

# Population Dynamics of the Concho Water Snake in Rivers and Reservoirs

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**The Concho Water Snake (*Nerodia harteri paucimaculata*) is confined to the Concho–Colorado River valley of central Texas, thereby occupying one of the smallest geographic ranges of any North American snake. In 1986, *N. h. paucimaculata* was designated as a federally threatened species, in large part because of reservoir projects that were perceived to adversely affect the amount of habitat available to the snake. During a ten-year period (1987–1996), we conducted capture–recapture field studies to assess dynamics of five subpopulations of snakes in both natural (river) and man-made (reservoir) habitats. Because of differential sampling of subpopulations, we present separate results for all five subpopulations combined (including large reservoirs) and three of the five subpopulations (excluding large reservoirs). We used multistate capture–recapture models to deal with stochastic transitions between pre-reproductive and reproductive size classes and to allow for the possibility of different survival and capture probabilities for the two classes. We also estimated both the finite rate of increase ( $\lambda$ ) for a deterministic, stage-based, female-only matrix model using the average litter size, and the average rate of adult population change,  $\hat{\lambda}$ , which describes changes in numbers of adult snakes, using a direct capture–recapture approach to estimation. Average annual adult survival was about 0.23 and similar for males and females. Average annual survival for subadults was about 0.14. The parameter estimates from the stage-based projection matrix analysis all yielded asymptotic values of  $\lambda < 1$ , suggesting populations that are not viable. However, the direct estimates of average adult  $\lambda$  for the three subpopulations excluding major reservoirs were  $\hat{\lambda} = 1.26$ ,  $S\hat{E}(\hat{\lambda}) = 0.18$  and  $\hat{\lambda} = 0.99$ ,  $S\hat{E}(\hat{\lambda}) = 0.79$ , based on two different models. Thus, the direct estimation approach did not provide strong evidence of population declines of the riverine subpopulations, but the estimates are characterized by substantial uncertainty.**

RAPIDLY expanding human populations are increasingly modifying the environment and thereby reducing the amount of habitat available for numerous species (Ehrlich, 1988; Wilson, 1988). Habitat loss and degradation are perhaps the greatest threats for species that are specialized and that range over a relatively small geographic area. In light of this, one of the challenges facing conservation biologists is estimating demographic parameters for species of conservation concern to infer something about their future viability (Soulé, 1986). In particular, we need to know if populations that exist in modified habitats are more susceptible to extinction compared to populations in relatively undisturbed habitats.

The Concho Water Snake (*Nerodia harteri paucimaculata*) not only occupies one of the smallest ranges of any North American snake, but it is also a habitat specialist. Unlike other *Nerodia*, it is thought to have a reduced dispersal capacity (Whiting et al., 1998) and rarely ventures more than a few meters from water (Whiting et al., 1997; USFWS, 2004). Although adult snakes are able to occupy a range of habitat types that include lakes and river pools, juveniles are dependent on exposed, rocky areas. In rivers, juveniles are most commonly associated with riffles (shallow, fast flowing rocky areas with a broken water surface), while in lakes they

are typically found along low gradient, rocky shorelines. The construction of water impoundments has significantly reduced the availability of suitable riverine habitat for juveniles. Even when impoundments are constructed outside of the snakes' range, the consequence is a reduction in flow rate and a cascade of events that result in the downstream siltation of riffles and vegetation encroachment from weedy species such as saltcedar, *Tamarix* spp., an exotic invasive tree (Scott et al., 1989). Habitat alteration, therefore, may have potentially far reaching effects for this species.

