed Rattlesnakes was 0.60:1.00 during 2009–2011 and did not differ from unity (X^2 = 0.5, df = 1, P > 0.05). Adults generally comprised approximately two-thirds of actively moving individuals. Excluding individuals of unknown category, juveniles comprised 33.33% of observations during 2009–2011. When individuals of unknown category were included, percentages of young comprised 28.57% of the sample.

Monthly movements- The Eastern Diamond-backed Rattlesnake was detected nearly continuously in Everglades National Park. Collectively, most individuals were encountered in October, concomitant with mating, but seasonal movements may have been multi-modal in pattern (**Figure 97**). In an earlier study on Long Pine Key (Dalrymple et al., 1991a), movements were distinctly unimodal, strongly peaking in November. Relationships between monthly movements by the Eastern Diamond-backed Rattlesnake and environmental factors were not significant (**Table 19**).

Ambient temperatures associated with nightly activity- Ambient temperatures associated with all individuals averaged 25.6 °C (± 2.2 °C; range = 20.8–28.0; n = 12) (**Figure 98**).

Roadkill dynamics- Eastern Diamond-backed Rattlesnakes were killed by vehicles on the road. DOR Eastern Diamond-backed Rattlesnakes comprised 1.02% of all DOR snakes and 35.71% of all conspecifics recorded during 2009–2011. Eastern Diamond-backed Rattlesnakes were killed during the cooler months, with the highest incidence of DOR individuals in February (**Figure 99**). A negative relationship (Multiple R = 0.59, P = 0.045) was detected between the %DORs and total individuals per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 86.1 cm SVL ± 10.6 cm SVL; range = 74.0–94.1; n = 3) and females (Mean = 106.5 cm SVL ± 11.8 cm SVL; range = 89.6–120.5; n = 5) were available. Male:female sexual size dimorphism of this sample was 0.81:1.00. Monthly distribution of body sizes indicates appearance of the smallest individuals, 46.5–49.1 in October and February (**Figure 100**). Mean adult body sizes of males (mean = 93.7 cm SVL) and females (103.2 cm SVL) from coastal islands of Everglades National Park (Mealey et al., 2005) were similar in mean body size to those of this study, and male:female body size dimorphism was 0.91:1.00. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. From a small sample size, we combined samples from Meshaka and Layne (2015) with those of this study and calculated a mean value of adult body size from males (mean = 109.8 ± 21.2 cm SVL; range = 74.0–140.0; N = 11) and females (mean = 107.8 ± 10.8 cm SVL; range = 89.6–120.5; N = 8). Only the variance of adult body size differed between the sexes (F = 3.860, P = 0.04; t = 0.260, df = 16, P = 0.80). The male:female sexual size dimorphism ratio for this combined sample was 1.02:1.00.

Table 19. Relationship of environmental conditions to monthly movements of the Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*, in Everglades National Park during 2009–2011.

Environmental factors	2009–2011
Mean monthly maximum air temperature	r = 0.10, P = 0.77
Mean monthly minimum air temperature	r = 0.20, P = 0.71
Total monthly rainfall volume	r = 0.13, P = 0.68
Mean monthly water level	r = 0.43, P = 0.16

Figure 95. An Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*, from Everglades National Park. (A) In a hammock. Photographed by M. Rochford. (B) Along road edge, and (C) along hammock edge where it is not so easily seen. (B, C) Photographed by Arik Hartmann.

Figure 96. Distribution of the Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*, in Everglades National Park.

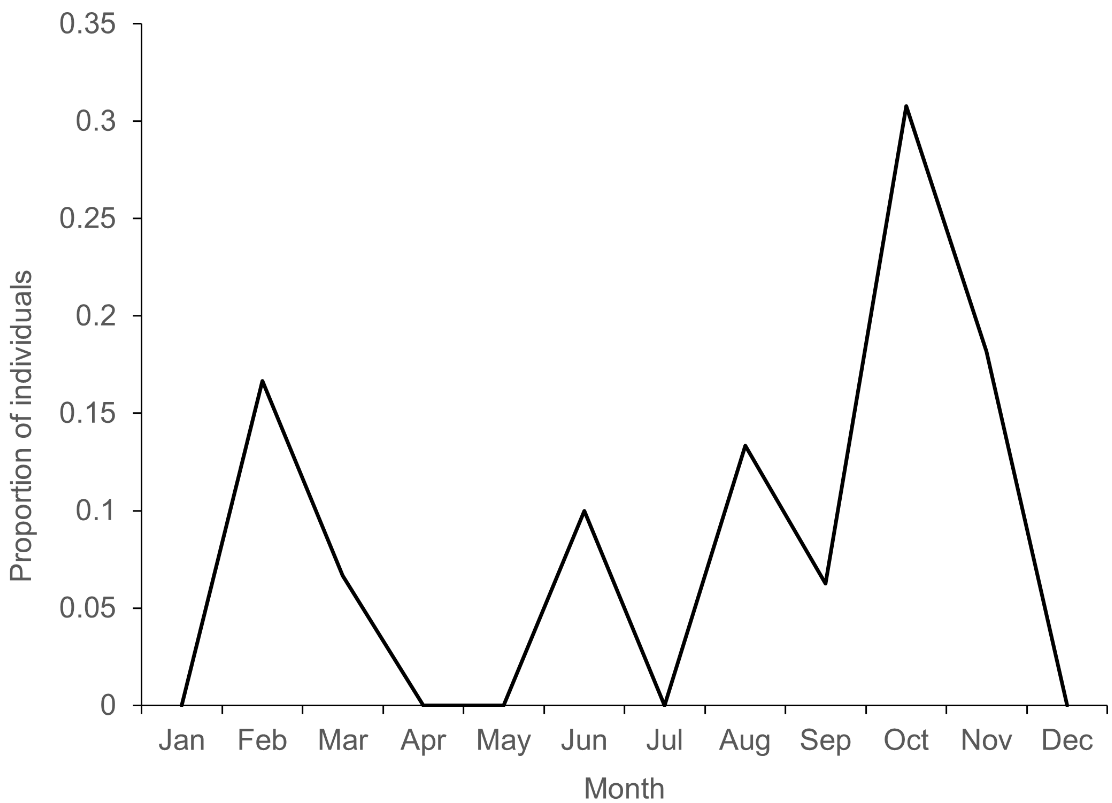

Figure 97. Monthly distribution of the Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*, crossing roads in Everglades National Park during 2009–2011.

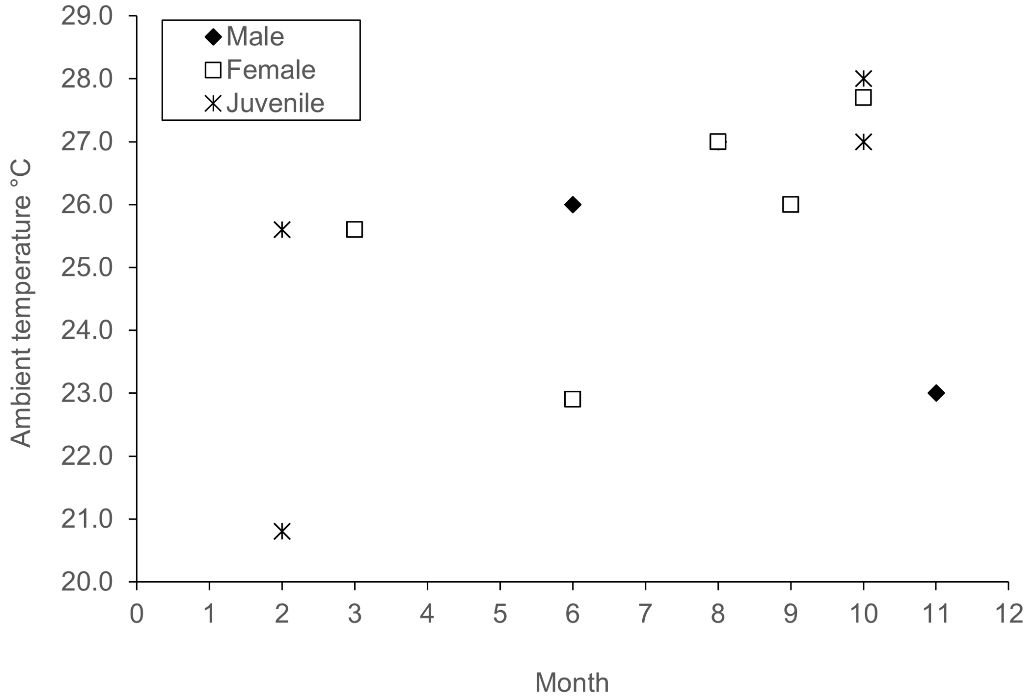

Figure 98. Ambient temperatures associated with the Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*, crossing roads at night in Everglades National Park during 2009–2011.

