

Relevance of Life-History Parameter Estimation to Conservation Listing: Case of the Sharp-tailed Snake (*Contia tenuis*)

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ABSTRACT.—Optimizing conservation efforts requires distinguishing between rare and potentially endangered species (few extant individuals, functionally rare) and species that are difficult to find (operationally rare). Certain suites of life-history parameters such as slow growth, late maturity, low fecundity, and long interbreeding intervals are thought to be associated with functional rarity and with intrinsic vulnerability to population declines. We estimated life-history parameters by using capture-recapture data of one such elusive species, the Sharp-tailed Snake (*Contia tenuis*), from 1997 to 2005 in northern portions of its range in British Columbia, Canada. Body size ranged from 84 mm (smallest juvenile) to 323 mm (largest female). Mean snout–vent lengths were 212 ± 14 mm (mean \pm SD) for adult males and 251 ± 28 mm for females. They were slow growing (adult growth rate, 4.3 ± 3.8 mm/yr), had extended time-to-sexual maturity (5–6 yr), and had small clutch size (3.6 ± 1.1 eggs). Estimated adult survival was 0.71 (95% confidence interval [CI] = 0.59–0.81). Estimated population growth rate for one population over the 8-yr study period was 0.89 (95% CI = 0.79–1.1). Compared with populations farther south and other similarly sized colubrid snakes, Sharp-tailed Snakes at our study site exhibited many “slow” life-history traits that could increase their vulnerability to population declines. Our analysis validated Sharp-tailed Snakes as a species of conservation concern in British Columbia with traits that could lead to functional rarity and highlighted research into mortality, migration, and recruitment patterns as key needs for conservation planning.

Distinguishing between rare and potentially endangered species (few extant individuals, functionally rare) and just elusive species that are difficult to find (operationally rare) is an overlooked problem in conservation biology (McDonald, 2004; Hoyer et al., 2006; Christy et al., 2010). Species that are difficult to find are sometimes perceived as rare and are therefore also rated to be of high conservation concern. For example, the Coeur d’Alene Salamander (*Plethodon idahoensis*) was listed as “critically imperiled” in British Columbia in 1993 and then rose rapidly through the conservation listings as survey methods for this species improved, until it was listed as “apparently secure” in 2007 (British Columbia Conservation Data Centre, 2009), even though threats or population trends had changed little over this time. Other examples of this trend include plants (*Corydalis scouleri* and *Hackelia ciliata*) and insects (*Coenagrion interrogatum*, *Somatochlora cingulata*, and *Lestes forcipatus*; Ramsay and Cannings, 2005; British Columbia Conservation Data Centre, 2009). To optimize conservation efforts, it is necessary to distinguish between functionally rare and operationally rare species, although the two are not mutually exclusive (Partel et al., 2005; Fontaine et al., 2007).

A species can be difficult to find because it is fossorial or nocturnal, is inactive for long periods, or has large home ranges (Parker and Plummer, 1987). These factors also often contribute to a poor understanding of a species’ ecology and life history (Eggert et al., 2003; Bellemain et al., 2005; Whitman et al., 2006). Information on ecology and life history can help distinguish true rarity and endangerment from just elusiveness (Reed and Shine, 2002). Certain suites of ecological and life-history traits, such as slow growth, late maturation, long interbirth intervals, and small litters, make some species rarer and also more vulnerable to population declines (Webb et al., 2002; Oli, 2004; Bekker and Kwak, 2005; Cofre et al., 2007). A species that is difficult to find that possesses these “slow” life-history traits (Oli, 2004) can warrant ranking as a species of conservation concern. A good example of such a species is the Sharp-tailed Snake (*Contia tenuis*), ranked as a species of conservation concern in parts of its range (NatureServe, 2009). However, this designation is questioned by some who argue that the snake

may be difficult to find but is neither rare nor a species of conservation concern in some areas (Hoyer et al., 2006).

The Sharp-tailed Snake is a small (20–30 cm snout–vent length [SVL]), semifossorial snake that was first described from specimens collected in the state of Washington in 1852, and it remained almost unknown until the mid-20th century (Cook, 1960). At the northern limits of its range in Canada, the species is designated as “endangered” because of its restricted geographic range in British Columbia, and because it occurs in disjunct populations in areas under heavy development pressure (Leonard and Ovaska, 1998; COSEWIC, 2010). At the time of its initial assessment, it was known from only 11 records from southern Vancouver Island and the Gulf Islands (Spalding, 1993). Although the survey effort over the past 10 yr has increased the number of localities where the snake is found, the life history and ecology of the species remain poorly understood (COSEWIC, 2010).

