Ecology of an Insular Snake Assemblage in Coastal Maine

John D. Willson[1,*], Ethan J. Royal[1], Jacquelyn C. Guzy[1,2],
Meredith C. Swartwout[1,3,4], and Chelsea S. Kross[1,5]

Abstract - Wildlife populations at the peripheries of their distributions or on isolated islands often display divergent and poorly understood morphological or life-history characteristics compared to core populations. We used a capture–mark–recapture dataset collected over a 19-year period to characterize a northern, insular snake assemblage in coastal Maine. We captured 611 individual snakes of 4 species (*Thamnophis sirtalis* [Common Gartersnake; *n* = 221 individuals], *Diadophis punctatus* [Ring-necked Snake; *n* = 258 individuals], *Storeria occipitomaculata* [Red-bellied Snake; *n* = 81 individuals], and *Opheodrys vernalis* [Smooth Greensnake; *n* = 51 individuals]) and recorded 104 recaptures. We provide some of the first data on growth, reproduction, and movement for these species in northern New England, expanding our understanding of insular and northern snake populations. Specifically, we found that Common Gartersnakes fed primarily on earthworms and amphibians and grew rapidly, in accordance with mainland populations, but exhibited smaller size at maturity and average litter sizes. We captured an unusually large number of Ring-necked Snakes, which are uncommon elsewhere in Maine, and recorded an apparently localized nesting area for this species, as well as relatively long-distance (230–300 m) dispersal away from that location. In our population, female Ring-necked Snakes mature in their third year, and this species exhibits weak sexual size dimorphism (SSD). We found the ecology of Red-bellied Snakes at our study site to be similar to other populations, with individuals feeding on slugs, and females maturing in their second year; however, our population exhibited the strongest pattern of (female-biased) SSD. Smooth Greensnakes were restricted to the most extensive old-field habitat within our study site and fed on a variety of arthropods. We confirmed communal nesting and short incubation period for this species and provide among the first data on growth and longevity (at least 7 years) of this relatively understudied species.

Introduction

Snakes play important trophic and ecological roles within ecosystems, but are often overlooked because their cryptic coloration, low and variable activity, and fossorial or arboreal behavior make them inconspicuous. Although the secretive nature of snakes has rendered them among the most challenging vertebrate groups to study (Parker and Plummer 1987), they can be important predators in many ecosystems (Campbell et al. 2012, Godley 1980, Patten and Bolger 2003, Willson and Winne 2016). Many snakes, especially small-bodied species, are also important

[1]Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701. [2]US Geological Survey, Wetland and Aquatic Research Center, 3321 College Avenue, Davie, FL 33314. [3]Department of Biology, University of Toronto Mississauga, 3359 Mississauga Road, Mississauga, ON L5L 1C6, Canada. [4]Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON M5S 3B2, Canada. [5]Stephen A. Forbes Biological Station, Illinois Natural History Survey, University of Illinois at Urbana-Champaign, Havana, IL 62644. [*]Corresponding author - jwillson@uark.edu.

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prey for a variety of predators (Ernst and Ernst 2003). Yet, small, semi-fossorial species are among the most understudied of all snake species (Willson and Dorcas 2004). Although these snake species can be wide-ranging and occur in high abundances, in some cases at densities greater than 1000 individuals/ha (Fitch 1975), few have been the subject of direct research. The sparse life-history data available for many common small snake species can inhibit our ability to understand their biology and conservation status (Greene 2005).

Studies examining variation in life-history traits (e.g., demography, age at maturity, fecundity, growth rates) within species can yield insights into factors that dictate distribution and abundance, as well as identify evolutionary patterns of local adaptation that drive speciation. For example, coastal populations of *Thamnophis elegans* (Baird and Girard) (Western Terrestrial Gartersnake) are locally adapted to a specialized diet of slugs and can transfer 62% more ingested energy towards production, compared to inland populations of generalist Western Terrestrial Gartersnakes (Britt et al. 2006). Additionally, populations at the periphery of a species' range often exhibit different life-history patterns compared to populations at their range core. *Crotalus horridus* L. (Timber Rattlesnake) in the Adirondacks of New York can live longer than 32 years but may have only a single reproductive event (Brown 2016), greatly differing from populations in the southern United States that reproduce biennially (Gibbons 1972). Life-history trait variation in peripheral populations is often of clear ecological importance yet it remains understudied, including for North American snake species that reach their northern range limits in New England (Hunter et al. 1999).

Islands provide an ideal setting for understanding life-history variation, drivers of community assemblage, and how selection acts on small populations (e.g., Darwin 1859, Lillywhite and Martins 2019, MacArthur and Wilson 1967, Ricklefs and Bermingham 2007). These processes have been documented in some insular snake populations. For example, the island endemic rattlesnake *Crotalus catalinensis* Cliff (Santa Catalina Rattlesnake) may have lost its rattle through selection (Greene 1997). Populations of *Agkistrodon piscivorus* (Lacépède) (Cottonmouth) on Florida islands have a different feeding strategy (scavenging fish dropped by seabirds) than populations on the mainland (Lillywhite et al. 2002). In addition, island populations of *Notechis* spp. (Australian tiger snakes) and *Elaphe quadrivirgata* (H. Boie) (Japanese Four-lined Ratsnake) have been the subject of long-term studies to determine the origins of gigantism and dwarfism in body size (Aubret 2012, Hasegawa and Mori 2008, Keogh et al. 2005, Vincent et al. 2009). Thus, natural history data collected from insular snake populations at their northern range limits provide context for the trait variation exhibited within these species and can be valuable for future comparative work.

We used a long-term capture–mark–recapture dataset to examine the natural histories of the 4 species of snakes (*Thamnophis sirtalis* (L.) [Common Gartersnake], *Diadophis punctatus* (L.) [Ring-necked Snake], *Storeria occipitomaculata* (Storer) [Red-bellied Snake], and *Opheodrys vernalis* (Harlan) [Smooth Greensnake]) that occur on an island in coastal Maine. We present data on community composition as well as the habitat associations, demography, growth, movement, diet, and reproduction of each species. These data are among the most comprehensive for these species and for any reptile species in New England, providing a valuable baseline for comparison to other regions and for understanding the ecology of reptiles at their northern range limits.

Field-Site Description

We studied snakes within a ~1-km^2 study site located on private property on the island of Islesboro, Waldo County, ME. Islesboro is located in the mid-coast region of Maine at the head of the Penobscot Bay. The island runs ~18 km north–south and is <4 km wide at its widest point. It is surrounded by salt water on all sides, with the mainland and other major islands 2–9 km distant across water 15 to >60 m deep. Islesboro is characterized by relatively rough topography of limestone ledge and is primarily forested with maximum elevation of ~60 m. The island lies along the boreal transition zone, with the northern parts of the island being primarily conifer forest, transitioning to mixed or primarily deciduous forest to the south. Much of the island is mid-age (<100 years) second-growth forest, but parts of the study site contain numerous large trees >100 years old. The island has 1 large (10 ha) freshwater pond, located just to the east of the study site.

Islesboro has a temperate maritime climate, with cool, foggy, summers (average daily high = 25 °C [78 °F], daily low = 14 °C [57 °F] in July and August) and cold winters (average daily high = -1 °C [30 °F], daily low = -13 °C [9 °F], in January and February) (www.wunderground.com; accessed 5 Sept 2022). Frost is expected between early October and early May.

