Sunning themselves in heaps, knots, and snarls: The extraordinary abundance and demography of island watersnakes

Richard B. King

Follow this and additional works at: https://huskiecommons.lib.niu.edu/allfaculty-peerpub

Original Citation
King, RB., Stanford, KM, and Jones, PC. 2018. Sunning themselves in heaps, knots, and snarls: The extraordinary abundance and demography of island watersnakes. Ecology and Evolution DOI: 10.1002/ece3.4191
Sunning themselves in heaps, knots, and snarls: The extraordinary abundance and demography of island watersnakes

Richard B. King1,2 | Kristin M. Stanford3 | Peter C. Jones1

Abstract
Snakes represent a sizable fraction of vertebrate biodiversity, but until recently, data on their demography have been sparse. Consequently, generalizations regarding patterns of variation are weak and the potential for population projections is limited. We address this information gap through an analysis of spatial and temporal variation in demography (population size, annual survival, and realized population growth) of the Lake Erie Watersnake, Nerodia sipedon insularum, and a review of snake survival more generally. Our study spans a period during which the Lake Erie Watersnake was listed as threatened under the U.S. Endangered Species Act, recovered, and was delisted. We collected capture–mark–recapture data at 14 study sites over 20 years, accruing 20,000 captures of 13,800 individually marked adults. Lake Erie Watersnakes achieve extraordinary abundance, averaging 520 adults per km of shoreline (ca. 260 adult per ha) at our study sites (range = 160–1,600 adults per km; ca. 80–800 adults per ha) and surpassing population recovery and postdelisting monitoring criteria. Annual survival averages 0.68 among adult females and 0.76 among adult males, varies among sites, and is positively correlated with body size among study sites. Temporal process variance in annual survival is low, averaging 0.0011 or less than 4% of total variance; thus, stochasticity in annual survival may be of minor significance to snake extinction risk. Estimates of realized population growth indicate that population size has been stable or increasing over the course of our study. More generally, snake annual survival overlaps broadly across continents, climate zones, families, subfamilies, reproductive modes, body size categories, maturation categories, and parity categories. Differences in survival in relation to size, parity, and maturation are in the directions predicted by life history theory but are of small magnitude with much variation around median values. Overall, annual survival appears to be quite plastic, varying with food availability, habitat quality, and other ecological variables.

Keywords
body size, capture–mark–recapture, life history, population estimation, process variance, realized population growth, survival, vital rates
1 | INTRODUCTION

The availability of accurate demographic parameter estimates is central to understanding population dynamics (Caswell, 2001), evaluating life history evolution (Roff, 1992; Stearns, 1992), and modeling extinction risk (Açkakaya, 2004; Lacy, 1993, 2000). Generating such estimates requires long-term monitoring data, often of marked individuals. Historically, game species and species of economic importance have been the targets of such monitoring, but increasingly, efforts have broadened to include species of conservation concern. At the same time, analytical methods for generating demographic parameter estimates have improved and increased in sophistication (Halstead, Wylie, Coates, Valcarcel, & Casazza, 2012; White & Burnham, 1999). Consequently, demographic parameter estimates are becoming available for a widening range of taxa (Mesquita et al., 2015; Salguero-Gómez et al., 2015, 2016), offering the possibility of improved interpretation and generalization, including evaluations of r-K, slow-fast, and pace-of-life syndromes (Bielby et al., 2007; Dunham, Miles, & Reznick, 1988; Gaillard et al., 1989, 2005; Gangloff et al., 2017; Hille & Cooper, 2015; Réale et al., 2010; Ricklefs & Wikelski, 2002; Wiersma, Muñoz-Garcia, Walker, & Williams, 2007) and niche classification (Pianka, Vitt, Pelegrin, Fitzgerald, & Winemiller, 2017; Winemiller, Fitzgerald, Bower, & Pianka, 2015).

Snakes represent a sizable fraction of vertebrate biodiversity; their 3,400 species constitute 10% of extant tetrapods and 35% of extant squamates (lizards and snakes; http://www.reptile-database.org/db-info/SpeciesStat.html). Although often secretive and infrequently encountered, snakes can be abundant and, as tertiary predators, exert top-down influences on ecosystem function (Jones, King, Stanford, Lawson, & Thomas, 2009; Willson & Winne, 2016 and citations therein). Despite their diversity, snakes are poorly represented among life history data compilations, comprising, for example, just four entries among the 1,927 matrix population models in the COMADRE Animal Matrix Database (Salguero-Gómez et al., 2016; http://www.compadre-db.org/ accessed 19 October 2017).

Here, we provide a case study of the demography of the Lake Erie Watersnake, Nerodia sipedon insularum (Conant & Clay). Using data from 14 study sites collected over 20 years, we estimate population size, annual adult survival, and its variance and realized population growth. We characterize the degree to which annual survival and realized population growth vary among sexes, sites, and years. Sex effects are likely to arise from differences in body size and reproductive allocation between males and females. Females exceed males in length and mass, possibly making them less vulnerable to predation. Males engage in active mate-searching behaviors in spring, and females frequently bask, while gestating during summer, both potentially risky behaviors; females also produce large litters of energetically expensive offspring. Site and year effects are likely to arise from spatial and temporal variation in biotic (predator and prey abundance) and abiotic (weather and microclimate) factors. Thus, our analyses provide insight into the degree to which adult survival is influenced by year-to-year and local site-to-site variation in the environment.

We place the variation we see in annual adult survival of Lake Erie Watersnakes in context by reviewing other studies of snake survival that have utilized contemporary estimation techniques. Our review updates a summary compiled 30 years ago (tables 9-5 in Parker & Plummer, 1987) that relied heavily on survival estimates from return rates of marked animals (e.g., to overwintering dens) and from life tables generated from inferred age structure; methods that do not account for imperfect and varying detection probability. Following Parker and Plummer (1987), we consider variation in annual adult survival among families, subfamilies, continents, and climate zones and its relationship to reproductive mode, body size, age at maturity, and reproductive frequency.

2 | MATERIALS AND METHODS

2.1 | Study species

The Lake Erie Watersnake, Nerodia sipedon insularum, is endemic to the islands of western Lake Erie (North America; Figure 1). It differs in color pattern from mainland Northern Watersnakes (N. s. sipedon, Linnaeus) due to a dynamic balance between natural selection favoring less patterned individuals along rocky island shorelines and gene flow from nearby mainland populations (King & Lawson, 1997). Lake Erie Watersnakes consume amphibians and fish, including the invasive Round Goby (Neogobius melanostomus), in the nearshore waters of Lake Erie (Jones et al., 2009; King, Ray, & Stanford, 2006; King, Stanford, & Ray, 2008). They utilize shoreline retreats and basking sites during the active season and both shoreline and inland hibernation sites during winter (Stanford, King, & Wynn, 2010). Like other New World natricines, Lake Erie Watersnakes are viviparous, and adult females produce large litters (mean litter size = 26, King et al., 2008) of independent young annually.

Restricted geographic distribution and declining population size led to listing of the Lake Erie Watersnake as threatened under the U.S. Endangered Species Act in fall 1999 (U.S. Fish and Wildlife Service, 1999). Recovery efforts focused on population monitoring, habitat management, and a reduction in human-caused mortality (U.S. Fish and Wildlife Service, 2003). These efforts occurred simultaneously with an exponentially growing Round Goby population (Johnson, Allen, Corkum, & Lee, 2005) and a shift in watersnake diet to this new and abundant food source (Jones et al., 2009; King, Ray, et al., 2006; King et al., 2008). Successful achievement of recovery criteria resulted in the delisting of the Lake Erie Watersnake in summer 2011 (U.S. Fish and Wildlife Service, 2011). As required under the Endangered Species Act, postdelisting monitoring was implemented to ensure that the Lake Erie Watersnake sustained itself following delisting (U.S. Fish and Wildlife Service, 2011). Population monitoring prior to listing, during recovery, and postdelisting provides an extensive database for the demographic analyses presented here.
2.2 | Field protocols

Data analyzed here were collected from 1996 through 2015 at study sites on five U. S. islands in western Lake Erie (Figure 1). Data collection accelerated in 2001 when a program of intensive annual population censuses was initiated. These censuses spanned a period of about 2 weeks (late May to mid-June) each spring. Some sites were also sampled outside of this period, either to provide more accurate population estimates or to meet other research objectives. As of 2005, 14 intensive study sites were included (Figure 1), encompassing 0.7–2.8 km of shoreline each and accounting for about 30% (17.9 km) of the total shoreline (57.7 km) of these islands. The number of study sites was reduced to 13 in 2011 and 12 in 2012 when two sites with inconsistent and low capture rates were dropped.

Censuses consisted of area-constrained searches of suitable shoreline habitat. Watersnakes were captured by hand, classified by sex, measured to obtain snout-vent length (SVL), and weighed. Watersnakes were permanently marked using passive integrated transponders (PIT tags) injected under the skin. Following marking, snakes were released at their site of capture. Watersnakes were also temporarily marked using a latex paint stick (All-Weather Paintstik® Livestock Marker, LA-CO Industries, Inc.). Temporary marks alerted field workers that a snake had been recently processed and that it needs only be scanned before release. Watersnakes were classified as adults if SVL ≥ 430 mm (males) or ≥ 590 mm (females) (King, 1986; King, Queral-Regil, & Stanford, 2006; King, Stanford, Jones, & Bekker, 2016). Processing was carried out in the field, at the F. T. Stone Laboratory, our research base during censuses of sites on South Bass, Middle Bass, North Bass and Gibraltar island, or at “South Bay,” a rental property used as our research base during censuses of sites on Kelleys Island. Less intensive censuses occurred at additional study sites periodically throughout the study (King, Queral-Regil, et al., 2006). Results from those sites are included here only as they pertain to documenting movements of animals among study sites. Census participants included federal and state agency staff, university faculty and students, zoo staff, naturalists, and area residents working in teams of ca. 3–8 individuals. Correctly identifying marked animals was a primary goal of snake processing, and errors resulting from ca. 3–8 individuals. Correctly identifying marked animals was a primary goal of snake processing, and errors resulting from tag loss, tag failure, detection failure, scanner failure, or observer error were minimal (more details are provided in Supporting Information Data S1).

2.3 | Population size

Adult Lake Erie Watersnake population sizes were estimated using the Jolly–Seber model (Jolly, 1965; Seber, 1965) via the program JOLLY (http://www.mbr-pwr.usgs.gov/software.html) with 95% confidence intervals calculated using Manly’s method (Krebs, 1998; Manly, 1984). Capture histories were created for each snake using 0’s to denote years in which a given snake was not captured, 1’s to denote years in which a snake was captured, and 2’s to denote snakes that were found dead or that were released unmarked. Multiple captures of the same animal within a year were treated as a single capture for the purposes of population estimation. Because capture probabilities differed between sexes (Results), estimates were computed separately for males and females. Population estimates and confidence intervals were rounded to the nearest 10. Population density was computed by dividing population estimates by the linear extent of shoreline sampled within each study site (King, Queral-Regil, et al., 2006).