The primary objective of this study is to provide life-history estimates for the Sharp-tailed Snake by using capture-mark-recapture (CMR) data from a long-term monitoring study and to examine whether this species possesses a suite of life-history traits that would make it intrinsically vulnerable to population declines. We also compare the estimates from our study in the northern limits of the species’ range to available information from the central and southern parts of its range to assess whether regional differences in life-history characteristics can lead to varying perceptions of conservation concern.

MATERIALS AND METHODS

Study Sites.—The Sharp-tailed Snake is known from scattered locations on southern Vancouver Island and the Gulf Islands in British Columbia (COSEWIC, 2010). All known populations in British Columbia occur in the Coastal Douglas-fir Biogeoclimatic Zone (Meidinger and Pojar, 1991), and individuals are mainly found along edges and openings of forests dominated by Douglas-fir (*Pseudotsuga menziesii*), arbutus (*Arbutus menziesii*), and Garry oak (*Quercus garryana*) (Wilkinson et al., 2007; COSEWIC, 2010). Most of these areas are modified by human activity and are typically surrounded by residential developments.

We monitored snake populations for various durations from 1997 to 2005 at four study sites on North Pender Island, on

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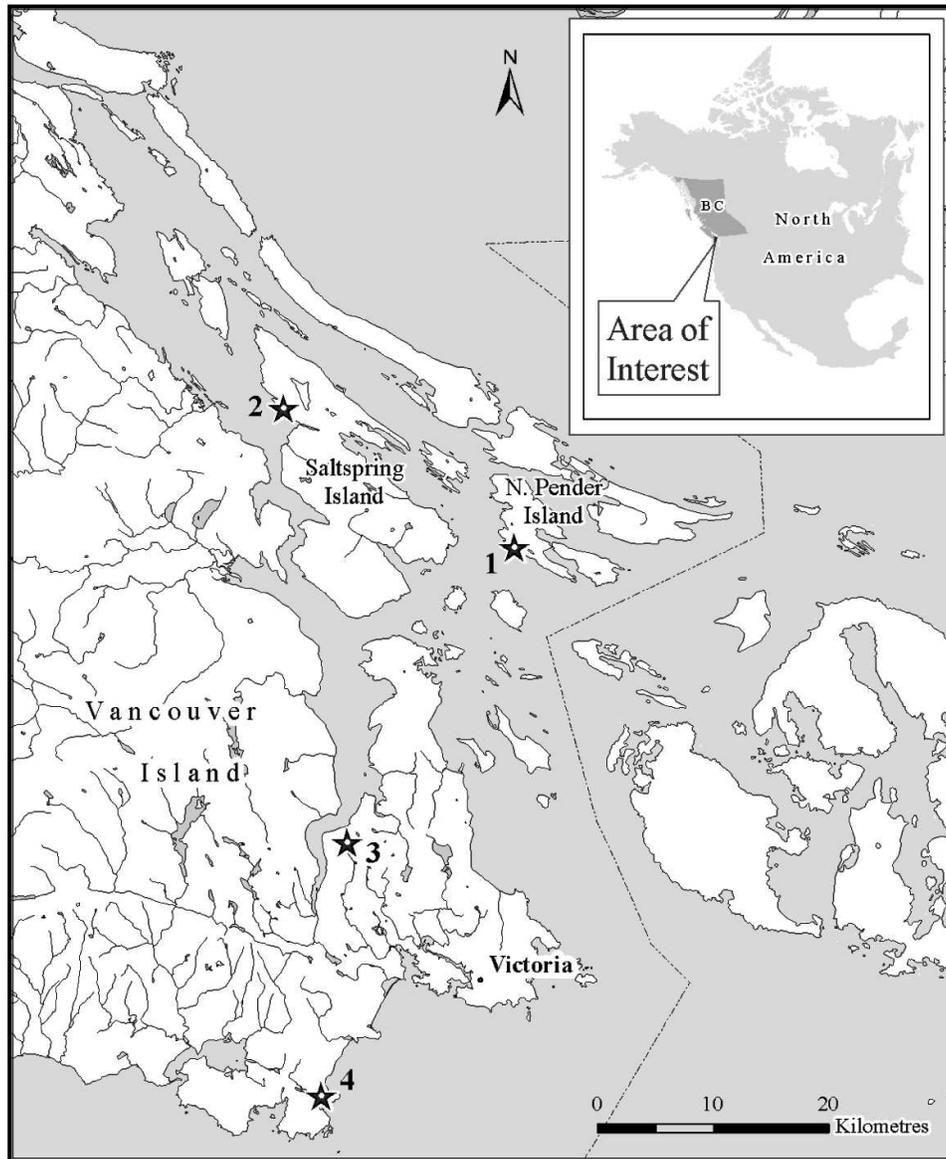


FIG. 1. Location of Sharp-tailed Snake study sites: North Pender Island (1), Saltspring Island (2), Cole Hill (3), and Mary Hill (4).

