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Trapping Efficiency, Demography, and Density of an Introduced Population of Northern Watersnakes, *Nerodia sipedon*, in California

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Abstract.—Northern Watersnakes, *Nerodia sipedon*, have been introduced into California's Central Valley and pose an important new challenge for the management of biodiversity in the state's already greatly distressed freshwater ecosystems. Nonnative watersnakes will likely compete with federally threatened Giant Gartersnakes, *Thamnophis gigas*, and prey on native amphibians and fish, including young salmonids, many of which are imperiled. We used three types of aquatic funnel traps and three different methods to estimate the abundance and density of *N. sipedon* in a small wetland in Roseville, California. Capture rates did not differ significantly among the three trap types but snakes captured in large box funnel traps were nearly 300 mm longer on average than those captured in minnow traps. Our estimates of the abundance of *N. sipedon* in our 2-ha trapping area were similar for the mark–recapture model, Leslie depletion curve, and the actual number of snakes removed over 57 days (112.4–119 individuals; approximately 56.2 snakes/ha). Extrapolating to the entire 6.2-ha aquatic area, the population likely numbered approximately 348 individuals. Several females were gravid, demonstrating successful reproduction by this species outside its native range. We caught more small *N. sipedon* compared with studies in its native range. This may be due to a sampling bias in our trapping methods but more likely reflects a population growing rapidly from a few initial founders with relatively fewer large adults. We recommend immediate action to prevent the spread and broader establishment of *N. sipedon* across the Central Valley of California.

Invasive species may pose one of the greatest threats to biodiversity and native communities globally (Wilcove et al., 1998; Clavero and Garcia-Berthou, 2005). Introduced species can disrupt food webs via their interactions with native competitors, prey, and predators (Case and Bolger, 1991; Vander Zanden et al., 1999). Although invasive species are taxonomically diverse (Lowe et al., 2000), many reptiles and amphibians have proven successful invaders (Kraus, 2009). Two invasive snakes in particular have received much media and scientific attention because of their high population densities in nonnative habitats and their subsequent effects on native fauna. The Brown Tree Snake (*Boiga irregularis*), native to Australia and New Guinea, now reaches high densities on Guam and has had a devastating effect on the island's native birds and lizards (Savidge, 1987; Rodda and Fritts, 1992; Rodda et al., 1997). More recently, the Burmese Python (*Python molurus bivittatus*) has become established widely in the Everglades of southern Florida, where its increasing abundance has been linked to severe declines of mammal populations (Holbrook and Chesnes, 2011; Dorcas et al., 2012). These studies illustrate the potential impacts of snake introductions and highlight the need to prevent the establishment and spread of nonnative snakes in the future.

Studying the population biology of invasive species can lend insight into the invasion process and guide management and eradication efforts (Sakai et al., 2001; Willson et al., 2011a). For example, estimates of vital rates and other demographic data can reveal whether a population is growing rapidly or in a lag period that precedes broader establishment and population growth (Crooks and Soulé, 1999), can identify possible introduction scenarios (Willson et al., 2011a), and can be used to target the removal of life stages that have the greatest contribution to population growth (Govindarajulu et al., 2005). The need for detailed population data can present a problem for snakes because it can be difficult to obtain precise estimates of abundance, fecundity, and survival using mark–recapture efforts, due in part to their low detectability (Parker and Plummer, 1987; Willson et al., 2011b). Nevertheless, recent studies have shown that intensive and coordinated trapping can raise capture and recapture rates enough to robustly estimate abundance and survival (Willson et al., 2011b).

