

GARTER SNAKE POPULATION DYNAMICS FROM A 16-YEAR STUDY: CONSIDERATIONS FOR ECOLOGICAL MONITORING

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Abstract. Snakes have recently been proposed as model organisms for addressing both evolutionary and ecological questions. Because of their middle position in many food webs they may be useful indicators of trophic complexity and dynamics. However, reliable data on snake populations are rare due to the challenges of sampling these patchily distributed, cryptic, and often nocturnal species and also due to their underrepresentation in the ecological literature. Studying a diurnally active stream-associated population of garter snakes has allowed us to avoid some of these problems so that we could focus on issues of sampling design and its influence on resulting demographic models and estimates. From 1986 to 2001, we gathered data on a population of the Pacific coast aquatic garter snake (*Thamnophis atratus*) in northwestern California by conducting 3–5 surveys of the population annually. We derived estimates for sex-specific survival rates and time-dependent capture probabilities using population analysis software and examined the relationship between our calculated capture probabilities and variability in sampling effort. We also developed population size and density estimates and compared these estimates to simple count data (often used for wildlife population monitoring). Over the 16-yr period of our study, we marked 1730 snakes and had annual recapture rates ranging from 13% to 32%. The best approximating demographic model for our data demonstrated higher survival rates for females than males and showed low and annually variable capture probabilities for both. Annual population size estimates (converted to linear densities), ranged from 58 to 131 snakes/km. Mean annual field counts typically accounted for only 5–10% of the total population size estimated using capture–recapture models. We found no evidence for a changing population size throughout the study. We found a positive relationship between sampling effort and capture probabilities. We evaluate survey design options that would help us approach recommended levels of capture probabilities and thus increase the precision of our estimates, allowing derivation of more complex demographic models. Our results should be useful in the development of monitoring programs for snakes and other secretive wildlife species and provide target demographic rate values for restoration of related at-risk snake species.

Key words: capture probability; long-term study; northwestern California, USA; Pacific coast aquatic garter snake; population size; Program MARK; sampling effort; survival rate; *Thamnophis atratus*.

INTRODUCTION

Snakes have gained recent attention as potential model organisms for studying both evolutionary and ecological questions because of their unique body form (elongate body with no limbs) and their ectothermic nature (Shine and Bonnet 2000). Unfortunately, snakes have received less ecological study than other reptiles, and the studies that do exist may be underrepresented

in the literature (Seigel 1993, Bonnet et al. 2002). Snakes typically occupy middle to higher levels in ecological food webs and as such may have strong effects on web dynamics. This is especially likely to be true in lotic aquatic systems, where food chains are often relatively short with some taxa having strong and readily detectable influences (e.g., Power 1990). Understanding snake population dynamics is essential for assessing their role and influence in ecological systems. Rigorously collected demographic data can reveal important aspects of a species' ecology, provide insights into life history evolution, and are critical for detecting changes in population size. With reliable demographic models, snakes could be used as status and trend indicators in trophic dynamics, community, and ecosystem monitoring. For example, declines in numbers of garter snakes have been linked to declines in their amphibian prey (Jennings et al. 1992, Matthews et al. 2002), and snakes have been found to be useful indi-

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cators for certain environmental toxins (Stafford et al. 1976, Olendorf 1988). However, in order to use snake populations as metrics of ecological trends, we need to better understand how sampling effort and design can impact our ability to derive appropriate and precise demographic models.

Much of the work that has been done on snakes, and a variety of other species for that matter, utilizes unadjusted field counts for estimates of abundance (Thompson 2002). Capture–recapture studies give more reliable estimates of abundance that can aid in interpretation of count data (Nichols 1992, Pollock et al. 2002), as well as to provide estimates of demographic characteristics, such as survival rates. However, deriving precise estimates of population parameters for snakes has proved challenging due to difficulties in detection resulting from their patchy distributions, secretive and cryptic natures, and often nocturnal habits (Fitch 1987). In addition, there is typically substantial variation in catchability based on sex or age (e.g., Bonnet and Naulleau 1996). Though long-term data exists for a number of species (e.g., Bronikowski and Arnold 1999, Fitch 1999), studies designed to develop demographic models and especially to derive sex- and age-specific survival rates are rare (Parker and Plummer 1987, Rossman et al. 1996). The challenges of field sampling combined with the underrepresentation of snake studies in the literature hinder the development of methods that would improve demographic models and make monitoring programs and conservation strategies more ecologically relevant and effective. Our study system provided an opportunity to avoid many of the difficulties associated with sampling snakes. The population of garter snakes we studied is confined to a relatively narrow landscape feature (the stream) in which it feeds primarily on aquatic prey and is active in relatively open habitats in the daytime.