Saltspring Island, and on Mary Hill and Cole Hill on Vancouver Island (Fig. 1; Table 1). At each site, we installed 0.6×0.6 -m artificial cover objects (ACOs) made of asphalt roofing (50 lb [22.7 kg]), which is an accepted sampling method for these snakes (Engelstoft and Ovaska, 2000). We inspected ACOs from March to November, focusing on peak activity periods in the spring–early summer (March–June) and fall (September–October; Ovaska and Engelstoft, 2008). The number of visits varied among sites and years: >30 times per year in 1997 and 1998 at North Pender Island and Saltspring Island, to approximately 10 times per year at the other sites in other years (Table 1). Such variation in sampling effort resulted from

logistical constraints, mainly due to funding pressures. In the CMR analysis, variation in sampling effort is taken into account.

Upon capture, we measured SVL and determined mass and sex of each individual. Sex was determined using tail shape, width at tail base, and tail length in relation to body length (Fitch, 1960). Toward the end of the project, we verified sex of larger individuals by everting the hemipenes (Gregory, 1983). Due to our inability to determine sex of small individuals (<180 mm SVL) with confidence, we classified all individuals below this size as either small juveniles (<120 mm) or large juveniles (120–180 mm). We assessed reproductive condition

TABLE 1. Sites where CMR population monitoring was conducted using ACOs. The duration of monitoring (years) and density of ACOs per 1,000 m² varied among sites. The total number of individual snakes (N) seen at each site is indicated along with the number of snakes that were seen again at least once following initial capture (R). Mean \pm SD SVL and weight of adults are shown for each site.

Site	Area (m ²)	Yr	ACO density/1,000 m ²	N (R)	SVL (mm)	Mass (g)
North Pender Island	733	1997–2004	8.2	38 (16)	236 \pm 28	6.5 \pm 2.3
Saltspring Island	983	1997–1998	36.6	18 (7)	236 \pm 43	5.8 \pm 2.6
Cole Hill	11,950	2004–2005	7.9	19 (6)	211 \pm 9	4.8 \pm 0.5
Mary Hill	20,435	2004–2005	4.7	13 (6)	209 \pm 16	4.7 \pm 1.3

by gently palpating the lower abdomen of each female and counting oviductal eggs or enlarged follicles to estimate clutch size (Santos and Llorente, 2001). Then, we photographed the unique markings on the chin and tail region of each snake to allow for individual identification, and we released the snake at the original capture location.

Data Analysis.—Due to the small number of snakes captured at three of the study sites, it was not always possible to test for differences among sites. We calculated growth rate estimates from snakes that were repeatedly captured over the sampling period and pooled estimates of growth rate across sites. We used increases in SVL to estimate growth rate because measurements of mass for the same snakes were more variable, probably as a result of recent feeding, body condition, and reproductive status. We estimated growth rate only for large juveniles (≥ 120 mm SVL) and adults; we did not recapture any of the smaller individuals. When animals were captured multiple times, we used only one estimate of that individual's growth rate calculated as the SVL at last capture minus SVL at first capture divided by the number of years between first and last capture (Aresco and Guyer, 1999). Due to the lack of age estimates, we plotted growth rate against the individual's average SVL over the growth interval (Aresco and Guyer, 1999). We compared difference in growth rate between males and females by using analysis of covariance (ANCOVA; Stanford and King, 2004), including juvenile growth rates twice with both male and female growth rates (Aresco and Guyer, 1999). To test that increased sample size from using juvenile growth rates twice in the analysis did not bias our results, we repeated the ANCOVA by sorting the juveniles by SVL and alternately assigning half of them to males and half to females, and then reversing the order of assignment. The results were similar in all analyses, providing confidence in the robustness of the analysis. Only results from the first analysis are shown.

We estimated time to sexual maturity from direct observation of snakes that were captured repeatedly and by using estimated growth rates to infer the time a hatchling snake would need to reach adult size. We estimated fecundity by counting eggs in gravid females. Life expectancy was calculated as follows: $-1/\ln(\text{annual survival rate})$ (Brownie et al., 1985; Schaub and Vaterlaus-Schlegel, 2001). We also present expected number of years of survival for 25 and 10% of the population as indicators of longevity (Claisse et al., 2009).