North American watersnakes of the genus *Nerodia* are native to eastern North America and have not occurred west of the continental divide historically (Gibbons and Dorcas, 2004). Instead, garter snakes (genus *Thamnophis*) have radiated along the western coast of North America to fill semiaquatic niches similar to those occupied by *Nerodia* species elsewhere in North America (Rossman et al., 1996). Recently, at least two species of *Nerodia* have been introduced into western environments outside of their native range. For example, the Banded Watersnake, *N. fasciata*, has been found in Los Angeles County, California since at least 1976 (Bury and Luckenbach, 1976; Fuller and Trevett, 2006) and in the Central Valley in Sacramento County, California since at least 1992 (Balfour and Stitt, 2002). Additionally, the Northern Watersnake, *N. sipedon*, has been introduced to California's Placer County in the Central Valley where it was first documented in 2007 (Balfour et al., 2007). *Nerodia sipedon* fills a niche superficially similar to that of the Giant Gartersnake, *Thamnophis gigas*, a species endemic to the Central Valley and listed as threatened under both the United States Endangered Species Act and California's similar state legislation. Both species inhabit emergent wetlands, are aquatic foragers, and prey primarily on amphibians and fish (Rossman et al., 1996; Gibbons and Dorcas, 2004). In addition to competitive effects on native species, introduced watersnakes could present a novel threat to California's many endangered fish and amphibians as predators of these aquatic species. Thus, there is growing concern that the wider establishment of *N. sipedon* or other closely related *Nerodia* species may represent an important new threat to California's native species. In light of the possible negative impact this species may have on California's wetland communities, it is vital to collect basic population-level information to direct management and eradication efforts.

Here, we report the results of a short-term study of an introduced population of *N. sipedon* in California's Central Valley in the city of Roseville. We address several questions covering two main topics: 1) the abundance/density and demography of this introduced population and 2) the effectiveness of various different trap types in capturing these snakes.

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We compare three different estimates or counts of abundance of this population and present information on the demography and reproductive biology. We also compare three different types of aquatic traps that may vary in their capture efficiencies and in the size of individuals captured. The results of this study will aid risk assessment and future eradication or management efforts aimed at this and closely related species.

Materials and Methods

Data Collection.—We sampled *N. sipedon* at a wetland in Roseville, California. The wetland lies in a sprawling residential area along a greenway adjacent to a suburban high school. *Nerodia sipedon* were first reported at the wetland in 2007 (Balfour et al., 2007). The wetland is fed by a small stream that drains a golf course lying approximately 800 m upstream. The stream flows an additional 400 m beyond the wetland study site before it disappears beneath a roadway overpass from which it did not emerge on the other side during the 2011 study period. *Nerodia sipedon* is not yet known to occur elsewhere in California. However, our study site lies just 2.7 km from Dry Creek, a tributary of the much larger Sacramento River. There are also multiple water bodies found within 2 km, including drainage ditches, lakes, and small streams. Finally, our study site is approximately 13 km from the eastern edge of the Natomas Basin, where the closest occurrence of threatened *T. gigas* is reported.

From 15 July to 10 September 2011, we deployed 156 aquatic minnow traps in aquatic vegetation along the periphery of the wetland, covering approximately 2 ha of the total 6.2-ha wetland. Minnow traps have been used previously to great effect in other studies of *Nerodia* (Willson et al., 2005, 2011b). Half of the minnow traps were plastic (model 700, Gator Buckets, New Market, Indiana), and half were made of a metal mesh (Gee's minnow trap, Tackle Factory, Fillmore, New York). Both the plastic and metal traps had a funnel opening initially 2.5 cm wide, and we widened the openings of the metal traps to 3.0–3.5-cm diameter to allow capture of larger snakes (Willson et al., 2008). We paired the plastic and metal minnow traps such that each plastic trap had a metal trap located ~1 m adjacent to it. This was done to minimize habitat differences between plastic and metal traps and to allow comparison of capture efficiency and characteristics of captured snakes between trap types. We also used seven hand-built, large box funnel traps (BFTs) with 3-m aquatic drift fences, designed originally to capture amphibian larvae (Mushet et al., 1997). These traps had a larger, vertically slotted funnel opening that measured 3.75-cm wide (Mushet et al., 1997). All traps were checked daily between 0900 and 1500 hours for 57 days, resulting in 9,283 trap-nights. Traps were allowed to accumulate fish and amphibian larvae to serve as potential bait but any adult bullfrogs or crayfish that were captured were removed from traps each day.

We split our sampling into two periods. The first 10 days of the study represented a closed mark–recapture period wherein we marked all captured snakes with a unique code by branding ventral scales (Winne et al., 2006), and recorded their sex, snout–vent length (SVL), tail length, and mass before releasing them near their point of capture. The remainder of the study represented a removal study wherein all captured snakes were removed upon capture, returned to the laboratory, and euthanized via overdose of an inhalant gas isofluorane. We recorded sex, SVL, mass, and tail length of these snakes in the laboratory. In the laboratory, we dissected all euthanized snakes to record their reproductive status and, in the case of females, the number of fertilized embryos and unfertilized ova present to determine fecundity.