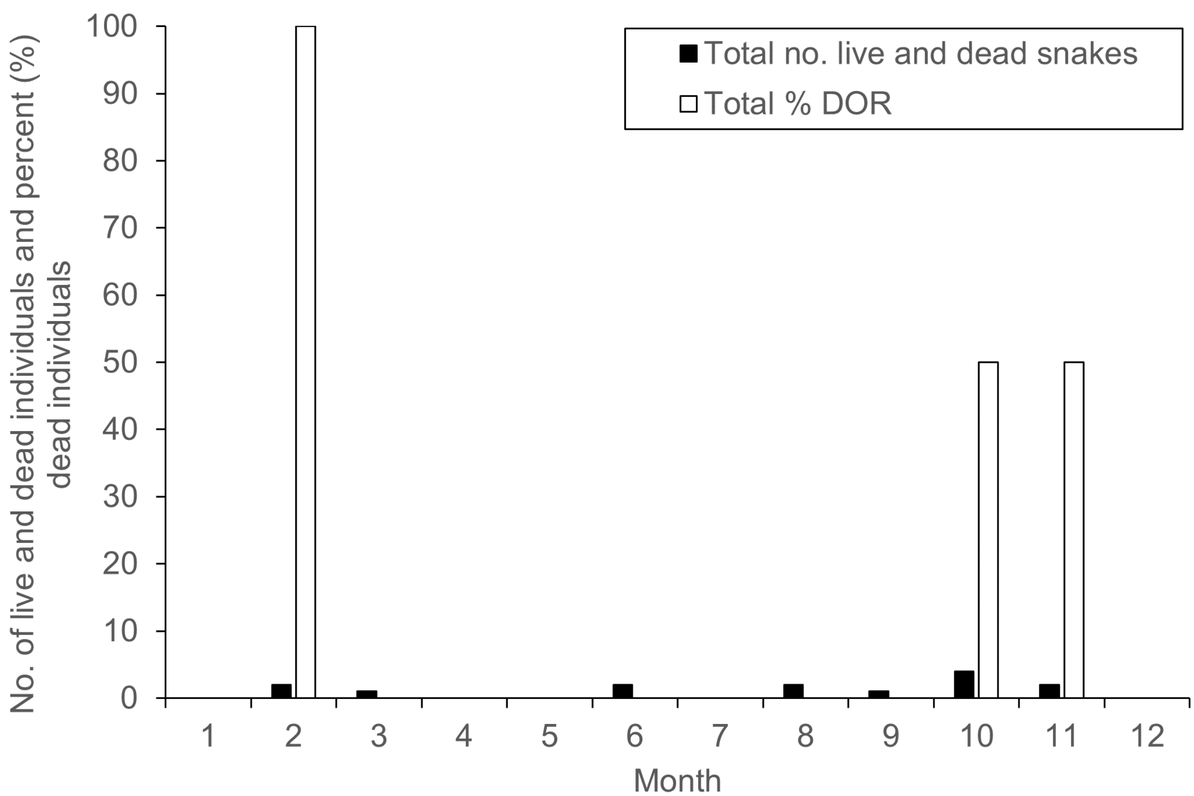

Figure 99. Monthly distribution of all and percent dead individuals of the Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*, on roads at night in Everglades National Park during 2009–2011.

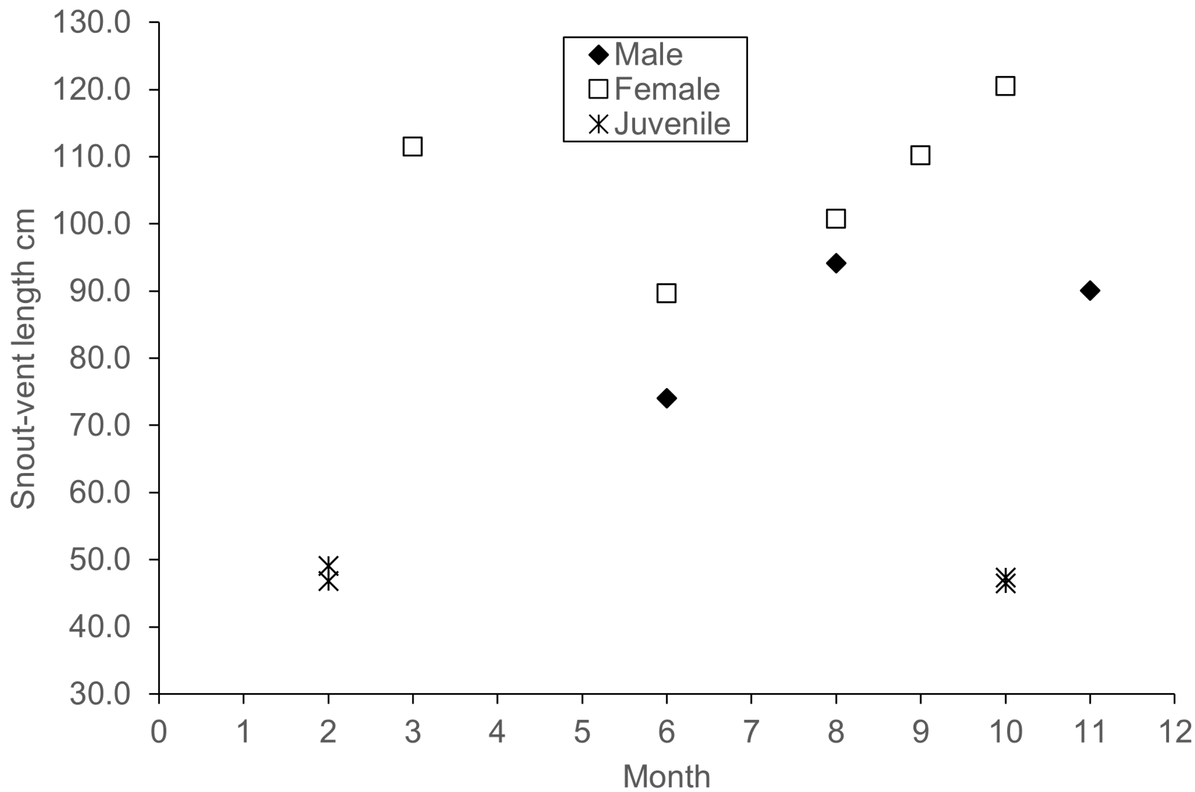

Figure 100. Monthly distribution of body sizes of the Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*, from Everglades National Park during 2008–2011.

Sistrurus miliarius barbouri Gloyd, 1935- Dusky Pygmy Rattlesnake. (**Figure 101**).

Habitat association- The Dusky Pygmy Rattlesnake was absent from Long Pine Key (**Table 4; Figure 102**). Fewer individuals were encountered in Pahayokee than the saline glades (X^2 = 33.03, df = 2, *P* < 0.001) (**Table 4**). On Long Pine Key, this species was much less abundant during June–August at the time of our study than it was in the 1980s (Dalrymple et al., 1991a) (**Table 5**).

