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SAMPLING BIASES IN DEMOGRAPHIC ANALYSES OF BLACK RAT SNAKES (*ELAPHE OBSOLETA*)

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ABSTRACT: Population ecology requires reliable population samples. We assessed sampling reliability for black rat snakes (*Elaphe obsoleta*) using 1724 captures obtained by two different methods: trapping at communal hibernacula and opportunistic capture of snakes at large. Recapture intervals indicated that opportunistic captures were biased by size (larger snakes were over-represented) but not by sex. Furthermore, opportunistic captures of snakes seen on roads (while observers were driving) had a stronger size bias than other opportunistic captures. Trapping at hibernacula sampled the respective hibernacula populations reliably, but the hibernacula populations themselves were not representative samples of the local population. Among 13 hibernacula, sex ratios ranged from 31–65% females and age structure from 42–86% sexually mature individuals. Because rat snakes can take many years before they join communal hibernacula, young snakes were under-represented in all hibernacula samples. We found highly significant differences in the size and sex composition of our samples from the Ontario population and from samples from a population in Maryland (from published data). Those differences seem more likely to be a consequence of biases associated with how snakes were sampled at each location than a reflection of real population differences. We recommend that future sampling of rat snakes include opportunistic sampling of snakes at large combined with sampling at several hibernacula. Also, researchers sampling snakes should assess biases in their samples, because biases that are not recognized will be more problematic than those of which researchers are aware.

Key words: *Elaphe obsoleta*; Population sampling; Snake populations; Sampling bias; Demography; Size structure

PRIOR to the advent of radio-telemetry, research on snake population ecology relied primarily on data obtained from opportunistic captures. Telemetry revealed that snakes encountered opportunistically tended to be the most visible members of the population (by virtue of their size or

activity), and they were found where they were most easily seen rather than in habitats that they used most (Burger and Zappalorti, 1988; Weatherhead and Charland, 1985; Weatherhead and Prior, 1992). Although tests for biased catchability are recommended whenever possible (Parker and Plummer, 1987), few studies have attempted to quantify the degree to which data obtained by different sampling techniques are representative of the population (Iverson, 1990; Shine, 1986*a,b*). For many species, opportunistic captures of snakes at large remains the only method for quan-

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tifying demographic parameters or for monitoring populations through time. However, for species that aggregate for hibernation, it may be possible to obtain more reliable information by sampling those aggregations. Our general goal in this study was to compare alternative methods of sampling black rat snakes (*Elaphe obsoleta obsoleta*) to identify biases inherent in each technique and to determine how best to sample populations in the future.

Our first objective was to compare demographic data from black rat snakes captured opportunistically during the active season with data from snakes trapped during emergence from communal hibernacula. We expected that opportunistic captures would be biased toward larger individuals because they are more easily seen. We expected an even stronger size bias in hibernacula samples because the mean ages at which black rat snakes begin using communal hibernacula in our population is 8.3 yr for males and 9.6 yr for females (Blouin-Demers, Prior, and Weatherhead, unpublished data). A comparison of samples collected by two different methods can tell us whether the methods produce different demographic patterns but not which method, if either, provides samples that are representative of the population. However, it is possible to use recapture data to assess biases in both sampling methods. If a method is biased toward capturing a particular class of snakes, then individuals in that class should be recaptured at shorter intervals relative to individuals in other classes. Among opportunistic samples, we expected that larger snakes should be recaptured at shorter intervals than smaller snakes because the former should be seen more easily, and among sexually mature individuals, males should be recaptured at shorter intervals because they tend to be more active than females (Weatherhead and Hoysak, 1989). We expected that samples at a hibernaculum should be representative of the hibernaculum population. Thus, recapture intervals at hibernacula should not vary consistently with the size or sex of individuals.

If hibernacula populations are small and chance plays a role in determining which individuals happened to find a particular hibernaculum, the demographic profiles of individual hibernacula sub-populations may vary substantially. Determining the extent to which demographic profiles of samples from different hibernacula vary is important because hibernacula will provide excellent opportunities for long-term population monitoring if there is little variation among them. Our second objective was to compare demographic profiles from several different hibernacula in the same area to assess the extent to which they vary, and whether that variation was related to the number of snakes sampled at a hibernaculum. We also tested the assumption underlying this objective, that once a snake finds a hibernaculum, it remains faithful to that site for the rest of its life.

Our final objective was to compare the demographic profile of our study population with a profile previously published for a widely separated population of black rat snakes sampled with a different technique. We generated the demographic profile for our Ontario population by combining samples from communal hibernacula with individuals not caught at the hibernacula but captured opportunistically in the vicinity of the hibernacula the same year. The second population, studied by Stickel et al. (1980) in Maryland, was only sampled opportunistically, and primarily by field workers conducting projects on taxa other than snakes (unlike the Ontario samples). Given the differences in how samples were obtained in each population, we expected that, relative to our Ontario samples, the samples from Maryland would be biased toward larger snakes.