Statistical Analyses.—We estimated population size via three methods. In program MARK (White and Burnham, 1999), we used the closed-captures model to estimate abundance from our 10-day mark–recapture period. We defined 4 a priori candidate models to test for time dependence in capture (p) and recapture (c) probabilities and a behavioral response to traps ($p \neq c$). Our models included: 1) constant and equal p and c; 2) time-varying but equal p and c; 3) constant p and time-varying c; and 4) constant but unequal p and c. We identified the model that best fit the data using Akaike's information criterion adjusted for small sample size (AIC_c; Burnham and Anderson, 2002) and we used model averaging to incorporate model selection uncertainty into our estimates of N, p, and c.

As our second estimation method, we used the Leslie depletion method to examine changes in removal rates over the complete 57-day sampling period (Leslie and Davis, 1939). Using the Leslie depletion method, individuals are removed from the population during sampling. As the catch per unit effort (CPUE; captures per trap-night) declines with the cumulative number of individuals caught, a regression can be used to estimate initial population size. We incorporated data from the mark–recapture period into our Leslie depletion curve by treating snakes captured multiple times as if they had been removed from the population on first capture. We used the "FSA" package in R version 2.12.1 (R Development Core Team, 2011) to calculate the estimate of population size from the depletion method. Our third and final estimate of population size was simply a count of the total number of individual snakes captured during the study, including a separate tally that included hand captures.

For size comparisons among groups (i.e., between sexes or among the three trap types), we log-transformed size variables using the natural logarithm to better meet assumptions of normality. We used Levene's test (Levene, 1960) to test the assumption of homogeneity of variances among groups. If variances were homogenous, we used standard one-way analysis of variance to test for differences in group means, with the exception of using an analysis of covariance to compare relative tail lengths between the sexes. If variances were not homogeneous, we used Welch's one-way test for differences among group means because it does not assume equal variances between the groups (Welch, 1951). If a snake was caught multiple times, we used only its first capture to compare sizes and sex ratios between trap types. We used chi-square contingency table analysis to test for differences in capture rate among trap types. We also tesed for sex-biases among trap types and deviations from a 1 : 1 sex ratio using contingency tables.

Results

We captured 56 snakes a total of 75 times during the initial 10-day mark–recapture period. One hundred thirteen snakes were caught in traps over the entire 57 days of the study. Of these 113 snakes, 104 were removed from the population and nine were marked during the initial 10-day period but were not recaptured or seen again. The number of snakes captured (standardized by trapping effort) decreased over time as snakes were removed from the population (Fig. 1) until several consecutive days of trapping resulted in no captures. Including hand captures, we removed 119 individual *N. sipedon* from the wetland.

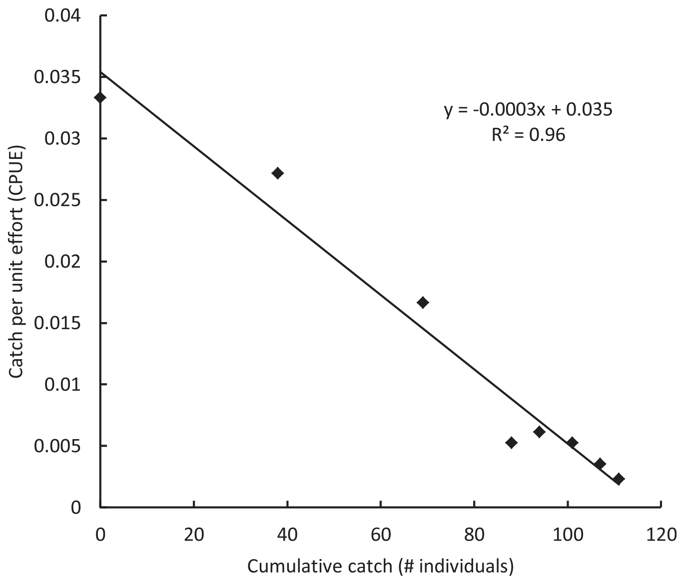

FIG. 1. Leslie depletion curve depicting weekly catch of *Nerodia sipedon* per unit effort (CPUE) and cumulative catch of *Nerodia sipedon*.