Only one site (North Pender Island) provided sufficiently long-term data to enable estimation of survival rates and population trends. Ovaska and Engelstoff (2008) presented preliminary survival estimates from these data but did not examine factors that affect survival and capture probabilities. Our analyses followed protocols described in Lebreton et al. (1992). Survival and capture probabilities, population size, and realized population growth rate were estimated using maximum-likelihood methods implemented in program MARK (White and Burnham, 1999). The CMR modelling method accounts for the fact that not all marked living individuals are recaptured at every sampling occasion and separates survival probability from recapture probability, wherein recapture refers to the probability of capturing an individual given that it is alive and in the study area on that occasion (Lebreton et al., 1992; Mazerolle et al., 2007). This method cannot distinguish permanent emigration from mortality.

We used the Cormack-Jolly-Seber (CJS) model that estimates survival and recapture probabilities separately for each year and for each size/sex class (Lebreton et al., 1992) as the starting point for model selection. Subsequently, we constructed simpler models using factors thought to affect survival and recapture rates, and we used these factors to frame hypotheses that were expressed as an a-priori set of alternate models (Anderson et al., 2000). For this analysis, we modeled yearly

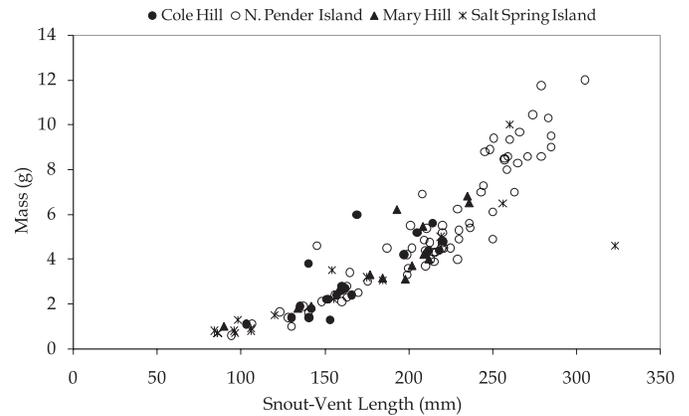


FIG. 2. Mass (g) versus SVL (mm) for all snakes captured at each of the four sites from 1997 to 2005: Cole Hill, $n = 20$; North Pender Island, $n = 69$; Mary Hill, $n = 15$; and Salt Spring Island, $n = 17$. A greater number of large and heavy snakes were caught at the North Pender Island site, and most of the smallest snakes were caught at the Salt Spring Island site.

survival probability as dependent on size (SVL), size/sex class (male, female, and juvenile), varying over the years and constant over the years of the study. We modeled recapture probability as dependent on number of capture days per year, number of ACOs inspected over the year, varying independently over the years and remaining constant over the years.

We used information-theoretic methods to estimate the formal likelihood of each model given the data and rank support for each model (Anderson et al., 2000; Mazerolle, 2006), and we based model selection on the sample size adjusted Akaike's Information Criterion (AIC_c) (Burnham and Anderson, 2002). AIC_c mediates the trade-off between deviance explained and the number of parameters used, and simulations have shown that this method is better at recovering the true underlying model compared with likelihood ratio tests (Burnham et al., 1995). The model with the lowest AIC_c value is the model best supported by the data. Akaike weights indicate the support from the data for a particular model relative to the other models in the set, and sum up to 1 across all models. The ratios between the Akaike weights of two models give their relative support (e.g., a model with Akaike weight of 0.5 is twice as well supported as a model with Akaike weight of 0.25).

The CMR modeling approach assumes equal probability of survival and recapture among individuals within a recapture interval. These assumptions were tested for the starting CJS model by using a bootstrap goodness of fit analysis with 500 replicates, using program RELEASE implemented within MARK (Burnham et al., 1987). No significant deviations from assumptions were detected ($P = 0.29$). Comparison of means were done with t -tests and one-way analysis of variance (ANOVA) using SPSS for Windows, Release 16.0 (SPSS, Chicago, IL). We assessed significance at $\alpha = 0.05$. Results are presented as mean \pm SD.