MATERIALS AND METHODS

We sampled black rat snakes from hibernacula at four locations in eastern Ontario: Queen's University Biological Station (QUBS; 11 hibernacula, 1981–1996 and 1996–1998, depending on the hibernaculum), Murphy's Point Provincial Park (two hibernacula, 1992–1994), La Rue Mills (one hibernaculum, 1992–1994), and Hill Island (two hibernacula, 1984–1997). All

hibernacula had been located previously by tracking snakes implanted with radio-transmitters. We used three different techniques to catch snakes at hibernacula. First, we enclosed hibernacula openings with 1.5 m high perimeter fences made of plastic sheeting fixed to a wooden frame. We buried the bottom edge of the plastic and placed a funnel trap along the fence. Second, we used drift fences near hibernacula when the terrain prevented us from surrounding the openings with a perimeter fence. Drift fences were similar to perimeter fences, but they were linear rather than circular and typically had a funnel trap at each end. Third, because black rat snakes often bask close to hibernacula for several days after emerging, we carefully searched the ground and trees around each hibernaculum on each visit to find snakes that had avoided the traps. We constructed fences and initiated daily searches in early April, prior to the start of emergence, and ending late May, when emergence was completed (Blouin-Demers et al., 2000).

QUBS was the only site at which we captured snakes opportunistically. We made these captures during the active season (May through September) away from hibernacula. The opportunistic captures consist of a long-term and a short-term sample. We collected the long-term sample from 1981–1995 in a 7-ha study area that we refer to as Station Point. A telemetry study had indicated that rat snakes in this study area hibernated in one of two local hibernacula (Weatherhead and Hoy-sak, 1989). The short-term opportunistic sample was collected from 1996–1998 in a 1600-ha study area with 11 known hibernacula. This larger study area included Station Point and its two hibernacula.

We processed snakes captured at all sites in a similar manner. We determined a snake's sex by gently probing for the presence of hemipenes. We measured snout–vent length (SVL) to the nearest 1 mm with a metric tape and mass to the nearest 1 g with a calibrated spring-scale. We marked each snake individually by heat-branding caudal scutes (1981–1991) or by PIT-tagging (1992–1998), except at

Murphy's Point Provincial Park where snakes were never marked. We released snakes within 24 h at their point of capture. All protocols were approved by the Carleton University Animal Care Committee.

We used the hibernacula captures supplemented with opportunistic captures from 1981–1998 at Station Point for comparison with samples from a population in Maryland. For the Station Point data, our annual samples consisted of all snakes captured at the two local hibernacula plus any additional individuals captured opportunistically within the Station Point study area. Thus, an individual captured at a hibernaculum and opportunistically was only represented once in an annual sample. We combined the annual samples to produce our overall population sample (see below). For the Maryland population, we obtained original capture records from the study by Stickel et al. (1980) at the Patuxent Wildlife Research Center (L. Garrett, personal communication).

Data Analysis

For many of our analyses, we either had to combine samples obtained from a particular location over multiple years or combine samples obtained by a particular sampling technique over multiple years. To do so, we simply combined all the annual samples from a particular locality into a single pooled sample and, likewise, we pooled the annual samples obtained by different sampling techniques at a given locality. With the exception of our analysis of recapture latencies (days between captures), we only used data obtained from an individuals' first capture each year. However, data from individuals recaptured in successive years were included each year in which they were captured, thereby treating each year as an independent sample of the population. Had we excluded recaptures in successive years, our sample would have become progressively biased towards smaller snakes (i.e., individuals captured for the first time), and thus would not have been representative of the population.

To quantify demographic structure, we

categorized individuals into four size-classes. Male and female black rat snakes in our population mature at 1050 mm SVL (Blouin-Demers and Weatherhead, unpublished data), so we used this size criterion to first divide the snakes into mature or immature. We then divided each of these two classes in two, with the divisions intended to produce symmetrical size classes and a reasonable balance of sample sizes in each class. This produced the following four size classes: (1) 250–799 mm SVL, (2) 800–1049 mm SVL, (3) 1050–1299 mm SVL, and (4) 1300–1800 mm SVL. We calculated sex ratios as the percentage of females in a sample of individuals.

For analyses of recapture latencies, we used the opportunistic captures at Station Point, which we had sampled from 1981–1998, and data from one hibernaculum at Station Point (Curtis) and one at Hill Island (Lower Hill). These hibernacula had been sampled continuously from 1981–1998 and 1984–1997, respectively. We defined recapture latency as the number of days that a snake could potentially have been recaptured between its first and second captures. Calculation of recapture latencies for opportunistic captures required excluding the periods that snakes were in hibernacula or emerging from hibernacula. Hibernation in our study area lasts from early October to mid-April (approximately 190 days: Weatherhead, 1989) and spring emergence lasts an average of 40 days (Blouin-Demers et al., 2000). Thus, the active season (from the end of emergence to the start of hibernation) is approximately 135 days. Therefore, for opportunistic captures between years, we calculated recapture latency as the number of days between two successive captures minus 230 days per year (number of days in hibernation and emergence). For hibernacula captures between years, we estimated recapture latency as the number of days between the successive captures minus 325 days per year (the number of days in hibernation plus the number of days in the active season). We used ANCOVA to determine whether recapture latencies dif-

fered by sex or size, or by some interaction between these two variables.