Population Estimates.—The most highly supported mark–recapture model had equal and time-varying *p* and *c* but did not significantly outperform the second-best model (ΔAIC_c 0.30). The second-best model had constant and equal capture and recapture probabilities (Table 1). The model-averaged estimate for *N* was 112.4 snakes (95% confidence interval [CI] 72.3–251.9), from which we estimate the density of the population to be approximately 56.2 snakes/ha. The model-averaged estimates of *p* (0.067) and *c* (0.068) indicated nearly equal capture and recapture probabilities.

There was a high degree of congruence between abundance estimates from mark–recapture and the Leslie depletion method. Regression of daily CPUE on cumulative catch estimated *N* as 114.6 (95% CI 104.7–124.6), and regression of weekly CPUE estimated *N* as 117.2 (95% CI 107.1–127.4; Fig. 1). Weekly CPUE had a much stronger relationship with cumulative catch ($r^2 = 0.961$) than did daily CPUE ($r^2 = 0.569$), likely because weekly grouping of CPUE obscured some of the day-to-day variation in snake captures. Both weekly and daily CPUE declined over time as the number of snakes removed from the population increased, indicating that our removal efforts had the intended effect of reducing the population.

Trap Comparisons.—Over the 57 days of trapping, we made 86 total captures of *N. sipedon* in plastic minnow traps, 76 in metal minnow traps, and 5 in BFTs; these numbers include repeated captures of some individuals. The captures adjusted by trapping effort did not vary significantly from random expectation over the entire study period ($\chi^2 = 1.33$, $P = 0.514$) or during the 10-day mark–recapture period ($\chi^2 = 1.24$, $P = 0.537$). During the 10-day mark–recapture period, before snakes were removed from the population, CPUE was 19.5 trap-nights/snake for plastic minnow traps, 23.6 trap-nights/snake for metal minnow traps, and 35 trap-nights/snake for box funnel traps.

Metal minnow traps caught longer (mean = 424.3 mm SVL vs. 358.4 mm SVL; $F_{1,108} = 7.81$, $P = 0.006$) and heavier (106.4 g vs. 52.7 g; $F_{1,108} = 7.49$, $P = 0.007$) snakes than did plastic traps. The maximum SVL (890 mm) and mass (775 g) of snakes caught in BFTs were greater than that of metal (max. SVL = 724 mm, mass = 503 g) and plastic (max. SVL = 680 mm, mass = 287 g) minnow traps, but too few BFTs were used to allow statistical comparisons among mean sizes of captured snakes (Fig. 2). Plastic minnow traps caught the smallest snake (minimum SVL = 194 mm, mass = 8.4 g), followed by metal traps (minimum SVL = 220 mm, mass = 10.8 g).

TABLE 1. Model results for *N. sipedon* sampled at Roseville, California during July 2011. *p* = capture probability, *c* = recapture probability, *t* = time varying, "." = constant, ΔAIC_c, Akaike information criterion adjusted for small sample size.

	Description				
Model	*p*	*c*	No. parameters	ΔAIC_c	Wt.
1	(*t*)	(*t*)=*p*	11	–	0.44
2	(.)	(.)=*p*	2	0.30	0.38
3	(.)	(.)	3	2.22	0.14
4	(.)	(*t*)	11	4.67	0.04

There was no significant sex bias in captures between minnow trap types; metal traps captured 22 males and 25 females and plastic traps captured 30 males and 33 females ($\chi^2 = 0.007$, $P = 0.933$). All three individuals captured in BFTs were large females.

Population Characteristics.—Fifty-four male and 65 female snakes were captured during the study , a ratio that did not differ significantly from 1 : 1 ($\chi^2 = 0.\ 1.017$, $P = 0.3132$). Females were significantly longer than males (Fig. 3; $F_{1,114.3} = 7.18$, $P = 0.0084$) and significantly heavier ($F_{1,112.1} = 5.68$, $P = 0.019$). There was a significant interaction between SVL and sex such that, above 350 mm SVL, males had relatively longer tails than females but tail lengths were similar at sizes below 350 mm SVL ($F_{1,109} = 21.8$, $P < 0.001$).