The Jolly–Seber model is an open population model, allowing for recruitment, death, immigration, and emigration between sampling occasions (Jolly, 1965; Seber, 1965). However, emigration is assumed to be permanent, and thus, animals that are captured at one study site were treated as new individuals if they are later recaptured at another study site. To assess the extent of movement among study sites and the degree to which emigration was permanent, we tallied...
cases of recaptures that occurred at a site different from the site of prior capture.

2.4 | Annual survival

We estimated adult survival ($\phi$) and recapture ($p$) parameters for Lake Erie Watersnakes using the Cormack–Jolly–Seber (CJS) model in RMark version 2.1.7 (Laake, 2013) and Program MARK version 8.0 (White & Burnham, 1999). We used R version 3.2.2 (R Core Team, 2015) to construct and run all models. For sites where sampling began after 2000 or ended prior to 2015, recapture parameters were fixed to zero by deleting the model’s design data for years when no sampling occurred. We used the fully parameterized model $\phi(sex\times site\times time)p(site\times time\times sex)$ as our global model. Goodness of fit was assessed for the global model in U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009). We calculated $\hat{c}$ for the global model to check for over-dispersion. We anticipated an interactive effect of site and time on recapture probabilities based on site-to-site and year-to-year variation in capture success arising from constraints imposed by weather and sampling logistics. Therefore, in addition to the global model, we evaluated candidate models that included $p(site\times time)$, $p(site\times time\times sex)$, and $p(site\times time\times sex)$ and additive and interactive effects of site, time, and sex on $\phi$ (Supporting Information Table S1). We excluded several highly parameterized models with $\phi(sex\times site\times time)$ and $\phi(sex\times site\times time)$ because of data sparseness and the likelihood of inestimable parameters.

2.5 | Process variance in annual survival

Temporal process variance is the portion of the total variance that is attributable to the actual variation in a demographic parameter over time and can be estimated via a variance components approach as total variance minus sampling error (Gould & Nichols, 1998). Similarly, spatial process variance is the portion of the total variance that is attributable to actual variation among sites. We used Program MARK version 8.0 (White & Burnham, 1999) to estimate the temporal process variance in survival from the highest ranked model that included time effects on $\phi$ and spatial process variance in survival from the highest ranked model that included site effects on $\phi$.

2.6 | Realized population growth

We estimated realized population growth ($\lambda$) using the Pradel $\phi$ and $\lambda$ parameterization within Program MARK. We used our top-ranked CJS model, $\phi(sex\times site)p(site\times time\times sex)$ (cf. Cam, 2012; Anthony et al., 2006; Seamans & Gutierrez, 2007; Mullin, Colwell, McAllister, & Dinsmore, 2010; Kofanta, Newmark, & Kauffman, 2012), and then considered additive and interactive effects of site, sex, and time on $\lambda$ (Supporting Information Table S2). Because sampling was initiated in different years among sites, candidate Pradel models all included $\lambda(site)$ in their parameterization to avoid the effects of a changing study area (Cooch & White, 2017; Pradel, 1996).

2.7 | Associations between demography and body size among sites

Watersnakes continue to grow after reaching reproductive maturity and so may achieve greater body size at sites where survival is high. However, there is also much individual variation in the asymptotic size of Lake Erie Watersnakes (King et al., 2016) so larger individuals are not necessarily older. Consequently, it is unclear whether body size might show an association with survival, and if it does, whether high survival promotes increased body size, large body size promotes increased survival (e.g., by making snakes difficult for predators to subdue; King, 1993), or some other mechanism underlies variation in both. To determine if any such association exists, we computed the mean SVL of the largest 10% of individuals of each sex captured at each site. We then used one-tailed Pearson’s correlation with test for positive associations between SVL and $\phi$ separately for males and females.

2.8 | Review of snake survival

We collated estimates of survival that utilized maximum likelihood-based methodologies (including known-fate analyses) to analyze capture–mark–recapture data while accounting for imperfect detection. We categorized species by family, subfamily, continent, climate zone of study location (temperate, >40°N or S; subtropical, 23.5–40°N or S; tropical, <23.5°N or S), and reproductive mode (oviparous and viviparous). In addition, we classified species by body size as small (lower adult size limit from 150 to 350 mm SVL and upper adult size limit from 250 to 800 mm SVL), medium (400–500 and 600–1,200 mm SVL), or large (600–1,400 and 1,000–3,000 mm SVL); by attainment of reproductive maturity as early (3 years or less), intermediate (3–4 years), or late (more than 4 years); and by parity as reproducing on an annual or shorter interval vs. biennial or longer interval.

3 | RESULTS

From 1996 to 2015, a total of 13,802 individual adult Lake Erie Watersnakes were captured 20,025 times at 14 intensive study sites (Supporting Information Table S3). Included among these were 129 animals that had been marked in 1 year and found dead in a subsequent year, 117 unmarked individuals found dead, and 27 live individuals that were released unmarked. Excluding dead and unmarked animals, the number of individual adult Lake Erie Watersnakes ranged from 284 to 1,854, and the number of captures ranged from 330 to 2,694 per study site (Supporting Information Table S3).

Most snakes were captured in just a single year, but some individuals were recaptured in as many as 8 or 9 years (Supporting Information Table S4). Of animals captured in more than 1 year, most were captured in two successive years but gaps of 1 or more years between captures were common (Supporting Information Table S4).
At the extreme were two animals first captured in 2002 and subsequently in 2014 (a gap of 11 years) and 2015 (a gap of 12 years). The time span between first and last capture ranged up to 15 years (Supporting Information Table S4).

3.1 | Extent and permanence of emigration

We identified 57 cases of Lake Erie Watersnakes that moved among our 14 study sites (more details are provided in Supporting Information Data S2, Table S5, Figure S1). In contrast, 9,358 recaptures that occurred at the same site as prior capture. Thus, only 0.6% of recaptures involved moves among sites.

3.2 | Population size

Capture–mark–recapture data allowed use of the Jolly–Seber method to estimate adult male and female population size at most sites in most years from 2001 to 2014 (Table S1, Supporting Information Table S6, Figure S2). Combining males and females and averaging across years, estimated population size varied among study sites from fewer than 200 (Kelleys Island Minshall, Kelleys Island State Park) to more than 1,000 adults (Kelleys Island South Shore; Table S1, Supporting Information Table S6, Figure S2). Density estimates were also highly variable, ranging from 100 to 1,600 adults per km (Table 1). In general, 95% confidence limits of population estimates

### TABLE 1 | Population size and density, annual adult survival (ϕ) and associated temporal process variance, realized population growth (λ), and maximum body size of adult female and male Lake Erie Watersnakes at 14 study sites

| Site (length, km) | Sex  | Adults per km | Adults | Annual adult survival ϕ (CI) | Process variance | Realized population growth λ (CI) | Maximum body size (mm) | SVL (Range) |
|-------------------|------|---------------|--------|-----------------------------|------------------|-----------------------------------|-----------------------|------------|
| KI Long Point     | Female Male | 230 210 | 160 650 | 0.85 (0.79–0.89) 0.84 (0.77–0.89) | <0.0001 0.0006 | 1.06 (1.01–1.11) 1.11 (1.06–1.17) | 28 27 | 1,046 (1,034–1,057) 793 (783–802) |
| KI SE Shore       | Female Male | 270 380 | 650 1,600 | 0.70 (0.67–0.73) 0.79 (0.76–0.81) | 0.0006 0.0004 | 1.01 (0.98–1.03) 1.02 (1.00–1.04) | 82 103 | 981 (976–987) 769 (764–774) |
| KI South Shore    | Female Male | 270 850 | 1,600 1.04 | 0.55 (0.49–0.61) 0.81 (0.78–0.83) | 0.0006 0.0002 | 0.97 (0.94–1.00) 1.04 (1.02–1.07) | 54 142 | 965 (956–975) 760 (756–764) |
| KI Minshall       | Female Male | 50 80 | 100 1.04 | 0.51 (0.36–0.65) 0.71 (0.59–0.80) | 0.0080 0.0001 | 0.96 (0.85–1.08) 0.95 (0.85–1.06) | 11 16 | 969 (952–986) 750 (738–762) |
| KI State Park     | Female Male | 60 90 | 210 0.72 (0.68–0.76) | 0.0005 0.004 | 1.05 (1.02–1.08) 1.04 (1.01–1.07) | 31 33 | 1,002 (991–1,013) 767 (762–773) |
| SBI East Point    | Female Male | 230 200 | 330 800 | 0.71 (0.66–0.76) 0.74 (0.70–0.78) | 0.0079 0.0007 | 1.09 (1.04–1.15) 1.00 (0.95–1.05) | 51 57 | 991 (983–1,000) 783 (776–790) |
| SBI East Shore    | Female Male | 330 450 | 780 1.00 | 0.71 (0.67–0.76) 0.85 (0.82–0.87) | 0.0006 0.0002 | 1.00 (0.97–1.04) 0.98 (0.95–1.01) | 54 78 | 1,010 (1,002–1,017) 785 (780–789) |
| SBI State Park    | Female Male | 170 230 | 570 1.01 | 0.71 (0.68–0.73) 0.71 (0.69–0.74) | 0.0006 0.0006 | 1.01 (0.99–1.03) 0.96 (0.94–0.98) | 102 104 | 930 (923–937) 719 (713–725) |
| MBI East Point    | Female Male | 250 560 | 810 0.83 (0.78–0.87) | 0.0009 0.0003 | 0.94 (0.89–0.99) 0.96 (0.91–1.00) | 32 63 | 995 (983–1,007) 756 (750–761) |
| MBI State Park    | Female Male | 200 250 | 450 0.65 (0.61–0.69) 0.67 (0.62–0.71) | 0.0007 0.0007 | 1.00 (0.97–1.04) 0.99 (0.95–1.03) | 64 59 | 1,006 (999–1,013) 772 (765–779) |
| MBI West End      | Female Male | 540 460 | 910 0.74 (0.64–0.82) 0.92 (0.81–0.97) | 0.0003 – | 1.07 (1.00–1.15) 1.12 (1.05–1.19) | 48 64 | 1,062 (1,052–1,071) 786 (779–793) |
| NBI NE,SE Shore   | Female Male | 180 240 | 180 0.70 (0.64–0.75) 0.66 (0.59–0.72) | 0.0008 0.0009 | 1.05 (1.00–1.10) 1.02 (0.96–1.07) | 44 43 | 970 (958–982) 727 (714–740) |
| NBI South Shore   | Female Male | 240 300 | 270 0.72 (0.69–0.75) 0.67 (0.63–0.72) | 0.0006 0.0006 | 1.11 (1.09–1.14) 1.14 (1.11–1.17) | 122 106 | 993 (986–1,000) 746 (739–753) |
| Gibraltar        | Female Male | 70 160 | 260 0.74 (0.69–0.78) 0.73 (0.69–0.77) | 0.0005 0.0005 | 1.04 (1.00–1.08) 1.02 (0.98–1.06) | 45 49 | 1,014 (1,003–1,024) 772 (764–779) |

Note. To remove effects of year, population size was averaged and λ was estimated from ϕsex/site*p thriftsex/site*time*sex)/site*sex. Dashes indicate unestimable values. Estimates of λ that are significantly greater than 1.0 are indicated in bold; CI refers to 95% confidence interval; n refers to the number of animals constituting the largest 10%.
were broad with lower and upper limits frequently differing by a factor of two or more (Supporting Information Table S6, Figure S2). However, estimates were often quite consistent among years, sometimes varying by just a few 10 s of individuals (e.g., South Bass Island State Park, Kelleys Island State Park, and Gibraltar Island; Table 1, Supporting Information Table S6, Figure S2). Males typically had a higher population estimate than females at a given site; however, male and female confidence intervals overlapped broadly (Table 1, Supporting Information Table S6, Figure S2).