In 1986, *N. h. paucimaculata* was declared a federally threatened species (Stefferd, 1986) because of its limited distribution and the perceived threat to its existing habitat through current and proposed reservoirs. Shortly thereafter, we began monitoring populations as part of a general study of the life history and ecology of *N. h. paucimaculata*. One aspect of this study was to estimate annual survival of *N. h. paucimaculata* in multiple populations, including both natural snake habitat (rivers) and highly modified habitat (reservoirs). Specifically, we had the following four aims: to determine if survival was population-specific and if it differed between lake and river systems; to determine whether annual survival was dependent on snake size (a

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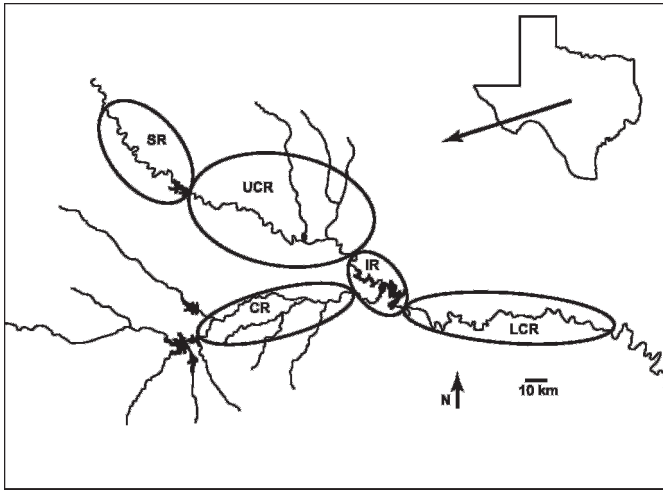
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**Fig. 1.** Map depicting the locations of the five subpopulations: Spence Reservoir and above (SR), Upper Colorado River (UCR), Ivie Reservoir (IR), Lower Colorado River (LCR), and Concho River (CR).

proxy for age) and/or sex; to estimate the rate of change in population size; and to determine the minimum survival rate required for population persistence. Because this species evolved in rivers and has only recently occupied water impoundments, we predicted higher survival rates in river systems than reservoirs. We also predicted higher survival rates for larger versus smaller snakes because smaller snakes are generally susceptible to a wider range of predators.

## MATERIALS AND METHODS

**Study animal.**—*Nerodia h. paucimaculata* is a relatively small piscivorous natricine snake (maximum snout–vent length [SVL], male: 616 mm, female: 827 mm) endemic to the Concho–Colorado River drainage of Central Texas, where it occurs along 238 km of river habitat and over 67 km of man-made lake habitat (Greene et al., 1994; USFWS, 2004). The taxonomic and systematic status of this species is controversial, with some authors proposing an elevation to specific status (Rose and Selcer, 1989; Densmore et al., 1992). However, because the external character states are variable and therefore not diagnostic (JRD, unpubl. data), we have opted to retain the subspecific designation. Males mature at 380 mm SVL, while females mature at 460 mm SVL (Greene et al., 1999). Females produce their first litter at either 24–25 months or 36–37 months, depending on their growth rate (Werler and Dixon, 2000). Parturition occurs from late July through September and mean litter size is 11.1 (range: 4–29; Greene et al., 1999).

**Study area and designation of subpopulations.**—We conducted a capture–recapture field study of *N. h. paucimaculata* in the Concho Valley of west central Texas (Fig. 1). We sampled snakes at multiple sites on the Concho–Colorado River drainage, including several reservoirs, during a ten-year period (1987–1996). These sites are described in detail elsewhere (Mueller, 1990; Greene, 1993; Whiting, 1993; Greene et al., 1994; Whiting et al., 1997). The most intensive sampling took place during 1987–1991 (Table 1), prior to the construction of a major water impoundment, O. H. Ivie Reservoir (Fig. 1). Following the construction of Ivie Reservoir, several new populations in the flood basin were also monitored. Our initial analyses found no evidence of a

difference in survival among the five subpopulations (Fig. 1), and therefore we pooled data into three groups for survival estimation: the ten-year data set (1987–1996); the same data set excluding the Spence and Ivie Reservoirs, which were not sampled in all years; and the 1987–1991 data set (all subpopulations excluding Ivie Reservoir), during which sampling was most intensive. Sampling occasions for all analyses were from 25 August–20 October each year. These were the periods of consistently large numbers of captures, in part because this corresponds to when females gave birth (Greene et al., 1999), and therefore when the most juveniles are likely to be present.

