Measuring snake activity patterns: The influence of habitat heterogeneity on catchability

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Abstract. Activity patterns for two populations of the Concho water snake (*Nerodia harteri paucimaculata*) were studied in a large lake system in central Texas, USA, and compared to a river population. Trap data suggested different activity patterns for the two geographically proximate lake populations. Testing of the trap data using the program CAPTURE revealed differences in catchability rather than activity cycles. Based on these results, the apparent activity patterns for one of the lake sites was considered erroneous; and the differences in catchability were ascribed to habitat differences. It is suggested that future studies should incorporate a test of equal catchability when making interpopulational comparisons.

Introduction

Sampling of snake populations and communities is typically difficult due to the intractable nature of snakes in general (Fitch, 1987; Parker and Plummer, 1987; Shine, 1987). This difficulty often saddles the researcher with insufficient sample sizes resulting in analyses incorporating several different age and/or reproductive classes, masking intra- and interpopulational differences in life history traits. Because life history traits often differ as much within a population as they do between populations, any population level analysis must account for differences between the appropriate population subsects (Macartney et al., 1988; Reinert, 1992; Secor, 1992, 1994). Also, interpopulational comparisons are hampered by differential adaptive responses of snakes to local environmental conditions (Gregory et al., 1987; Plummer and Congdon, 1994).

One confounding factor related to population level comparisons is that of habitat structure. When interpopulational habitat heterogeneity exists, a sampling design appropriate for one population may not be appropriate for another—radiotelemetric studies not withstanding. Herein we describe an instance where two disjunct populations of the Concho water snake (*Nerodia harteri paucimaculata*), from the same lake system, provided conflicting data on seasonal activity patterns due to differences in catchability between the

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two populations. Unfortunately this problem was detected *a posteriori*, therefore the hypothesis that differences in activity patterns between the two sites were real, and not an artifact of sampling, was not rigorously tested in the field. Instead, we test our capture data using equal catchability tests to determine if a real difference in activity patterns existed between the two populations. This paper also characterizes activity cycles for lacustrine snakes, with comparison to a river site; detailed analyses of riverine Concho water snake activity cycles and analysis of proximate environmental factors will be presented elsewhere (Greene in prep.; see also Greene, 1993).

Nerodia harteri, the only endemic Texas snake, is a relatively small natricine found in the upper reaches of two river basins. The Brazos water snake (*Nerodia h. harteri*) is restricted to the upper Brazos River drainage while the Concho water snake (*Nerodia h. Paucimaculata*), is primarily restricted to about 25 km of lake shore and about 396 km of shoreline along the Concho-Colorado River drainage of central Texas (Scott et al., 1989). Due to its conservation status, a number of studies have been conducted on this snake (references in Greene, 1993). The low vagility and relatively high local abundance of the Concho water snake makes it amenable to a variety of ecological studies, including activity cycles.

Materials and methods

Study area

Primary field work took place at E. V. Spence Reservoir (hereafter referred to as Spence). At the time of study, Spence was a 21-year-old reservoir of 14950 ha surface area at maximum pool level, located in Coke County, Texas (fig. 1). The shoreline was devoid of vegetation, generally consisted of a silt substrate, and was rocky in some areas. Spence was a dynamic system constantly fluctuating in elevation (see Whiting, 1993), causing variation in habitat availability.

Two primary study sites were selected at Spence (fig. 1). The two sites were disjunct, and based on recapture records no evidence of population exchange was found. Pump Station was located on the northwestern shoreline, facing the main body of the lake. Pecan Creek was located in the upper reaches of the lake, in a more sheltered environment. The differences in location resulted in Pump Station receiving more intensive wave action from winds blowing off the main body of the lake, than Pecan Creek. Another important site difference was the abrupt shoreline at Pump Station, compared to the more gradual shoreline of Pecan Creek. Both sites were characterized by rocky shorelines devoid of vegetation; however, when the lake rose in 1992, the new shoreline at Pecan Creek entered a growth of salt cedar with less exposed rock.