3.3 | Annual survival

An overall goodness of fit test of the global model was nonsignificant ($p = 0.91$), indicating a good fit of the data to CJS open population models. The resultant estimate for $\hat{c}$ was 0.87, indicating an absence of overdispersion and precluding the need to adjust AICc values (Burnham & Anderson, 2002). The most parsimonious CJS model from our candidate set, $\phi$(sex*site)$p$(site*time+sex), included interactive effects of sex and site on survival and interactive effects of site and time and an additive effect of sex on recapture probability (Supporting Information Table S1). This model had weight $= 0.76$. The second highest ranked model, $\phi$(sex*site+time)$p$(site*time+sex) (weight $= 0.24$), differed only in that it included an additive effect of time on survival.

Recapture probability was highest at South Bass Island (SBI) State Park, exceeding 0.25 in all years and frequently exceeding 0.5 (Supporting Information Figure S3, Table S7). In contrast, recapture probability was consistently low at KI South Shore, SBI East Shore, MBI East Point, and MBI West End, falling below 0.25 in nearly all years. Recapture probabilities were frequently between 0.25 and 0.5 at other sites. Recapture probabilities were 3%-5% higher among females than males.

Overall, annual adult male survival averaged 0.76 and annual adult female survival averaged 0.68 (Figure 2, Table 1). However, the difference in survival between males and females varied among sites. Male survival was approximately equal to female survival at some sites (KI Long Point, SBI East Point, SBI State Park, MBI State Park, NBI NE, E, SE Shore, NBI South Shore, and Gibraltar) but exceeded female survival, by 0.09–0.26, at other sites (KI Southeast Shore, KI South Shore, KI Minshall, KI State Park, SBI East Point, and MBI West End; Figure 2, Table 1). Confidence intervals for sex- and site-specific estimates averaged 0.10 (range $= 0.05–0.29$; Table 1).

3.4 | Process variance in annual survival

Temporal process variance in annual adult survival could be estimated for 26 of 28 sex–site combinations (Table 1) and was generally low, averaging just 0.0011 (range $= <0.0001$ to 0.0080 among sites; Table 1). In contrast, total variance in adult survival over time averaged 0.0264 (range $= 0.0132–0.0773$ among sites). Thus, temporal process variance averaged less than 4% of total variance (range $= <0.1\%-30.2\%$ among sites). Spatial process variance in annual adult survival was 0.005 for both males and females (24% of total variance).

3.5 | Realized population growth

The most parsimonious Pradel model from our candidate set, $\lambda$(site*sex+time), included interactive effects of site and sex and an additive effect of time on realized population growth (Supporting Information Table S2). This model had weight $= 1.00$, indicating its clear precedence over other candidate models. Confidence intervals for realized population growth were wide for the early years of the study but decreased over time (Figure 3). Of 28 site–sex combinations, realized population growth was significantly greater than one in nine, did not differ from one in 17, and was significantly less
than one in only two. Realized population growth was similar in males and females, averaging 1.025 and 1.026, respectively (range = 0.95–1.14 and 0.94–1.11; Table 1, Figure 4, Supporting Information Table S8).

### 3.6 Associations between survival and body size among sites

Mean SVL of the largest 10% of animals captured from 2000 to 2015 varied among sites from 719 to 793 mm in males and from 930 to 1,062 mm in females (Table 1). Across sites, mean SVL was positively correlated between the sexes ($r = 0.81$, $df = 12$, $p < 0.001$). Furthermore, mean SVL was positively correlated with $\phi$ in both males ($r = 0.61$, $df = 12$, $p = 0.010$) and females ($r = 0.52$, $df = 12$, $p = 0.030$; Figure 4).

### 3.7 Review of snake survival

We collated information from 65 studies of 45 species that provided estimates of survival for one or more age classes of snakes (Table 2, Supporting Information File S1, Figure 5). After averaging across sexes, years, and local populations, we identified 55 estimates (48 species) of adult annual survival, 18 estimates (16 species) of annual juvenile survival, and 12 estimates (10 species) of annual neonatal survival (Table 2). Thirteen studies provided separate estimates of adult male and adult female annual survival (Supporting Information File S1).

Across studies, estimates of annual adult survival ranged from 0.23 to 0.94 (median = 0.73). Three estimates appeared to be outliers based on their standard $z$ scores: *Nerodia harteri* ($\phi = 0.23$, $z = -2.81$), *Tropidonophis mairii* ($\phi = 0.26$, $z = -2.62$), and *Trimersurus albolabris*.
models with varying frequency. For example, survival frequently differed among study sites (nine of 10 studies in which site was included among candidate models) and among size, stage, or age classes (17 of 26 studies). Year and sex appeared among high-ranking models less frequently (just 14 of 36 and 13 of 38 studies, respectively). Only a single study included size as a continuous covariate. Using a growth function to estimate the size of snakes when not encountered, Hansen, Scherer, White, Dickson, and Fleishman (2015) demonstrated that, for Thamnophis gigas (Giant Gartersnake), survival increased as function of SVL from 0.37 among neonates to 0.73 among large adults. Similarly, survival consistently increased with increasing size, stage, or age in studies using these grouping variables.

Survival was frequently associated with environmental factors. In Thamnophis elegans (Wandering Gartersnake), adult survival was higher in lakeshore than in meadow populations and covaried with body size, age at first reproduction, reproductive frequency, and food availability (relatively constant at lakeshore sites, highly variable at meadow sites; Bronikowski & Vieck, 2010; Miller, Clark, Arnold, & Bronikowski, 2011). Adult survival was also associated with prey availability in Liasis fuscus (Water Python, Madsen, Ujvari, Shine, & Olsson, 2006; Ujvari, Brown, Shine, & Madsen, 2016) and Vipera berus (European Adder, Forsman & Lindell, 1997). Changes in adult survival were associated with the arrival of nonnative toxic toads in the Tropidonophis majorii (Common Keelback) and Acanthophis praelongus (Northern Death Adder) but not Stegonotus cucullatus (Slatey-grey Snake; Brown, Ujvari, Madsen, & Shine, 2013; Phillips, Greenlees, Brown, & Shine, 2010). Other variables associated with variation in survival included degree of habitat fragmentation (Drymarchon couperi, Indigo Snake, Breininger et al., 2012), fire (Vipera ursinii, Ursini's Viper; Rhinolophus nigrescens, Small-eyed Snake; Webb & Shine, 2008; Lyet, Cheylan, Prodon, & Besnard, 2009), color morph (Vipera berus, European Adder; Crotalus horridus, Timber Rattlesnake; Forsman, 1995; Brown, Kery, & Hines, 2007; Brown, 2008), and possibly, disturbance by researchers (Crotalus oreganus, Pacific Rattlesnake; Diller & Wallace, 2002).

4 | DISCUSSION

4.1 | Population size and realized population growth

Population size of the Lake Erie Watersnake is of interest for two reasons. The first is the sheer density that this snake achieves. Descriptions by French explorers of watersnakes "sunning themselves in heaps, knots, and snarls" (Ballou, 1878) and by mid-twentieth-century biologists of catching hundreds in a single day (Conant, 1997) seemed steeped in hyperbole when efforts to quantify population density began in the 1980s (King, 1986). Currently, watersnake density varies from 160 to 1,600 adults per km of shoreline among study sites (mean = 520/km, Table 1), a dramatic increase from early quantitative estimates (King, 1986; King, Queral-Regil, et al., 2006). Furthermore, capture rates exceeding 100 adults per site per day during annual population censuses are once again a
regular occurrence, suggesting that past abundance has been regained at many sites.

Lake Erie Watersnakes occupy a narrow band of shoreline habitat during the active season (90% of on-shore activity occurs within 21 m of shore, Stanford et al., 2010). Thus, linear density estimates translate into ca. 260 adults per ha (range = 80–800 adults per ha). In contrast, densities of Northern Watersnakes (N. s. sipedon) occupying marshes and ponds in southern Michigan and southern Ontario are an order of magnitude lower (26 adults per ha, Brown & Weatherhead, 1999), as is an introduced population in California (15 adults per ha estimated from Figure 3 in Rose, Miano, & Todd, 2013). Among congeners, N. fasciata achieves a density of 45 adults per ha in a South Carolina bay (Willson & Winne, 2016), and N. taxispilota achieves a density of 200 juveniles and adults per km of the Savannah River (Mills, 2002). To our knowledge, only two other snake species similar in body size to the Lake Erie Watersnake achieve comparable densities. Natrix tessellata has a density >500/ha at a study site in Macedonia (Ajtic et al., 2013), and Gloydius shedaoensis has a density of ca. 200/ha at a study site in China (Shine, Sun, Kearney, & Fitzgerald, 2002). Both involve island populations. Like the Lake Erie Watersnake, N. tessellata feeds on locally abundant fish, whereas G. shedaoensis feeds on temporally abundant migratory birds.

Lake Erie Watersnake population size is also of practical interest; criteria for delisting and for postdelisting monitoring both included island-specific and total adult population size targets (U.S. Fish and Wildlife Service, 2003, 2011). Summing population estimates across sites within islands and across all 14 study sites (Table 1) demonstrate that these targets have been met. In addition to population size criteria, the Lake Erie Watersnake postdelisting monitoring plan included analyses of realized population growth (U.S. Fish and Wildlife Service, 2011). Specifically, the plan specified that 95% confidence intervals for \( \lambda \) that included or exceeded one represented evidence of stable or increasing population size. Taken together, estimates of population size and realized population growth indicate that, during postdelisting monitoring, the species has remained secure without Endangered Species Act protections (U.S. Fish and Wildlife Service, 2011).