Population structure- During the three full calendar years of 2009–2011, seven males, six females, zero juveniles, and five individuals of unknown status comprised the 18 total Dusky Pygmy Rattlesnakes, live and dead, encountered on the road at night. Counterparts recorded during March–December 2008 were one male, one female, zero juveniles, and zero individuals of unknown status comprising a total of two individuals.

The Dusky Pygmy Rattlesnake was uncommonly encountered during our study. The total number of sightings comprised 1.37% of all snakes seen during January–December of 2009–2011 (**Table 2**) and 1.41% of all snakes seen during March–December of 2008–2011 (**Table 3**). Numbers of individuals differed significantly during 2009–2011 in association with a very low water table in 2011.

The male:female ratio among adult Dusky Pygmy Rattlesnakes was 1.17:1.00 during 2009–2011. On Long Pine Key, males outnumbered females (Dalrymple et al., 1991a). Adults were evenly distributed between the sexes and comprised the entirety of the sample. Thus, recruitment was 0.00% when excluding or including individuals of unknown category.

Monthly movements- The Dusky Pygmy Rattlesnake was encountered in low numbers during May–October, bimodally peaking in numbers of encounters in May and in October (**Figure 103**), concomitant with the wet season. In an earlier study on Long Pine Key (Dalrymple et al., 1991a) activity peaked distinctively in October. Relationships between monthly movements by the Dusky Pygmy Rattlesnake and environmental factors were not statistically significant (**Table 20**).

Ambient temperatures associated with nightly activity- Most ambient temperatures ranged 26.0–27.0 °C (**Figure 104**). Mean temperatures were available for four males (mean = 26.4 ± 0.5 °C; range = 26.0–27.0) four females (mean = 25.8 ± 1.3 °C; range = 24.0–27.0). Ambient temperatures associated with all eight individuals combined averaged 26.1 °C (± 0.9 °C; range = 24.0–27.0.

Roadkill dynamics- Dusky Pygmy Rattlesnakes were killed by vehicles on the road. DOR Dusky Pygmy Rattlesnakes comprised 1.63% of all DOR snakes and 44.44% of all conspecifics recorded during 2009–2011. Dusky Pygmy Rattlesnakes were killed in four of the eight months there were encountered, especially in June, October, and December (**Figure 105**). No significant relationship (Multiple R = 0.45, *P* = 0.15) was detected between %DORs and total individual per month during 2009–2011.

Adult body size and age at sexual maturity- From individuals encountered during 2008–2011, adult body size of males (Mean = 41.1 ± 7.0 cm SVL; range = 32.8–54.6; n = 8) did not differ significantly from that of females (Mean = 46.0 ± 4.9 cm SVL; range = 41.5–55.2) with respect to variance (F = 1.998, *P* = 0.21) or mean (t = -1.558, df = 13, *P* = 0.14). Male:female sexual size dimorphism of this sample was 0.89: .00. Mean adult body sizes of males (mean = 43.5 cm SVL) and females (mean = 42.0 cm SVL) and sexual size dimorphism (1.04:1.00) from Everglades National Park (Tohulka, 1992) differed from those of this study. A subset of data from Meshaka and Layne (2015) was used to calculate mean adult body sizes from Everglades National Park, no later than 2000, for comparison with those of this study. In this sample, body sizes of 20 males (Mean = 43.5 ± 4.5 cm SVL; range = 35.0–53.2) and nine females (Mean = 42.8 ± 8.2 cm SVL; range = 30.6–53.9) differed significantly only in variance (F = 0.281, P = 0.01; t = 0.230, df = 10, P = 0.82). Male:female sexual size dimorphism of this sample was 1.02:1.00.

Injury- From individuals encountered on the road during 2008–2011, one individual, a 40.5 cm SVL male, was found with a bobbed tail. Consequently, 12.50% of males and 5.00% of the sampled population were missing some portion of their tail.

Table 20. Relationship of environmental conditions to monthly movements of the Dusky Pygmy Rattlesnake, *Sistrurus miliarius barbouri*, in Everglades National Park during 2009–2011.

Environmental factors	2009–2011
Mean monthly maximum air temperature	r = 0.24, *P* = 0.46
Mean monthly minimum air temperature	r = 0.25, *P* = 0.43
Total monthly rainfall volume	r = 0.08, *P* = 0.81
Mean monthly water level	r = 0.05, *P* = 0.88

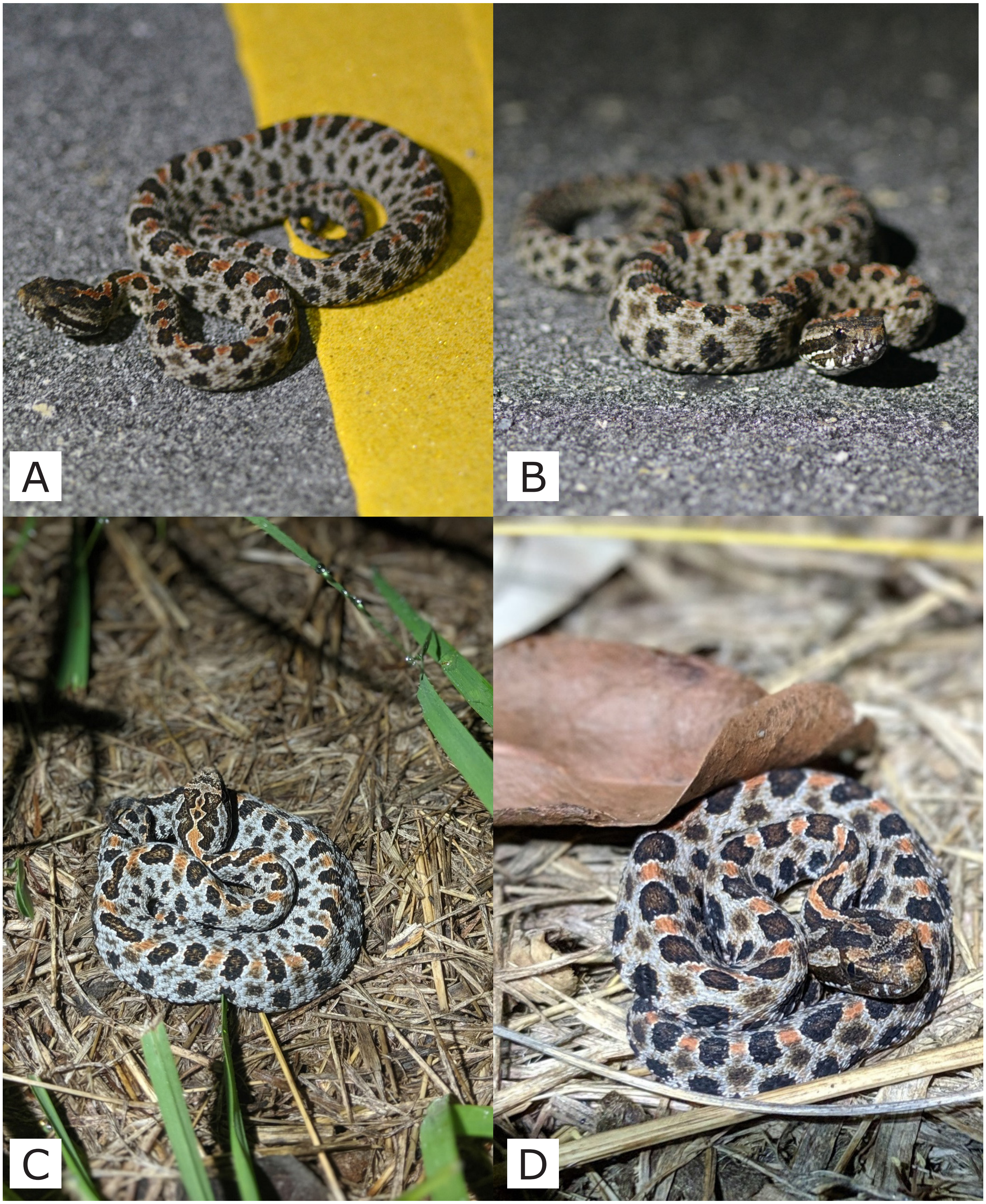

Figure 101. Dusky Pygmy Rattlesnakes, *Sistrurus miliarius barbouri*. (A, B) Individuals on road and (C, D) in hunting posture in Everglades National Park. Photographed by Arik Hartmann.