RESULTS

Body Size.—SVL of the smallest snakes captured was 85–95 mm (weight = $0.8 \text{ g} \pm 0.2$, $n = 10$), and these small individuals were assumed to be hatchlings. The largest snake measured 323 mm SVL (weight = 12 g; Fig. 2) and was female. Adult males were significantly shorter and lighter than adult females (male SVL = 212 ± 14 mm, $n = 40$; female SVL = 251 ± 28 mm, $n = 37$; $t_{75} = 7.9$, $P < 0.001$; and male mass = 4.6 ± 0.9 g, $n = 38$; female mass = 7.6 ± 2.2 g, $n = 35$; $t_{71} = 7.6$, $P < 0.001$). A greater number of large adults were captured at

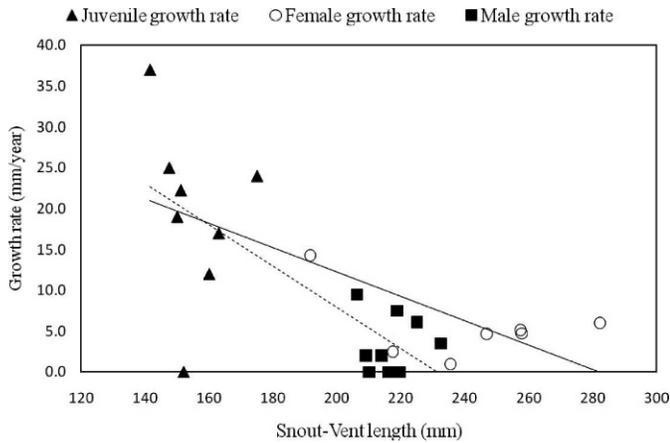


FIG. 3. Growth rate (mm/yr) versus size (SVL) for juveniles, adult females, and adult males based on snakes recaptured from 1997 to 2005. Juveniles had a higher growth rate than adults and growth rate started to asymptote at approximately 180 mm SVL, presumably indicating the attainment of sexual maturity. Adults of both sexes had comparable relative growth rates.

North Pender Island compared with the other sites (SVL: $F_{3,73} = 4.0$, $P = 0.01$; weight: $F_{3,69} = 3.0$, $P = 0.03$; Fig. 2). Summing across all years, a very small proportion of the snakes captured were in the small juvenile class (<120 mm SVL) at all sites (North Pender Island, 3%; Cole Hill, 5%; and Mary Hill, 7%), except at Saltspring Island, where 40% of the snakes captured were in this size class (Fig. 2).

Growth.—The mean growth rate of large juveniles (120–180 mm SVL) was 19.5 ± 10.7 mm/yr ($n = 9$) and declined with SVL until we were able to accurately tell sexes apart at approximately 180 mm (Fig. 3). The mean growth rate of adult females and adult males was 5.5 ± 4.3 mm/yr ($n = 7$) and 3.3 ± 3.4 mm/yr ($n = 9$), respectively. Although growth rate declined significantly with SVL, there were no detectable differences between males and females (Fig. 3; Table 2A–B).

Reproduction.—We found gravid females from March to early May. Two females were recaptured regularly over the 7 yr and were not gravid in all years, suggesting that individual females may not breed annually; average laying frequency cannot be calculated due to low recapture rates. The mean SVL of gravid females was 260 ± 22.5 mm, and their mean weight was 9.0 ± 2.4 g ($n = 16$). The smallest gravid female measured 219 mm SVL (5 g), and the largest gravid female measured 305 mm SVL (12 g). Palpation through the abdominal wall suggested a mean clutch size of 3.6 ± 1.1 eggs. However, this estimate should be interpreted with caution because it is easy to miss eggs when palpating through the body wall (false negatives), and it is also possible that some enlarged follicles that we counted as eggs may be resorbed before egg maturation and laying (false positives; Gilman and Wolf, 2007).

Time to sexual maturity was extrapolated using size-specific growth rates. We did not recapture any juveniles <120 mm SVL and so could not estimate their growth rate; therefore, we used the maximum estimated growth rate of 30 mm/yr (Fig. 3) for these small juvenile snakes. Based on this rate, it would take the smallest observed snakes (84 mm) approximately 2 yr to reach the size at which repeated recapture made it possible to directly estimate growth rates (>120 mm SVL). Using the average juvenile growth rate (19 mm/yr), it would then take 3 yr for these large juveniles to reach the size at which we could reliably determine the sex of the snakes (180 mm). This extrapolation is supported by two snakes that were captured as large juveniles (156 and 140 mm SVL) and took 3 yr to reach adult size. Therefore, the best conservative estimate of time to

TABLE 2. ANCOVA of growth rate with sex as a factor and SVL as a covariate. Large juvenile (>120 mm) growth rates were included in both male and female growth data sets. Test for equality of slope (A) and intercept (B).