Reproductive Status.—Six of 56 female snakes that were dissected were gravid and one female captured 15 August appeared to have just given birth because of the presence of recent embryo attachment scars. Gravid females had on average 20.5 embryos (range 2–48). Nine females (16.1%) were reproductively mature judging by physiological development of the ova during necropsies, with the smallest reproductively mature female measuring 594 mm SVL. Only three of the mature females were not gravid or did not appear to have given birth in the preceding weeks. On the basis of the presence of sperm in the vas deferens, 23.4% of male snakes were sexually mature, and the smallest male with sperm in the vas deferens was 347 mm SVL.

Additional Results.—No specific effort was made to document the diet of captured snakes because of possible bias introduced by prey accumulation in minnow traps. However, some snakes that clearly contained prey were manually palpated to force regurgitation and a least a few did so voluntarily upon handling. Stomach contents regurgitated by snakes included nonnative American Bullfrogs (*Lithobates catesbeianus*) and native Pacific Chorus Frogs (*Pseudacris regilla*). Nonnative Mosquitofish (*Gambusia affinis*) were abundant in traps and presumably were also common prey for *N. sipedon* but no individuals regurgitated these fish.

Snakes moved on average a distance of 21.4 m between captures. The maximum distance moved by a snake between captures was 70.8 m over 22 days and one individual moved 46.6 m between captures on consecutive days. Because our study site measured only 200 m × 100 m, it is likely that snakes moved throughout the area on a regular basis.

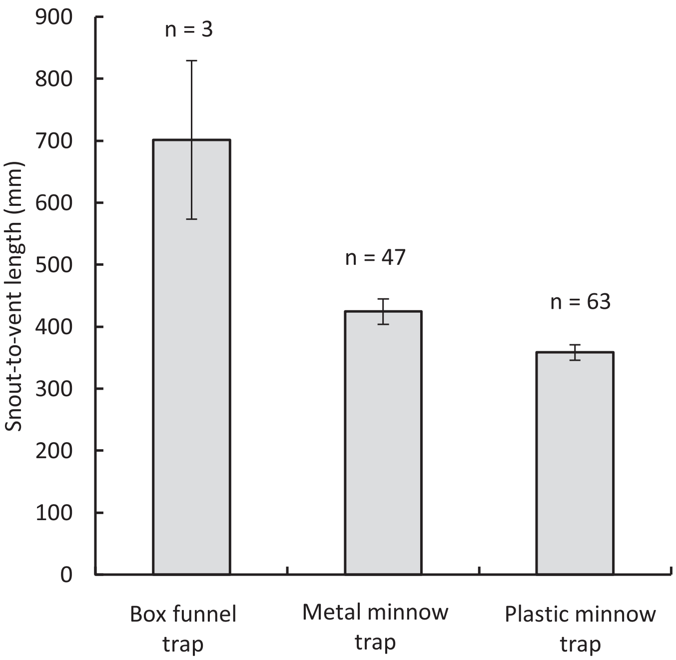

FIG. 2. Mean snout-to-vent length (SVL) of *Nerodia sipedon* captured for each trap type. Sample sizes indicate number of individuals captured and exclude repeat captures of the same individual. Error bars represent ±1 standard error.