Figure 102. Distribution of the Dusky Pygmy Rattlesnake, *Sistrurus miliarius barbouri*, in Everglades National Park.

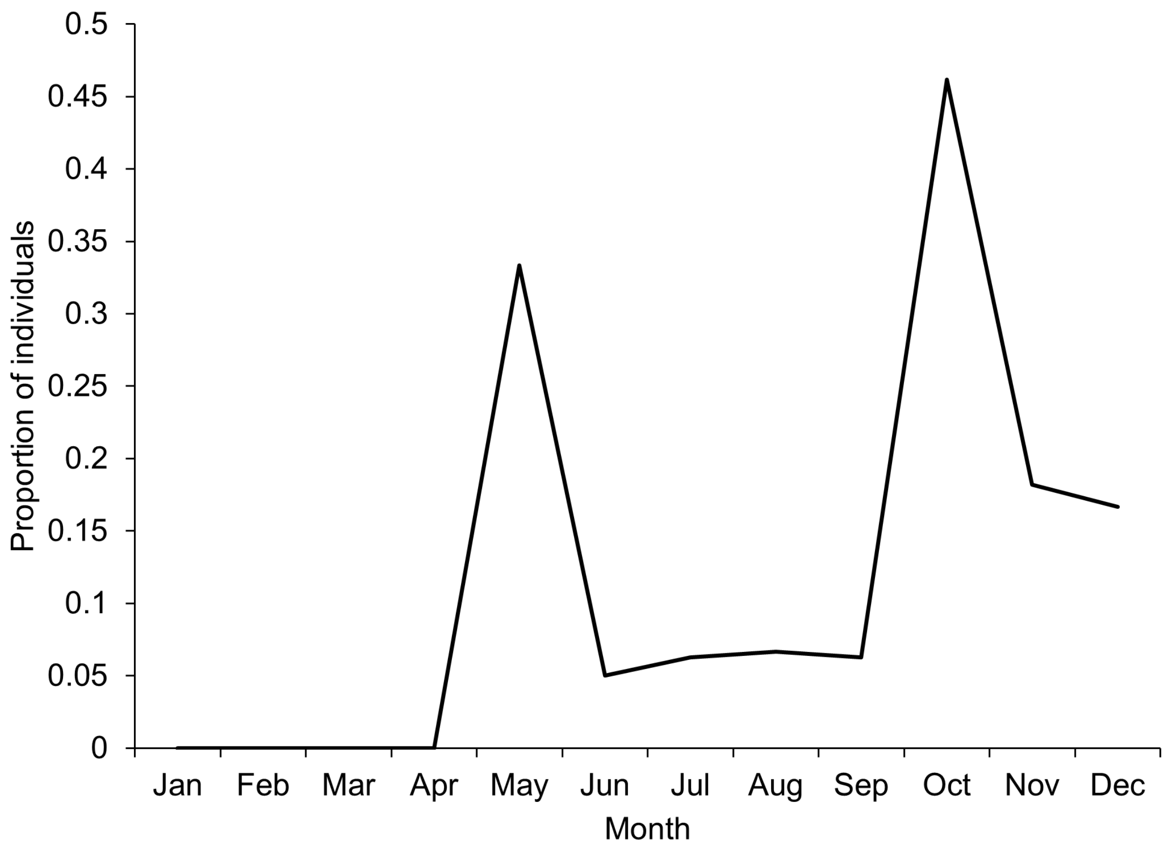

Figure 103. Monthly distribution of the Dusky Pygmy Rattlesnake, *Sistrurus miliarius barbouri*, crossing roads in Everglades National Park during 2009–2011.

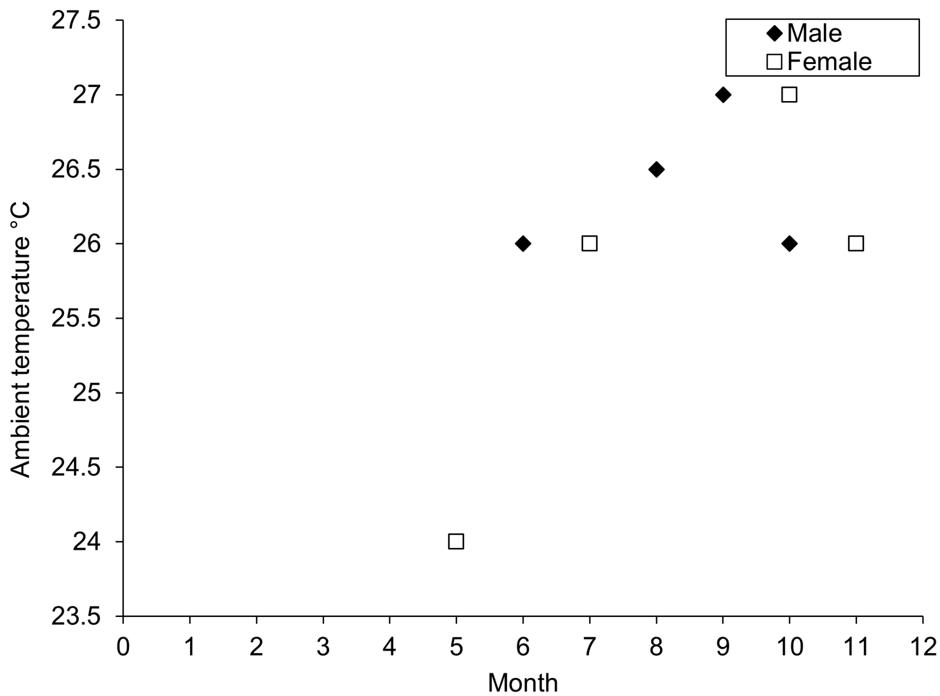

Figure 104. Ambient temperatures associated with the Dusky Pygmy Rattlesnake, *Sistrurus miliarius barbouri*, crossing roads at night in Everglades National Park during 2009–2011.

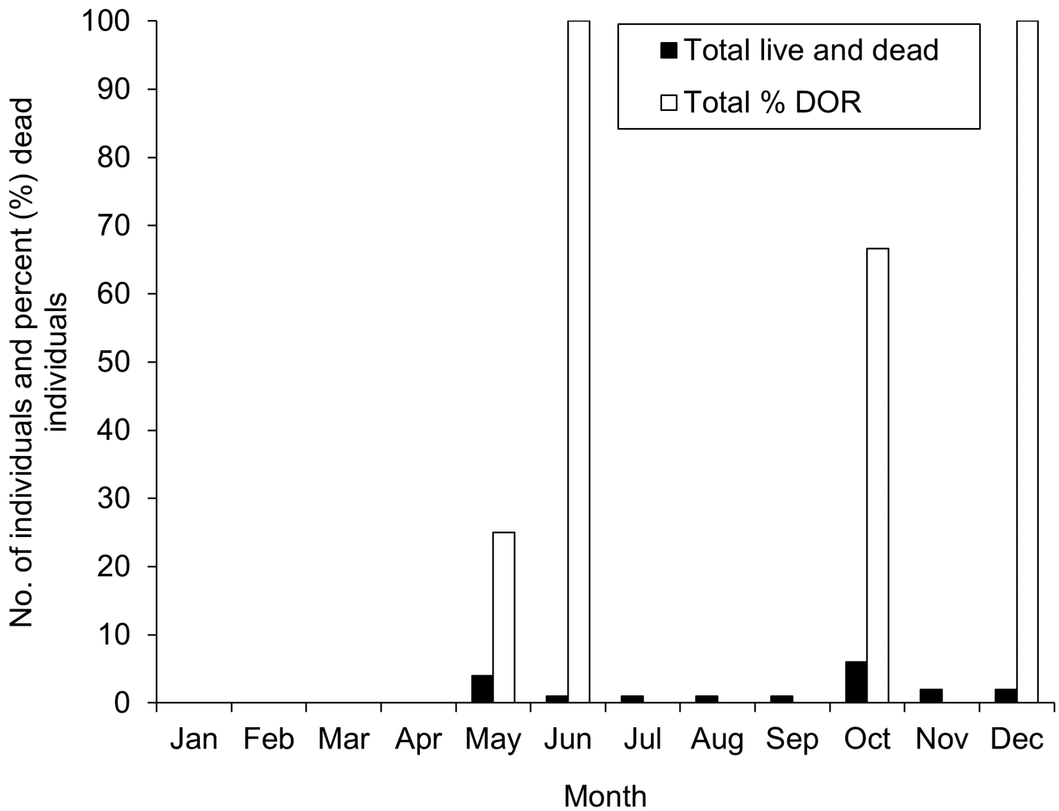

Figure 105. Monthly distribution of all and percent dead individuals of the Dusky Pygmy Rattlesnake, *Sistrurus miliarius barbouri*, on roads at night in Everglades National Park during 2009–2011.