**Sampling procedure.**—We captured snakes using a combination of sampling by hand and trapping. Because first year snakes are typically found under small, exposed rocks, we systematically sampled all shoreline and river-bank rock that could potentially harbor a snake. We also trapped snakes using funnel traps (commercial minnow traps), placed along the shoreline and/or in riffles. Following capture, each snake was individually marked with a passive integrated transponder (PIT tag) injected into the lower body cavity, sexed, measured (SVL, tail to nearest 1 mm), and weighed (nearest 1 g). All snakes were processed on site and returned to their point of capture on the same day.

**Survival analyses.**—In all analyses, snakes were grouped as male or female and adult (reproductive size, >510 mm for females, >420 mm for males) or juvenile (pre-reproductive, ≤510 mm for females, ≤420 mm for males). We selected these size cut-offs because in the case of males, all individuals >420 mm SVL contained motile sperm in their testes and the vast majority of females >510 mm SVL were gravid during the breeding season (Greene et al., 1999). The transition probability between juvenile and adult stages was also then a parameter to be estimated. We focused on local survival,  $S_i$ , the probability that a snake alive and in the population at sampling occasion  $i$  was still alive and in the population (i.e., snake did not die or permanently emigrate) at sampling occasion  $i+1$ .

We conducted two kinds of analysis. First, we focused on survival and recruitment and used multistate capture–recapture models (Brownie et al., 1993; Williams et al., 2002). These models were selected to allow stochastic transitions from pre-reproductive to reproductive size classes and to permit the possibility of different survival and capture probabilities for the two classes. We implemented the models using program MARK (White and Burnham, 1999) and used a model selection approach involving  $AIC_c$  (Burnham and Anderson, 2002) to select the most appropriate model for each data set. Initial analyses showed that data were inadequate (e.g., produced numerical convergence problems) to support models with multiple types of parameters (e.g., capture and survival probabilities) modeled as time-specific (denoted by  $t$ ) and location-specific ( $l$ ). We thus focused on models that permitted all parameters to vary by sex (denoted  $s$ ), size ( $r$ ), or neither variable ( $.$ ). Annual apparent survival rate and capture probability were also permitted to vary by year ( $t$ ) in some models. Similarly, we fitted a small number of models with location-specific parameters. Model notation generally follows that recommended by Lebreton et al. (1992). State (size) is indicated by superscript. Other sources of variation in a parameter (time, sex) are denoted via subscript with \* denoting a model with

**Table 1.** Number of Individual Males and Females Captured during 25 August–20 October Each Year for Three Capture–Recapture Data Sets of the Concho Water Snake (*Nerodia h. paucimaculata*). The five subpopulations are abbreviated as follows: Spence Reservoir and above (SR), Upper Colorado River (UCR), Ivie Reservoir (IR), Lower Colorado River (LCR), and Concho River (CR). Ivie Reservoir was inundated to become a reservoir in April 1990 and so IR populations in 1988–1989 were therefore riverine. <sup>1</sup> We excluded Ivie and Spence Reservoirs from this analysis, and therefore those cells have been left blank in this column. Otherwise, this column is identical to the previous column (data from five subpopulations). <sup>2</sup> These studies only collected data through 1991, and therefore cells for 1992–1996 have been left blank in this column.