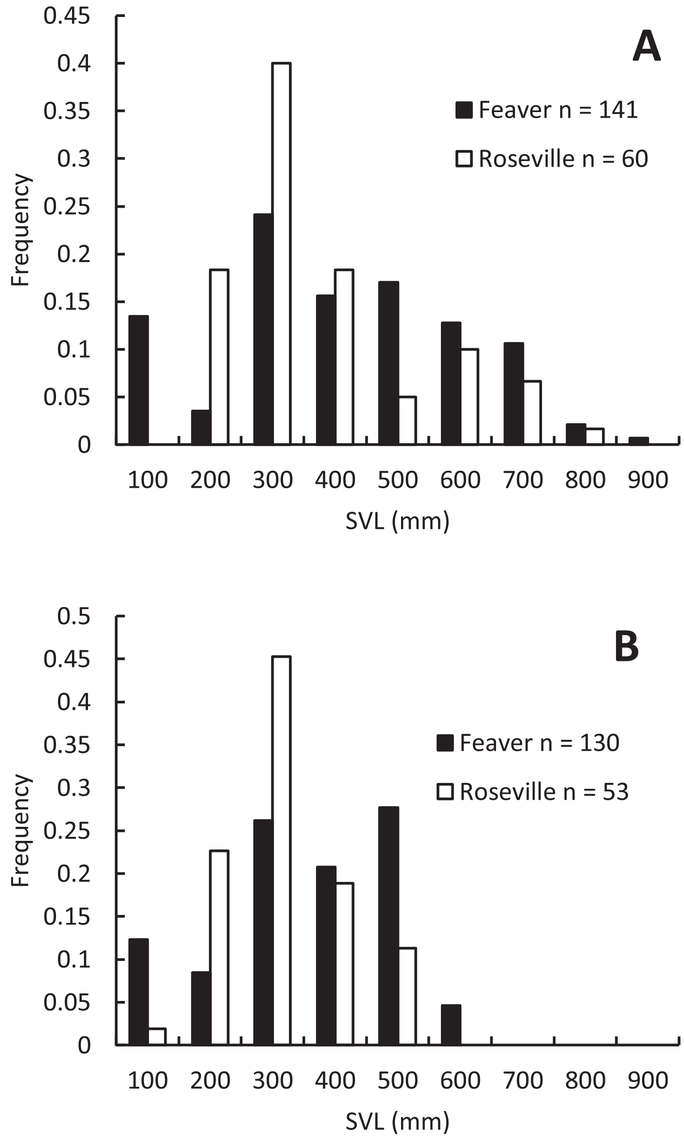

FIG. 3. Comparison of size frequencies of (A) female and (B) male *Nerodia sipedon* from the present study and that of Feaver (1977). Sample sizes are indicated in the legend.

Only six of 119 snakes (two males, four females) had stubbed or injured tails, representing 5% of snakes captured. Of those snakes greater than 300 mm SVL, 6.5% had stubbed tails.

In addition to *N. sipedon*, we made 13 captures of *T. sirtalis* and 1 capture of *T. elegans* in our traps. These snakes were not marked individually; therefore abundances were not estimated for these species.

DISCUSSION

Our study demonstrates that *N. sipedon* is abundant, actively reproducing, and well established in at least one area of suitable habitat in the Central Valley of California. Using aquatic traps, we were able to obtain relatively high capture/recapture rates for this species and to deplete the trapped portion of the population via removal of snakes after capture. The congruence between our abundance estimates using mark–recapture and depletion models and the actual number of snakes we removed demonstrates that both mark–recapture and the Leslie depletion method can provide an accurate measure of abundance for this species. It is particularly noteworthy that if we had concluded the study after only the 10-day mark–recapture period, our effort would have been sufficient to estimate the size of the population in the area for which we trapped. However, the additional 47 days of trapping and the use of the Leslie depletion method yielded much narrower CIs that may be useful when trying to assess the range of possible population sizes. If we assume that snake density is uniform across the 2 ha that we sampled and the adjacent unsampled aquatic habitat, the estimate of total population size would be approximately 348 snakes across the entire 6.2-ha area.

The density of 56.2 snakes/ha for *N. sipedon* derived from our mark–recapture estimate is greater than the only comparable estimate for this species in its native range. Brown and Weatherhead (1999a) reported densities of 25.4 snakes/ha and 33.4 snakes/ha for *N. sipedon* at two wetlands in Ontario. Other studies are not directly comparable with our results because they are based on the numbers of snakes along linear stretches of shoreline (90.5 adults/km; King, 1986) or because they do not report the area surveyed (e.g., 6,300 killed in 1 year at a fish hatchery; Bauman and Metter, 1975). The high density of snakes in the introduced population in the present study may be a reflection of the abundant prey at this site. We captured large numbers of known prey for *N. sipedon* in our traps throughout the summer, including adult and larval bullfrogs (*L. catesbeianus*), small Mosquitofish (*Gambusia affinis*), sunfish (*Lepomis* spp.), and catfish (Ictaluridae). Although we caught native *T. sirtalis* in our traps and they appeared to be relatively common, it is possible that sizeable prey populations prevented competition for resources. *Nerodia sipedon* may also be more abundant in this introduced population because they are subjected to less mortality from predation: the proportion of snakes >300 mm SVL with stub tails in the present study (6.5%) was much lower than that reported in the literature for this species. For example, King (1986) reported 12.8% of adult *N. sipedon insularum* in Ohio had stubbed tails, whereas populations of *N. sipedon* from Kansas (29%; Beatson, 1976) and South Carolina (20%; Kaufman and Gibbons, 1975) had even higher rates of tail loss. It is likely that predators are similar in both their native and invaded ranges (raccoons, opossums, wading birds, raptors, large bullfrogs), but these predators may be reduced in the invaded range of *N. sipedon*, thus allowing greater densities of snakes.