### 4.2 Annual survival and process variance in annual survival

Our analyses indicate that annual adult survival of the Lake Erie Watersnake is relatively high (ca. 0.72), is greater among males than females (0.76 vs. 0.68), and varies among sites (by 0.18 in males and 0.27 in females). Estimates provided by the CJS model are of “apparent survival,” the product of survival and emigration probability. Thus, some of the variation in survival that we see among sites could arise from variable emigration rates. However, high site fidelity of adult Lake Erie Watersnakes, as indicated by our recapture data (99.4% of recaptures occurred within study sites) and radio telemetry (Stanford et al., 2010), suggests that emigration is infrequent and likely has only minor effects on survival estimates.

In contrast, our top-ranked model suggests that variation in survival among years is of lesser significance. Temporal process variance averaged just 0.0011, less than 4% of total variance. This has implications for population projections and models of extinction risk that include stochasticity (Akçakaya & Root, 2002; Lacy & Pollak, 2014). In the absence of estimates like ours, total variance or arbitrary values (e.g., 10%) are sometimes used in place of process variance, potentially resulting in overly pessimistic assessments of extinction risk (Jones, King, & Sutton, 2017). Long-term data (10 or more years) are needed to calculate temporal process variance (Gould & Nichols, 1998; Burnham & Anderson, 2002; Anderson, 2008) and so estimates are scarce. However, those estimates for snakes that do exist are uniformly low (Table 3) suggesting that stochasticity in annual survival may be of minor significance to snake extinction risk. In cases where process variance cannot be estimated directly, values in Table 2 might serve as a proxy.

We found that adult survival was positively correlated with body size (mean SVL of the largest 10% of animals) across sites in both males and females. Interpreting this pattern is complicated by extensive individual variation in the asymptotic size of Lake Erie Watersnakes (King et al., 2016) such that larger individuals are not necessarily older. Consequently, it is unclear whether high survival leads to increased body size, large body size leads to increased survival, or some other mechanism underlies variation in both size and survival. Given that our 14 study sites are separated by less than 20 km, variation in climatic conditions is likely to be small and certainly far less than that seen in range-wide demonstrations of variation in survival (Jones et al., 2012) or body size (Hileman, King, et al., 2017; Hileman, Powell, et al., 2017). Study sites differ in the extent of human activity and may differ in predator abundance, but how these variables affect mortality awaits further investigation. Prey availability or foraging success may also differ among sites, and this could contribute to variation in both survival rates (e.g., through an effect on body condition) and size (e.g., through an effect on growth). Cases in which survival varies as a consequence of prey availability are well documented in our review of snake survival, suggesting that further investigation of this linkage in Lake Erie Watersnakes would be worthwhile.

### 4.3 Review of snake survival

Estimates of snake adult survival overlap broadly across continents, climate zones, families, subfamilies, reproductive modes, body size categories, maturation categories, and parity categories. There is some evidence for higher survival in subtropical (median = 0.78) vs. tropical areas (0.63), among Viperidae (0.79) vs. Colubridae (0.67), especially Crotalinae (0.81) vs. Natricinae (0.67), in large- (0.79) vs. small-bodied snakes (0.69),
### TABLE 2  Estimates of annual survival in snakes based on known-fate analyses of telemetry data (study type = T) or analyses of capture–mark–recapture data that account for imperfect detection (study type = CMR)

| Species                        | Study type | Grouping variables and covariates                                      | Annual survival |
|--------------------------------|------------|------------------------------------------------------------------------|-----------------|
|                                |            | Year | Sex | Size, Stage, or Age | Site | Other | Adult | Juvenile | Neonate |
| Colubridae, Colubrinae         |            |      |     |                   |      |        |        |          |          |
| Drymarchon couperi             | CMR        | –    | –    | +                  |      |        | 0.74   | 0.52      |          |
| Drymarchon couperi             | T          | –    | –    | +                  |      |        | 0.91   |           |          |
| Hierophis viridiflavus         | CMR        | +    | –    |                    |      |        | 0.55   |           |          |
| Lampropeltis triangulum        | CMR        | –    | –    |                    |      |        | 0.72   |           |          |
| Pantherophis obsoletus         | T          | +    | –    |                    |      |        | 0.76   |           |          |
| Pituophis catenifer            | T          | –    | –    |                    |      |        | 0.73   |           |          |
| Stegonotus cucullatus          | CMR        | –    | –    |                    |      |        | 0.57   |           |          |
| Zamenis longissimus            | CMR        | +    | –    |                    |      |        | 0.51   |           |          |
| Colubridae, Dipsadinae         |            |      |     |                   |      |        |        |          |          |
| Diadophis punctatus            | CMR        | –    | –    |                    |      |        | 0.79   | 0.62      | 0.76      |
| Colubridae, Natricinae         |            |      |     |                   |      |        |        |          |          |
| Natrix natrix                  | CMR        | –    | –    |                    |      |        | 0.66   |           |          |
| Natrix tessellata              | CMR        | +    | –    | +                  |      |        | 0.73   |           |          |
| Nerodia erythrogaster          | T          | +    | +    |                    |      |        | 0.71   |           |          |
| Nerodia fasciata               | CMR        | –    | –    |                    |      |        | 0.92   |           |          |
| Nerodia harteri                | CMR        | +    | –    | +                  | –    |        | 0.23   | 0.14      |          |
| Nerodia sipedon                | T          | +    | +    |                    |      |        | 0.50   |           |          |
| Nerodia sipedon                | CMR        | +    | +    | +                  |      |        | 0.72   |           |          |
| Nerodia sipedon                | CMR        | –    | +    | +                  | Marking+ | 0.53 | 0.18 |
| Nerodia sipedon                | CMR        | –    | +    | +                  | Marking+ | 0.55 | 0.19 |
| Nerodia sipedon                | CMR        | –    | +    | +                  | Marking+ | 0.31 | 0.19 |
| Nerodia sipedon                | CMR        | –    | +    | +                  | Marking+ | 0.88 | 0.60 |
| Seminatrix pygaea              | CMR        | –    | –    |                    |      |        | 0.88   |           |          |
| Thamnophis atratus             | CMR        | –    | +    |                    |      |        | 0.60   |           |          |
| Thamnophis butleri             | CMR        | +    | –    | Invasive plant management | 0.48 |
| Thamnophis elegans             | CMR        | +    | +    | +                  | +    |        | 0.63   | 0.56      | 0.35      |
| Thamnophis elegans             | CMR        | +    | +    | +                  | +    |        | 0.75   | 0.81      | 0.67      |
| Continent | Climate area | Reproductive mode | Size | Maturation | Parity | Source |
|-----------|--------------|-------------------|------|------------|--------|--------|
| NA        | Subt         | O                 | L    | I          | A      | Hyslop et al. (2012) |
| NA        | Subt         | O                 | L    | I          | A      | Breining et al. (2012), Hyslop et al. (2012) (maturation, parity) |
| E         | Temp         | O                 | L    | I          | A      | Leleivre et al. (2013), Zuffi, Fornasier, and Bonnet (2007) (size), Fornasiero, Bonnet, Dendi, and Zuffi (2016) (maturation), Capula, Filippi, Luiselli, and Jesus (1997) (parity) |
| NA        | Temp         | O                 | M    | I          | A      | Hileman, Kapfer, Muehlfeld, and Giovanni (2015), Fitch (1999) (maturation), other NA colubrinae (parity) |
| NA        | Subt         | O                 | L    | I          | A      | Sperry and Weatherhead (2008, 2009) (size), Fitch (1999) (maturation), other NA colubrinae (parity) |
| NA        | Temp         | O                 | L    | I          | A      | Williams, Hodges, and Bishop (2014), Parker and Brown (1960) (maturation in P. melanoleucus), Diller and Wallace (1996) (parity in P. melanoleucus) |
| Au        | Trop         | O                 | L    | E          | A      | Brown et al. (2013), Dubey, Brown, Madsen, and Shine (2009) (size), Brown, Shine, and Madsen (2002) (maturation, parity) |
| E         | Temp         | O                 | L    | I          | A      | Leleivre et al. (2013), Naulleau and Bonnet (1995) (size, parity), other temperate colubrinae (maturation) |
| NA        | Temp         | O                 | S    | E          | A      | Riedle (2014), Ernst and Ernst (2003) (parity) |
| E         | Temp         | O                 | L    | I          | A      | Sewell, Baker, and Griffiths (2015), Gregory (2004) (size), Madsen (1983) (maturation), Luiselli et al. (2011) (parity) |
| E         | Temp         | O                 | M    | I          | A      | Luiselli et al. (2011), Luiselli, Capula, and Shine (1997) (parity) |
| NA        | Temp         | V                 | M    | E          | A      | Roe, Attum, and Kingsbury (2013), Gibbons and Dorcas (2004) (maturation in other Nerodia, parity) |
| NA        | Subt         | V                 | M    | E          | A      | Willson, Winne, and Todd (2011), Conant (1975) (size); Gibbons and Dorcas (2004) (maturation in other Nerodia, parity) |
| NA        | Subt         | V                 | S    | E          | A      | Whiting et al. (2008), Greene, Dixon, Whiting, and Mueller (1999) (size, parity), Gibbons and Dorcas (2004) (maturation) |
| NA        | Temp         | V                 | M    | E          | A      | Roe et al. (2013), Gibbons and Dorcas (2004) (maturation, parity) |
| NA        | Temp         | V                 | M    | I          | A      | This study, King et al. (2016) (maturation), Stanford (2012) (parity) |
| NA        | Temp         | V                 | M    | I          | A      | Stanford (2012) |
| NA        | Temp         | V                 | M    | I          | A      | Brown and Weatherhead (1999), Weatherhead, Barry, Brown, and Forbes (1995) (size, parity) |
| NA        | Temp         | V                 |      |            |        | Kissner and Weatherhead (2005) |
| NA        | Temp         | V                 |      |            |        | Cecala, Price, and Dorcas (2010) |
| NA        | Subt         | V                 | S    | E          | A      | Willson et al. (2011), Winne, Willson, and Gibbons (2006) (size, parity), Gibbons and Dorcas (2004) (maturation) |
| NA        | Temp         | V                 | M    | I          | A      | Lind, Welsh, and Tallmon (2005), Rossman, Ford, and Seigel (1996) (size), other Thamnophis (maturation, parity) |
| NA        | Temp         | V                 | S    | E          | A      | E. T. Hileman, Personal Communication |
| NA        | Temp         | V                 | M    | I          | A      | Miller et al. (2011), Bronikowski and Vleck (2010) (size, maturation) |
| NA        | Temp         | V                 | S    | L          | B      | Miller et al. (2011), Bronikowski and Vleck (2010) (size, maturation) |