Year and subpopulation		Data from five subpopulations 1987–1996		Data <sup>1</sup> from three subpopulations 1987–1996		Data <sup>2</sup> from Mueller (1990) and Whiting (1993)	
		Males	Females	Males	Females	Males	Females
1987	SR	13	10			11	10
	UCR	131	129	131	129	82	73
	IR	0	0			0	0
	LCR	83	73	83	73	10	7
	CR	54	16	54	16	4	4
1988	SR	5	5			2	4
	UCR	102	122	102	122	63	81
	IR	42	39			42	39
	LCR	86	79	86	79	13	11
1989	CR	83	80	83	80	26	17
	SR	0	0			0	0
	UCR	124	127	124	127	54	50
	IR	29	44			28	46
	LCR	87	94	87	94	20	17
1990	CR	59	59	59	59	25	27
	SR	37	49			37	47
	UCR	138	139	138	139	70	62
	IR	0	0			0	0
1991	LCR	92	84	92	84	22	18
	CR	45	27	45	27	8	8
	SR	30	43			36	45
	UCR	136	124	136	124	71	64
	IR	27	27			0	1
1992	LCR	78	100	78	100	19	38
	CR	28	26	28	26	5	2
	SR	0	0				
	UCR	120	100	120	100		
	IR	8	9				
1993	LCR	82	62	82	62		
	CR	24	30	24	30		
	SR	0	0				
	UCR	113	80	113	80		
1994	IR	21	12				
	LCR	59	71	59	71		
	CR	33	36	33	36		
	SR	0	0				
	UCR	66	79	66	79		
1995	IR	19	27				
	LCR	58	79	58	79		
	CR	10	7	10	7		
	SR	0	0				
1996	UCR	48	56	48	56		
	IR	11	11				
	LCR	39	47	39	47		
	CR	20	14	20	14		
	SR	0	0				
1996	UCR	25	39	25	39		
	IR	0	2				
	LCR	43	53	43	53		
	CR	8	15	8	15		

interactions (different parameters for each combination of variables). For example, model  $(S_{t^*s_i}^r, p_{s_i}^r, \Psi_s)$  denotes a model in which annual apparent survival has a different parameter for every time–sex–size combination, capture probability is size dependent only, and transition probability is a constant over time and sex. Model  $(S_{t_i}^r, p_{s_i}^r, p_{m_i}^r, \Psi_s)$  indicates a model with survival rates varying by time and size, capture probabilities of females varying by size, capture probabilities of males not varying by size, and juvenile to adult transition probability varying by size. We estimated temporal variance of survival using a random effects approach with the best model that permitted survival to vary over time (Burnham and White, 2002). Such estimates of temporal variance are rare in demographic studies, but useful because sampling variance is removed from the estimates, leading to a better estimate of the true year-to-year variability in survival (Gould and Nichols, 1998).

**Finite rate of increase ( $\lambda$ ), asymptotics.**—We used the estimates of survival and transition probabilities generated from our analyses to estimate the finite rate of increase ( $\lambda$ ) for a deterministic, stage based, female only, post-breeding census matrix model using the average litter size (11.1 offspring of both sexes per breeding female) reported in Greene et al. (1999). We assumed that 85% of females of breeding size bred each year (Greene et al., 1999) and an equal sex ratio among neonates. We used RAMAS Metapop software (Akçakaya and Root, 2002) to perform these calculations using the following projection matrix:

$$\begin{bmatrix} N_j(t+1) \\ N_a(t+1) \end{bmatrix} = \begin{bmatrix} S_j(1 - \Psi + \Psi PF/2) & S_a PF/2 \\ S_j \Psi & S_a \end{bmatrix} \times \begin{bmatrix} N_j(t) \\ N_a(t) \end{bmatrix},$$

where  $N_j$  and  $N_a$  are the numbers of juveniles and adults (at times  $t$ , and  $t+1$ ),  $\Psi$  is the transition probability (per year) from juvenile to adult,  $P$  is the percentage that breeds each year (0.85),  $F$  is fecundity (11.1), and  $S$  is the survival rate, with subscript “ $a$ ” indicating adult and subscript “ $j$ ” indicating juvenile females.

After calculating the asymptotic rate of increase ( $\lambda$ ) using the average annual survival and transition probabilities, we then calculated how much higher average adult and juvenile survival would need to be to attain  $\lambda = 1$  (stable population), a parameter which we term the ‘survival multiplier.’ Because each matrix element contains a survival rate, the survival multiplier for our particular stage-based matrix, can be estimated as the reciprocal of  $\lambda$ . This calculation assumes an equal survival multiplier for juvenile and adult survival, and other approaches would certainly be possible (e.g., juvenile survival could remain the same and one could ask how much higher adult survival would need to be to achieve stability).