Synthesis

Assemblage structure– Our study, conducted at night from Long Pine Key to Mahogany Hammock detected a species-rich, even if highly uneven, snake assemblage of 24 species. The Florida Cottonmouth was the dominant species in the park and at Pahayokee and Long Pine Key. Although numerous in the saline glades, the Mangrove Saltmarsh Snake-Florida Watersnake hybrid was the most frequently encountered snake in the saline glades. This snake was in turn replaced in higher frequencies by the Florida Watersnake in the deep-water freshwater glades of Pahayokee.

Historical comparisons- Previously, the Southern Watersnake, *N. fasciata* (Linnaeus, 1766), was considered polytypic and included what is now considered the Mangrove Saltmarsh Watersnake, *N. clarkii compressicauda*. Comparable to our study were road surveys during 1984–1986 that detected 20 snake species on Long Pine Key (Dalrymple et al., 1991a). Road surveys during February–March 1986 and February 1987–January 1989 detected 16 species in Pahayokee (Bernardino and Dalrymple, 1992). The combined totals of the two studies were 22 taxa (21 species and one polytypic species, *N. fasciata*). In light of contemporary taxonomy that recognizes *N. fasciata compressicauda* of Bernardino and Dalrymple (1992) as the Mangrove Saltmarsh Watersnake, *N. c. compressicauda*, as in our study, we recognize 21 species in Pahayokee (Bernardino and Dalrymple, 1992) and 22 species in the combined species list of Dalrymple et al. (1991a) and Bernardino and Dalrymple (1992). We note, however, that our category of the Mangrove Saltmarsh Watersnake was accepted as including hybrids with the Florida Watersnake, *N. f. pictiventris*. Surveys of the former study shifted from primarily diurnal in cooler months to nocturnal in hotter, wetter months. Timing of surveys of the latter study were not reported.

The four most numerous species on Long Pine Key were the Common Gartersnake, *T. sirtalis,* Eastern Ribbonsnake, *T. saurita,* North American Racer, *Coluber constrictor,* and Rough Greensnake, *Opheodrys aestivus* (Dalrymple et al., 1991a). The four most numerous species at Pahayokee were the Common Gartersnake, Eastern Ribbonsnake, Southern Watersnake*, N. fasciata,* and Northern Cottonmouth, *A. piscivorus* (Bernardino and Dalrymple, 1992). In our study, which subsumed the areas of the aforementioned studies, the top four species were the Florida Cottonmouth, Florida Watersnake*,* Peninsula Ribbonsnake, and Eastern Gartersnake. Common to the top four species of all three studies were the latter three species*.* Species richness was similar between our study and the combined findings Dalrymple et al. (1991a) and Bernardino and Dalrymple (1992). Two species detected in our study were not reported in the other two studies. The first, the Southern Florida Swampsnake, was represented by only one sighting. The other species, the Burmese Python, although present in the park at the time, was rare and restricted to the extreme southern end (Meshaka et al., 2000).

Some of the differences in abundances between the mid-1980s and our study can be explained by sampling times when diurnally active species (Everglades Racer*,* Eastern Diamond-backed Rattlesnake, Eastern Indigo Snake*,* Florida Rough Greensnake*,* and South Florida Coralsnake) would not be found alive on roads at night. For still others, the Eastern Ring-necked Snake and Florida Brownsnake, we are unsure of the reason for such striking differences between the time periods; however, we have seen them moving at night. Concurrent to the road survey on Long Pine Key (Dalrymple et al., 1991a), funnel traps along drift fences and nearby cover boards were used to sample the herpetofauna of prairie, pineland, tropical hardwood hammock, and disturbed habitat on Long Pine Key (Dalrymple, 1988). Seventeen species of snakes were detected in that study. The four most trapped species were the Northern Racer*,* Common Gartersnake*,* Pygmy Rattlesnake, *Sistrurus miliarius*, and equal numbers of the Ring-necked Snake, and the Eastern Ribbonsnake. Sampling techniques by Dalrymple (1988) and Dalrymple et al. (1991a), provided two different measures of abundance, and the same four species figured most prominently.

A direct comparison of results was possible between our study and that of Dalrymple et al. (1991a) on Long Pine Key. By restricting counts to June–August, we could compare numbers of snakes captured from dusk through dark. A comparison of three environmental conditions between the time periods of our study (2009–2011) and that of Dalrymple et al. (1991a) (1984–1986) points to a distinctly wetter and cooler environment during our study (Table 21) than during 1984–1986 (Table 22).

Table 21. Water stage data (cm) from Station TSB, rainfall totals (cm) from Station RPL, and maximum/minimum air temperatures (°C) from Station RPL in Everglades National Park during 2009–2011.

Year	Water stage (cm)	Rainfall totals (cm)	Maximum/minimum air temperatures (°C)
2009	105.5	135.0	24.6/23.1
2010	111.4	142.7	23.5/22.0
2011	86.7	165.9	24.5/22.9
Mean 2009–2011	101.2	147.9	24.2/22.7

Table 22. Water stage data (cm) from Station TSB, rainfall totals (cm) from Station RPL, and maximum/minimum air temperatures (°C) from Station RPL in Everglades National Park during 1984–1986.

Year	Water stage (cm)	Rainfall totals (cm)	Maximum/minimum air temperatures (°C)
1984	85.5	117.3	30.1/17.6
1985	81.6	115.0	29.9/18.6
1986	87.6	102.2	29.8/20.6
Mean 1984–1986	84.9	111.5	29.9/19.9

Numbers of species and number of individuals significantly exceeded those of their study (**Table 5**). Among the species, a strong shift towards semi-aquatic and aquatic species took place, evident in seven native species, while the Southern Ring-necked Snake, Florida Rough Greensnake and Florida Brownsnake plummeted in abundance since the late 1980s (**Table 5**). Temporal comparisons in two native species stand out as having been unexpected for hydrology-induced changes in community assemblage. In light of habitat affinities and trophic position, we expected the Peninsula Ribbonsnake and Dusky Pygmy Rattlesnake to respond with higher numbers of individuals in our study. We do not know why numbers of the Peninsula Ribbonsnake remained unchanged nor why the Dusky Pygmy Rattlesnake experienced a population crash. We can only hypothesize that for the Peninsula Ribbonsnake, hydrological changes were not sufficient to enhance prey availability of small frogs and tadpoles. On the other hand, the Dusky Pygmy Rattlesnake was expected to have responded positively to hydrological changes significant enough to affect ranid prey. We hypothesize that the contemporary loss of this species in Everglades National Park may be the result *of Raillietiella orientalis*, an Asian pentasome parasite presumed to have been introduced into Florida with the Burmese Python (Miller et al., 2018), a species not encountered by Dalrymple et al. (1991a).