Within the study site (Fig. 1), snake captures were concentrated within 4 general areas, broadly representing the major areas of open canopy cover and encompassing

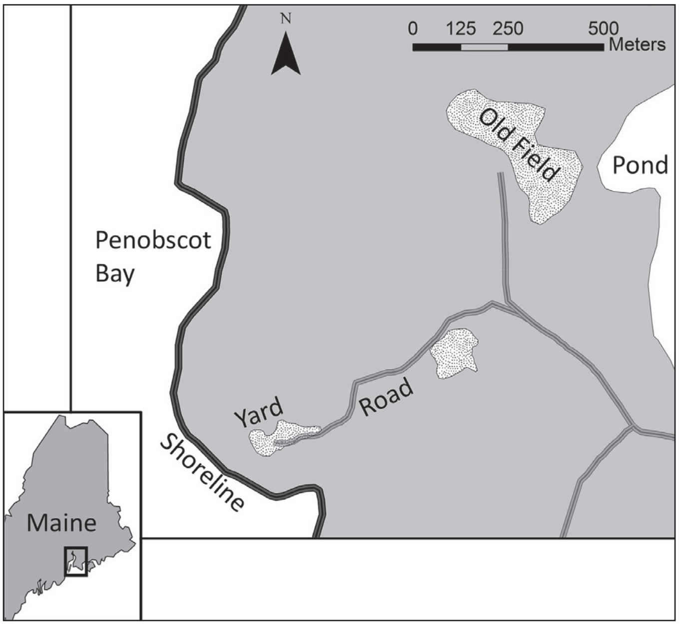

Figure 1. Map of study site on Islesboro Island, in coastal Maine, with primary study areas indicated. See text for detailed descriptions of study areas. Gray shading represents forest; stippled areas represent open-canopy grassy areas. Sampling primarily occurred in the open-canopy habitats and along the road and shoreline, an area totaling ~8.5 ha.

an total of ~8.5 ha. The western side of the study site is boreal, primarily vegetated by mature *Picea rubens* Sarg. (Red Spruce), *Abies balsamea* (L.) Mill. (Balsam Fir), and *Betula* spp. (birch) with thin soil and a groundcover of ferns, lichens, and mosses. Within this area, snakes were captured along the shoreline, where steep slope and abundant limestone ledge and talus create gaps in the canopy, and around the yard (~0.15 ha), comprised of lawn, garden, and forest edge surrounding a house. Along the unpaved road leading northeast from the yard, the forest transitions to mixed conifer-deciduous (adding *Acer rubrum* L. [Red Maple], *Fraxinus americana* L. [White Ash], and *Populus* spp. [aspen]), interspersed with wet, boggy areas dominated by *Thuja occidentalis* L. (Northern White Cedar), *Larix laricina* (Du Roi) K. Koch (Tamarack), and *Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton (Skunk Cabbage). There is minimal open canopy along the road, and we captured most snakes under rocks along a <2 m-wide road embankment that receives partial sun. The house and road were constructed in 1991, whereas another open area bordering the road to the south was cleared in the early 2000s; this area was not sampled for snakes. The final study area, the old field, is a much larger (~3 ha) grassy field, adjacent to the pond. The western section of this field, where we captured most snakes, is dry and grassy, with several rocky outcrops and clumps of *Vaccinium angustifolium* Aiton (Lowbush Blueberry) and *Juniperus communis* L. (Juniper). This area has been a field for >100 years and at the start of the study contained an old, partially deconstructed stone foundation that yielded large numbers of snake captures until the foundation was replaced with a modern barn in 2012. The remainder of the study area is primarily closed-canopy forest where we seldom encountered snakes.

Methods

Snake sampling

We sampled snakes opportunistically between 2003 and 2021 by turning natural cover objects, primarily rocks, and visually searching for active individuals. Because most sampling occurred during recreational visits by the first author, effort was variable within and among years, but when sampling occurred, we sampled all sub-sites with approximately equal effort and collected data on all snakes encountered. We conducted most sampling during May–September, with most captures occurring in July and August. Following capture, we recorded sex (by visual inspection of tail morphology and/or probing) and snout–vent length (SVL; nearest mm by stretching along a meter stick) of each individual, and identified recently ingested prey items by palpation and regurgitation. Additionally, we palpated females and counted any enlarged follicles or ova detected to determine clutch size for oviparous species (Ring-necked Snake and Smooth Greensnake) or litter size for viviparous species (Common Gartersnake and Red-bellied Snake). Palpation yields a less accurate assessment of litter size than more involved methods, such as ultrasound or maintaining females until parturition, especially for large or heavy-bodied species. However, our species were relatively small and developing ova could usually be clearly differentiated. Moreover, mean litter size for our largest species, the

Common Gartersnake, was very similar between palpated ova counts (mean = 13.2; *n* = 63) and litters born to females that were held until parturition (mean = 13.6; *n* = 10), suggesting that palpation rendered a reasonably accurate measure of litter size for our study species.

We individually marked snakes with a unique code by branding ventral scales (Winne et al. 2006). Following processing, we released each snake at its capture location within 48 h. In 1 year, we held 10 gravid female Common Gartersnakes in captivity for 9–21 (mean = 14.2) days to gather reproductive data. These females were housed individually in 75.7-L aquaria with a substrate of aspen shavings, a hide box, and a large water bowl. We positioned a 75-W incandescent bulb above an end of each aquarium, providing a thermal gradient (~20–40 °C) within the cage during the day and allowing the cage to cool to ambient temperature at night. We checked females several times per day. We measured mass and SVL of neonates, as well as total mass of the litter (including any unfertilized ova), immediately after their birth. One female Red-bellied Snake gave birth in captivity while being held overnight for processing.

Analyses

We described species composition of the snake assemblage among the 4 primary sampling areas by tabulating the number of individual snakes of each species captured (i.e., excluding recaptures) and visually examining the relative abundance of species in each sampling area. We examined movements by calculating the linear distance between initial capture location and recapture location for all recaptures where location was noted to within 5 m. We then created a frequency histogram of movement distances for each species.

We examined demography of each species by creating size–frequency histograms of all field captures for each species, separated into males and females. We could not sex some small Ring-necked Snakes (*n* =19, <200 mm SVL) and omitted these from the histograms. We evaluated sexual size dimorphism (SSD) in each species by comparing SVL of the 15 largest individual snakes of each sex among the sexes using an individual *t*-test for each species in the 'stats' package in program R (v.4.1.2) (R Core Team 2021), with statistical significance recognized at $\alpha = 0.05$. We limited our SSD analyses to the 15 largest individuals to eliminate the influence of variable demography on our results (Forsman 1991, Winne et al. 2010). For Ring-necked Snakes, we also visually examined size–frequency histograms for each of the 4 primary sampling sites, irrespective of sex.

We examined growth in 3 ways. First, for each species, we amassed all recaptures and calculated growth in SVL (mm) and time interval between recaptures. More specifically, we calculated the change in SVL between recaptures over time for each individual, excluding portions of each year (i.e., 1 November–1 April) where negligible growth is assumed because of seasonally cold temperatures. We also excluded recaptures occurring more than 2 years apart because growth is not likely to be linear over longer time intervals. We then plotted growth rate in mm/day versus SVL for males and females separately and fit those relationships with linear best-fit lines.

Some individuals exhibited slightly negative growth rates due to measurement error; these values were retained to avoid bias towards faster growth.

We then used the program Growth II (Pisces-Conservation Ltd, Lymington, Hants, UK) to fit all incremental growth data to a Von Bertalanffy growth model, $SVL_t = SVL_\infty (1 - be^{-rt})$, where SVL_t is the SVL at time t, SVL_∞ is the asymptotic snout–vent length, SVL_0 is the hatchling SVL, b is a parameter related to hatchling SVL ($\sim 1 - SVL_0/SVL_\infty$), r is the growth rate, and t is the time since birth. Based on our reproductive and field data (see below), we set SVL_0 at 136 mm for Common Gartersnakes, 100 mm for Ring-necked Snakes, 72 mm for Red-bellied Snakes, and 100 mm for Smooth Greensnakes. We plotted age versus SVL curves generated using the mean and upper and lower bounds of the 95% CI of the growth parameter (r) and asymptotic size parameter (SVL∞) for both sexes of Common Gartersnakes and Ring-necked Snakes. Low recapture rates of male Red-bellied Snakes and Smooth Greensnakes precluded meaningful analyses; thus, we only plotted growth curves for females of those species.