Cervenka Dam, a site on the Colorado River located near the junction of Coke and Runnels Counties, Texas, is included for comparison as a river locality. Cervenka Dam was considered an artificial riffle because the dam was constructed more than 20 years

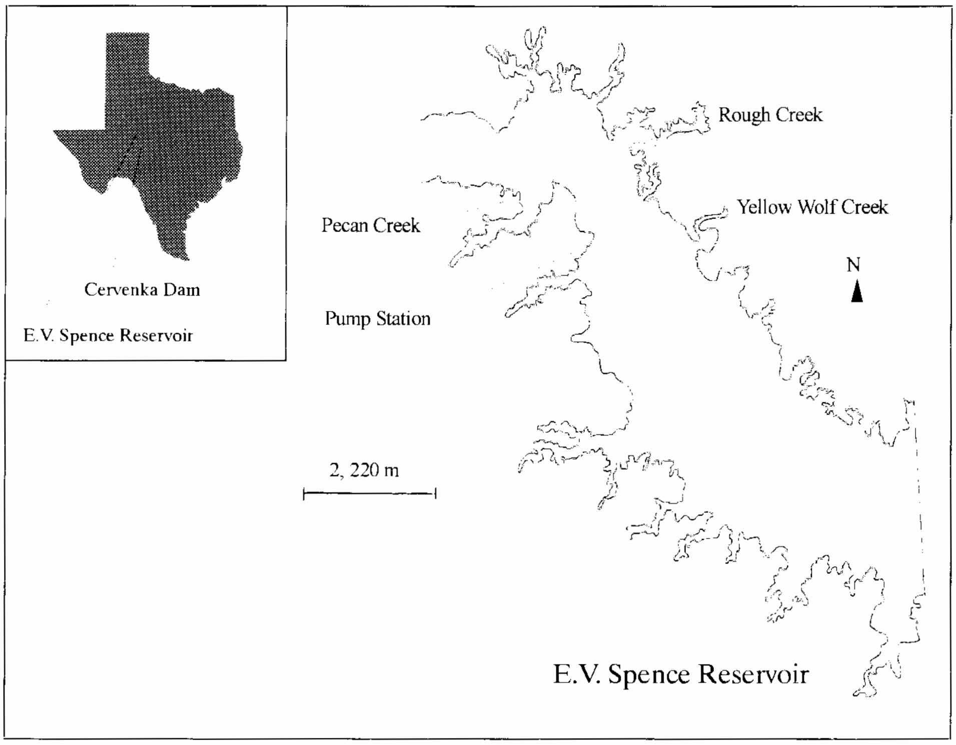

Figure 1. Map of study sites; the inset shows the location of study areas in the state of Texas.

prior to our investigation (J. Cervenka, personal communication), by partially blocking the river with slabs of rock. Long pools occurred for several kilometers upstream and downstream of the riffle.

Data analyses

Seasonal activity patterns were investigated using funnel traps (commercially available minnow traps). Unbaited traps were placed along the shoreline at Spence; at Cervenka Dam traps were placed along each river bank and adjacent to rocks within the riffle. The number of traps set varied according to site, and depended on weather conditions and water levels. For any one site, as few as 10 and as many as 35 traps were set. Capture success, the ratio of the number of snakes caught divided by the number of trap-days (as a percentage), was used as a measure of snake activity. Activity was assessed from mid-May to the end of August, for a single season (1991).

Activity (trap) data were analyzed by life history category using SVL. Snakes were placed in the following life history categories based on size at maturity and/or reproductive condition: (1) juveniles (males under 380 mm SVL, females under 460 mm

SVL); (2) adult males; (3) nongravid adult females; and (4) gravid females. Because most adult females were gravid, nongravid females were excluded from analysis due to small sample size. Additionally, nost neonates (average parturition in August) were only large enough to be caught in traps the following spring. Some individuals were captured multiple times in a single month. In cases where a snake was captured on consecutive days, the second capture was discarded.

CAPTURE (Vers. 30 Dec 1991; Otis et al., 1978), a program for the demographic analysis of closed populations, contains a model selection procedure that detects various forms of capture heterogeneity. Variation in the probability of capture is examined by: (1) capture probability varying with time, Model M_t, (2) capture probability varying by behavioral response, Model M_b, and (3) capture probability varying by individual animal, Model M_h. In addition to the above three models, all possible combinations are considered by CAPTURE (i.e. Models M_{tb}, M_{th}, M_{bh}, and M_{tbh}); if capture probability is constant, the "null" case, Model M_o, is selected. By allowing for changes in capture probability over time, Model M_t accounts for differences in seasonal catchability; for example during the heat of summer snakes are typically less active (Greene, 1993). Model M_h allows for variation in capture probability due to a behavioural response or "capture history". Under Model M_h, individual capture heterogeneity may occur due to individual accessibility to traps (as a function of an individual's activity range), or due to differences in age or sex (Otis et al., 1978). Capture heterogeneity was compared between snakes of similar age but from different sites, in an attempt to evaluate the validity of the activity data for the Spence populations as revealed by funnel traps.