We are reluctant to make direct comparisons of encounter rates of snakes at Pahayokee between our study and that of Bernardino and Dalrymple (1992) because, as mentioned earlier, we do not know the times of day they sampled along the road. In their January–March study, they encountered 1,272 individuals of 16 species. In our study, we encountered 184 individuals of 11 species. From these counts, we note an assemblage structure dominated by the Eastern Gartersnake, Peninsula Ribbonsnake, and Florida Watersnake, respectively, by Bernardino and Dalrymple (1992).

Monthly activity– For all years combined, snake movement was greatest in March and during July–November and was significantly related only to mean monthly high and low air temperatures. On Long Pine Key, seasonal snake movements were trimodal and positively associated with monthly volumes of rainfall (Dalrymple et al., 1991a). Collectively, snake movement was bimodal and not related to rainfall. On Long Pine Key, seasonal snake movements were trimodal and positively associated with monthly volumes of rainfall (Dalrymple et al., 1991a). At Pahayokee, highest numbers of snakes were encountered during April–May and October–November, and overall movements were negatively associated with water level, rainfall, and mean minimum air temperature (Bernardino and Dalrymple, 1992).

Several findings in seasonal movements of snakes on Long Pine Key by Dalrymple et al. (1991a) were also evident in our study. In both studies, modality of seasonal movements could vary among size-classes within a species. To that finding, our study detected interannual differences in modality in monthly activity of the Florida Cottonmouth. In Everglades National Park, both the Southern Watersnake and Florida Green Watersnake moved extensively in the winter (Bernardino and Dalrymple, 1992; this study); however, we also detected an August peak of movements by the Florida Watersnake and July and November peaks in movements by the Florida Watersnake. To this group, we add findings of only June and November peaks in movements by the Mangrove-Florida Watersnake hybrid.

Species-specific comparisons of seasonal activity patterns between Long Pine Key (Dalrymple et al., 1991a) and our study varied in overlap. Common to both studies, male ratsnakes were encountered more often than females, including an absence of females in our study. The Red Cornsnake in our study peaked in activity in June, one month later than the largest of three seasonal activity peaks on Long Pine Key (Dalrymple et al., 1991a). In our study, males were more frequently encountered than females but not to the extent reported by Dalrymple et al. (1991a). Seasonal movements of the Eastern Gartersnake peaked in November, one month later than found by Dalrymple et al. (1991a). On the other hand, females in our study moved most frequently in June, one month earlier than found by Dalrymple et al. (1991a); potentially indicating a response to climate change. Monthly activity of the Dusky Pygmy Rattlesnake peaked in October in both studies; however, we also detected a May peak though with a much smaller sample size. Activity on roads by the Eastern Diamond-backed Rattlesnake peaked in November on Long Pine Key (Dalrymple et al., 1991a) and in October in our study, supporting fall mating (Meshaka and Layne, 2015). Exceptionally, seasonal activity of the Peninsula Ribbonsnake was unimodal on Long Pine Key (Dalrymple et al., 1991a) and trimodal in our study. On Long Pine Key, activity of the Florida Cottonmouth generally peaked in March or April and again in September in our study. Peaks in activity were apparent in June and during September–October (Dalrymple et al., 1991a); however, the authors noted that because of small sample sizes they could not be certain of patterns. In several species annual activity patterns differed between our studies. Just as Dalrymple et al. (1991a) identified intraspecific differences in annual activity, we found interannual differences in the Florida Cottonmouth a species for which we had sufficient data to examine the question. Therefore, apart from generalities, the incongruences in annual activity between studies is not surprising even if not explained.

Life history traits– Clutch sizes and nesting and parturition seasons from snakes of this study were comparable to those of other studies in Everglades National Park (Dalrymple et al., 1991a; data from Meshaka and Layne, 2015). The male:female sex ratio of seven species could be compared between those of our study and those of Dalrymple et al. (1991a). In five of the species, overall sex ratios were similar between studies. Males were more numerous than females in the Everglades Racer, intergrade ratsnake, and Red Cornsnake. Females were more numerous than males in the Southern Ring-necked Snake and Eastern Gartersnake. Females of the Peninsula Ribbonsnake outnumbered males in our study but were similar to numbers of males in the study by Dalrymple et al. (1991a). In the Dusky Pygmy Rattlesnake, numbers of males and females were similar in our study, but males outnumbered females in the study by Dalrymple et al. (1991a). Sample sizes of males and females were provided for the Peninsula Ribbonsnake and Eastern Gartersnake from Long Pine Key (Dalrymple et al., 1991a). Our analysis of sex ratios for these two species from both studies statistically corroborated an even sex ratio in the Peninsula Ribbonsnake and a female-biased sex ratio in the Eastern Gartersnake.

Incidence of roadkill– In our study, greater than one third of all snakes encountered were dead and that percent decreased with increasing numbers of all snakes combined. Bernardino and Dalrymple (1992) found a significant correlation between the monthly number of vehicles at Flamingo and monthly number of snakes found dead on the road, which ranged 70.0–92.9%. Those months, fall-spring, of high mortality and cars overlapped highest incidences of road-killed snakes in our study. Our highest numbers of DORs were during February–March and November, and February and December by Bernardino and Dalrymple (1992).

Demographic responses to environmental factors– One question in our study was the response of species to interannual differences in water levels, temperatures, or rainfall volumes. Seven species shifted in numbers during 2009–2011, six of which were related to water table. During 2009–2011, annual rain volumes totaled 165.5 cm, 120.2 cm, 137.8 cm, respectively. Maximum temperatures averaged 24.6, 23.5, and 24.5 ºC, respectively, and minimum temperatures averaged 23.1, 22.0, and 22.9 ºC, respectively. However, respective values of water level averaged 86.8 cm, 90.2 cm, and 70.4 cm. The lower water table in 2011 corresponded to the significant drops in total numbers of snakes but not number of species. Species affected by the low water table in 2011 were principally semi-aquatic and shallow-water aquatic species and collectively accounted for the most captures in this study. Specifically, the Florida Cottonmouth, *N. clarkii compressicauda* X *N. f. pictiventris,* Florida Watersnake, Peninsula Ribbonsnake, and Eastern Gartersnake accounted for the five most frequently encountered snakes during both time periods. In common with one another, these five species could have perished for lack of water and associated wetland food, such as anurans and they may have been reluctant to move much.

The Dusky Pygmy Rattlesnake and Everglades Racer are primarily terrestrial in southern Florida (Meshaka and Layne, 2015). Both species feed heavily on anurans in southern Florida (Meshaka and Layne, 2015). Their abundances were unsurprisingly lowest in 2011. Among fossorial species with sufficient sample sizes to examine water table-related responses in abundances was the Florida Scarletsnake. Numbers of individuals encountered on the road varied significantly across years. During both time periods, its abundance was least in 2009 and highest in 2010, which suggests that interannual variation in abundance of the Florida Scarletsnake was not related to a low water table. We do not know why its abundances varied as it did, with only a modest drop in 2011. However, the Florida Scarletsnake, least common on Long Pine Key, is specialized to eating eggs, including turtle eggs. Thus, its food base could have been unaffected by a low water year in Everglades National Park, especially in light of the near extirpation of many mammals, including the Raccoon, *Procyon lotor*, through the depredation of the Burmese Python (Dorcas et al., 2014). The Southern Ring-necked Snake, another fossorial snake sharply declined in abundance during 2009–2011 unrelated to changes in the water table. It was most abundant on Long Pine Key, where it feeds on small frogs, lizards, and eggs. Disease or a crash in prey are potential causes for the observed trend.

The Red Cornsnake is a terrestrial-arboreal species and it responded to the low water table of 2011 with significantly lower abundances. This species likewise could have been negatively impacted by food limitation and/or its movements could have been inhibited by a low water table. Its nearest relative in Everglades National Park, the ratsnake (*P. a. quadrivittatus* X *P. a. rossalleni*), provides a sharp contrast in response and biology. This species was evenly distributed across years. It is strongly arboreal in southern Florida, where, to a great extent, it includes birds in its diet (Meshaka and Layne, 2015). Perhaps, then, the ratsnake remained unaffected in trees while its more terrestrial and shallow wetland counterparts starved, were too reluctant to move far, or both? Like the ratsnake, the Burmese Python did not significantly vary in abundance. It was detected in 2010 and 2011 and in low abundances. Body size data were available for only a few juveniles, so we cannot examine recruitment as a possible clue in their demographic response among years. We are inclined to believe that the Burmese Python, like the ratsnake, was unaffected by the low water table in light of its arboreal habits and, all the more so, because of both its wide trophic breadth and inclusion of terrestrial habits.