Source	Sum of squares	df	Mean square	F	P
A					
Sex \times SVL	122.495	1	122.495	1.91	.177
Sex	80.662	1	80.662	1.26	.271
SVL	1864.481	1	1864.481	29.15	.000
Error	1790.954	28	63.963	1.91	.177
B					
Sex	90.220	1	90.220	1.36	.252
SVL	1750.045	1	1750.045	26.52	.000
Error	1913.448	29	65.981		

reach size of sexual maturity is 5 or 6 yr and may be longer given that the minimum size of gravid females is 219 mm.

Survival.—The top five models were relatively equally supported, whereas the remaining models had no support (Table 3; models with AIC_c weights <3% are not shown). There was variation in capture probability over the years (model 2). This variation can be explained in some measure by capture effort (number of capture days over the year or number of ACOs inspected, models 1 and 3–5, respectively).

Those models where survival probability was constant for all individuals over all years (models 2, 3, and 5, sum of AIC_c weights = 49%) were only slightly better supported than models where survival rates were correlated with SVL (models 1 and 4, sum of AIC_c weights = 37%). Model-predicted annual survival rates showed a positive correlation with SVL and ranged from 66% for small juveniles (95 mm SVL) to 75% for large adults. Mean survival for all size classes was 0.71 (95% confidence interval [CI] = 0.59–0.81). There was no evidence that survival rates of males and females differed (females: 0.73, 95% CI = 0.53–0.87 and males: 0.74, 95% CI = 0.56–0.87; model not shown in Table 3 because AIC_c weight was <3%).

Life Expectancy.—The average life expectancy of Sharp-tailed Snakes at North Pender Island was 2.9 yr (95% CI = 1.9–4.7). Life expectancy calculated from mean annual survival rates indicates the average length of time an individual in the population is expected to survive. Some snakes can survive for much longer than this average, and 25% of the population is expected to survive for 5 yr and 10% of the population up to 8 yr. This is supported by field observations at this site where five of the individually identified snakes first caught as adults continued to be recaptured even six years after initial capture.

Population Density and Population Growth Rate.—There were insufficient data to estimate population size and trends in all sites except North Pender Island. We estimated the mean population size at North Pender Island at 49 individuals (95% CI = 43–65). The entire area surveyed was approximately 1 ha, but the species was found only within an area of 733 m², resulting in a density estimate of 0.067 snakes/m² within the occupied patch. The mean realized growth rate (N_{t+1}/N_t) of this population was estimated at 0.89 (95% CI = 0.79–1.1). Although λ is <1, which suggests that the population is declining, the CI overlaps 1.

DISCUSSION

Recent morphological and molecular evidence suggests that there are two species within the range limit of the nominal taxon *C. tenuis* (Hoyer, 2001; Feldman and Spicer, 2002; Feldman and Hoyer, 2010), a northern coastal clade and a southern interior clade in southern Oregon and California (Feldman and Spicer, 2002). Sharp-tailed Snakes in British Columbia belong to the northern clade. Although Sharp-tailed

TABLE 3. Model selection for survival rate and recapture probability estimation by using CMR data from North Pender Island (1997–2003). Model factors are shown in parentheses for each parameter. Φ = survival rate; p = recapture rate; SVL = dependent on SVL; (c) = held constant for all years/capture-occasions; (t) = different for each year/capture-occasions; capdays = number of capture days per year; ACO = number of ACOs checked per year. AIC_c = sample size adjusted Akaike's Information Criterion, where a lower number indicates a better model; ΔAIC_c = difference between the best model and a particular model; Akaike weight = percentage of support for a given model over the set of candidate models; N = number of parameters; and Deviance = model deviance. Only models with Akaike weight >0.03 are shown in the table.

No.	Model	AIC_c	ΔAIC_c	Akaike weight	Likelihood	N	Deviance
1	Φ (SVL) p (capdays)	152.72	0.00	0.22	1.00	4	144.03
2	Φ (c) p (t)	153.02	0.30	0.19	0.86	8	134.35
3	Φ (c) p (capdays)	153.10	0.37	0.18	0.83	3	146.69
4	Φ (SVL) p (ACO)	153.42	0.70	0.15	0.70	4	144.74
5	Φ (c) p (ACO)	153.88	1.16	0.12	0.56	3	147.47

Snakes remain abundant in the central and southern parts of their range in Oregon and California (Hoyer et al., 2006), they are rare and patchily distributed in British Columbia (Leonard and Ovaska, 1998; COSEWIC, 2010). Sharp-tailed Snakes at our study sites at the northern limits of the species' distribution exhibited a suite of "slow" life-history traits associated with intrinsic vulnerability to population declines. Life history and population biology of the species in the United States are poorly known, but some data are available, allowing comparisons of body size, growth, and densities from different parts of the species' range.