Finally, for comparison with growth curves generated via capture–recapture, we visualized seasonal shifts in demography of Common Gartersnakes and Ring-necked Snakes by plotting SVL versus Julian day of capture for all field-captured individuals.

To characterize reproduction, we calculated summary statistics (mean, standard error, min–max) for various reproductive traits for each species based on field data (palpated litters from field-captured females, egg clutches observed in the field, and neonates captured in the field) and based on lab-born litters for Common Gartersnakes and Red-bellied Snakes. We examined correlations between female body size (SVL) and clutch/litter size using linear regression for all species except for Ring-necked Snakes (due to small sample size).

To assess diet, we tabulated prey within various taxonomic groups for each snake species.

Results

Snake community assemblage

In total, we had 715 snake captures across 19 years, of which 104 captures were recaptures of previously marked individuals. Variable sampling precluded formal comparisons of seasonal or inter-annual shifts in relative abundance. However, snakes were frequently found active (i.e., crawling on the surface) and under cover objects between May and October and were seldom found in other seasons. However, 1 juvenile female Ring-necked Snake (SVL = 119 mm) was captured on 23 November 2009 (rainy, air temperature = ~4 °C) and another juvenile Ring-necked Snake (sex and SVL not recorded) was captured on 21 December 2006 (overcast, air temperature = -1 °C). Both snakes were found under small surface rocks along the shoreline in areas of deep rocky talus.

Overall, Common Gartersnakes (n = 221 individuals; 51 recaptures) and Ring-necked Snakes (n = 258 individuals; 27 recaptures) were more commonly captured than Red-bellied Snakes (n = 81 individuals; 12 recaptures) and

Smooth Greensnakes (n = 51 individuals; 14 recaptures), but there was substantial variation in relative abundance of species among the study areas (Fig. 2). Ring-necked Snakes dominated captures in the more boreal/forested areas of the shoreline (84% of individuals captured) and along the road (89% of individuals captured), whereas Common Gartersnakes were more common in grassy habitats of the yard and especially the old field (66% of individuals captured). Red-bellied Snakes were found in small numbers (<15% of individuals captured) at all sites. Smooth Greensnakes were only found in the old field, where they comprised 15% of individuals captured.

Movement

We gathered data on movements between successive captures of 98 individuals that were captured more than 1 time. Recapture intervals varied from 1 day to 2131 days (almost 6 years) and averaged 248 days; the longest recapture interval was an adult female Smooth Greensnake (SVL = 341 mm at initial capture) that was captured in the same general area on 13 Sept 2006 and on 14 July 2012. Two additional adult female Smooth Greensnakes were recaptured ~3 years (1050 days) after their initial captures. The longest recapture intervals for other species were 431 days for Red-bellied Snakes, 751 days for Ring-necked Snakes, and 712 days for Common Gartersnakes.

Across all species, the majority (66%) of recaptured individuals were captured <5 m from their initial capture location (see Supplemental Figure S1 in Supplemental File 1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n31-1-N1981-Willson-s1 and, for BioOne subscribers, at https://www.doi.org/10.1656/N1981.s1). However, some individual Ring-necked Snakes and Common Gartersnakes moved considerable distances. Specifically, 3 juvenile Ring-necked Snakes (110–123 mm SVL) moved from either the yard or shoreline to the road, representing straight-line distances of 230–300 m. Five individual Common Gartersnakes were documented making 150–200 m movements, all within the old field. Three individual adult Red-bellied Snakes were recorded

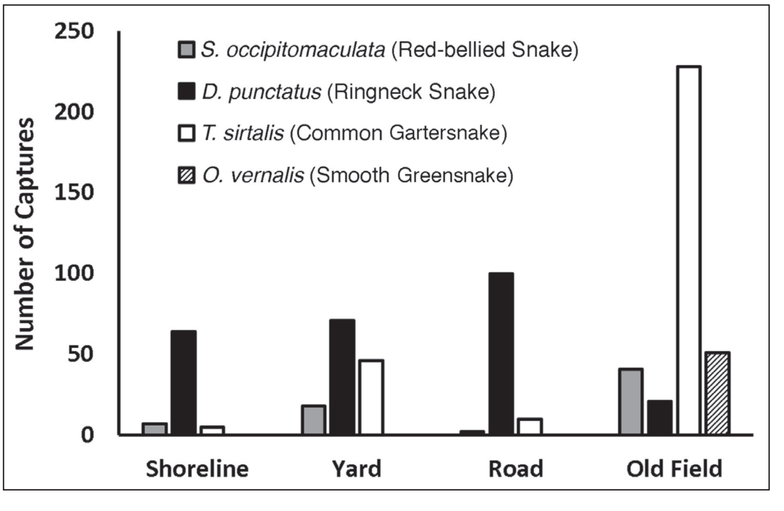

Figure 2. Composition of the snake assemblage (total individuals captured per species) at 4 study areas within study site in coastal Maine. See Figure 1 and text for spatial configuration and descriptions of study areas.

moving between the shoreline and yard or within the old field, representing straight-line movements of 50–120 m. Although Smooth Greensnakes had the most multi-year recapture events, no individual was recorded having moved >40 m from its initial capture location. In addition to movements of marked snakes, we observed a male Common Gartersnake (SVL ~350 mm) swimming in the ocean on 24 July 2020, ~200 m off the coast of the island, heading towards the mainland, which was ~2 km away. At the capture location, the water was ~27 m deep, with a surface temperature of 19 °C.

Demography

Common Gartersnakes exhibited a unimodal and normally distributed pattern of body-size variation (Fig. 3A). Relatively few small juveniles were captured, with individuals <250 mm SVL comprising 12% of captures. Likewise, only 4 individuals (1% of captures) measured >600 mm SVL. Common Gartersnakes displayed pronounced sexual size dimorphism in SVL among the 15 largest individuals of each sex (*t*-test; $t_{28} = 10.27$, $P < 0.01$), with females (mean SVL of 15 largest = 593 mm, maximum SVL = 698 mm) being substantially larger than males (mean SVL of 15 largest = 456 mm, maximum SVL = 526 mm). Ring-necked Snakes displayed a strongly bimodal distribution of body sizes (Fig. 3B), with juveniles <200 mm SVL comprising 61% of captures overall. However, this bimodal pattern was driven by