Statistical analyses were performed using the Statistical Analysis System (SAS Institute Inc., 1989). The procedure CATMOD with orthogonal comparisons were used to test for differences in capture frequency by site and cohort. This procedure provides a method for performing analysis of variance on frequency data. Differences were considered significant at the 0.05 alpha level.

Results and discussion

Activity patterns

Activity patterns as a function of capture success, are presented for juveniles, adult males, and gravid females in table 1. Pecan Creek and Cervenka Dam had the greatest trapping success, and this data probably more accurately reflects Concho water snake activity patterns. Trapping success at Pump Station was far poorer, and alone, appeared to be an inadequate technique for the measurement of activity patterns.

A large amount of literature exists on snake activity patterns and movements; however, much of it is anecdotal and a number of crucial gaps still exist (Gibbons and Semlitsch, 1987). One such area is information on the activity patterns of juvenile snakes relative to adults, as only a few studies have made this distinction. Due to the smaller size

Table 1. Monthly activity patterns revealed by trapping, for juvenile, adult male, and gravid female Concho water snakes for 1991. Capture rates were calculated as the number of captures divided by the number of trap-days ×100. The numbers in parentheses represent the actual number of snakes caught. PC = Pecan Creek; PS = Pump Station; and CD = Cervenka Dam. Trapping data from Pump Station should not be regarded as an indication of activity patterns (see text).

Month	Juveniles			Adult males			Gravid females		
	PC	PS	CD	PC	PS	CD	PC	PS	CD
May	4.4 (14)	0.6 (4)	2.9 (3)	4.4 (14)	1.4 (9)	3.8 (4)	2.2 (7)	1.4 (9)	2.9 (2)
June	4.4 (29)	0.7 (4)	8.5 (12)	2.6 (17)	1.2 (7)	4.5 (8)	2.0 (13)	0.7 (4)	1.0 (2)
July	4.6 (24)	1.4 (7)	3.3 (11)	1.2 (6)	1.8 (9)	3.3 (11)	1.7 (9)	1.4 (7)	1.5 (4)
August	2.0 (17)	0.5 (4)	2.5 (3)	0.4 (3)	1.2 (9)	3.4 (3)	2.1 (17)	1.0 (8)	3.4 (4)

of juveniles and their absence from activities associated with reproduction, they are presumably under different selective pressures. Accordingly, juveniles may devote larger amounts of time to feeding to assimilate energy for growth. The relatively uniform activity level of juveniles throughout the activity season perhaps reflects the high level of feeding necessary for rapid growth. Concordantly, juveniles in the Colorado River exhibited little seasonality to their activity (Greene, 1993). This is in contrast to adult males who were primarily active in May-early June, at the end of the mating season. Greene (1993) reported late April and early May as a peak activity period for male Concho water snakes, overlapping the mating period. Unfortunately, our April samples were limited to shoreline searches, a less effective technique for sampling adult Concho water snakes than trapping. Gravid females were equally active in the months sampled. However, the greatest number of gravid females were caught in August (table 1). In the river system, adult female activity peaked during late August and September, the postpartum feeding period prior to hibernation (Greene, 1993). The classic activity model of high adult male activity during mate location and low adult female activity during gestation (Secor, 1994; and references therein) appears to fit the Concho water snake (see also Greene, 1993).

Capture success is summarized for Spence and Cervenka Dam (table 2). Maximum likelihood ANOVA revealed a difference in capture frequency (activity patterns) by site ($\chi^2 = 29.44$, df = 15, $P = 0.014$), and by cohort ($\chi^2 = 62.47$, df = 15, $P < 0.0001$; intercept: $\chi^2 = 259.32$, df = 5, $P < 0.0001$; likelihood ratio: $\chi^2 = 47.78$, df = 45, $P = 0.36$). Differences in capture frequency between cohorts was expected because snakes from different age/sex classes typically behave differently (e.g. Reinert, 1992); this was not evaluated further (see Whiting, 1993). A specific treatment comparison of Pecan Creek and Pump Station, using contrasts of maximum likelihood estimates, showed capture frequency to be significantly greater at Pecan Creek ($\chi^2 = 15.37$, df = 5, $P =$ 0.0089). Differences in capture frequency between the Spence sites and Cervenka Dam were nonsignificant ($P > 0.05$). Radiotelemetry at Spence provided additional evidence for differences in catchability between Pecan Creek and Pump Station. Telemetered

Table 2. Trapping success at E. V. Spence Reservoir and Cervenka Dam for adult and large juvenile Concho water snakes, for a single year (1991). Numbers in parentheses are numbers of individuals.