(Continues)
| Species                  | Study type | Year | Sex | Size, Stage, or Age | Site | Other                                      | Annual survival |
|--------------------------|------------|------|-----|--------------------|------|--------------------------------------------|-----------------|
|                          |            |      |     |                    |      | Condition−, terrestrial vs. aquatic habitat+; linear vs. areal habitat− | Adult | Juvenile | Neonate |
| Thamnophis gigas         | T          | +    | −   | +                  |      |                                           | 0.61            |
| Thamnophis radix         | CMR        | +    | +   |                    |      |                                           | 0.43 0.42 0.16  |
| Thamnophis sirtalis      | CMR        | +    |     |                    |      |                                           | 0.67            |
| Thamnophis sirtalis      | CMR        | +    |     |                    |      |                                           | 0.76            |
| Tropidonophis mairii     | CMR        | −    | −   |                    |      | Pre− vs. posttoad invasion+               | 0.26            |
| *Colubridae, Xenodonta*  |            |      |     |                    |      |                                           |                 |
| Borikenophis portoricensis| CMR        | +    |     |                    |      |                                           | 0.50            |
| Contia tenuis            | CMR        | −    | −   | +                  |      |                                           | 0.75 0.66       |
| *Elapidae, Elapinae*     |            |      |     |                    |      |                                           |                 |
| Naja kaouthia            | CMR        | +    |     |                    |      |                                           | 0.93 0.48       |
| *Elapidae, Hydrophiinae* |            |      |     |                    |      |                                           |                 |
| Acanthophis praelongus   | T          |      |     |                    |      | Toad experience+                          | 0.73            |
| Emydcephalus annulatus   | CMR        | −    | −   |                    |      | Color morph−                               | 0.69            |
| Hoplocephalus bungaroides| CMR        | −    | −   | −                  |      | Pre− vs. postfire−                         | 0.74 0.68       |
| Notechis scutatus        | CMR        | −    | +   | +                  |      |                                           | 0.79 0.57       |
| Rhinoplocephalus nigrescens| CMR        | −    | −   | −                  |      | Pre− vs. postfire+                         | 0.61            |
| *Pythonidae*             |            |      |     |                    |      |                                           |                 |
| Liasis fuscus            | CMR        | −    |     |                    |      | Prey abundance−, pre− vs. postflood+      | 0.80            |
| *Viperidae, Crotalinae*  |            |      |     |                    |      |                                           |                 |
| Agkistrodon piscivorus   | CMR        | −    | −   | −                  |      | Season−, transience+                       | 0.79            |
| Agkistrodon piscivorus   | CMR        | −    | −   |                    |      | Area−                                      | 0.81            |
| Bothrops insularis       | CMR        | +    |     |                    |      | Season+                                    | 0.49            |
| Crotalus adamanteus      | CMR/T      | −    | −   |                    |      | Season+, condition+                        | 0.82            |
| Crotalus horridus        | CMR        | −    | −   | +                  |      | Morph+, marking treatment−, cohort−        | 0.89 0.84 0.65  |
| Crotalus horridus        | T          | +    |     | +                  |      | Season+, weather−, time since marking+, female reproductive state−, condition−, prey abundance+| 0.88            |
| Crotalus oreganus        | CMR        | +    | −   | +                  |      |                                           | 0.82 0.76 0.66  |
| Crotalus pricei          | CMR        | −    |     |                    |      |                                           | 0.71            |
| Sistrurus catenatus      | CMR        | −    | +   | +                  |      |                                           | 0.69 0.66 0.38  |
| Sistrurus catenatus      | CMR        | −    | −   |                    |      | Transience+                                | 0.74            |
| Sistrurus catenatus      | CMR        | −    | −   |                    |      |                                           | 0.94 0.85 0.65  |
| Continent | Climate area | Reproductive mode | Size | Maturation | Parity | Source |
|-----------|--------------|--------------------|------|------------|--------|--------|
| NA        | Temp         | V                  | M    | L          | A      | Halstead et al. (2012), Wylie, Casaza, Gregory, and Halstead (2010) (size), Rossman et al. (1996) (maturation); other Thamnophis (parity) |
| NA        | Temp         | V                  | M    | E          | A      | Stanford and King (2004) |
| NA        | Temp         | V                  | M    | E          | A      | Larsen and Gregory (1989), Rossman et al. (1996) (maturation, parity) |
| NA        | Temp         | V                  | M    | E          | A      | Halstead et al. (2011), Rossman et al. (1996) (maturation, parity) |
| Au        | Trop         | O                  | M    | E          | A      | Brown et al. (2013), Brown and Shine (2002) (size, maturation, parity) |
| NA        | Trop         | O                  | M    | E          | A      | Hileman, King, et al. (2017), Hileman, Powell, et al. (2017) |
| NA        | Temp         | O                  | S    | L          | B      | Govindarajulu, Isaac, Engelstoft, and Ovaska (2011) |
| As        | Trop         | O                  | L    | I          |        | Chaitae (2011) |
| Au        | Trop         | V                  | M    | E          | B      | Phillips et al. (2010), Webb, Brook, and Shine (2002) (size, maturation) |
| Au        | Trop         | V                  | S    | E          | A      | Shine, Brischoux, and Pile (2010), Shine, Shine, and Shine (2003) (size); Masunaga and Ota (2003) (maturation and parity in E. imae) |
| Au        | Subt         | V                  | M    | L          | B      | Webb and Shine (2008), Webb, Christian, and Fisher (2002) (size, maturation, parity) |
| Au        | Subt         | V                  | L    | E          | A      | Bonnet et al. (2011), Shine (1977) (parity) |
| Au        | Subt         | V                  | S    | I          | A      | Webb and Shine (2008), Shine (1984) (size), Webb, Christian et al. (2002) (maturation, parity) |
| Au        | Trop         | O                  | L    | E          | A      | Ujvari et al. (2016), Madsen et al. (2006) (size, parity), Madsen and Shine (2000) (maturation) |
| NA        | Subt         | V                  | L    | L          | B      | Koons, Birkhead, Boback, Williams, and Greene (2009), Conant (1975) (size), Ford (2002) (maturation, parity) |
| NA        | Subt         | V                  | M    | L          | B      | Rose, Simpson, Ott, and Manning (2010), Rose, Simpson, Ott, Manning, and Martin (2010) (size), Ford (2002) (maturation, parity) |
| SA        | Trop         | V                  | M    | E          | B      | Guimaraes, Munguia-Steyer, Doherty, Martins, & Sawaya (2014), Marques, Kasperoviczus, and Almeida-Santos (2013) (size, parity), Hartmann, Marques, and Almeida-Santos (2004) (maturation in B. neuwiedi) |
| NA        | Subt         | V                  | L    | L          | B      | Waldron, Welch, Bennett, Kalinowsky, and Mousseau (2013) |
| NA        | Temp         | V                  | L    | L          | B      | Brown et al. (2007), Brown (1991) (size), 1993 (size), Brown et al. (2007) (maturation, parity), Brown (2008) (maturation, parity) |
| NA        | Temp         | V                  | L    | L          | B      | Olson, MacGowan, Hamilton, Currylow, and Williams (2015), Brown (1991) (size), 1993 (size), Brown et al. (2007) (maturation, parity), Brown (2008) (maturation, parity) |
| NA        | Temp         | V                  | M    | E          | B      | Diller and Wallace (2002) |
| NA        | Subt         | V                  | M    | I          | B      | Prival and Schroff (2012) |
| NA        | Temp         | V                  | M    | I          | B      | Hileman (2016), Hileman, King, and Faust (2018) |
| NA        | Temp         | V                  | M    | I          | B      | Jones et al. (2017), Hileman (2016) (size, maturation, parity) |
| NA        | Temp         | V                  | M    | I          | B      | Baker (2016) |

(Continues)
in biennially (0.75) vs. annually (0.69) reproducing snakes, and in later (0.75) vs. earlier (0.71) maturing snakes. Notably, differences in survival in relation to size, parity, and maturation are in the directions predicted by life history theory (Roff, 1992; Stearns, 1992) but are of small magnitude with much variation around median values. In contrast to Parker and Plummer (1987, tables 9-5), we found that annual survival differed little among early maturing temperate colubrids (median adult survival = 0.67, range = 0.43–0.79, n = 7), late maturing temperate colubrids (median = 0.66, range = 0.51–0.75, n = 13), and late maturing temperate vipers (median = 0.70, range = 0.64–0.94, n = 11; Table 2).

Covariation in demographic traits is well documented in mammals, birds, lizards, and fishes (e.g., Gaillard et al., 1989,
| Continent | Climate area | Reproductive mode | Size | Maturation | Parity | Source |
|-----------|--------------|-------------------|------|------------|--------|--------|
| NA        | Temp         | V                 | M    | I          | B      | Johnson (2013), Johnson, Gibbs, Shoemaker, and Cohen (2016), Hileman (2016) (maturation) |
| NA        | Temp         | V                 | M    | I          | B      | Jones et al. (2012), Seigel (1986) (size, maturation, parity) |
| As        | Trop         | V                 | M    | I          | B      | Devan-Song (2014), Nishimura and Kamura (1994) (maturation in T. flavoviridis) |
| Af        | Trop         | V                 | S    | E          | A      | Maritz (2011), Maritz and Alexander (2012) |
| E         | Temp         | V                 | M    | I          | B      | Flatt, Dumermuth, and Anholt (1997), Altweeg, Dumermuth, Anholt, and Flatt (2003), Naulleau and Bonnet (1995) (size) |
| E         | Temp         | V                 | M    | I          | B      | Forsman and Lindell (1997), Forsman (1995) (size, maturation, parity) |
| E         | Temp         | V                 |      |            |        | Baron, Le Galliard, Tully, and Ferriere (2010) |
| E         | Temp         | V                 | S    | L          | B      | Lyet et al. (2009), Baron, Le Galliard, Ferriere, and Tully (2013) (size, maturation, parity) |
| E         | Temp         | V                 | S    | L          | B      | Baron et al. (2013) |

2005; Mesquita, Faria, Colli, Vitt, & Pianka, 2016; Mesquita, Costa, et al., 2016; Promislov & Harvey, 1990; Winemiller & Rose, 1992), but whether this covariation conforms to a single (slow-fast) axis or two (opportunistic-periodic-equilibrium) axes (Dunham & Miles, 1985; Winemiller, 2004; Bielby et al., 2007) and the ways in which demography covaries with physiology and behavior remain areas of active research (Pianka et al., 2017; Réale et al., 2010; Ricklefs & Wikelski, 2002; Winemiller et al., 2015). At the same time, species or larger taxonomic groups that represent exceptions to general patterns provide interesting insights regarding demographic variability. For example, crocodilians and turtles exhibit a suite of demographic traits that are unusual among vertebrates; delayed maturity and high adult survival coupled with high fecundity (BriggsGonzalez et al., 2017). The variation in annual survival revealed in our case study, and review suggests that demography may be unusually plastic in snakes compared to more frequently studied taxa. Our review reveals a strong bias favoring North American and temperate/subtropical species with few representatives from centers of snake diversity in the tropics (compare Figure 6 with figure 1d in Roll et al., 2017), thus much remains to be learned regarding snake demography. We suspect that, as additional studies accumulate, future analyses, which might also include juvenile survival, offspring size, offspring number, growth parameters, and generation time, will clarify ecological and evolutionary determinants of snake life history. Additional studies are also likely to provide further information on the magnitude of process variance in annual survival, possibly confirming our suggestion, based on existing examples, that such variance is generally low. This has practical implications for making accurate projections of future population trajectories (e.g., for species of conservation concern) and may offer insight into the stability of snake population dynamics more generally.