We used 16 yr of capture–recapture data from a population of the Pacific coast aquatic garter snake (*Thamnophis atratus*) to address two primary objectives: (1) to develop estimates of population density, survival rates, and capture probabilities and (2) to evaluate sampling design and assess the potential to use this species for monitoring lotic system status and trends. We developed both age-structured and non-age-structured models for estimating demographic parameters for several subsets of this population: neonates, juveniles/adults combined, females, and males. We also compared snake abundance estimates from count data and capture–recapture methods, with the goal of improving sampling designs for long-term monitoring. Our research on an aquatic snake in a relatively pristine stream system could be used as a model for evaluating the status of related species in more altered habitats and as a baseline for population restoration of declining species.



PLATE 1. Pacific aquatic garter snakes (*Thamnophis atratus*) are occasionally seen foraging from branches overhanging our study stream. Photo credit: Clara Wheeler.

METHODS AND ANALYSIS

Study area and study species

All field work was conducted at Hurdygurdy Creek in Del Norte County, California, USA (start of study reach, latitude, 41.687°, longitude, 123.911°). This stream is a large tributary to the South Fork of the Smith River ranging from 200 to 250 m in elevation. It contains typical lotic habitats such as riffles, runs, and pools and has a narrow riparian vegetation zone dominated by alders and willows. The Pacific coast aquatic garter snake (*Thamnophis atratus*; see Plate 1) ranges from southern Oregon to southern California, from sea level to 1920 m (Stebbins 2003). It has been classified in the “subfamily” *Natricinae* of the largest (and possibly paraphyletic) snake family, Colubridae. New World members of this group of snakes, which include water snakes, garter snakes, earth snakes, and crayfish snakes among others, are completely viviparous and can be terrestrial or aquatic (Pough et al. 2001). For Pacific coast aquatic garter snakes, mating may occur in spring or fall and young are born in the late summer. While most garter snakes will forage in lentic waters, Pacific coast aquatic garter snakes forage primarily in running waters on aquatic prey (see Lind and Welsh [1990, 1994] and Welsh and Lind [2000]

for foraging and prey data and further details on the study area).

Field data collection

We collected capture–recapture data on the Pacific coast aquatic garter snakes at Hurdygurdy Creek from 1986 to 2001. A 4.7-km section (the study area) of the stream was surveyed 3–5 times each year on partly sunny or sunny days during the primary activity period of the snakes (10:00–18:00 hours, May–October). These visits are hereafter called sampling periods; over the 16 yr of this study we gathered data in 58 sampling periods. Sampling was conducted by 1–3 individuals who methodically searched the stream channel and adjacent banks. In sampling periods with two or more observers, individuals searched on opposite sides of the stream, beginning at the downstream end of the 4.7-km section and proceeding upstream. In the few sampling periods with a single observer (7 of 58 sampling periods), the observer worked upstream searching along one bank in the morning and then walked downstream in the afternoon searching along the opposite bank. Three consecutive days were typically required to cover the entire study area, though surveys early in the study (1986–1988) and those with only one observer took up to 7 d. Air and water temperatures were recorded at the start and end of daily sampling. The following data were collected for each snake: date and time of capture, capture status (new or marked) and mark number, sex, age class, reproductive status (gravid and number of ova, nongravid, etc.), behavior, position and substrate, water depth, stream habitat type, distance from water, location (on a map of the stream), snout-to-vent and total lengths, mass, head diameter, and stomach contents (via forced regurgitation, prey species and size). All data were collected at the point of capture of each snake; snakes were then marked, using ventral scale clipping (Fitch 1987), and released.

Snakes were assigned age classes based on the time of year of sampling and sex-specific information on sexual maturity (i.e., analysis of cloacal smears to detect sperm presence and sizes of gravid females; A. J. Lind and H. H. Welsh, Jr., *unpublished data*). The neonate age class extended from birth (August/September) through the first “hibernation” period. Upon emergence the following spring, snakes were considered to be juveniles until reaching a snout–vent length of 358 mm for males and 510 mm for females, at which point they were considered adults.