Location	Trap-days	#Captures	Capture success
Pecan Creek	2011	169 (52)	0.084 = 8.4%
Pump Station	2048	71 (37)	0.035 = 3.5%
Cervenka Dam	675	67 (39)	0.099 = 9.9%

snakes at Pecan Creek were captured in minnow traps significantly more often ($\chi^2 = 7$, df = 1, $P < 0.01$) than at Pump Station.

Capture heterogeneity

Differences in capture frequency may be ascribed to one of two sources: either a real difference in activity patterns existed, or the populations were not equally catchable. The actual numbers of snakes caught at Pecan Creek and Pump Station were very similar over the two year period (table 3; Whiting, 1993) and, given the close proximity of the two lake sites, it is unlikely that a real difference in seasonal activity patterns existed, as suggested by the trap data. Therefore, catchability of snakes belonging to the three populations was evaluated by comparing snakes of the same age class, using CAPTURE. Model selection by CAPTURE was remarkably similar for the Pecan Creek and Cervenka Dam populations, but different from that of Pump Station (table 4). The similarity in model selection (and therefore catchability of individuals), between Pecan Creek and Cervenka Dam, appears to be correlated with habitat. Water turbidity was high at Cervenka Dam and Pecan Creek, while the water at Pump Station was typically clear. The shoreline at Pump Station was abrupt, compared to a relatively gradual shoreline at Pecan Creek; Cervenka Dam was a riffle adjoined by shallow pools. Possibly the most important physical factor causing a difference in catchability between the Spence populations was wave action. Pump Station received constant wave action due to a predominantly southeasterly wind, while Pecan Creek received minimal wave action due to the sheltered nature of its environment. Wave action in the immediate area of the trap presumably influenced catchability. This is further supported by observations of snakes released into shoreline waves, during which they struggled against the repeated wave action.

When model selection by program CAPTURE was compared between Pecan Creek and Pump Station, for the same cohorts, different models were selected for all but one cohort (table 4). This suggests that the two populations experienced different capture probabilities; and therefore, a different sampling protocol would be necessary to adequately assess activity patterns for the Pump Station population. Radio telemetry would avert sampling problems at Pump Station for adults, but because of size constraints, juveniles and subadults would be precluded from telemetric monitoring, although radio transmitters are becoming increasingly smaller and sophisticated. Unfortunately, radio

Table 3. Actual numbers of snakes (males : females) caught by hand and funnel trap at E. V. Spence Reservoir and Cervenka Dam, over a two year period. See Whiting (1993) for a breakdown by age and sex.

Location	1990	1991
Pecan Creek	46 : 42	45 : 49
Pump Station	42 : 44	41 : 52
Cervenka Dam	44 : 32	55 : 50

Table 4. Results of model selection by program CAPTURE for the Spence and Cervenka Dam populations. In some instances CAPTURE selected a second model; the model selection value is given in parentheses beside the model.

Study site	Cohort	Sample period	Model
Pump Station	1988†	21 May '90-13 May '92	M_h
	1989	21 May '90-15 May '92	M_h
	1990	31 Aug '90-14 Jun '92	M_h
			M_{th}(0.98)
	1991	06 Aug '91-10 Jun '92	M_{th}
Pecan Creek	1988†	06 Jul '90-16 Apr '92	M_h
	1989	06 Jul '90-23 May '92	M_o
	1990	18 Aug '90-23 May '92	M_{tbh}
	1991	20 Aug '91-16 Apr '92	M_{th}
Cervenka Dam	1988†	19 Jun '90-12 Jun '92	M_o
			M_h(0.92)
	1989	19 Jun '90-08 Jul '92	M_o
	1990	13 Aug '90-08 Jun '92	M_o
	1991	29 Jul '91-21 Jun '92	M_{th}

†Includes snakes born prior to 1988.

telemetry as a means of monitoring snake activity patterns becomes prohibitively expensive with increasing sample size. Radio telemetry also provides a further test for heterogeneity in capture that can be applied to interpopulational comparisons.

Gibbons and Semlitsch (1987) identified a bias towards studying readily identifiable, conspicuous species; adding that the development of snake activity models was thereby constrained. Based on the results of this study we further advocate tests of capture heterogeneity for interpopulational comparisons (for nontelemetric sampling), similar to those proposed by Parker and Plummer (1987) for snake demographic studies. Other factors such as prey and predator density may be important factors distinguishing activity patterns between populations, particularly when the geographic locations are distant.

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