Body Size.—Sharp-tailed Snakes in British Columbia were similar in size to snakes in Washington and Oregon but smaller than the new species of *Contia* from parts of southern Oregon and California, where maximum sizes exceed 400 mm (Hoyer, 2001; Feldman and Hoyer, 2010). The size structure of populations depends on a variety of factors, including growth rate and size-specific mortality rates (Parker and Plummer, 1987). Typically, the ratio between adults and juveniles is approximately 4.3:1 in long-lived colubrids (Parker and Plummer, 1987), but this was true only at two of four study sites (North Pender Island and Mary Hill), assuming that body size reflects age structure. The reason for the difference in size structure among Sharp-tailed Snake populations at our study sites remains unclear. We found very few hatchlings and small juveniles, possibly resulting from a methodological bias associated with ACOs, which may favor the capture of larger snakes (Engelstoft and Ovaska, 2000). Only one site (Saltspring Island) had a relatively higher number of small juveniles (Fig. 2). In addition to methodological bias, the poor representation of small juveniles at most of our study sites could represent recruitment failure either due to high mortality rates or dispersal from natal sites, or use of different habitats by young juveniles.

Growth Rate.—Comparison of growth rates of small colubrids (mean adult SVL = 250 mm) suggests growth rates of up to 52 mm/yr (Parker and Plummer, 1987). The maximum estimated growth rate of Sharp-tailed Snakes in British Columbia was <30 mm/yr, although the growth rate of small juveniles (≤ 120 mm) could not be estimated due to low recapture rates (Fig. 3). This growth rate seems to be slow compared with other similar sized fossorial snakes such as the Eastern Ring-necked Snake (*Diadophis punctatus edwardsii*) that exhibits growth rates of approximately 50 mm/yr in the initial years and growth rates >20 mm/yr even after year 5 (Blanchard et al., 1979). The Southeastern Crowned Snake (*Tantilla coronata*) grew from 90 to 130 mm in the first year (Todd et al., 2008), whereas the Eastern Worm Snake (*Carphophis amoenus*) had estimated growth rates from 95 to 170 mm in the first growing season (Willson and Dorcas, 2004).

Most colubrid snakes mature at 60–75% of maximum SVL (Parker and Plummer, 1987), and this seems to match maturation of Sharp-tailed Snakes in British Columbia. The smallest gravid female that we captured was 219 mm SVL and the largest 305 mm SVL. There are no comparable data available from other Sharp-tailed Snake populations, but

comparisons with other fossorial oviparous snakes show similar values: male and female juvenile Eastern Ring-necked Snakes reached 68 and 60%, respectively, of their lifetime growth during the juvenile period (Blanchard et al., 1979). However, compared with other small fossorial snakes (Eastern Worm Snake, maturity in 1 yr [Willson and Dorcas, 2004]; Southeastern Crowned Snake, maturity in 2 yr [Todd et al., 2008]; Eastern Ring-necked Snake, maturity in 4 yr [Clark et al., 1997]), the estimated time to sexual maturity of Sharp-tailed Snakes in British Columbia is relatively long (5–6 yr). Snakes with delayed maturity are particularly vulnerable to population declines and range contractions (Webb et al., 2002).

Reproduction.—In British Columbia, gravid females were captured from March to May, suggesting that eggs might be laid by early summer (June or July). In Washington and California, field-collected gravid females laid eggs in the laboratory in the last weeks of July (Cook, 1960; Nussbaum et al., 1983; Leonard et al., 1996). We found preliminary evidence that individual female Sharp-tailed Snakes may not oviposit every year. Long interbreeding intervals can have a strong effect on population growth rate and can be associated with rarity and susceptibility to population decline (Webb et al., 2002; Horne et al., 2003; Saba et al., 2007).

Our estimated clutch size of 3.6 ± 1.1 eggs closely matches the clutch size of three to five eggs reported for the species previously (Brodie et al., 1969; Leonard et al., 1996). Clutch size in Sharp-tailed Snakes is lower than that recorded for most colubrids (mean \pm SD = 10.2 ± 6.1 eggs) and may simply reflect the constraints of small body size (Seigel and Ford, 1987). Clutch size of Sharp-tailed Snakes is similar to that reported for Eastern Worm Snakes (Willson and Dorcas, 2004) but slightly below average of mean clutch sizes reported for other similarly sized semifossorial snakes (Shine et al., 1996; Marques and Puerto, 1998; Goldberg and Rosen, 1999; Willson and Dorcas, 2004; Shine et al., 2006; Todd et al., 2008).