**ACKNOWLEDGMENTS**

We are grateful to the many agency staff members, naturalists, colleagues, students, island residents, and volunteers who assisted us in the field and to agencies and landowners who allowed access to study sites. We thank E. Hileman for sharing results, P. Ruback for assistance with maps, and reviewers for improvements to the manuscript. Funding and logistical support were provided by the U.S. Fish and Wildlife Service, Ohio Department of Natural Resources, Toledo Zoo, Columbus Zoo, Northern Illinois University, and the Ohio State University F. T. Stone Laboratory. Protocols regarding the use
of live vertebrate animals were approved by the Northern Illinois University Institutional Animal Care and Use Committee (ORC 238, ORC 282, ORC 326, LA12-003) and The Ohio State University Institutional Animal Care and Use Committee (2004A0048, 2007A0046, 2010A0000148). Permits were provided by the U. S. Fish and Wildlife Service and the Ohio Division of Wildlife.

**FIGURE 6** Box plots showing variation in adult snake survival among continents, climate zones, families, subfamilies, modes of reproduction, body size, maturation, and parity. Bars represent medians, boxes represent 50th percentiles, and whiskers represent ranges excluding outliers (points). The number of estimates and the number of species are listed above each box plot.
AUTHOR CONTRIBUTIONS

All authors conceived the ideas, designed methodology, analyzed the data, wrote the manuscript, contributed to revisions, and gave final approval for publication.

DATA ACCESSIBILITY

Relevant data will be available via Dryad.

ORCID

Richard B. King http://orcid.org/0000-0002-1466-0232

REFERENCES

Ajtic, R., Tomovic, L., Sterijovski, B., Crnobrnja-Isailovic, J., Djordjevic, S., Djurakic, M., ... Bonnet, X. (2013). Unexpected life history traits in a very dense population of dice snakes. Zoologischer Anzeiger, 252, 350–358. https://doi.org/10.1016/j.zjac.2012.10.001

Akçaçay, H. R. (2004). Using models for species conservation and management: An introduction. In H. R. Akçaçay, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjögren-Gulve, J. S. Hatfield & M. A. McCarthy (Eds.), Species conservation and management: Case studies (pp. 3–14). New York, NY: Oxford University Press.

Akçaçay, H. R., & Root, W. (2002). RAMAS Metapop: Viability analysis for stage-structured metapopulations. Setauket, NY: Applied Biomathematics.

Altwegg, R., Dummermuth, A., Anholt, B. R., & Flatt, T. (2005). Winter weather affects asp viper Vipera aspis population dynamics through susceptible juveniles. Oikos, 110, 55–66. https://doi.org/10.1111/j.0030-1299.2001.13723.x

Anderson, D. R. (2008). Model based inference in the life sciences: A primer on evidence. New York, NY: Springer.

Anthony, R. G., Forsman, E. D., Franklin, A. B., Anderson, D. R., Burnham, K. P., White, G. C., ... Sovern, S. G. (2006). Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monographs, 163, 1–48. https://doi.org/10.2193/0084-0173(2006)163[1:SATO]2.0.CO;2

Baker, S. J. (2016). Life and death in a corn desert oasis: reproduction, mortality, genetic diversity, and viability of Illinois’ last eastern massasauga population. PhD thesis, University of Illinois, Urban-Champaign.

Ballou, W. H. (1878). The natural history of the islands of Lake Erie. Field and Forest, 3, 135–137.

Baron, J. P., Le Galliard, J. F., Ferriere, R., & Tully, T. (2013). Intermittent breeding and the dynamics of resource allocation to reproduction, growth and survival. Functional Ecology, 27, 173–183. https://doi.org/10.1111/1365-2656.12023

Baron, J. P., Le Galliard, J. F., Tully, T., & Ferriere, R. (2010). Cohort variation in offspring growth and survival: Prenatal and postnatal factors in a late-maturing viviparous snake. Journal of Animal Ecology, 79, 640–649. https://doi.org/10.1111/j.1365-2656.2010.01661.x

Bielby, J., Mace, G. M., Bininda-Emonds, O. R., Cardillo, M., Gittleman, J. L., Jones, K. E., ... Purvis, A. (2007). The fast-slow continuum in mammalian life history: An empirical reevaluation. The American Naturalist, 169, 748–757.

Bonnet, X., Lorioux, S., Pearson, D., Aubret, F., Bradshaw, D., Delmas, V., & Fauvet, T. (2011). Which proximate factor determines sexual size dimorphism in tiger snakes? Biological Journal of the Linnean Society, 103, 668–680. https://doi.org/10.1111/j.1095-8312.2011.01633.x

Breininger, D. R., Mazerolle, M. J., Bolt, M. R., Legare, M. L., Drese, J. H., & Hines, J. E. (2012). Habitat fragmentation effects on annual survival of the federally protected eastern indigo snake. Animal Conservation, 15, 361–368. https://doi.org/10.1111/j.1469-1795.2012.00524.x

Briggs Gonzalez, V., Bonenfant, C., Basille, M., Cherikiss, M., Beauchamp, J., & Mazzotti, F. (2017). Life histories and conservation of long-lived reptiles, an illustration with the American Crocodile (Crocodylus acutus). Journal of Animal Ecology, 86, 1102–1113. https://doi.org/10.1111/1365-2656.12723
Brown, W. S. (1991). Female reproductive ecology in a northern population of the timber rattlesnake, Crotalus horridus. Herpetologica, 47, 101–115.

Brown, W. S. (1993). Biology, status, and management of the Timber Rattlesnake (Crotalus horridus): A guide for conservation. Society for the Study of Amphibians and Reptiles Herpetological Circulars, 22, 1–78.

Brown, W. S. (2008). Sampling timber rattlesnakes (Crotalus horridus): Phenology, growth, intimidation, survival, and a syndrome of undetermined origin in a northern population. In W. K. Hayes, K. R. Beaman, M. D. Cardwell, & S. P. Buse (Eds.), The biology of rattlesnakes (pp. 235–256). Loma Linda, CA: Loma Linda University Press.

Brown, W. S., Kery, M., & Hines, J. E. (2007). Survival of timber rattle snakes (Crotalus horridus) estimated by capture-recapture models in relation to age, sex, color morph, time, and birthplace. Copeia, 2015, 656–671. https://doi.org/10.1643/0045-8511(2007)0656:SOTRCH.2.0.CO;2

Brown, G. P., & Shine, R. (2002). Reproductive ecology of a tropical natrix-cine snake, Tropidonophis mairii (Colubridae). Journal of Zoology, 258, 63–72. https://doi.org/10.1017/S0952836902001218

Brown, G. P., Shine, R., & Madsen, T. (2002). Responses of three sympatric snake species to tropical seasonality in northern Australia. Journal of Tropical Ecology, 18, 549–568. https://doi.org/10.1017/S0266467402002365

Brown, G. P., Ujvari, B., Madsen, T., & Shine, R. (2013). Invader impact clarifies the roles of top-down and bottom-up effects on tropical snake populations. Functional Ecology, 27, 351–361. https://doi.org/10.1111/1365-2435.12044

Brown, G. P., & Weatherhead, P. J. (1999). Demography and sexual size dimorphism in northern water snakes, Nerodia sipedon. Canadian Journal of Zoology-Revue Canadienne De Zoologie, 77, 1358–1366. https://doi.org/10.1139/z99-112

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach. New York, NY: Springer.

Cam, E. (2012). Each site has its own survival probability, but information is borrowed across sites to tell us about survival in each site: Random effects models as means of borrowing strength in survival studies of wild vertebrates. Animal Conservation, 15, 129–132. https://doi.org/10.1111/j.1469-1795.2012.00533.x

Capula, M., Filippi, E., Luiselli, L., & Jesus, V. T. (1997). The ecology of the western whip snake, Coluber viridiflavus (Lacepede, 1789) in Mediterranean central Italy (Squamata: Serpentes: Colubridae). Herpetozoa, 10, 65–79.

Caswell, H. (2001). Matrix population models: Construction, analysis, and interpretation. Sunderland, MA: Sinauer Associates.

Cecala, K., Price, S., & Dorcas, M. (2010). Ecology of juvenile Northern watersnakes (Nerodia sipedon) inhabiting low-order streams. Amphibia-Reptilia, 31, 169–174. https://doi.org/10.1163/156853810791069029

Chaitae, A. (2011). Demography of the Monocled Cobra (Naja kaouthia) in the central region of Thailand. MS thesis, University of Louisville, Louisville, KY.

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A. M., & Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CArture-RECapture data. Ecography, 32, 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Conant, R. (1975). A field guide to reptiles and amphibians of Eastern and Central North America. Boston, MA: Houghton Mifflin Company.

Conant, R. (1997). A field guide to the life and times of Roger Conant. Provo, UT: Selva Canyonlands Publishing Group, L.C.

Cooch, E. G., & White, G. C. (2017). Program MARK – a gentle introduction’. Retrieved from http://www.phidot.org/software/mark/docs/book/

Devan-Song, E. A. (2014). Ecology and conservation of the Bamboo Pit Viper: natural history, demography and effects of translocation. MS thesis, University of Rhode Island, Kingston, RI.

Diller, L. V., & Wallace, R. L. (1996). Comparative ecology of two snake species (Crotalus viridis and Pituophis melanoleucus) in Southwestern Idaho. Herpetologica, 52, 343–360.

Diller, L. V., & Wallace, R. L. (2002). Growth, reproduction, and survival in a population of Crotalus viridis oreganus in north central Idaho. Herpetological Monographs, 16, 26–45. https://doi.org/10.1655/0733-1347(2002)016[0026:GRASIA]2.0.CO;2

Dubey, S., Brown, G. P., Madsen, T., & Shine, R. (2009). Sexual selection favours large body size in males of a tropical snake (Stegonotus cucullatus, Colubridae). Animal Behaviour, 77, 177–182. https://doi.org/10.1016/j.anbehav.2008.09.037

Dunham, A. E., & Diller, D. B. (1985). Patterns of covariation in life history traits of squamate reptiles: The effects of size and phylogeny reconsidered. The American Naturalist, 126, 231–257. https://doi.org/10.1086/284411

Dunham, A. E., Miles, D. B., & Reznick, D. N. (1988). Life history patterns in squamate reptiles. In C. Gans, & S. R. Huey (Eds.), Biology of the reptilia 16 (pp. 441–522). New York, NY: Alan R. Liss Inc.