Analysis of demographic data

Capture and recapture rate summaries and graphical presentations were used to describe patterns over time and to help interpret results of demographic modeling. Mean annual field counts were derived by averaging capture totals (regardless of whether new or a recapture) across all sampling periods within each year. These values were calculated to provide an example of

unadjusted field counts often seen in wildlife monitoring projects. These count data were then compared to annual estimates of population size derived from a Lincoln-Peterson estimate of our capture–recapture data using graphical analyses.

Our demographic models, which included only survival rate (Φ) and capture probability (p) parameters, were built following recommendations in E. Cooch’s and G. White’s Introduction to Program MARK (*available online*).³ In this approach, a general (or global) model including all parameters of interest (e.g., time, age, sex) is first tested for overall goodness-of-fit to the capture–recapture data. Then, reduced models containing a subset of parameters or in which some parameters are restricted to be equal are examined to find the model or models that exhibit optimal fit and precision. We derived capture probabilities (the probability of a marked animal that is alive at time t being encountered at time t) and annual survival rates (probability of survival from time t to time $t + 1$) for this population using the mark–recapture software Program MARK, version 3.1 (hereafter referred to as “MARK”; White and Burnham 1999). Because we anticipated low capture probabilities, we combined data from the 3–5 sample periods within each year to create annual capture histories for each individual (0 = not captured in a given year, 1 = captured in a given year), resulting in 16 capture–recapture periods. Only one of the age classes (neonates) consistently transitioned to the next age class (juvenile) within 1 yr, thus we could not easily develop age-structured models for all age classes (i.e., the juvenile age class included multiple and variable numbers of years). Consequently, our age-structured models included just two age classes for each sex: (1) neonates and (2) all others (juveniles and adults combined). This resulted in four uniquely coded groups (neonate females, neonate males, juvenile/adult females, juvenile/adult males). We examined Pacific coast aquatic garter snake survival rates and capture probabilities relative to age and sex and over time by analyzing 25 a priori Cormack-Jolly-Seber capture–recapture models (E. Cooch and G. White, see footnote 3) that were developed based on field experience and perceptions about likely sources of variation in these parameters (Table 1). We expected there to be age-specific differences in survival, but we also included some simplified models with no age structure in anticipation that low capture probabilities might lead to poor support for more complex models.

We tested for adequate fit of the most general (global) model to the data set with the MARK bootstrap goodness-of-fit test, using deviance values as follows. We examined the relative ranking of the deviance scores of our global model with regard to 500 bootstrapped data sets created using MARK (E. Cooch and G. White, see footnote 3). The deviance values from the boot-

³ <http://www.phidot.org/software/mark/docs/book/>

strapped data were also used to estimate the variance inflation factor (\hat{c}), which adjusts for the overdispersion of the data (i.e., lack of fit of the data to the underlying general model). After it was determined that the global model adequately fit the data (i.e., the global model deviance ranked 390 among 500 bootstrap deviances), we examined the candidate reduced models. Model rankings and weights were based on QAIC_c values, which included the variance adjustment ($\hat{c} = 1.07$). The QAIC_c is a modified version of the Akaike Information Criterion which ranks models based on optimization of fit and precision and accounts for differences in effective sample size and lack of fit (E. Cooch and G. White, see footnote 3). The model with the lowest QAIC_c value is considered the most parsimonious model of the candidate set (Burnham and Anderson 2002).

Population size estimates were calculated within each year (May–September) using the least biased Chapman (1951) version of the Lincoln-Peterson estimator. Because this estimate requires only two distinct periods and assumes closure (no births, deaths, immigration, emigration), we combined information from sampling periods within each year to create two periods, a marking period and a recapture period. We used only the juvenile/adult snake age class in this analysis (no neonates) to minimize violation of the closure assumption. Snakes first encountered in the marking period of a given year, even those that had originally been marked in previous years, were considered new captures. Snakes captured multiple times within either the marking or the recapture period were considered to have been captured only once within that period. From the population size estimates we calculated both linear and area densities. For the linear density we divided the estimated population size by the length of our study area. The area density was calculated based on available data showing a mean stream width of 9.75 m (M. McCain and D. Fuller, *unpublished data*), so the study area, if considered a long, narrow rectangle, would encompass 4.62 ha.