Survival.—Survival rates predicted from our best-fit model ranged from 66% for juveniles to 75% for large adults. However, a relationship between size and survival rate was not strongly supported by our data, and the size-dependent survival model was only slightly better supported than the model that estimated constant survival rates for all size classes at 0.71 (95% CI = 0.59–0.81). Our estimates are close to the average adult survival rate (0.70) for late maturing colubrids (Parker and Plummer, 1987). Most colubrid snakes show Type II mortality curves with low juvenile survival and fairly constant adult survival (Parker and Plummer, 1987).

The low recapture rate of small juveniles could be due to low survival rates, juveniles not using ACOs, or because of emigration of juveniles from natal sites. Although adult Sharp-tailed Snakes seem to move fairly short distances (Ovaska and Engelstoft, 2008), as seems typical of many fossorial snakes (Blanchard et al., 1979), it is not known whether hatchling and juvenile Sharp-tailed Snakes emigrate from natal sites. In snakes, highest mortality rates are observed for dispersing hatchlings and juveniles (Bonnet et al., 1999),

which is of conservation concern due to the rapid rate of fragmentation of Sharp-tailed Snake habitat in British Columbia.

Very little is known about the mortality factors that affect Sharp-tailed Snakes. Other snakes (*Diadophis punctatus*), fish (*Salvelinus fontinalis*), amphibians (*Bufo boreas*), and birds (based on body scars) have all been suggested as potential predators (Leonard and Ovaska, 1998), but the relative predation rate is not known. Road-kill, accidental mortality from landscaping and gardening, and predation by domestic cats have all been documented in British Columbia, but their significance to Sharp-tailed Snake populations is unknown (COSEWIC, 2010). These sources of mortality are likely to increase as habitats continue to fragment. Life-history theory suggests that survival (compared with age at first reproduction or fecundity) is the most important demographic parameter for the persistence of relatively long-lived, slow-growing vertebrates (Oli, 2004; Fletcher et al., 2006).

Population Density and Population Growth Rate.—Several studies have reported dense aggregations of Sharp-tailed Snakes from relatively small areas, which suggest fairly high population densities. For example, 54 specimens have been found under a plastic sheet in Oregon (Hoyer et al., 2006). Leonard et al. (1996) found 22, 10, and six snakes on subsequent visits to a 1- × 35-m study site on the eastern slope of the Cascades Range in Washington. In another instance, 238 individual snakes were found within 2 days within a 1-km stretch of gravel road in Oregon (Hoyer et al., 2006). At the North Pender Island site, CMR analysis estimated a mean population size of 49 individuals, although we typically captured only a few individuals (from zero to four) at any given occasion. Compared with reports from other parts of the range, the population density of Sharp-tailed Snakes in British Columbia seems to be low. Relative population density in Sharp-tailed Snakes may follow the general pattern of Brown's (1984) model of higher density in the central parts of the range compared with the periphery in British Columbia.

In British Columbia, the estimated population growth rate from North Pender Island indicates that the population is declining, even though the 95% CI just overlaps 1. In Oregon, surveys at historical Sharp-tailed Snake locations have confirmed population persistence; combined with high abundance at certain sites, Hoyer et al. (2006) suggest that Sharp-tailed Snakes are not declining in southern Oregon. High adult survival and longevity can in some cases mask and buffer short-term population declines (Leigh, 1981; Saether et al., 2005) but only if there is sufficient juvenile recruitment into the population (Hughes and Tanner, 2000). We were unable to estimate recruitment rate in our study.

It has been suggested that elusive and cryptic animals may become unnecessary targets for conservation (Gibbons et al., 1997). Systematic searches in Oregon have uncovered new populations of Sharp-tailed Snakes, often in abundance, suggesting that this species may be an example where elusiveness has been wrongly equated with endangerment (Hoyer et al., 2006). However, in British Columbia, this snake remains a rare species even with increased survey efforts since it was first listed nationally as a species of conservation concern in 1999. In addition, our study of the life history of Sharp-tailed Snakes in British Columbia shows that they have many "slow" life-history traits such as slow growth, late maturation, long interbirth intervals, and small clutch sizes that may make them rare and vulnerable to population declines (Webb et al., 2002). Life-history studies in difficult-to-find species not only help resolve the debate as to whether the species is just elusive or truly rare and endangered but also highlight research needs for effective conservation planning. Our analysis reveals that assessment of mortality factors in adults and juveniles, and estimation of recruitment rates of small juveniles are important research priorities for conservation planning for this species.

Investment in long-term CMR studies on endangered species that are difficult to find can help optimize conservation efforts.

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