Ernst, C. H., & Ernst, E. M. (2003). Snakes of the United States and Canada. Washington, DC: Smithsonian Institution Press.

Feaver, P. E. (1977). The demography of a Michigan population of Natrix sipedon with discussions of ophidian growth and reproduction. PhD dissertation, University of Michigan, Ann Arbor, MI.

Fitch, H. S. (1999). A Kansas snake community: Composition and changes over 50 years. Malabar, FL: Krieger Publishing Company.

Flatt, T., Dummermuth, S., & Anholt, B. R. (1997). Mark-recapture estimates of survival in populations of the asp viper, Vipera aspis aspis. Journal of Herpetology, 31, 558–564. https://doi.org/10.2307/1565609

Ford, N. B. (2002). Ecology of the western cottonmouth (Agkistrodon piscivorus leucostoma) in northeastern Texas. In G. W. Schuett, M. Hoggren, M. E. Douglas, & H. W. Green (Eds.), Biology of the vipers (pp. 167–178). Eagle Mountain, UT: Eagle Mountain Publishing, LC.

Fornasiero, S., Bonnet, X., Dendi, F., & Zuffi, M. A. L. (2016). Growth, longevity and age at maturity in the European whip snakes, Hierophis viridiflavus and H. carbonarius. Acta Herpetologica, 11, 135–149.

Forsman, A. (1995). Opposing fitness consequences of color pattern in male and female snakes. Journal of Evolutionary Biology, 8, 53–70. https://doi.org/10.1046/j.1420-9119.1995.8010053.x

Forsman, A., & Lindell, L. E. (1997). Responses of a predator to variation in prey abundance: Survival and emigration of adders in relation to vole density. Canadian Journal of Zoology, 75, 1099–1108. https://doi.org/10.1139/z97-132

Gaillard, J.-M., Pontier, D., Allaïne, D., Lebreton, J. D., Trouvilliez, J., & Clobert, J. (1989). An analysis of demographic tactics in birds and mammals. Oikos, 56, 59–76. https://doi.org/10.2307/356088

Gaillard, J.-M., Yoccoz, N. G., Lebreton, J.-D., Bonenfant, C., Devillard, S., Loison, A., … Allaïne, D. (2005). Generation time: A reliable metric to measure life-history variation among mammalian populations. The American Naturalist, 166, 119–123. https://doi.org/10.1086/430330

Gangloff, E. J., Chow, M., Leos-Barajas, V., Hynes, S., Hobbs, B., & Sparkman, A. M. (2017). Integrating behaviour into the pace-of-life continuum: Divergent levels of activity and information gathering in fast-and slow-living snakes. Behavioural Processes, 142, 156–163. https://doi.org/10.1016/j.beproc.2017.06.006

Gibbons, J. W., & Dorcas, M. (2004). North American watersnakes a natural history. Norman, OK: University of Oklahoma Press.
Gould, W. R., & Nichols, J. D. (1998). Estimation of temporal variability of survival in animal populations. Ecology, 79, 2531–2538. https://doi.org/10.1890/0012-9658(1998)079[2531:EOTVOS]2.0.CO;2

Govindarajulu, P., Isaac, L. A., Engelstoft, C., & Ovaska, K. (2011). Relevance of life-history parameter estimation to conservation listing: Case of the sharp-tailed snake (Contia tenuis). Journal of Herpetology, 45, 300–307. https://doi.org/10.1670/10-086.1

Greene, B. D., Dixon, J. R., Whiting, M. J., & Mueller, J. M. (1999). Reproductive ecology of the Concho water snake, Nerodia harteri paucimacula. Copeia, 1999, 701–709. https://doi.org/10.2307/447602

Gregory, P. T. (2004). Sexual dimorphism and allometric size variation in a population of Grass Snakes (Natrix natrix) in Southern England. Journal of Herpetology, 38, 231–240. https://doi.org/10.1670/122-03A

Guimaraes, M., Mungua-Steyer, R., Doherty, P. F. Jr, Martins, M., & Sawaya, R. J. (2014). Population Dynamics of the Critically Endangered Golden Lancehead Pitviper, Bothrops insularis: Stability or Decline? PLoS ONE, 9(4), e95203. https://doi.org/10.1371/journal.pone.0095203

Halstead, B. J., Wylie, G. D., Amarello, M., Smith, J. J., Thompson, M. E., Routman, E. J., & Casaza, M. L. (2011). Demography of the San Francisco gartersnake in coastal San Mateo County, California. Journal of Fish and Wildlife Management, 2, 41–48. https://doi.org/10.3996/012011-JFWM-009

Halstead, B. J., Wylie, G. D., Coates, P. S., Valcarcel, P., & Casaza, M. L. (2012). Bayesian shared frailty models for regional inference about wildlife survival. Animal Conservation, 15, 117–124. https://doi.org/10.1111/j.1469-1795.2011.00495.x

Hansen, E. C., Scherer, R. D., White, G. C., Dickson, B. G., & Fleishman, J. H. (2016). Revising the pace-of-life framework. Journal of Herpetology.

Hansen, E. C., Sistrurus catenatus threatened by vegetation. Journal of Animal Ecology, 74, 105–118. https://doi.org/10.1111/1365-2656.2005.00919.x

Hensel, E. T. (2015). Filling in the gaps in demography, phenology, and life history of the Eastern Massasauga Rattlesnake (Sistrurus catenatus). PhD dissertation, Northern Illinois University, DeKalb, IL.

Hileman, E. T., Kaper, J. M., Muehlfeld, T. C., & Giovanni, J. H. (2015). Recoup ing lost information when mark-recapture data are pooled: A case study of milksnakes (Lampropeltis triangulum) in the upper mid-western United States. Journal of Herpetology, 49, 428–436. https://doi.org/10.1670/13-217

Hileman, E. T., King, R. B., Adamski, J. M., Antong, T. G., Baker, S. J., ... Yagi, A. (2017). Climatic and geographic predictors of life history variation in Eastern Massasauga (Sistrurus catenatus): A range-wide synthesis. PLoS One, 12, e0172011. https://doi.org/10.1371/journal.pone.0172011

Hileman, E. T., King, R. B., & Faust, L. J. (2018). Eastern Massasauga demography and extinction risk under prescribed-fire scenarios. Journal of Wildlife Management, 1–14. https://doi.org/10.1002/jwmg.21457

Hileman, E. T., Powell, R., Perry, G., Mougey, K., Thomas, R., & Henderson, R. W. (2017). Demography of the Racer Borkinophis portoricensis (Squamata: Dipsadidae) on Guana Island, British Virgin Islands. Journal of Herpetology, 51, 454–460. https://doi.org/10.1670/16-147

Hille, S. M., & Cooper, C. B. (2015). Elevational trends in life histories: Revising the pace-of-life framework. Biological Reviews, 90, 204–213. https://doi.org/10.1111/brv.12106

Hyslop, N. L., Stevenson, D. J., Macey, J. N., Carlile, L. D., Jenkins, C. L., Hostetler, J. A., & Oli, M. K. (2012). Survival and population growth of a long-lived threatened snake species, Drymarchon couperi (Eastern Indigo Snake). Population Ecology, 54, 145–156. https://doi.org/10.1007/s10144-011-0292-3

Johnson, B. D. (2013). Management and status of an endangered Massasauga Rattlesnake population in New York State. MS thesis, State University of New York, Syracuse.

Johnson, T. B., Allen, M., Corkum, L. D., & Lee, V. A. (2005). Comparison of methods needed to estimate population size of roundgobies (Neogobius melanostomus) in western Lake Erie. Journal of Great Lakes Research, 31, 78–86. https://doi.org/10.22323/0090-3300(2005)023[78:COMNTE]2.0.CO;2

Kingsolver, J. G., Ovaska, K., & Johnson, P. D. (2016). Demography of a small and isolated population of Eastern Massasauga Rattlesnakes (Sistrurus catenatus) threatened by vegetation succession. Journal of Herpetology, 50, 534–540. https://doi.org/10.1670/16121

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika, 52, 225–247. https://doi.org/10.1093/biomet/52.1.225

Jones, P. C., King, R. B., Bailey, R. L., Bieser, N. D., Bissell, K., Campa, H., ... Yagi, A. (2012). Range-wide analysis of eastern massasauga survivorship. Journal of Wildlife Management, 76, 1576–1586. https://doi.org/10.1002/jwmg.418

Jones, P. C., King, R. B., Stanford, K. M., Lawson, T. D., & Thomas, M. (2009). Frequent consumption and rapid digestion of prey by the Lake Erie Watersnake with implications for an invasive prey species. Copeia, 2009, 437–445. https://doi.org/10.1643/CH-08-119

Jones, P. C., King, R. B., & Sutton, S. (2017). Demographic analysis of imperiled Eastern Massasaugas (Sistrurus catenatus catenatus). Journal of Herpetology, 51, 383–387. https://doi.org/10.1670/15-058

King, R. B. (1986). Population ecology of the Lake Erie water snake, Nerodia sipedon insularum. Copeia, 1986, 757–772. https://doi.org/10.2307/1444959

King, R. B. (1993). Color-pattern variation in Lake Erie Water Snakes: Prediction and measurement of natural selection. Evolution, 47, 1819–1833. https://doi.org/10.1111/1558-5646.1993.tb01273.x

King, R. B., & Lawson, R. (1997). Microevolution in island water snakes. BioScience, 47, 279–286. https://doi.org/10.2307/1313189

King, R. B., Queral-Regil, A., & Stanford, K. M. (2006). Population size and recovery criteria of the threatened Lake Erie watersnake: Integrating multiple methods of population estimation. Herpetological Monographs, 20, 83–104. https://doi.org/10.1655/0733-1347(2007)20[83:PSARCO]2.0.CO;2

King, R. B., Ray, J. M., & Stanford, K. M. (2006). Gorging on gobies: Beneficial effects of alien prey on a threatened vertebrate. Canadian Journal of Zoology-Revue Canadienne De Zoologie, 84, 108–115. https://doi.org/10.1139/05-205

King, R. B., Stanford, K. M., Jones, P. C., & Bekker, K. (2016). Size matters: Individual variation in ectotherm growth and asymptotic size. PLoS One, 11, e0146299. https://doi.org/10.1371/journal.pone.0146299

Kingsolver, J. G., & Weatherhead, P. J. (2005). Phenotypic effects on survival of neonatal northern watersnakes Nerodia sipedon. Journal of Animal Ecology, 74, 259–265. https://doi.org/10.1111/j.1365-2656.2005.00919.x

Koons, D. N., Birkhead, R. D., Boback, S. M., Williams, M. I., & Greene, M. P. (2009). The effect of body size on cottonmouth (Agkistrodon piscivorus) survival, recapture probability, and behavior in an Alabama swamp. Herpetological Conservation and Biology, 4, 221–235.