In order to better understand the relationship between our sampling efforts and capture probabilities of the garter snakes, we plotted and correlated an index of sampling effort relative to the capture probabilities derived for each year from the best approximating model in MARK analyses. In this situation, we used the correlation value (r) as a summary statistic only and did not evaluate statistical significance, as capture probabilities among years are not independent data points. The index considered both the number of sampling periods and the number of observers per sampling period (1–3). This was straightforward for two or three observers but with a single observer, he/she actually covered the same area of stream on any given day as would two observers. One-observer samples were thus equivalent to two-observer samples in terms of area coverage. Thus, the effort index for each year was calculated as: “number of one- or two-observer sampling

periods” \times 2 + “number of three-observer sampling periods” \times 3.

RESULTS

Over the 16 yr of our field study, we marked 1730 snakes: 240 neonate females, 174 neonate males, 638 juvenile females, 434 juvenile males, 82 adult females, and 162 adult males (Fig. 1). The overall observed sex ratio was slightly female-biased at 1.2:1 (females : males). We recaptured a total of 532 snakes with annual percentage of recaptures for all ages and sexes averaging 23.4% (range 13.2–32.4%; Fig. 2).

Survival rates and capture probabilities

The analysis of the candidate model set showed little support for either the most complex or the simplest models. Rather, the best approximating model, $\Phi_g P_{g*P}$ included an intermediate number of parameters (17) with sex-specific differences in survival and annual variation in capture probabilities, but no age-class effect. This model received more than 10 times the support of the next best model (Table 1, model number 1, QAIC_c weight). In this best approximating model, females showed higher survival rates ($\Phi = 0.636 \pm 0.021$ [SE]) than males ($\Phi = 0.558 \pm 0.026$), with little overlap in the 95% confidence interval (Fig. 3). Capture probabilities were generally low and varied from 0.089 (in 2000) to 0.288 (in 1987) (Fig. 4). The temporal variation in capture probabilities was expected because sampling effort varied among years. We found a positive relationship ($r = 0.728$) between field sampling effort and capture probabilities (derived from our best demographic model using MARK) (Fig. 5). In general, these analyses indicated that increasing both the number of sampling periods within a year and the number of observers per sampling period would have a positive influence on capture probabilities. Effort indices representative of multiple observers and four or more sampling periods per year showed the highest capture probabilities.

Population size and trends over time

Population size estimates, calculated separately for each year (15 yr with appropriate data using the adjusted Lincoln-Peterson estimator [Chapman 1951]), ranged from 274 to 615 individuals for the 4.7-km long study area, with a mean of 445.01 individuals (SE = 24.28) (Fig. 6). Converting this to a linear density gives a range of 58–131 snakes/km with a mean of 94.70 (SE = 5.17) snakes/km. Converting to an area density would give a mean of 96.3 snakes/ha (SE = 5.26) with a range of 59–133 snakes/ha. Examining abundance data for years where both field counts and Lincoln-Peterson estimates were available, there was never any overlap in the standard errors of these estimates (Fig. 6). Mean field counts typically represented only 5–10% of the population size estimated using the capture–recapture data. Patterns through time are fairly consistent

TABLE 1. Candidate models for survival rates (Φ) and capture probabilities (p) of Pacific coast aquatic garter snakes (*Thamnophis atratus*) at Hurdygurdy Creek, California, USA.