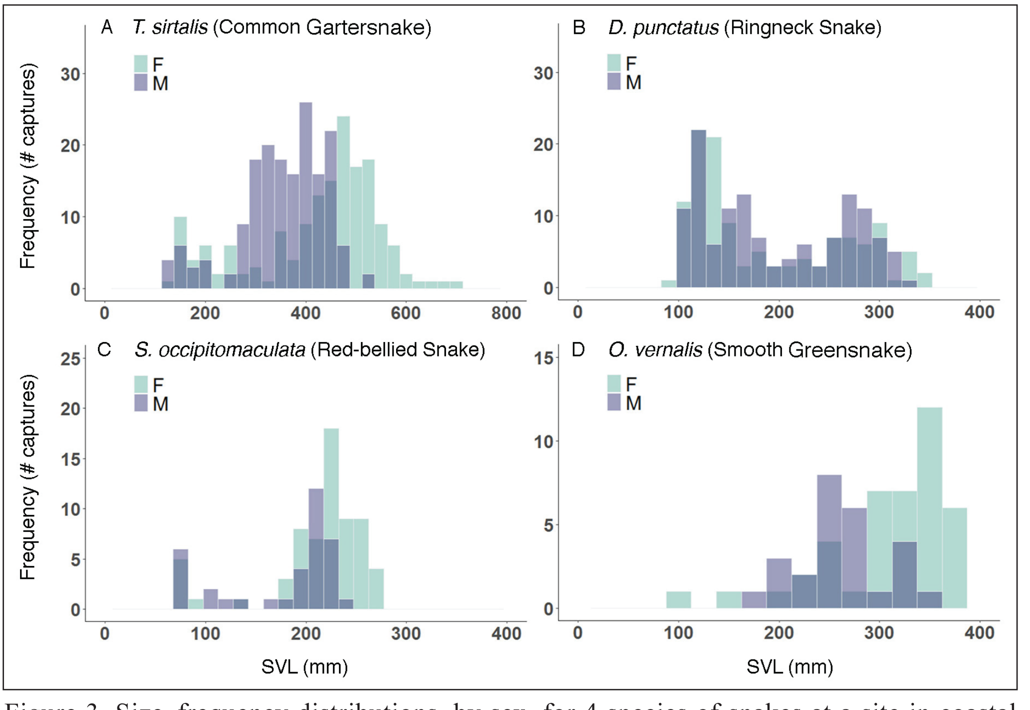

Figure 3. Size–frequency distributions, by sex, for 4 species of snakes at a site in coastal Maine. Some juvenile (<200 mm SVL) *D. punctatus* (Ring-necked Snake) of unknown sex (n = 19) were omitted. M = male, F = female, SVL = snout–vent length. Note that darker colors represent areas of overlap between sexes.

strong variation in demography among sampling locations (Fig. 4). Captures at the shoreline were almost exclusively (90% of captures) very small juveniles <150 mm SVL, with only 5 individuals >200 mm SVL captured in that location. Captures in the yard and road were also skewed towards juveniles, with most individuals being 125–200 mm SVL, yet with a fair number of adults also present (Fig. 4). Captures in the old field were few and were mostly large adults. Ring-necked Snakes exhibited significant sexual size dimorphism among the 15 largest individuals of each sex, with females (mean SVL = 313 mm, maximum SVL = 346 mm) larger than males (mean SVL = 303 mm, maximum SVL = 324 mm; Fig. 3B; *t*-test; $t_{28} = 2.31$, $P = 0.01$). The Red-bellied Snake was the smallest species, on average, and most individuals were adults between 200 and 250 mm SVL; relatively few juveniles were captured (Fig. 3C). Red-bellied Snakes exhibited sexual size dimorphism among the 15 largest individuals of each sex (*t*-test; $t_{28} = 6.84$, $P < 0.01$), with females (mean SVL = 246 mm, maximum SVL = 267 mm) substantially larger than males (mean SVL = 216 mm,

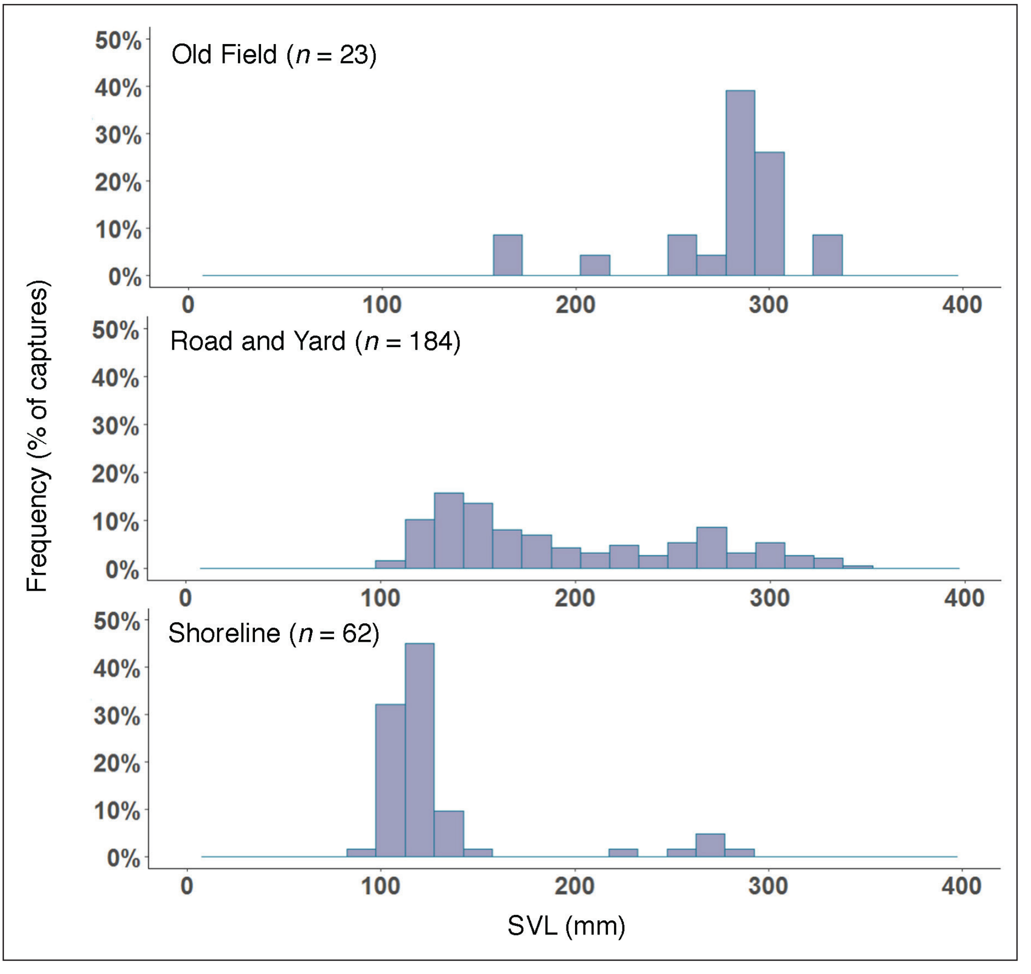

Figure 4. Size frequency distributions, by capture location, for *Diadophis punctatus* (Ring-necked Snake) from coastal Maine. SVL = snout–vent length.

maximum SVL = 245 mm). Smooth Greensnakes were strongly sexually dimorphic with females (mean SVL of 15 largest = 355 mm, maximum SVL = 384 mm) larger than males (mean SVL of 15 largest = 274 mm, maximum SVL = 343 mm; *t*-test; t_{28} = 9.20, $P < 0.01$). There were few captures of small juvenile Smooth Greensnakes, with individuals <200 mm SVL comprising just 7% of captures (Fig. 3D).

Growth

Based on recaptures of marked individuals over time, Common Gartersnakes grew rapidly, with neonates averaging ~0.8 mm per day during the active season (April–November; Fig. 5A). Examination of body lengths plotted against Julian day of capture (Fig. 6A) suggested that juveniles grow from ~135 mm SVL at birth in early August (see below) to ~200 mm SVL by the time they enter hibernation in the fall, and most individuals surpass 300 mm SVL by 1 year of age. Many adults, especially females, continued to grow well past maturity (Fig. 5A). Fitting Von Bertalanffy growth models to data for males and females yielded the following growth-parameter estimates (mean [95% CI]): male r = 0.85 (0.42–1.28), SVL_∞ = 444 (411–477); female r = 0.59 (0.29–0.89), SVL_∞ = 625 (539–710). Size-by-age plots based on these estimates (Fig. 5E) suggest that average females surpassed minimum size at sexual maturity (~400 mm SVL) around age 1 (i.e., summer of their second calendar year) and likely first reproduced at age 2 (summer of their third calendar year).