**Finite rate of increase ( $\lambda$ ), direct estimation.**—When finite rate of increase ( $\lambda$ ) is computed as above from a projection matrix with matrix elements representing averages of field estimates, there is typically an asymmetry in the treatment of movement in population losses and gains. Survival rate estimated from capture–recapture data is best viewed as apparent or local survival because it includes both death and permanent emigration. However, the upper rows of projection matrices are typically based on reproductive data (in our case average number of female offspring per female), and nowhere in the matrix are gains from immigration entered (usually). This asymmetry (losses include movement

**Table 2.** Multistate Model Selection Statistics for the Concho Water Snake (*Nerodia h. paucimaculata*) Capture–Recapture Data from Three Riverine Subpopulations, 1987–1996 (Column 2 of Table 1). The best model has the smallest  $AIC_c$  and the largest  $AIC_c$  weight. See text for details on notation.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	Number of parameters
$(S_{t_i}^r, p_{s_i}^r, p_{m_i}^r, \Psi_s)$	1412.1	0.00	0.66	22
$(S_{t_i}^r, p_{s_i}^r, \Psi_s)$	1414.1	2.02	0.24	23
$(S_{t_i}^r, p_{s_i}^r, \Psi_s)$	1416.0	3.92	0.09	24
$(S_{t^*s_i}^r, p_{s_i}^r, p_{m_i}^r, \Psi_s)$	1422.9	10.79	0.00	22
$(S_{t_i}^r, p_{t^*s_i}^r, \Psi_s)$	1423.4	11.26	0.00	39
$(S_{t_i}^r, p_{s_i}^r, \Psi_s)$	1425.3	13.25	0.00	7
$(S_{s_i}^r, p_{s_i}^r, \Psi_s)$	1425.7	13.58	0.00	10
$(S_{t_i}^r, p_{t^*s_i}^r, \Psi_s)$	1427.8	15.68	0.00	52
$(S_{s_i}^r, p_{s_i}^r, \Psi_s)$	1429.0	16.95	0.00	8
$(S_{t_i}^r, p_{t^*s_i}^r, \Psi_s)$	1432.2	20.09	0.00	53
$(S_{s_i}^r, p_{s_i}^r, \Psi_s)$	1437.3	25.21	0.00	7
$(S_{t_i}^r, p_{s_i}^r, \Psi_s)$	1440.1	27.98	0.00	5
$(S_{t_i}^r, p_{s_i}^r, \Psi_s)$	1442.4	30.30	0.00	15

but gains do not) tends to produce estimated  $\lambda$ s that are too low and that do not reflect changes in numbers of animals on the study areas from which estimates are obtained.

To estimate the average  $\lambda$  that describes changes in numbers of adult snakes on a given study area, we used the direct capture–recapture approach to estimation of  $\lambda$  (Pradel, 1996; Nichols and Hines, 2002). We combined males and females and used data from adult snakes only. We conducted this analysis for the medium-sized data set only (ten years of data), excluding Ivie and Spence because sampling was not consistent over the ten years of study at the two reservoirs, and because sampling did not occur over enough years to estimate  $\lambda$  for the small data set (Mueller, 1990; Whiting, 1993). We fitted several models to the data set, using  $AIC_c$  to evaluate the applicability of the different models. We focused on the low- $AIC_c$  model and on a model with fully time-specific survival and capture probabilities with  $\lambda_t$  modeled using a random effects approach (Burnham and White, 2002).

## RESULTS

Our estimates of survival are based on the capture of 4641 unique individual snakes at all sites combined during ten years of sampling (Table 1). Of these snakes, 2316 were males (71 recaptured) and 2325 were females (68 recaptured); the recaptures only include snakes caught in subsequent years, and during the period of interest (25 August–20 October). These data to some degree reflect sampling effort (e.g., no snakes at Spence in 1989 but 86 in 1990). Model selection statistics for the multistate models for the three riverine subpopulations (i.e., data shown in middle column of Table 1) are presented in Table 2.