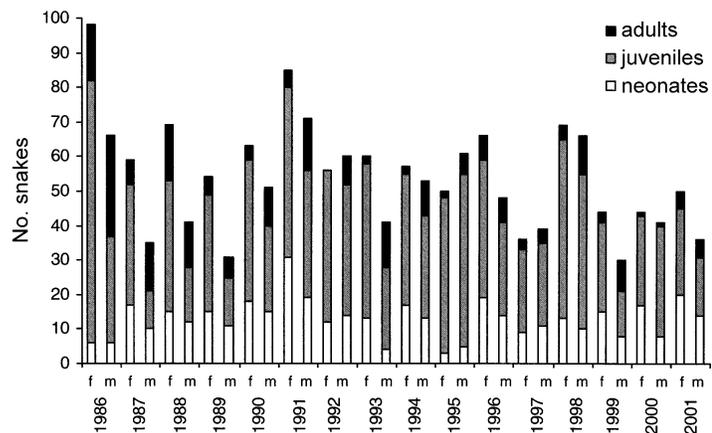
Model no.	Φ	p	Description	No. parameters	Δ QAIC _c	QAIC _c weight
1	g	t	no age cohorts; survival rates vary by group (= sex); capture probabilities vary over time	17	0.00	0.89300
2	g	$g \times t$	no age cohorts; survival rates vary by group (= sex); capture probabilities vary by group and over time	32	4.57	0.09079
3	t	g	no age cohorts; survival rates vary over time; capture probabilities vary by group (= sex)	17	9.48	0.00782
4	$a2 - g/g$	$a2 - g/g$	age cohorts have different estimates; survival rates and capture probabilities vary by group	8	12.57	0.00166
5	$a2 - g/g$	$a2 - ./.$	age cohorts have different estimates; survival rates vary by group; capture probabilities are constant	6	12.57	0.00166
6	g	$.$	no age cohorts; survival rates vary by group (= sex); capture probabilities are constant	3	12.79	0.00149
7	$a2 - T/T$	$a2 - ./.$	age cohorts have different estimates; survival rates vary with a linear time trend; capture probabilities are constant	6	13.01	0.00134
8	$a2 - ./.$	$a2 - g/g$	age cohorts have different estimates; survival rates are constant; capture probabilities vary by group	6	13.02	0.00133
9	$a2 - g/g$	$a2 - t/t$	age cohorts have different estimates; survival rates vary by group; capture probabilities vary over time	34	15.57	0.00037
10	$a2 - g \times T/g \times T$	$a2 - ./.$	age cohorts have different estimates; survival rates vary by group with a linear time trend; capture probabilities are constant	10	16.42	0.00024
11	$a2 - ./.$	$a2 - ./.$	age cohorts have different estimates; survival rates and capture probabilities are constant	4	17.06	0.00018
12	$a2 - ./.$	$a2 - t/t$	age cohorts have different estimates; survival rates are constant; capture probabilities vary over time	32	19.31	0.00006
13	$.$	$.$	no age cohorts; survival rates and capture probabilities are constant	2	19.46	0.00005
14	$g \times t$	$g \times t$	no age cohorts; survival rates and capture probabilities vary by group (= sex) and over time	58	23.66	0.00001
15	$a2 - t/t$	$a2 - g/g$	age cohorts have different estimates; survival rates vary over time; capture probabilities vary by group	34	25.69	0.00000
16	$a2 - t/t$	$a2 - ./.$	age cohorts have different estimates; survival rates vary over time; capture probabilities are constant	32	29.17	0.00000
17	$a2 - T/T$	$a2 - g \times t/g \times t$	age cohorts have different estimates; survival rates vary with a linear time trend; capture probabilities vary by group and over time	64	32.52	0.00000

TABLE 1. Continued.

Model no.	Φ	p	Description	No. parameters	Δ QAIC _c	QAIC _c weight
18	$a2 - g \times T/g \times T$	$a2 - g \times t/g \times t$	age cohorts have different estimates; survival rates vary by group with a linear time trend; capture probabilities vary by group and over time	68	34.50	0.00000
19	$a2 - g/g$	$a2 - g \times t/g \times t$	age cohorts have different estimates; survival rates vary by group; capture probabilities vary by group and over time	64	37.35	0.00000
20	$a2 - t/t$	$a2 - t/t$	age cohorts have different estimates; survival rates and capture probabilities vary over time	58	41.78	0.00000
21	$a2 - g \times t/g \times t$	$a2 - ./.$	age cohorts have different estimates; survival rates vary by group and over time; capture probabilities are constant	62	46.07	0.00000
22	$a2 - g \times t/g \times t$	$a2 - g/g$	age cohorts have different estimates; survival rates vary by group and over time; capture probabilities vary by group	64	47.14	0.00000
23	$a2 - t/t$	$a2 - g \times t/g \times t$	age cohorts have different estimates; survival rates vary over time; capture probabilities vary by group and over time	88	58.10	0.00000
24	$a2 - g \times t/g \times t$	$a2 - t/t$	age cohorts have different estimates; survival rates vary by group and over time; capture probabilities vary over time	88	61.99	0.00000
25	$a2 - g \times t/g \times t$	$a2 - g \times t/g \times t$	age cohorts have different estimates; survival rates vary by group and over time; capture probabilities vary by group and over time	116	95.05	0.00000

Notes: Models are ranked by Δ QAIC_c values. Models were developed using both grouping variables and hypotheses about variation over time, both in general (*t*) and considering a linear trend (*T*). Age cohorts (*a*) include neonates and juveniles/adults; groups (*g*) include sex and age classes (neonate female, neonate male, juvenile/adult female, juvenile/adult male); time is in terms of sample periods from 1986 to 2001.