On the other hand, aquatic species that are strongly associated with long hydroperiods and deep water, the Striped Swampsnake, Florida Green Watersnake, and Brown Watersnake, were unaffected by the lower water table. The absence of a response by these three species to a lower water table is not surprising and lends credence to the notion that low water by virtue of habitat loss and prey loss would negatively impact terrestrial, semi-aquatic, and short hydroperiod wetland species before it would impact inhabitants of deep water.

Among the six species whose changes in 2011 abundance were significant, a shift in sex ratio was evident only in the Red Cornsnake. Overall sex ratio (1.50:1.00) and those of the first two years of the study (1.80:1.00 and 3.00:1.00, respectively) were male biased. In 2011, the number of males dropped to zero from nine in each of the previous years while numbers of females remained steady (5, 3, and 4, respectively). Among these same six species, however, changes in recruitment associated with 2011 were striking among five of them. Recruitment increased in four species, the Florida Cottonmouth, Florida Scarletsnake, Peninsula Ribbonsnake, and Eastern Gartersnake, following distinct downward trends from 2009. Recruitment decreased to 0.00% in two species, the Mangrove-Florida Watersnake hybrid and the Red Cornsnake. The trend among years was downward in the former species and upward in the latter species before the 2011 crash in recruitment.

The two species whose abundances were unaffected by low water, the Florida Green Watersnake and Brown Watersnake, differed in their respective sex ratios in 2011. The male:female sex ratio of the Florida Green Watersnake trended to more females, then spiked towards males in 2011. The same was true of the Brown Watersnake; however, the high in 2011 was only slightly lower than that of 2009. Both of these species strikingly responded in a spike of recruitment following downward trends from 2009. Thus, changes in recruitment associated with a low water table were generally positive among the aquatic and semi-aquatic species regardless of their response in abundances. Recruitment was unaffected in the Florida Watersnake and affected in opposite in the Florida Scarletsnake and Red Cornsnake, whose responses in abundance differed from one another**.**

A short-term response by the snake assemblage presages its future- A severe population-wide demographic response was evident by these species to even moderate changes in water table levels in Everglades National Park. Do these demographic-related responses to a low water table by snakes in Everglades National Park provide a "Ghost of Christmas Future" in a system subject to the climatic, hydrological, and physical restructuring associated with human-mediated climate change? A varyingly predictable interplay of human-mediated changes in environmental temperatures, amounts and delivery patterns of annual precipitation, and sea level rise is underway globally. The trajectory of modeled changes in the environment will result in a stepwise restructuring of the southern Everglades ecosystem within which a successional timeline forms for the Everglades comprised of human-mediated ecological seres. What sort of future is projected for this youthful alternohygric system to be faced by its snake assemblage, and do the findings of our present study provide a glimpse into their future responses?

By 2100, environmental temperatures will be 2.0–2.5 C higher than the 2000 average (IPPC, 2007). Globally, fewer but more intense cyclones are predicted (Knutson et al., 2010). In the Southeastern US, the future precipitation patterns will be of more intense events separated by longer extreme droughts (Selman et al., 2013). By 2100, the global mean sea level increase will range 0.3–1.0 m (Sweet et al., 2018), the pattern of which is not steady (Noss, 2011). At even the conservative low-end prediction category of 0.3 m rise in regional sea level, most areas along the US. coast excluding Alaska will experience 25-fold annual increase in damaging floods by 2080.

Globally and regionally, then, a directional, even if wobbly, theme exists of increasing air temperatures, less rainfall delivered in more powerful events, and concomitant increase in evapotranspiration, all occurring under a backdrop of rising sea level. A combination of higher air temperatures and reduced precipitation alone affect prey species and amphibian habitat (Corn, 2005).

But what sequence of events awaits the southern Everglades, the immense shallow river that encompassed our site? Increased air temperatures will affect the species composition of the Everglades in at least two ways. First, although the increase in air temperature will be lower than elsewhere, the increase alone will stress many native species in the Everglades that are already at the edge of temperature tolerances (Pearlstine et al., 2010). The increase in air temperature in the Everglades will also increase the time between cold weather events, advantageous conditions for many potentially colonizing exotic species (Catano et al., 2015). The decrease in annual volume of rainfall in the Everglades will be substantial (Todd et al., 2012), exacerbated by a projected decrease by as much as 11% because of the type of extensive landscape changes over the past 100 years (Pielke et al., 1999). The decrease in annual rainfall in the Everglades is predicted to alter the mean shallow water depth from 20–40 cm at present to 0–15 cm and inundation from 80–100% at present to 0–20% (Todd et al., 2012). Maximum water depths will drop from 102.1 cm to 57.7 cm, and the number of distinct hydrologic classes will drop from 116 to 67 types (Todd et al., 2012). In response to these changes, xeric vegetation communities will replace hydric vegetation communities. Sawgrass will lose 13.6% coverage from its present-day coverage of 57.5% with colonization of xeric species such as muhly grass, Brazilian pepper, and slash pine with hardwoods (Todd et al., 2012).

From a different angle, a combination of less rain and more evapotranspiration will change the present-day interannual range of water height above the slough soil surface of 1.8 –1.2 m above the soil; only 25–35 cm difference in this value is enough to change vegetation types (Van der Valk et al., 2015). The combination of less rainfall and greater evapotranspiration negatively impacts a wide range of Everglades wildlife (Catano et al., 2015). For example, models for 2060 that expect less rainfall and more evapotranspiration at a 1.5 °C increase in air temperature predict reduced fish density and negative impacts on the American Alligator, the American Crocodile, and wading birds (Catano et al., 2015). Pearlstine et al. (2010) note that even a small increase in air temperatures and reduction of rainfall during the May–Oct wet season could result in extended droughts and changes to the Everglades. In such circumstances, a shift in geographic range in some species is a likely outcome, thereby changing community structures. However, the species at greatest risk in the Everglades will be those at the edge of their geographic ranges, that depend on environmental cues for life history phenologies, or those that disperse poorly (Pearlstine et al., 2010). To that end, Pearlstine et al. (2010) argue for greater investment in phenological studies of Everglades species.

Adding to changes in air temperature and rainfall patterns is sea level rise. Across its great expanse, the water level of the Everglades rises 5 cm per km (Pearlstine et al., 2010). However, during 1952–2010, water levels at Key West and in Everglades National Park rose 2.36 mm/yr (Stabenau et al., 2011), and sea level is expected to rise 0.8–2.0 m over next century (Pearlstine et al., 2010). Rapid sea level rise will easily spill ocean water over natural marl berms resulting in rapid loss of freshwater wetlands (Wanless et al., 1997); however, this is preceded by an intermediate step of inundation of saline water rising up from underground that will itself cause restructuring of the Everglades. A case in point is the natural berm, north of Florida Bay between Cape Sable and Joe Bay, that stands 65–100 cm above current mean sea level. Salt marsh and mangrove forest populate either side of the berm, buttonwood forest occurs up the slope of the berm, and coastal hammock exists along the top (Stabenau et al., 2011). Saline water rising from underground to buttonwood forests will precede saltwater inundation as sea level rises (Stabenau et al., 2011), and prior to that sustained inundation, initial sea level rise is predicted to result in the reduction of coastal hammocks and buttonwood forests in the Everglades, (Saha et al., 2011).