**Annual survival.**—Estimates of average annual adult survival varied by model and data set and are shown in Table 3. The average annual adult survival estimates ranged from 0.23 to 0.34 and, in all cases, could be modeled with a single parameter for the two sexes. Estimates of average annual juvenile survival ranged from 0.14 to 0.16 (Table 3), and



**Table 3.** Demographic Parameter Estimates (Standard Errors in Parentheses) for the Best-Fitting Models (as determined by AIC<sub>c</sub>) from Three Capture–Recapture Data Sets for the Concho Water Snake (*Nerodia h. paucimaculata*). Asymptotic  $\lambda$  is the finite rate of increase assuming a stable population using a deterministic projection matrix analysis. The survival multiplier, which is the reciprocal of  $\lambda$ , estimates how much higher adult and juvenile survival would need to be in order to have asymptotic  $\lambda = 1$ . <sup>1</sup> We excluded Ivie and Spence Reservoirs from this analysis. <sup>2</sup> Capture probabilities are not reported for this data set because they varied by year.

Parameter	Data from five subpopulations 1987–1996	Data <sup>1</sup> from three subpopulations 1987–1996	Data <sup>2</sup> from Mueller (1990) and Whiting (1993)
Capture probability: males (both stages)	0.14 (0.03)	0.15 (0.04)	
Capture probability: females $\leq$ 510 mm	0.31 (0.09)	0.32 (0.10)	
Capture probability: females $>$ 510 mm	0.07 (0.02)	0.07 (0.02)	
Transition probability: males and females	0.61 (0.06)	0.62 (0.06)	0.48 (0.20)
Annual survival: juveniles	0.14 (0.03)	0.14 (0.03)	0.16 (0.05)
Temporal variance in survival of juveniles	0.0059	0.0062	
	95% $\hat{C}\hat{I} = 0.0022$ to 0.0245	95% $\hat{C}\hat{I} = 0.0022$ to 0.0258	
Annual survival: adults	0.23 (0.05)	0.23 (0.06)	0.34 (0.10)
Temporal variance in survival of adults	0.0073	0.0110	
	95% $\hat{C}\hat{I} = 0.0000$ to 0.0932	95% $\hat{C}\hat{I} = 0.0000$ to 0.1374	
Asymptotic $\lambda$	0.67	0.68	0.74
Survival multiplier	1.49	1.47	1.35

again, could be modeled with a single parameter for the two sexes. The survival estimates from the data set excluding Ivie and Spence were 0.23 (SE = 0.06) for adult snakes and 0.14 (SE = 0.03) for subadults. Estimates of the annual transition probability (pre-reproductive to reproductive stage) ranged from 0.48 to 0.62, depending on the data set (Table 3).

**Finite rate of increase ( $\lambda$ ), direct estimation.**—We fitted several models to the data set, and the low-AIC<sub>c</sub> model ( $S_t, p_t, \lambda_t$ ) included time-specific parameters for capture probabilities, but not for survival probability or finite rate of increase. The estimate of average  $\lambda$  under this model for the three riverine subpopulations was  $\hat{\lambda} = 1.26$ ,  $SE(\hat{\lambda}) = 0.18$ . Although the point estimate is  $>1$ , the degree of uncertainty is large (e.g., the approximate 95%  $\hat{C}\hat{I} = 0.95$ –1.66), as the capture–recapture data set is relatively sparse. As noted above, we also fitted model ( $S_t, p_t, \lambda_t$ ), where  $\lambda_t$  was modeled using a random effects approach (Burnham and White, 2002). The average population growth rate under this approach was estimated as  $\hat{\lambda} = 0.99$ ,  $SE(\hat{\lambda}) = 0.79$ , again reflecting substantial uncertainty.

**Finite rate of increase ( $\lambda$ ), asymptotics.**—Because all the  $\lambda$  values for the stage-based matrix analyses were  $< 1$ , suggesting declining populations, we estimated how much higher survival would need to be to obtain a stable population. If there is no immigration to the system, we estimated that survival would have to be at least 1.5 times higher than current estimates for the various subpopulations (Table 3). Therefore, for the five subpopulations, the combination of juvenile survival of at least 0.21 and adult survival of at least 0.34 would yield  $\lambda = 1$ . For the three subpopulations, juvenile survival of at least 0.21 combined with adult survival of at least 0.33 would yield  $\lambda = 1$ .