Growth patterns of marked individuals support these conclusions (see Supplemental Fig. S2A in Supplemental File 1). A neonate male Common Gartersnake (see Supplemental Fig. S2, line A1, in Supplemental File 1) first marked on 2 September (SVL = 151 mm) was recaptured after ~1 year (14 August) at 293 mm SVL, and again at age 2 (3 July; 400 mm SVL). A neonate female (see Supplemental Fig. S2, line A2, in Supplemental File 1) first marked on 13 September (167 mm SVL) was recaptured in July, almost 2 years later, measuring 526 mm SVL and gravid with 10 ova. Another female (see Supplemental Fig. S2, line A3, in Supplemental File 1) was captured in the spring after her first hibernation (22 June; SVL = 212 mm). She was recaptured in June both of the next 2 years (second June SVL = 349 mm; third June SVL = 461 mm), and was gravid in her third summer (age 2; SVL = 480 on 14 Aug). Growth of male Common Gartersnakes slows after reaching ~400 mm SVL, whereas females continue to grow, even at larger body sizes (Fig 5E; see also Supplemental Fig. S2A in Supplemental File 1).

Growth of Ring-necked Snakes decreased from ~0.4 mm/day in hatchlings to negligible growth in large adults; growth rates were highly variable among individuals, but similar between the sexes (Fig. 5B). Fitting Von Bertalanffy growth models to growth data for males and females yielded the following growth-parameter estimates (mean [95% CI]): male r = 0.49 (0.12–0.87), SVL_∞ = 286 (249–323); female r = 0.68 (0.07–1.29), SVL_∞ = 287 (232–342). Examination of body-size distributions by Julian day of capture (Fig 6B) suggests that growth of neonates did not start until after their first hibernation; in May–June, many juveniles were still approximately the same size as hatchlings in the fall (100–130 mm SVL). By the

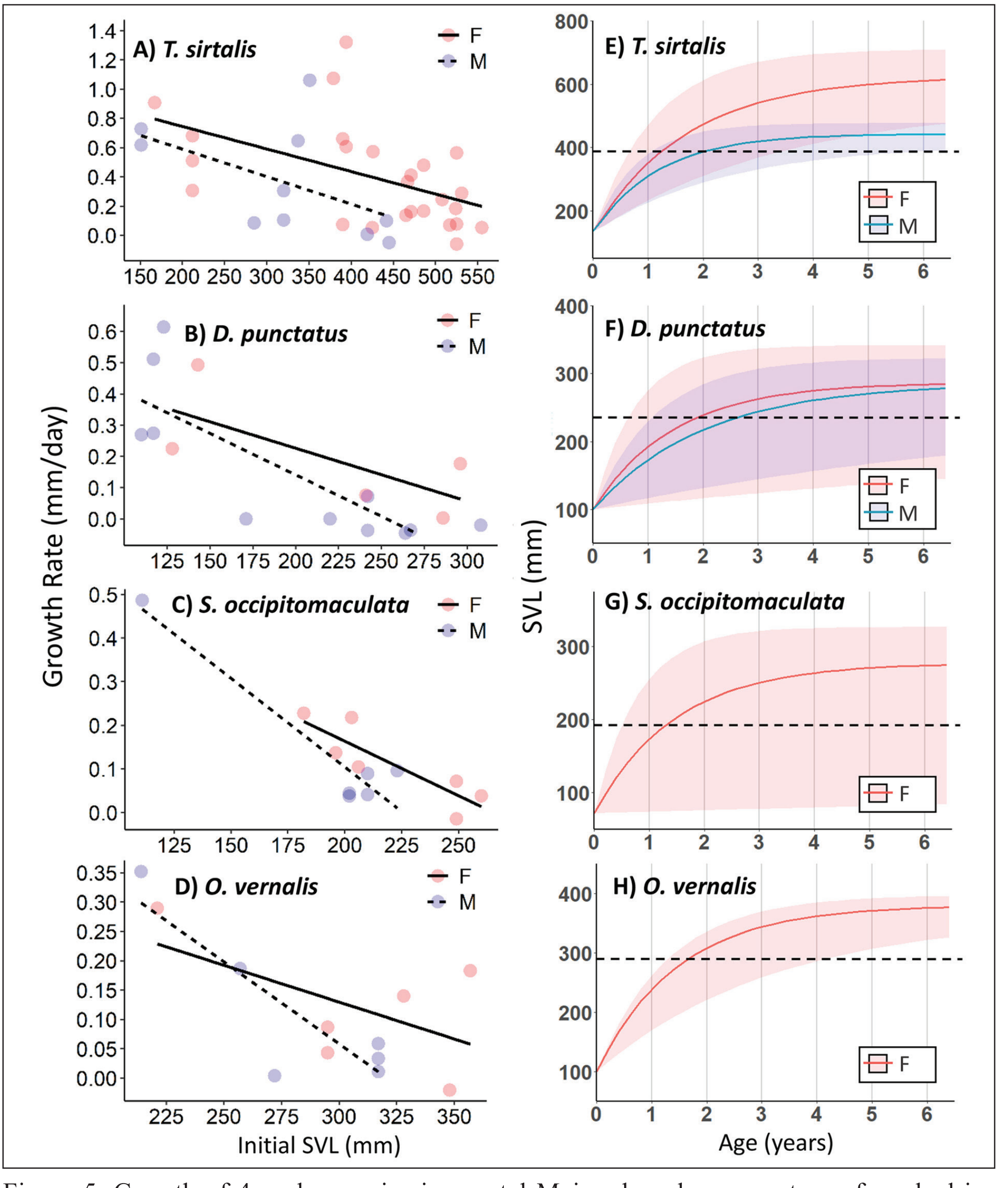

Figure 5. Growth of 4 snake species in coastal Maine, based on recapture of marked individuals over time. (A–D) Relationships between growth rate (mm per day, excluding November–March) and initial SVL of males (M) and females (F) recaptured less than 2 years after their initial capture, fit with linear regressions. (E–H) Von Bertalanffy growth curves, generated from all capture–recapture intervals. Lines represent mean (solid line) and 95% CI (shading) of size at age, generated by the von Bertalanffy growth model. Dashed horizontal lines in E–H represent minimum size at maturity for females based on our data for *T. sirtalis* (Common Gartersnake), *S. occipitomacula* (Red-bellied Snake), and *O. vernalis* (Smooth Greensnake), or the literature for *D. punctatus* (Ring-necked Snake; Hulse et al. 2001). Sample sizes were too small to yield meaningful growth curves for male Red-bellied Snakes and male Smooth Greensnakes.

end of their second calendar year (i.e., age 1), most individuals reached at least 150 mm SVL. Size-by-age plots based on these estimates (Fig. 5F) suggest that average females surpassed minimum size at sexual maturity (~230 mm SVL; Hulse et al. 2001) at ~2 years of age (i.e., summer of their third calendar year) and likely first reproduced at age 3 (summer of their fourth calendar year).

Although small sample sizes of recaptured Red-bellied Snakes and Smooth Greensnakes limited assessment of growth, females of both species appeared to reach maturity by age 2 (Fig. 5G, H). Male and female Red-bellied Snakes continued to grow, even at fairly large body sizes (i.e., >200 mm SVL; Fig. 5G; see also Supplemental Fig. S2D in Supplemental File 1), whereas 2 adult female Smooth Greensnakes grew just 78 and 43 mm in SVL, respectively, over recapture intervals of nearly 6 years (see Supplemental Fig. S2, line C1, in Supplemental File 1). Fitting Von Bertalanffy growth models to growth data for females yielded the following growth-parameter estimates (mean [95% CI]): female Red-bellied Snakes $r = 0.68$ (0.01–1.28), $SVL_{\infty} = 278$ (228–327); female Smooth Greensnakes $r = 0.68$ (0.31–0.79), $SVL_{\infty} = 380$ (363–398).