FIG. 1. New captures of Pacific coast aquatic garter snakes (*Thamnophis atratus*) by sex and age class at Hurdygurdy Creek, California, USA, from 1986 through 2001. For each year, female (f) and male (m) captures are represented by separate columns.



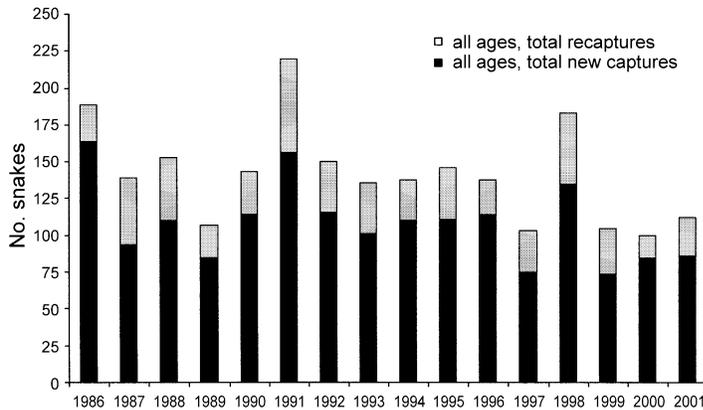


FIG. 2. Total captures of Pacific coast aquatic garter snakes at Hurdgyurdy Creek, California, showing the proportion of all (within- and between-year) recaptures from 1986 through 2001. The number of sampling periods varied across years as follows: 5 in 1986, 1987, 1988, and 1991; 4 in 1989 and 1990; 3 in 1992–2001.

between the field counts and the population size estimates. However, graphical analysis showed that at least in one instance field counts indicated that abundance from one year to the next changed in a different direction than did population size estimates. From 1998 to 2001, mean field counts drop consistently, while population size estimates show a drop from 1998 to 1999, but then rise through 2001 (Fig. 6).

We found no evidence of either increasing or decreasing linear trends in any of the demographic parameters over the 16 yr of our study. There also was no obvious increasing or decreasing trend over time in population size from graphical analysis of either field counts or population size estimates (Fig. 6). In addition, all of the survival rate models that included a linear time trend had very low QAIC_c weights (Table 1, model numbers 7, 10, 17, and 18).

DISCUSSION

The demographic models described in this paper are the first for this species and are among only a few developed for any snake species. Overall, we found sex differences in survival rates and temporal variation in capture probabilities for this apparently stable population. Specifically, female Pacific coast aquatic garter snakes had higher survival rates than males and capture probabilities were low for both sexes, with substantial variation over time.

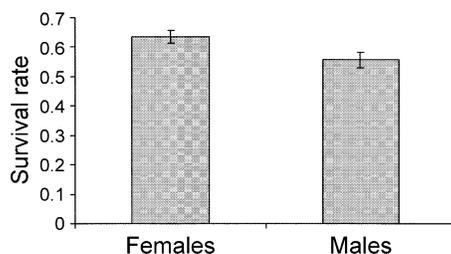


FIG. 3. Annual survival rate estimates (± 1 SE) for females and males, from the best approximating model derived using Program MARK, for Pacific coast aquatic garter snakes at Hurdgyurdy Creek, California (1986–2001).