## DISCUSSION

**Annual survival.**—Little is known about the annual survival of snakes in general, but the few data that exist suggest high first year mortality (Parker and Plummer, 1987). Mean annual first-year survival for seven species of early-maturing colubrids, a category that fits *N. h. paucimaculata*, was 24%

(range: 15–38; reviewed in Parker and Plummer, 1987). Other early-maturing colubrids for which first year survival has been subsequently reported include *Thamnophis elegans* (14–44%; Bronikowski and Arnold, 1999); *Thamnophis sirtalis fitchi* (29%; Jayne and Bennett, 1990); *Thamnophis radix* (16–17%; Stanford and King, 2004); *Nerodia sipedon insularum* (18%; King, 1987); *Nerodia s. sipedon* (20%; Brown and Weatherhead, 1999); and *Ophedrys aestivus* (21–22%; Plummer, 1997). The water snakes listed above (*Nerodia s. sipedon* and *Nerodia s. insularum*), and in Parker and Plummer (1987), had a first-year survival of 18–20%. Our data suggest an annual survival of about 14% for juvenile snakes, which included individuals older than one year. Therefore, first year survival is likely to be lower than this figure because snakes in their first year are vulnerable to a wider range of predators by virtue of their small body size and inexperience with potential predators. Mean annual adult survival for the same seven species of early-maturing colubrids was 49% (range: 35–63; Parker and Plummer, 1987). More recent studies of early-maturing colubrids report the following annual adult survival: *Thamnophis elegans* (34–86%; Bronikowski and Arnold, 1999); *Thamnophis radix* (35–45%; Stanford and King, 2004); *Thamnophis sirtalis* (large males: 68–98%; Larsen and Gregory, 1989); *Nerodia s. sipedon* (53–58%; Brown and Weatherhead, 1999); *Nerodia s. insularum* (63%; King et al., 2006); and *Ophedrys aestivus* (68–80%; Plummer, 1997). The water snakes listed above (*Nerodia s. sipedon* and *Nerodia s. insularum*), and in Parker and Plummer (1987) had an annual adult survival of 35–63%. Apparent annual adult survival for *N. h. paucimaculata* was considerably lower in our study, estimated to be about 23%. *Nerodia h. paucimaculata* may offset low survival by maturing rapidly and investing heavily in reproduction. Relative clutch mass (RCM) in Concho Water Snakes is considerably higher than values reported for other *Nerodia* (Greene et al., 1999), suggesting that snakes are offsetting high mortality with increased reproductive effort. Unfortunately we have no quantitative measures of emigration rates with which to estimate true survival (complement includes only mortality) and the nature of certain sites (e.g., dams)

would likely constrain migration. However, some individuals have moved substantial distances (6.4–19.3 km) over extended periods (Werler and Dixon, 2000), suggesting that local emigration is probably a factor at some sites. Indeed, the difference between the asymptotic  $\lambda$  (asymmetric treatment of movement) and the direct estimate of  $\lambda$  likely reflects dispersal or movement of individuals among locations.

We did not find evidence of variation in average survival among the five subpopulations, which is why we ultimately pooled them for the analyses presented here. Two of these subpopulations were in impoundments: E. V. Spence Reservoir (completed in 1969) and O. H. Ivie Reservoir (completed in 1990). Ivie is therefore a young reservoir and was never sampled adequately for any rigorous estimates of snake survival and population growth. Spence Reservoir has been surveyed intermittently during the late 1980s and the early 1990s, but the data were never sufficient for truly reliable estimates of snake survival and population growth. A recent survey in 2004 has confirmed that *N. h. paucimaculata* is still present in both Spence and Ivie reservoirs (JRD, unpubl. data). Lake Ballinger is a small municipal lake on a tributary of the upper Colorado River. This lake was included in the Upper Colorado River subpopulation and generally had a healthy population of *N. h. paucimaculata*. A recent survey in 2004 revealed Lake Ballinger almost devoid of water following a prolonged drought and no snakes were found (JRD, OWT, unpubl. data). However, in 2005 following refilling, these two authors found neonates along the rocky shoreline of this small reservoir.