The mean litter size (20.5 offspring/female) of the introduced Roseville population is similar to that reported for various populations in the native range of *N. sipedon*. King (1986) reported a mean litter size of 22.9 individuals (9–50) for *N. s. insularum*; Feaver (1977) found a mean of 11.8 individuals (4–24) for *N. sipedon sipedon* in Michigan; Beatson (1976) reported a mean litter size of 18.8 individuals for *N. s. sipedon* in Kansas; Prosser et al. (2002) reported a mean litter size of 18 individuals (5–28) in Ontario; and the number of offspring per female ranged from 15 to 63 in Missouri (Bauman and Metter, 1977). The minimum size of female snakes at maturity (594 mm SVL) was similar to that reported for *N. s. insularum* (590 mm; King, 1986) and for *N. sipedon* in Ontario (633 mm; Prosser et al., 2002), but larger than that reported for *N. s. sipedon* in Michigan (475 mm; Feaver, 1977). Our data do not suggest that females in the introduced population are able to produce larger litters, or are reaching sexual maturity at smaller sizes than females in the native range. However, a larger sample of gravid females would help elucidate the reproductive capacity of this species in its nonnative habitat. The smallest sexually mature male (347 mm SVL) was similar to the minimum size at maturity for *N. s. sipedon* in Michigan (375 mm; Feaver, 1977), and slightly smaller than the minimum size reported in Ontario (433 mm; Prosser et al., 2002) and for *N. s. insularum* in Ohio (430 mm; King, 1986). Although snakes of both sexes in the Roseville, California population may be reaching sexual maturity at sizes similar to those in their native range, we cannot rule out the possibility that snakes are able to grow more quickly and reach a reproductive size at a younger age in the introduced population.

There is one primary shortcoming related to using aquatic minnow traps to remove *N. sipedon* from wetlands. Specifically, we may have undersampled a portion of the population. Individuals may have been present in the study area but essentially uncatchable during the sampling period owing to behavioral variation (i.e., individuals not present at the study site and therefore not available to be captured [e.g., temporary emigration] or individual heterogeneity), or because they were too large or too small for our traps. These factors could cause our estimators to be overly conservative, and, thus, our estimates likely represent a minimum population size and density for the study area. The identification of temporary emigration would require a different temporal sampling regime, such as the robust design (Willson et al., 2011b).

The failure to capture the largest and smallest snakes, especially neonates, in aquatic minnow traps has been documented in other studies of aquatic snakes (Willson et al., 2008). Neonate *N. sipedon* range from 125 to 210 mm SVL (Bauman and Metter, 1977; King, 1986) and we only captured two snakes smaller than 210 mm SVL despite trapping through August and September when parturition takes place in many populations of this species (Fig. 3). Feaver (1977) reported that slightly more than 10% of individuals in a population from its native range in Livingston County, Michigan were <200 mm SVL. Although we caught only one snake of this size in our study, a greater proportion of our captures were in smaller size classes than reported in Feaver (1977) (Fig. 3). It is possible that a population could persist despite removal efforts if neonates evade capture; neonates may even experience increased compensatory survival and growth because of the removal of larger individuals.

Conversely, the failure to remove large females may be especially costly during eradication efforts because there is a positive relationship between the number of offspring produced and maternal body size (Bauman and Metter, 1977). There are at least two possible explanations for the relative scarcity of large animals in our sample. First, it is possible that we caught relatively few large snakes because we relied heavily on minnow traps that exclude large snakes, whereas Feaver (1977) caught many snakes by hand in addition to using minnow traps. This seems unlikely to have been the sole cause of the size discrepancy between the two studies because we did capture males and females in sizes comparable with the largest individuals found in other studies of *N. sipedon* (Feaver, 1977; Brown and Weatherhead, 1999b). The largest male we captured measured 561 mm SVL and the largest female we captured measured 890 mm SVL, which approaches the asymptotic SVL calculated for male (620 mm) and female (929 mm) *N. sipedon* in a study from their native range (Brown and Weatherhead, 1999b). An alternative explanation for the size distribution of our captures is that the Roseville population of *N. sipedon* is actively growing and, thus, a majority of individuals are in younger age (and smaller size) classes.