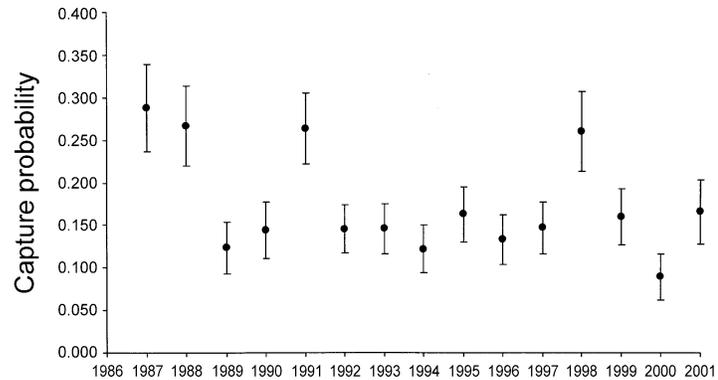
Survival rates of garter snakes

Our finding of higher survival rates for females (Fig. 3) is new for garter snakes though earlier studies have rarely addressed this question and possibly did not have the power to detect such trends (Parker and Plummer 1987). While sampling effort may play into this difference, inherent behavioral/activity patterns differ between the two sexes and are likely the main influences. Specifically, in studies of movements of this species within the same study area, our data show that distances moved (from one capture to the next) differed among both sexes and age classes, such that juvenile and adult males moved greater distances than juvenile and adult females (H. H. Welsh, Jr. and A. J. Lind, *unpublished manuscript*). This greater movement undoubtedly translates into higher exposure to predation and hence lower survival rates (e.g., Greene 1988, Allan 1995). The estimated values for survival fall within the range of survival rates observed in many (Parker and Plummer 1987, Rossman et al. 1996, Bronikowski and Arnold 1999) though not all (Larsen and Gregory 1989) other garter snake species. Age and habitat type have been shown to influence survival rates in a related species of garter snake (*Thamnophis elegans*) at a northeastern California study site, though no sex differences were found there (Bronikowski and Arnold 1999). Survival rates of northern water snakes (*Nerodia sipedon*), an ecologically similar and phylogenetically close relative to the Pacific coast aquatic garter snake, were found to differ between two study marshes but not between males and females (Brown and Weatherhead 1999). It is possible that heterogeneity of the habitat in these other studies overshadowed sex differences. Because our study only included one population in one stream, we could not assess potential differences in survival rates between habitats (e.g., stream vs. lake) or different geographic locations.

Population size and recapture rates of garter snakes

Our mean density estimates (95 snakes/km and 96 snakes/ha) are high for garter snakes, which typically

FIG. 4. Capture probability estimates (± 1 SE) for the best approximating model from Program MARK for Pacific coast aquatic garter snakes at Hurdygurdy Creek, California (1986–2001).



range from 10 to 20 snakes/ha (Parker and Plummer 1987, Fitch 1999). Water snakes (*Nerodia* sp.) have been found at comparable densities, both by area (24.5–128.5 snakes/ha) and for linear distance (22–381 snakes/km) (King 1986, Brown and Weatherhead 1999). Our snake-per-hectare density is an appropriate estimate for the spring/summer active season for this species. However, it is likely an overestimate from an annual perspective because it does not consider adjacent riparian and upland habitats that are used to an unknown extent during other times of the year. In addition, it is likely that our density estimates are biased upward because these estimates include individuals on the edges of the study area that may have territories extending beyond it (see Wilson and Anderson [1985] for further discussion of this problem). Finally, our estimates may be larger than those in the literature because by using capture–recapture data, we have explicitly incorporated capture probabilities, providing less biased estimates. For example, compare the difference in the abundance estimates in our count data with our capture–recapture results (Fig. 6). Nevertheless, this population appears to be large relative to other species of garter and water snakes (Parker and Plummer 1987).

Our recapture rates were very similar to those reported for other garter snakes (Parker and Plummer 1987, Fitch 1999). Improving recapture rates for this species is crucial because, in general, these rates need to be substantially higher to develop ecologically complex demographic models. Substantially more sampling effort, combined with a better understanding of the factors that influence daily and seasonal activity levels of snakes, is needed to improve capture probabilities and in turn increase the precision of estimates.

Capture probabilities, precision, and monitoring

Recent monitoring efforts have begun to integrate population size data with information on demographic rates, like survivorship and birth rates, to improve interpretations of observed trends (e.g., DeSante et al. 2001, Campbell et al. 2002, Schmidt et al. 2002). Even though the population of Pacific coast garter snakes we

studied appears to be nondeclining, our finding of sex differences in survival rates has implications for designing sampling schemes and monitoring efforts. This is especially true if survival rates are related to activity level differences among sexes and age classes. For example, more effort or different timing of sampling may be needed to detect and capture less active snakes.