The combined effects of higher air temperatures, lower annual rainfall volumes delivered in fewer and more violent events, and sea level rise form quantifiable predictions of an altered ecosystem. In a 50-yr window for Florida Everglades, the combination of a 1.5 °C increase in air temperature, 10% change in rainfall (decrease being the more likely direction), and 0.46 m rise in sea level will result in a 5–114 cm drop in median water depths and a 5-45% decrease in duration of inundations. The new hydrology will subject the Everglades to severe droughts, more wildfire, loss of slough, and the restructuring of plant and animal communities (Nungesser et al., 2015). In this scenario, the greater Everglades will dry out by 2060, altering the ecosystem and the water supply (Obeysekera et al., 2015).

Over the next century, the Everglades subjected to sea level rise $\geq$ 1m and increased drought punctuated by less rain delivered in intense storms will experience greater climate variability and extremes, fire, loss of freshwater graminoid and mangrove wetlands, and changes in flow to the two deep water sloughs, affecting many segments of the Everglades biota, including herpetofauna (Pearlstine et al., 2010). Everglades-adapted wildlife could migrate because of shifting habitats and climate or will vanish from an inability to adapt (Pearlstine et al., 2010).

From an examination of these projected changes in the climate it seems apparent to us that for the purposes of this study, the ecological changes over time can be best understood in the context of ecological succession. In this context, we recognize at least four distinct successional seres: Pre-saltwater inundation, partial saltwater inundation, full saltwater inundation shallow, full saltwater inundation deep. We describe these and relate those seres to the snake assemblage of Everglades National Park.

Prior to saltwater intrusion, the Everglades will become warmer. Punctuated by violent storms, the wet and dry seasons will become less distinct, and the water table will average lower in response to reduced annual volumes of precipitation. Everglades National Park will become floristically much more xeric, fire-prone, and colonized by more exotic species. In this sere, the deep water natricines, such as the Eastern Mudsnake, Southern Florida Swampsnake, Florida Green Watersnake, and Brown Watersnake will no longer be seen anywhere away from the two sloughs. Recruitment of the latter two species will be disrupted. In the freshwater glades, abundances of short-hydroperiod aquatic and semi-aquatic snakes, like the Florida Cottonmouth, *N. c. compressicauda X N. f. pictiventris*, Florida Watersnake, Peninsula Ribbonsnake, and Eastern Gartersnake will drop. The same would be true of the Dusky Pygmy Rattlesnake. Like midwestern snake assemblages whose associations with arroyos vary, these species will recede from much of their ranges within Everglades National Park and for a time live closely alongside the sloughs. In the saline glades of Everglades National Park to the south, these snakes would fare better and possibly for a longer time until the salinity level reaches a tipping point for want of rainfall. Regardless of location, recruitment will respond variably. Exotic species of amphibians and reptiles, on the other hand, may be conferred an advantage by the ensuing drier habitat (Howell et al., 2020).

Across the park, terrestrial-arboreal species, like the Everglades Racer, Red Cornsnake, ratsnake, and Burmese Python stand the best chance of persisting in terrestrial habitat for a time because of semi-arboreal and arboreal habits and a broad trophic breadth. This sere will end once saline water percolates up from the ground. Salt marsh and mangrove that typify the saline glades will evermore spread as the saltwater water becomes deeper, first by salt marsh, then mangrove. Accompanying this change will be loss and redistribution of the floristically unique buttonwood forests and coastal hammocks that grow along the southern berm. In this sere of inundation shallow, the ratsnake and Mangrove Saltmarsh Watersnake stand the best chance at success as the truly freshwater species and terrestrial species recede from estuarine and saline systems. Perhaps, selection will favor the morphology of Deckert's Ratsnake, *P. a. deckerti*, along extensive southern mangrove and the red morph of the Mangrove Saltmarsh Watersnake will dominate in the open saline glades. The Everglades Racer, Red Cornsnake, and Burmese Python share some likelihood of persistence in coastal hammock and buttonwood forest.

Ultimately, ocean water will spill over the berms and into the basin, changing the distribution of mangrove forests and salt marsh. The southern Everglades, Everglades National Park, known, treasured, and abused, will prematurely be buried under water leading to the fourth sere- the climax sere being shallow ocean, like that of much of the Gulf of Mexico. Facing each of these human-mediated ecological seres will be the members of the snake assemblage of which all members have shown varying adjustments in morphology and ecology in the few thousand years of their association with this youthful alternohygric evolutionary experiment (Meshaka and Layne, 2015). Regardless of how humans address climate change and its subsequent trajectories, global warming is a monster of our own making, and therefore, with a range of Ghosts of Christmas Futures of our choosing. Above is the result of one such choice.

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Appendix 1. Numbers associated with snake encounters in Everglades National Park, Miami-Dade and Monroe counties, Florida, during January–December 2009–2011.

Species	Jan–Dec	Jan–Dec	Jan–Dec	Jan–Dec
Species	2009	2010	2011	All years
Species	Total	Total	Total	Total
Agkistrodon conanti	127	130	65	322
Cemophora coccinea coccinea	9	32	19	60
Coluber constrictor paludicola	10	9	3	22
Crotalus adamanteus	2	7	5	14
Diadophis punctatus punctatus	4	1	0	5
Drymarchon couperi	0	1	0	1
Farancia abacura abacura	0	3	1	4
Lampropeltis elapsoides	0	0	1	1
Lampropeltis getula	0	0	1	1
Liodytes alleni	7	7	3	17
Liodytes pygaea cyclas	1	0	0	1
Micrurus fulvius barbouri	1	0	0	1
Nerodia clarkii compressicauda X N. fasciata pictiventris	31	35	3	69
Nerodia fasciata pictiventris	94	75	51	220
Nerodia floridana	19	20	22	61
Nerodia taxispilota	12	5	14	31
Opheodrys aestivus carinatus	3	1	0	4
Pantherophis guttatus	19	27	5	51
Pantherophis alleghaniensis quadrivittatus X P. a. rossalleni	10	8	10	28
Python bivittatus	9	6	5	20
Sistrurus miliarius barbouri	9	7	2	18
Storeria victa	1	2	0	3
Thamnophis saurita sackenii	76	80	30	186
Thamnophis sirtalis sirtalis	102	42	27	171
Total no. individuals	546	498	267	1311
Total no. species	20	20	18	24

Appendix 2. Numbers associated with snake encounters in Everglades National Park, Miami-Dade and Monroe counties, Florida, during March–December 2009–2011.

Species	Mar-Dec	Mar-Dec	Mar-Dec	Mar-Dec	Mar-Dec
Species	2008	2009	2010	2011	All years
Species	Total	Total	Total	Total	Total
Agkistrodon conanti	59	123	128	56	366
Cemophora coccinea coccinea	6	9	32	18	65
Coluber constrictor paludicola	10	9	9	3	31
Crotalus adamanteus	2	2	7	3	14
Diadophis punctatus punctatus	1	4	1	0	6
Drymarchon couperi		0	1	0	1
Farancia abacura abacura	1	0	3	1	5
Lampropeltis elapsoides	1	0	0	1	2
Lampropeltis getula	3	0	0	0	3
Liodytes alleni	0	7	7	2	16
Liodytes pygaea cyclas	0	1	0	0	1
Micrurus fulvius barbouri	0	1	0	0	1
Nerodia clarkii compressicauda X *N. fasciata pictiventris*	22	30	35	1	88
Nerodia fasciata pictiventris	30	68	74	38	210
Nerodia floridana	12	13	19	10	54
Nerodia taxispilota	7	10	5	12	34
Opheodrys aestivus carinatus	0	3	1	0	4
Pantherophis guttatus	11	18	24	5	58
Pantherophis alleghaniensis quadrivittatus X *P. a. rossalleni*	8	9	8	9	34
Python bivittatus	13	9	6	5	33
Sistrurus miliarius barbouri	2	9	7	2	20
Storeria victa	1	1	2	0	4
Thamnophis saurita sackenii	14	71	78	22	185
Thamnophis sirtalis sirtalis	41	85	40	20	186
Total no. individuals	244	482	487	208	1421
Total no. species	20	20	20	17	24