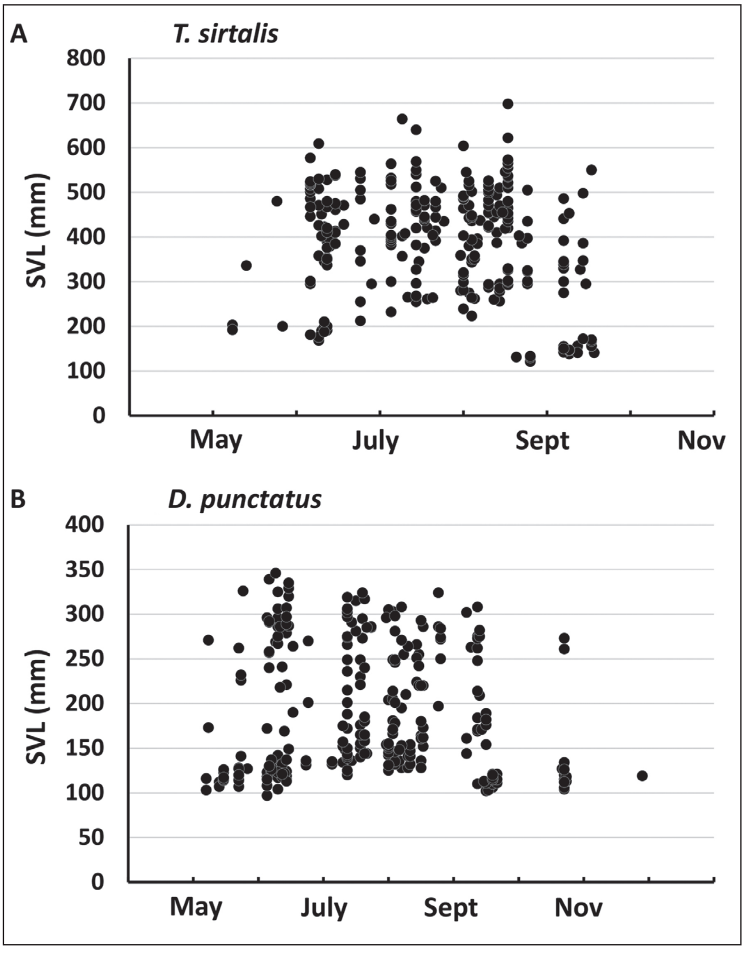

Figure 6. Snout–vent length (SVL) relative to Julian day of capture for (A) *Thamnophis sirtalis* (Common Gartersnake) and (B) *Diadophis punctatus* (Ring-necked Snake) in coastal Maine. Note clusters of very small individuals in August–November, representing newborn individuals, and of small individuals in the spring and summer, reflecting growth of juveniles in their second calendar year.

Reproduction

Reproductive data for the 4 focal species are summarized in Tables 1 and 2. Gravid female Common Gartersnakes were found in the field between 4 June and 14 August, and the smallest gravid female was 392 mm SVL. Litter size based on palpation averaged 13.2 ± 0.6 SE (*n* = 63), with a min–max of 3–28 ova. Ten gravid female Common Gartersnakes gave birth in captivity between 6 and 19 August, and the earliest date that a neonate was captured in the field was 17 August. Mean litter size for lab-born litters was 13.6 ± 1.5 SE (*n* = 10), with neonates averaging 136 ± 1.9 SE (*n* = 10) mm SVL (min–max = 127–147 mm) and 1.5 ± 0.1 SE (*n* = 10) g (min–max = 1.22–1.99 g). Across both lab-born and palpated litters (*n* = 73), litter size was positively related to female SVL (linear regression: $F_{72} = 18.1$, $P <$

Table 1. Reproductive characteristics of 4 species of snakes from a population in coastal Maine, based on palpation of gravid females.

	Thamnophis sirtalis (Common Garter) Snake)	*Diadophis punctatus* (Ring-necked Snake)	*Storeria occipitomaculata* (Red-bellied Snake)	*Opheodrys vernalis* (Smooth Greensnake)
# of gravid females	63	4	40	12
Min SVL	392	296	194	289
Dates collected	4 June–14 Aug	3 June–13 June	4 June–14 Aug	4 June–1 Aug
Mean ± SE clutch or litter size (min–max)	13.2 ± 0.6 (3–28)	3.0 ± 0.4 (2–4)	9.2 ± 0.5 (5–16)	7.2 ± 0.3 (6–10)

Table 2. Reproductive characteristics of 4 species of snakes from a population in coastal Maine, based on litters born in captivity (*T. sirtalis* and *S. occipitomaculata*) or clutches found in the field (*O. vernalis*).

	Thamnophis sirtalis (Common Garter) Snake)	*Diadophis punctatus* (Ring-necked Snake)	*Storeria occipitomaculata* (Red-bellied Snake)	*Opheodrys vernalis* (Smooth Greensnake)
# of clutches or litters	10	0	1	8
Mean ± SE clutch or litter size (min–max)	13.6 ± 1.5 (8–22)	-	5	10.3 ± 3.6 (1–33)^{C}
Dates collected	6 Aug–19 Aug	-	6 Aug	16 July–14 Aug
Mean ± SE neonate SVL (mm)	136 ± 1.9 (127–147)^{A}	-	72 ± 0.7 (69–73)	-
Mean ± SE neonate mass (g)	1.5 ± 0.1 (1.2–2.0)^{A}	-	Not recorded	-
Mean ± SE RCM^{B}	0.24 ± 0.02 (0.16–0.33)	-	-	-
Earliest neonate in field	17-Aug	7-Sep	11-Aug	8-Sep

[A]Mean/min–max across clutch/litter means.
[B]Relative clutch mass = total litter mass / female mass (including litter); Siegel and Fitch (1984).
[C]Some were communal clutches.

0.01, R^2 = 0.20, $y = 0.04x - 8.07$). Only 4 gravid female Ring-necked Snakes were captured, all in early June, and clutch size varied from 2 to 4, with an average of 3.0 ± 0.4 SE (n = 4). The smallest gravid female captured was 296 mm SVL. No Ring-necked Snake nests were discovered in the field, but the earliest date a hatchling was captured in the field was 7 September. Gravid female Red-bellied Snakes were captured between 4 June and 14 August, and the smallest gravid female was 194 mm SVL. Litter size based on palpation varied from 5 to 16, with an average of 9.2 ± 0.5 SE (n = 40), and was positively correlated with maternal SVL (linear regression: F_{39} = 16.21, P < 0.01, R^2 = 0.29, $y = 0.044x - 1.96$). One female Red-bellied Snake gave birth while being held for processing on 11 August, producing 5 offspring averaging 72 ± 0.7 SE (n = 5) mm SVL at birth. Twelve gravid female Smooth Greensnakes were captured between 4 June and 1 August; their clutch sizes varied from 6 to 10, with an average of 7.2 ± 0.3 SE (n = 12), and clutch size was not correlated with maternal SVL (linear regression: F_{11} = 0.51, df = 11, P = 0.46, R^2 = 0.04). The smallest gravid female measured 289 mm SVL. Eight Smooth Greensnake nests, some of which were clearly communal, were discovered under surface rocks in the old field. These nests contained 1–33 eggs, with an average of 10.3 ± 3.6 SE (n = 8). The largest communal nest contained groups of 7, 7, 8, 5, and 6 eggs, some of which were laid on different dates, suggesting use by 5 individual females. Smooth Greensnake nests were found between 16 July and 14 August and the earliest field-captured hatchling was on 8 September. Three clutches, numbering 5, 6, and 8 eggs, respectively, were laid between 16 and 20 July and had all hatched by 16 August, indicating an incubation period of no more than 30 days.