Our three trap types were complementary in their capture efficiencies and in the sizes of snakes captured. Despite no significant difference in capture success among the three trap types, BFTs took nearly twice the effort to capture a snake than did plastic minnow traps (35 trap-nights per snake vs. 19.5). However, BFTs also caught the largest snakes by far (nearly 300 mm longer on average than those captured in metal or plastic minnow traps), and these larger snakes may comprise a smaller portion of the population and thus be captured less frequently. Our results suggest that the combination of all three trap types would be most effective in any capture efforts aimed at depleting or eradicating populations of *Nerodia*. It would also be important to consider new trap designs or the use of other methods to effectively sample and remove neonates. Alternatively, if large, reproductive snakes are captured and removed adequately, neonates should grow to a catchable size and repeated trapping and removal in successive years may succeed in extinguishing a population before neonates grow large enough to reproduce. It would also be productive to include active searches and hand captures of *N. sipedon* to remove them; this may be especially effective at removing larger individuals, particularly in the spring when these animals emerge from shared hibernacula.

The introduction and potential spread of *Nerodia* in California presents a conservation concern for many native and endemic species. Native amphibians have undergone steep declines in the Central Valley because of habitat loss and introduced fish (Fisher and Shaffer, 1996). *Nerodia sipedon* feeds on a variety of amphibians in its native range (Gibbons and Dorcas, 2004), and has recently been documented feeding on native amphibians in California (Miano et al., 2012). Predation from *N. sipedon* may place additional pressures on threatened native species such as the California Red-legged Frog (*Rana draytonii*), the Foothills Yellow-legged Frog (*Rana boylii*), and the California Tiger Salamander (*Ambystoma californiense*). Likewise, a majority of native freshwater fish in California are imperiled (Moyle et al., 2011), and many of these species could serve as prey for *N. sipedon*. Further, the Roseville population of *N. sipedon* is ~13 km from known Giant Gartersnake habitat (Wylie et al., 2010). Thus it is likely that introduced watersnakes could soon come into contact with an imperiled, native snake. Unlike the Giant Gartersnake, which is restricted to stagnant or slow-moving bodies of water with emergent vegetation (Halstead et al., 2010), *N. sipedon* is a habitat generalist capable of living in wetlands, lakes, rivers, and streams. Therefore, although over 95% of the Central Valley's wetlands have been lost (Frayer et al., 1989), *N. sipedon* may still find abundant suitable habitat in which to expand its range because of its tolerance of human-dominated environments.

Our short-term study of a population of *N. sipedon* provides a foundation for our understanding of this species in its new environment, but much work remains to be done to prevent it from becoming a widespread invasive species. Demographic data, including age- or stage-specific rates of fecundity and survival, can be used in a sensitivity analysis to identify life stages that have the greatest effect on population growth and that should therefore be targeted in eradication efforts. Additional sampling should be performed in the area surrounding the known population to determine the breadth of distribution of *N. sipedon* around this site and whether it is still localized and contained. Molecular work could be used to determine the origin of this introduced population and to clarify whether new occurrences of this species in parts of California are the result of dispersal from established populations or represent new introductions and repeated releases. Ecological niche modeling of *N. sipedon* and *N. fasciata* could provide an overview of the risk of these species becoming established more widely in nonnative habitats. The fact that most of the Central Valley is now devoid of aquatic snakes, coupled with the generalist nature of this introduced species, suggests that watersnakes could become established throughout much of this lowland area should it be climatically suitable. Most importantly, it is critical that swift action be taken to prevent this species from establishing a firm foothold in California, as quick action may be the most important factor in determining the success of eradication (Simberloff, 2003). Preventing the Northern Watersnake from joining the ranks of the Brown Tree Snake and the Burmese Python should be a priority for those concerned with the conservation of California's native communities.

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