Our results relating sampling effort to capture probabilities, which are ultimately related to precision of survival rates (Pollock et al. 1990), can provide a context for designing sampling and monitoring plans for garter snakes and potentially other snake species. Field count results are a function of both N (the number of individuals actually present) and p (capture probabilities of those individuals). Since capture probabilities are usually unknown and likely nonuniform for typical field counts, the use of unadjusted field count data for detecting trends or even assessing relative abundance may not be appropriate (Nichols 1992, Pollock et al. 2002, Thompson 2002). The variation in capture probabilities that we found for Pacific coast aquatic garter snakes, even among years with the same sampling effort, illustrates this concern (Figs. 4 and 5). Thus, substantial effort should be directed toward determining

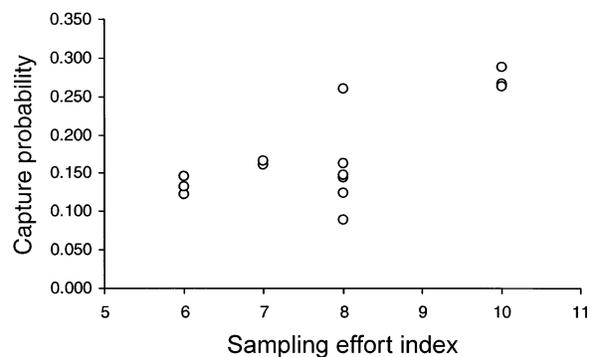


FIG. 5. Annual capture probabilities (from the best approximating population model, Program MARK) plotted with sampling effort as defined by a sampling effort index incorporating both the number of sampling periods and the number of observers per period for Pacific coast aquatic garter snakes at Hurdygurdy Creek, California (1986–2001).

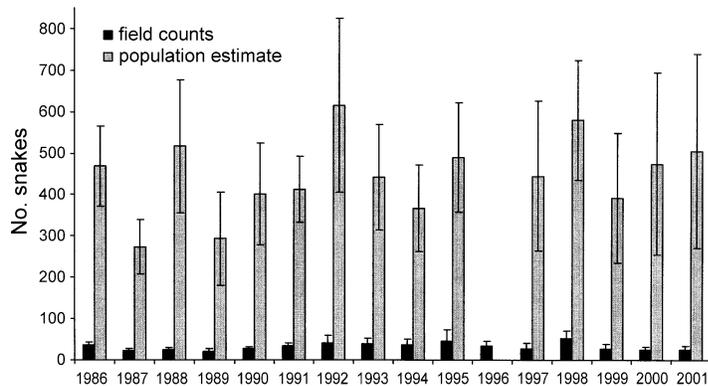


FIG. 6. Mean field counts and Lincoln-Peterson (Chapman) population estimates (± 1 SE) for pooled juvenile and adult Pacific coast aquatic garter snakes at Hurdygurdy Creek, California, from 1986 through 2001. Field counts are the mean of the 3–5 sampling periods per year. No Lincoln-Peterson estimate could be calculated for 1996 as there were no within-year recaptures.

capture or detection probabilities in research and monitoring programs for snakes and other secretive or cryptic species.

Based on the movements of the most mobile sex/age class (juvenile males), we believe the length of our study area (4.7 km) is sufficiently long to cover the home range of most snakes. Considering a mean monthly movement for juvenile males of ~ 73 m (H. H. Welsh, Jr. and A. J. Lind, *unpublished manuscript*), it would take 32 mo (almost 3 yr) for a snake moving consistently upstream or downstream to reach either end of our study area from the middle. Given these movement data, it may be possible to reduce the length of stream surveyed in our situation and in other monitoring efforts. By redirecting sampling effort to more (4–5), temporally proximate surveys of a shorter stream segment (e.g., 2–3 km) we would expect to increase capture probabilities substantially.

Our study of Pacific coast aquatic garter snakes emphasizes the importance of intensive sampling to obtain reliable estimates of population parameters critical to studies of autecology, the evolution of life history traits, and for design of effective conservation strategies. We recognize more work is needed to understand age-specific demographic rates for this and other species of snakes. However, we hope that our success in developing population models will encourage more research on these unique vertebrates. Because the population we studied appears to be stable, our data on survival rates, capture probabilities, and population sizes could be used as baseline or target values in the conservation of related declining species such as the giant garter snake, *Thamnophis gigas*, and two-striped garter snake, *T. hammondi* (U.S. Fish and Wildlife Service 1993; California Department of Fish and Game, California Natural Diversity Database, Special Animals, *available online*).⁴ With continued refinement of sampling approaches, snakes may indeed turn out to be useful model organisms for testing ecological and evolutionary theories (Seigel 1993, Shine and Bonnet 2000) and for ecological monitoring.

⁴ (<http://www.dfg.ca.gov/whdab/html/animals.html>)

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