**Finite rate of increase ( $\lambda$ ).**—None of the combinations of parameter estimates yielded values of asymptotic  $\lambda \geq 1$ , so there is no evidence from the stage-based matrix analysis supporting the conclusion that the populations are viable. However, this does not necessarily mean that populations of the Concho Water Snake are not viable, as these asymptotic  $\lambda$  do not deal symmetrically with animal movement. Our estimates of asymptotic  $\lambda$  assumed no stochasticity and would be even smaller if we included stochasticity in a full-blown population viability analysis (Boyce, 1977; Cohen, 1979; Akçakaya et al., 2004).

The direct capture–recapture approach yielded one estimate of  $\lambda > 1$  and another barely  $< 1$ , but both estimates were characterized by a large amount of uncertainty. Franklin et al. (2004:appendix 3) argued that this approach is likely better than the asymptotic, projection-matrix approach for estimating realized  $\lambda$  for a given population over a given time period, especially for organisms with high dispersal abilities and geographically open populations. *A priori* reasoning leads us to believe that our estimates of  $\lambda$  from the direct estimation approach may be more useful as a measure of population dynamics for the Concho Water Snake, at least over the period of study, 1987–1996, than the estimates of asymptotic  $\lambda$ . However, the resulting estimates had large variances and did not lead to strong inferences about population growth rate.

**Future prospects of the Concho Water Snake.**—Not only have large sections of the Concho–Colorado River system been altered through the construction of upstream reservoirs beyond the range of the snake, but several reservoirs have been constructed within the snakes' natural range (Scott et al., 1989). Given that *N. h. paucimaculata* naturally occurred

only along river courses and is relatively specialized (Scott et al., 1989), a key question is whether they can persist in highly modified habitats. A major aim of our study was to compare survival and population growth for river and lake populations. Unfortunately, this aim was hampered by a lack of consistent, multi-year samples for most of the lake populations. What our surveys have revealed is that snakes are currently able to persist in lakes, albeit at lower numbers (Table 1).

Extinction risk is governed by a myriad of factors that include geographic range size (Gaston, 1994), population size (Pimm et al., 1988), life history strategy (Webb et al., 2002), degree of specialization, and such anthropomorphic factors as amount of ecological overlap with humans where there is competition for space and resources (Hunter, 2002). Populations that experience high temporal variance in finite rates of increase ( $\lambda$ ) tend to be more susceptible to extinction based on stochastic fluctuations in population size (Lewontin and Cohen, 1969). One specific prediction links population density and life history: at low population densities, species that are short-lived, grow rapidly and are quick to mature, are at greater risk of extinction than large-bodied, slow-growing, late-maturing species (Pimm et al., 1988). Concho Water Snakes are fast-growing, early-maturing colubrids that are relatively short-lived. Under natural conditions in rivers, they can occur at high densities (unpubl. data), suggesting relatively low extinction risk. However, in reservoir systems they tend to occur at relatively low densities, suggesting that they may be more vulnerable to extinction in such locations. Since our primary survey period, west central Texas has suffered a prolonged, severe drought. Although our analyses have revealed low survival rates in the period prior to the drought, Concho Water Snakes are still persisting in both rivers and reservoirs, even in areas that experienced almost total water loss (Lake Ballinger). It is likely that the Concho Water Snake has evolved in a drought-prone, hydrologically dynamic system and is therefore equipped to handle stochastic environmental fluctuation. What is poorly understood is the contribution of movement to metapopulation dynamics and the likelihood of local recolonization of lower quality habitats. The difference between our asymptotic and directly estimated  $\lambda$ s suggests that movement is an important determinant of population dynamics on our study sites. Future studies addressing dispersal rates among subpopulations and the influence of dispersal on population persistence in degraded habitats would be invaluable.

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