Diet

Thirty-four prey items were recovered from 26 individual Common Gartersnakes. Earthworms accounted for 26 of these prey, along with 6 anurans (4 *Anaxyrus americanus* (Holbrook) [American Toad], 1 *Lithobates sylvaticus* (LeConte) [Wood Frog], 1 unidentified), 1 *Plethodon cinereus* (Green) (Red-backed Salamander), and 1 *Microtus* sp. (vole). Ring-necked Snakes fed almost entirely on salamanders, with the only local salamander species, Red-backed Salamander, comprising 11 of 12 total prey items collected from 10 individual Ring-necked Snakes. The remaining prey item was a small earthworm. Only 2 Red-bellied Snakes had detectable prey, with the 3 recovered prey consisting of 2 small slugs and 1 worm. Twenty-five prey items were recovered from 16 individual Smooth Greensnakes; all were arthropods, including 9 orthopterans (8 crickets, 1 grasshopper), 12 lepidopteran larvae (predominantly smooth-bodied, terrestrial, "cutworm-type" caterpillars), 3 spiders, and 1 harvestman.

Discussion

A coastal Maine snake community

Our long-term studies on Islesboro Island provide comprehensive data on the 4 most widespread and common snake species in Maine. No other species have been found on the island, despite the presence of *Lampropeltis triangulum* (Lacépède)

(Milk Snake) on the nearby mainland and other large islands (Mt. Desert and Deer Isle), and *Storeria dekayi* (Holbrook) (DeKay's Brownsnake) and *Thamnophis saurita* (L.) (Eastern Ribbonsnake) in neighboring counties (Hunter et al. 1999). Perhaps the most obvious contrast with mainland populations is the apparently greater abundance of Ring-necked Snakes, which are generally thought to be uncommon in Maine (Hunter et al. 1999). Indeed, Burgason (1999:166) stated that "the Ringneck Snake is apparently widespread in Maine, but not necessarily abundant or easily found." Whether the apparent abundance of Ring-necked Snakes at our study sites represents an unusual concentration of this species or simply targeted search effort is unknown. Otherwise, differences between our study populations and those elsewhere in North America are subtle. Below, we summarize natural- and life-history information for each species on Islesboro and discuss the relation to data from other populations and geographic regions.

***Thamnophis sirtalis* (Common Gartersnake)**

The Common Gartersnake is one of the most thoroughly studied snakes in North America (Rossman 1996). Consequently, there is research examining life-history and ecological characteristics of populations from across its range, covering much of the United States and Canada (Ernst and Ernst 2003, Rossman 1996). As in much of its range, we captured Common Gartersnakes most often in open habitat near a wetland (Ernst and Ernst 2003), and it was the dominant species in the old field, comprising 66% of captures. These captures consisted primarily of adult snakes encountered sheltering under rocks in the open-canopy areas of the old field. We seldom captured juvenile Common Gartersnakes, and gravid females made up a large proportion of total Common Gartersnake captures (73 gravid females out of 272 total captures). This result suggests that juveniles differ in habitat use, activity patterns, or detectability in a way that skews their capture rates relative to adults. Reproductive characteristics and growth rates of Common Gartersnakes in our population were generally similar to those exhibited by other northern populations (Carpenter 1952a, Gregory and Larsen 1993, Seibert and Hagen 1947), although the average litter size for Islesboro snakes (13.6) was notably lower than reported elsewhere (20 in Carpenter [1952b] and 27 in Ernst and Ernst [2003]).

Unlike the other species in our assemblage, a comparable maritime island population of Common Gartersnakes has been the subject of previous study on Georges Island, NS, Canada (Barnes et al. 2006). Generally, the life history and ecology of Common Gartersnakes on Islesboro mirrors the Georges Island population. As in most mainland populations (e.g., Barnes et al. 2006, Fitch 1999), individuals in the island populations appear to have small home ranges, and distances between capture locations are typically small, with most in this study moving <5 m between successive captures. In both island populations, Common Gartersnakes feed primarily on earthworms and occasional salamanders, but individuals in our population also included anurans and small mammals in their diet; these prey are apparently absent from Georges Island (Barnes et al. 2006). In both populations, females reached sexual maturity at shorter lengths than reported for mainland populations (Georges Island: 350 mm SVL, Islesboro: 392 mm SVL, a mainland Nova Scotia population: 464 mm SVL; Gregory and Larsen 1993). Interestingly, the Georges Island population exhibits smaller average and maximum sizes than mainland and Islesboro populations (Barnes et al. 2006). The Islesboro population exhibits significant female-biased sexual size dimorphism (SSD index for female-biased SSD: [average SVL of female / average SVL of male] - 1 = 0.19; Lovich and Gibbons 1992), which is typical of mainland populations but not seen in the Georges Island population (SSD index = 0.04; Barnes et al. 2006, Ernst and Ernst 2003). Controlled experiments are necessary to determine if smaller body size, reduced SSD, smaller size at maturity, and smaller litter sizes in the Georges Island population reflect a plastic response to the lack of larger anuran and mammalian prey for females or if isolation of this population has resulted in a heritable shift in body size (i.e., local adaptation or genetic drift; Barnes et al. 2006).

Diadophis punctatus **(Ring-necked Snake)**

In contrast to the 3 other species, which were most frequently encountered in the old field, Ring-necked Snakes were common along edges in predominantly forested habitats. Indeed, the Ring-necked Snake was the most frequently encountered species in the yard and along the road. Ring-necked Snakes also accounted for >80% of snake captures along the shoreline, but the prevalence of small juveniles in this area over multiple years suggests that Ring-necked Snakes use the shoreline as a nesting or rookery area. Captures of Ring-necked Snakes along the shoreline were concentrated around a steep, exposed headland located just a few meters from the high tide line, comprised of broken ledge and talus interspersed with patches of grass and low shrubs. Juvenile Ring-necked Snakes were found sheltering under surface rocks, suggesting nesting sites underground, but neither eggs nor egg shells were ever observed. In contrast, the eggs of Smooth Greensnakes were easily found under surface rocks in the old field. Other authors have noted communal nesting of Ring-necked Snakes in rocky substrates (Fitch 1975), but to our knowledge ours is the first description of a localized nesting area for this species in New England (Hulse et al. 2001). Given that we found Ring-necked Snakes under surface rocks at this location on 23 November and 26 December, this area also seems to be used for hibernation. In fact, the direct southern exposure and thermal inertia of the rocky headland apparently enables surface activity well into the fall and early winter; the active season of Ring-necked Snakes in the Northeast is generally presumed to end in October (Hulse et al. 2001).

Our capture of large numbers of juvenile Ring-necked Snakes allowed us to examine juvenile movements and growth, providing the first data of this type for northeastern populations of this wide-ranging species. We recaptured 3 Ring-necked Snakes that were marked as juveniles along the shoreline 230–300 m away at the yard and road, supporting the idea that individuals disperse widely from the nesting area. Hatchling Ring-necked Snakes exhibited little growth in their first fall, which might reflect low availability of salamander and earthworm prey along the shoreline or in the warm and dry late-summer weather. Our mark–recapture data suggested that most females reach mature size (~230 mm SVL; Hulse et al.

2001) in their third calendar year, a pattern of growth similar to that noted by Fitch (1975) in Kansas. As might be expected, the ecology of Ring-necked Snakes in our population aligns more closely with patterns reported in Pennsylvania (Hulse et al. 2001) than other regions of the country. For example, the largest individuals were females in both Pennsylvania and Maine. Additionally, slender plethodontid salamanders appear to be the preferred prey of Ring-necked Snakes in our population, Pennsylvania (Hulse et al. 2001), and Virginia (Mitchell 1994), despite more generalist, or vermivorous diets elsewhere (Ernst and Ernst 2003).