Korfan, N. M., Newmark, W. D., & Kauffman, M. J. (2012). Long-term demograhic consequences of habitat fragmentation to a tropical understory bird community. Ecology, 93, 2548–2559. https://doi.org/10.1890/11-1345.1

Krebs, C. J. (1998). Ecological methodology. San Francisco, CA: Benjamin Cummings.
Seigel, R. A. (1986). The physiology/life-history nexus. Trends in Ecology & Evolution, 17, 462–468. https://doi.org/10.1016/S0169-5347(02)2578-8

Riedle, J. D. (2014). Demography of an urban population of ring-necked snakes (Diadophis punctatus) in Missouri. Herpetological Conservation and Biology, 9, 278–284.

Roe, J. H., Attum, O., & Kingsbury, B. A. (2013). Vital rates and population demographics in declining and stable watersnake populations. Herpetological Conservation and Biology, 8, 591–601.

Roff, D. A. (1992). Evolution of life histories: Theory and analysis. New York, HW: Chapman and Hall.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., … Colli, G. R. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. Nature Ecology & Evolution, 1, 1677–1682. https://doi.org/10.1038/s41559-017-0332-2

Rose, F. L., Simpson, T. R., Ott, J. R., & Manning, R. W. (2010). Use of space by western cottontooths (Agkistrodon piscivorus) inhabiting a variable-flow stream. Southwestern Naturalist, 55, 160–166. https://doi.org/10.1894/GC-202.1

Rose, F. L., Simpson, T. R., Ott, J. R., Manning, R. W., & Martin, J. (2010). Survival of western cottontooths (Agkistrodon piscivorus leucostoma) in a pulsing environment. Southwestern Naturalist, 55, 11–15. https://doi.org/10.1894/WL-28.1

Rossman, D. A., Ford, N. B., & Seigel, R. A. (1996). The garter snakes evolution and ecology. Norman, OK: University of Oklahoma Press.

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Bein, C., de Buhr, H., Frack, C., … Vaupel, J. W. (2016). COMPADRE: A global data base of animal demography. Journal of Animal Ecology, 85, 371–384. https://doi.org/10.1111/1365-2656.12482

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., … Vaupel, J. W. (2015). The COMPADRE Plant Matrix Database: An open online repository for plant demography. Journal of Ecology, 103, 202–218. https://doi.org/10.1111/1365-2435.12334

Seamans, M. E., & Gutierrez, R. J. (2007). Habitat selection in a changing environment: The relationship between habitat alteration and spotted owl territory occupancy and breeding dispersal. Condor, 109, 566–576. https://doi.org/10.1650/8352.1

Seber, G. A. F. (1965). A note on the multiple recapture census. Biometrika, 52, 249–259. https://doi.org/10.1093/biomet/52.1-2.249

Seigel, R. A. (1986). Ecology and conservation of an endangered rattlesnake, Sistrurus catenatus, in Missouri, USA. Biological Conservation, 35, 333–346. https://doi.org/10.1016/0006-3207(86)90093-5

Sewell, D., Baker, J. M. R., & Griffiths, R. A. (2015). Population dynamics of grass snakes (Natrix natrix) at a site restored for amphibian reintroduction. Herpetological Journal, 25, 155–161.

Shine, R. (1977). Reproduction in Australian elapid snakes 2. Female reproductive-cycles. Australian Journal of Zoology, 25, 655–666. https://doi.org/10.1071/ZO9770655

Shine, R. (1984). Reproductive-biology and food-habits of the Australian elapid snakes of the genus Cryptopsis. Journal of Herpetology, 18, 33–39. https://doi.org/10.2307/1563669

Shine, R., Brischoux, F., & Pile, A. J. (2010). A seasnake’s colour affects its susceptibility to algal fouling. Proceedings of the Royal Society B-Biological Sciences, 277, 2459–2464. https://doi.org/10.1098/rspb.2010.0255

Shine, R., Shire, T., & Shine, B. (2003). Intraspecific habitat partitioning by the sea snake Emydocephalus annulatus (Serpentes, Hydrophiidae): The effects of sex, body size, and colour pattern. Biological Journal of the Linnean Society, 80, 1–10. https://doi.org/10.1046/j.1095-8312.2003.00213.x

Shine, R., Sun, L. X., Kearney, M., & Fitzgerald, M. (2002). Thermal correlates of foraging-site selection by Chinese pit-vipers (Gloydius shedoensis, Viperidae). Journal of Thermal Biology, 27, 405–412. https://doi.org/10.1006/jtbi.2002.0506

Sperry, J. H., & Weatherhead, P. J. (2008). Pre-mediated effects of drought on condition and survival of a terrestrial snake. Ecology, 89, 2770–2776. https://doi.org/10.1890/07-2017.1

Sperry, J. H., & Weatherhead, P. J. (2009). Sex differences in behavior associated with sex-biased mortality in an oviparous snake species. Oikos, 118, 627–633. https://doi.org/10.1111/j.1600-0706.2008.17404.x

Stanford, K. M. (2012). Spatial and temporal variation in demographic parameters of the Lake Erie Watersnake (Nerodia sipedon insularum). PhD dissertation. Northern Illinois University, DeKalb, IL.

Stanford, K. M., & King, R. B. (2004). Growth, survival, and reproduction in a Northern Illinois population of the plains gartersnake, Thamnophis radix. Copeia, 2004, 465–478. https://doi.org/10.1643/CH-03-212R

Stanford, K. M., King, R. B., & Wynn, D. (2010). Summer and winter spatial habitat use by the Lake Erie Watersnake. Journal of Fish and Wildlife Management, 1, 122–130. https://doi.org/10.3996/052010-JFWM-013

Stearns, S. C. (1992). The evolution of life histories. London, UK: Oxford University Press.

Ujvari, B., Brown, G., Shine, R., & Madsen, T. (2016). Floods and famine: Climate-induced collapse of a tropical predator-prey community. Functional Ecology, 30, 453–458. https://doi.org/10.1111/1365-2435.12505

U.S. Fish and Wildlife Service (1999). Endangered and threatened wild-life and plants; threatened status for Lake Erie water snakes (Nerodia sipedon insularum) on the offshore islands of western Lake Erie. Federal Register, 64, 47126–47134.

U.S. Fish and Wildlife Service (2003). Lake Erie Watersnake (Nerodia sipedon insularum) recovery plan. Retrieved from https://www.fws.gov/midwest/endangered/reptiles/pdf/lews-fnl-rpla-sm.pdf

U.S. Fish and Wildlife Service (2011). Endangered and threatened wild-life and plants; removal of the Lake Erie Watersnake (Nerodia sipedon insularum) from the Federal list of endangered and threatened wild-life. Federal Register, 76, 50680–50702.

Waldron, J. L., Welch, S. M., Bennett, S. H., Kalinowsky, W. G., & Mousseau, T. A. (2013). Life history constraints contribute to the vulnerability of a declining North American rattlesnake. Biological Conservation, 159, 530–538. https://doi.org/10.1016/j.biocon.2012.11.021

Weatherhead, P. J., Barry, F. E., Brown, G. P., & Forbes, M. R. L. (1995). Sex-ratios, mating-behavior and sexual size dimorphism of the northern water snake, Nerodia sipedon. Behavioral Ecology and Sociobiology, 36, 301–311. https://doi.org/10.1007/BF00167791

Webb, J. K., Brook, B. W., & Shine, R. (2002). What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. Ecological Research, 17, 59–67. https://doi.org/10.1046/j.1440-1703.2002.00463.x

Webb, J. K., Christian, K. A., & Fisher, P. (2002). Fast growth and early maturation in a viviparous sit-and-wait predator, the northern death adder (Acanthophis paeleon), from tropical Australia. Journal of Herpetology, 36, 505–509. https://doi.org/10.1670/0022-1511(2002)036[0505:FGAEMI]2.0.CO;2

Webb, J. K., & Shine, R. (2008). Differential effects of an intense wildfire on survival of sympatric snakes. Journal of Wildlife Management, 72, 1394–1398. https://doi.org/10.2193/2007-515

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. Bird Study, 46, 120–139. https://doi.org/10.1080/0006365990477239
Whiting, M. J., Dixon, J. R., Greene, B. D., Mueller, J. M., Thornton, O. W., Hatfield, J. S., ... Hines, J. E. (2008). Population dynamics of the Concho Water Snake in rivers and reservoirs. *Copeia*, 2008, 438–445. https://doi.org/10.1643/CE-06-271

Wiersma, P., Muñoz-Garcia, A., Walker, A., & Williams, J. B. (2007). Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences*, 104, 9340–9345. https://doi.org/10.1073/pnas.0702212104

Williams, K. E., Hodges, K. E., & Bishop, C. A. (2014). Phenology and demography of great basin gophersnakes (*Pituophis catenifer deserticolus*) at the northern edge of their range. *Herpetological Conservation and Biology*, 9, 246–256.

Willson, J. D., & Winne, C. T. (2016). Evaluating the functional importance of secretive species: A case study of aquatic snake predators in isolated wetlands. *Journal of Zoology*, 298, 266–273. https://doi.org/10.1111/jzo.12311

Willson, J. D., Winne, C. T., & Todd, B. D. (2011). Ecological and methodological factors affecting detectability and population estimation in elusive species. *Journal of Wildlife Management*, 75, 36–45. https://doi.org/10.1002/jwmg.317

Winemiller, K. O., Fitzgerald, D. B., Bower, L. M., & Pianka, E. R. (2015). Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, 18, 737–751. https://doi.org/10.1111/ele.12462

Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196–2218. https://doi.org/10.1139/f92-242

Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 872–885. https://doi.org/10.1139/f05-040

Winne, C. T., Willson, J. D., & Gibbons, J. W. (2006). Income breeding allows an aquatic snake *Seminatrix pygaea* to reproduce normally following prolonged drought-induced aestivation. *Journal of Animal Ecology*, 75, 1352–1360. https://doi.org/10.1111/j.1365-2656.2006.01159.x

Wylie, G. D., Casazza, M. L., Gregory, C. J., & Halstead, B. J. (2010). Abundance and sexual size dimorphism of the Giant Gartersnake (*Thamnophis gigas*) in the Sacramento Valley of California. *Journal of Herpetology*, 44, 94–103. https://doi.org/10.1670/08-337.1

Zuffi, M. A. L., Fornasiero, S., & Bonnet, X. (2007). Geographic variation in reproductive output of female European whip snakes (*Hierophis viridiflavus*). *Herpetological Journal*, 17, 219–224.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

---

**How to cite this article**: King RB, Stanford KM, Jones PC. Sunning themselves in heaps, knots, and snarls: The extraordinary abundance and demography of island watersnakes. *Ecol Evol*. 2018;00:1–22. [https://doi.org/10.1002/ece3.4191](https://doi.org/10.1002/ece3.4191)