***Storeria occipitomaculata* (Red-bellied Snake)**

Our study adds to a growing number of ecological studies of Red-bellied Snakes across this species' broad geographic range (Blanchard 1937, Brodie and Ducey 1989, Cairns et al. 2018, King 2022, Meshaka and Klippel 2011, Semlitsch and Moran 1984, Virgin and King 2019, Willson and Dorcas 2004). Despite ranking third among our 4 local species in terms of total captures, Red-bellied Snakes were nonetheless common, with 93 captures in our study; it has also been described as common in New York (Gibbs et al. 2007) and Pennsylvania (Hulse et al. 2001). This species was encountered regularly throughout the summer, and gravid females were particularly common under rocks in open areas leading up to parturition in July and early August. The abundance and seasonal activity of this species in our study area contrasts with observations from southern portions of this species' range, where Red-bellied Snakes are noted as being uncommon or rare (Werler and Dixon 2000) and most frequently encountered in the spring and fall (Ernst and Ernst 2003, Semlitsch and Moran 1984, Willson and Dorcas 2004). Likewise, although this species is generally described as being associated with forested or mesic habitats in the southern US (Johnson 2000, Semlitsch and Moran 1984, Willson and Dorcas 2004) and in New York (Gibbs et al. 2007), our captures of this species were highest in the old field and yard, indicating a preference for grassy, open-canopy habitats; only 1 Red-bellied Snake was ever captured along the road through dense spruce–fir forest. Semlitsch and Moran (1984) attributed use of mesic habitats by Red-bellied Snakes to availability of their primary prey, slugs. It is likely that the cool maritime climate of coastal Maine permits high densities of mollusk prey in open-canopy habitats (J.D. Willson, pers. observ.), allowing Red-bellied Snakes to simultaneously meet dietary and thermoregulatory needs in these habitats. Preference of open habitats in the north is supported by Diaz and Blouin-Demers (2017), who captured over 200 Red-bellied Snakes under cover objects systematically placed in fields in Quebec, but only 7 under objects placed in forested habitats, as well as by Cairns et al. (2018), who noted a preference for grassland habitats in Manitoba.

The Red-bellied Snake exhibits substantial variation in body size across its range. Adults from our population are smaller than those from South Carolina (Semlitsch and Moran 1984) and North Carolina (Willson and Dorcas 2004), but larger than those from Pennsylvania (Hulse et al. 2001). Similarly, there appears to be strong spatial variation in degree of SSD in this species. Though the largest individuals in all populations studied have been females, the sexes were similar (and not statistically different) in SVL (SSD index = 0.05) in South Carolina (Semlitsch and Moran 1984) and in Michigan (SSD index = 0.04; Blanchard 1937). Conversely, studies in North Carolina (SSD index = 0.13; Willson and Dorcas 2004), Pennsylvania (SSD index = 0.15; Hulse et al. 2001), and Virginia (SSD index = 0.12; Mitchell 1994) all found substantial female-biased SSD. Females in our study were 19% longer than males (SSD index = 0.19), making our populations the most strongly sexually dimorphic of those listed. Given the potential for patterns of SSD in snakes to be strongly shaped by reproductive behavior and mating systems (Shine 1994), the causes and consequences of regional variation in SSD in Red-bellied Snakes warrant further investigation.

Reproductive characteristics of Red-bellied Snakes in our study were comparable to those observed elsewhere. Specifically, average litter size was very similar to that of individuals from New York (Brodie and Ducey 1989), slightly larger than that of individuals from Manitoba (Cairns et al. 2018), and slightly smaller than that of those from Kansas (Meshaka and Klippel 2011). Size of neonates in our study was similar to those in Michigan (Blanchard 1937), but in accordance with larger female body size, average litter size was larger in our study (9.2 in Maine vs. 7 in Michigan). Comparatively, the smaller females in South Carolina have smaller neonates and larger litter sizes relative to body size (mean litter size = 9; Semlitsch and Moran 1984). Given that the latest gravid female we found was 14 August, timing of parturition in Maine appears similar to that of populations in other northern states (i.e., mid- to late August in Pennsylvania and Michigan [Blanchard 1937, Hulse et al. 2001] and late July to late August in New York [Brodie and Ducey 1989]).

Previous studies have suggested that Red-bellied Snakes have rapid growth (reaching maturity at age 2) and high rates of population turnover (i.e., short life span), based on seasonal body-size distributions and very low recapture rates (Blanchard 1937, Semlitsch and Moran 1984). Our data support this conclusion, suggesting first reproduction by females at 2 years of age. Likewise, the longest recapture interval for Red-bellied Snakes was just 14 months, compared to much longer maximum recapture intervals for other species (~2 years for Ring-necked Snakes, ~4 years for Common Gartersnakes, ~6 years for Smooth Greensnakes), suggesting a shorter life span. Alternatively, this species might range more extensively (i.e., out of the study area) than other species, a possibility supported by a smaller proportion of short-distance (<5 m) movements by this species, compared to our other focal species (see Supplemental Fig. S1 in Supplemental File 1). Although movements and longevity of Red-bellied Snakes clearly warrant future investigation, our limited data on movement of recaptured individuals and an overall recapture rate of 13% suggest that the spatial ecology and detectability of this species does not differ dramatically from the other species in our assemblage.

Although we had few diet records for Red-bellied Snakes, our study supports the idea that this species specializes on slugs and occasionally small worms as prey (Semlitsch and Moran 1984, Virgin and King 2019).

***Opheodrys vernalis* (Smooth Greensnake)**

Smooth Greensnakes occur throughout the northern US and southern Canada, but populations are patchily distributed, often uncommon, and may be declining in some regions (Ernst and Ernst 2003). Consequently, few field studies have focused on this species, and those that have are from the midwestern US and southern Canada. Our study offers the first comprehensive ecological study of this species in New England. These baseline data are particularly important, given that a recent phylogenetic study (Blais et al. 2021) demonstrated 2 distinct clades within this species: an eastern clade ranging from Ohio and Michigan east through the Appalachians and Maritime Canada, and a western clade containing populations in the Great Lakes, Midwest, northern Great Plains, and Rocky Mountains.

The Smooth Greensnake was the least common snake in our study and was restricted to open, grassy habitats, as has been noted for this species across its range (Grobman 1941, Rutherford and Cairns 2020). The fact that we only captured Smooth Greensnakes in the old field suggests that this species may have more specialized habitat requirements, require larger patches of open-canopy habitat, or have more limited dispersal than the other species we studied. Smooth Greensnakes exhibited strong female-biased sexual size dimorphism (SSD index = 0.17). This pattern is consistent across the species' range, although overall body sizes of males and females in Manitoba, Canada, were substantially smaller than ours (Rutherford and Cairns 2020). In conjunction with larger body size, average litter size in our population (mean = 7.3) was larger than in Manitoba (mean = 5.1), but litter size did not increase with female SVL within either population. The reproductive biology of Smooth Greensnakes is unusual in that females often lay communally, and eggs are laid at an advanced stage of development, hatching after only a 4–25 day incubation period in the field (Ernst and Ernst 2003). Coincidentally, communal nesting of Smooth Greensnakes was first reported from Islesboro Island (Lawson 1983). We confirmed both of these attributes in our population, with communal clutches of up to 33 eggs that likely belonged to at least 5 individual females. Three clutches that were checked more than once through incubation hatched after no more than 30 days in the field.

Our study yielded, to our knowledge, the first published data on growth and longevity of Smooth Greensnakes in the field. Two individuals, initially marked as adults, were recaptured 6 years later. The fact that, despite larger sample sizes, no individuals of other species were recaptured after such long intervals provides further support for longer lifespan in Smooth Greensnakes. Our data on diet of Smooth Greensnakes agrees well with dietary patterns reported previously in the literature (Ernst and Ernst 2003). Specifically, Smooth Greensnakes fed exclusively on terrestrial arthropods, especially smooth-bodied caterpillars, spiders, and crickets.

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