To determine the extent of demographic variation among hibernacula, we used contingency table analyses to compare size distributions and sex ratios among samples. We conducted these analyses on two groups of hibernacula. First, we compared seven broadly distributed hibernacula (maximum distance approximately 50 km) sampled from 1992–1994 (two hibernacula each at Station Point, Murphy's Point, and Hill Island, and one hibernaculum at La Rue Mills). Second, we compared a complex of six neighboring hibernacula (maximum distance approximately 6 km) at QUBS sampled from 1996–1998. To determine whether variation in demographic composition among hibernacula varied as a function of the number of snakes sampled, we first calculated the mean number of snakes captured at a site across years. We then calculated the difference between the mean SVL of all black rat snakes captured at each hibernaculum and the mean SVL across all hibernacula. Similarly, we calculated the difference between the sex ratio of each hibernaculum and the overall sex ratio across all hibernacula. We then used linear regression to determine if the magnitude of these deviations (i.e., the absolute values of the differences) was related to mean sample sizes.

In predicting that smaller hibernacula will be less representative of the overall population because of sampling effects, we have assumed that once a snake begins using a communal hibernaculum, it remains faithful to that site for the rest of its life. We assessed this assumption by quantifying movement between sites, using long-term recapture data from two pairs of nearby hibernacula at Station Point and Hill Island. At Station Point, Curtis and Cow Island hibernacula were 1.2 km apart, and at Hill Island, Lower Hill and Upper Hill hibernacula were 1 km apart.

We checked all data for non-normality and heteroscedasticity of variance using box plots. We applied a natural logarithm transformation to the recapture latency data to meet the normality assumption. We conducted statistical tests using JMP

version 3.0 software package for the Macintosh (SAS Institute, 1994). We reported all means with ± 1 SE.

RESULTS

Long- and short-term fieldwork across all our study sites produced 1724 captures (including recaptures) from QUBS (512 individuals captured 1051 times, 1981–1998), Murphy's Point (unmarked individuals captured 174 times, 1992–1994), La Rue Mills (41 individuals captured 65 times, 1992–1994), and Hill Island (172 individuals captured 434 times, 1982–1997).

Opportunistic versus Hibernacula Captures

Size distributions estimated from opportunistic captures differed significantly from those estimated from captures at hibernacula, both for the long-term samples from Station Point and for short-term data from the larger QUBS study area. However, we captured fewer small individuals at hibernacula in the long-term samples ($n = 522$, $\chi^2 = 27.90$, $df = 3$, $P < 0.001$; Fig. 1) and more small individuals at hibernacula in the short-term samples ($n = 747$, $\chi^2 = 34.28$, $df = 3$, $P < 0.001$; Fig. 1). The difference between the long- and short-term results appears to be primarily a consequence of a difference in the opportunistic captures. We found significant differences between the long- and short-term hibernacula samples ($n = 732$, $\chi^2 = 8.85$, $df = 3$, $P = 0.03$) and between the long- and short-term opportunistic samples ($n = 537$, $\chi^2 = 54.54$, $df = 3$, $P < 0.001$). However, the magnitude of the difference was much greater among the opportunistic samples; there were more large individuals in the short-term opportunistic samples than in the long-term opportunistic samples.

One reason that large individuals were more prevalent in the short-term samples may be that many more were captured as a result of being seen on roads by researchers commuting to study sites; 60.0% of short-term opportunistic captures were on roads compared to only 33.7% of long-term captures.

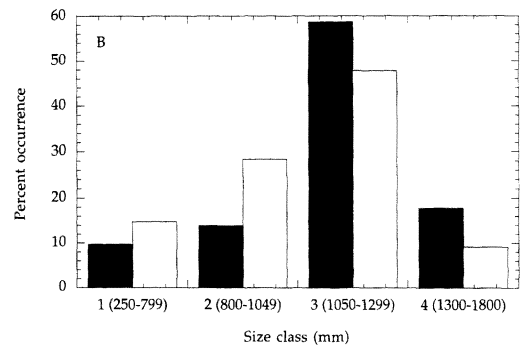
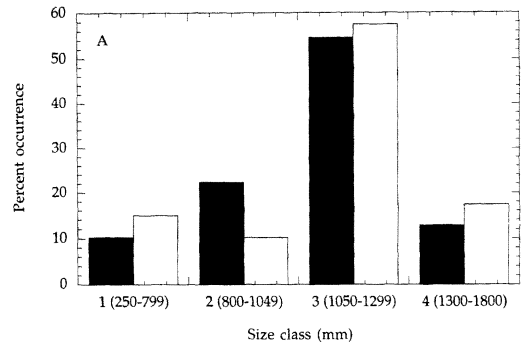


FIG. 1.—(A) Long-term size structure of black rat snakes sampled opportunistically (filled) and at hibernacula (open) at Station Point from 1981–1995. (B) Short-term size structure of opportunistic (filled) versus hibernacula-based (open) captures at QUBS from 1996–1998.

Recapture Latency

Among opportunistic samples from Station Point, latency to recapture relative to size did not differ between the sexes (sex \times SVL interaction, $F = 0.50$, $df = 1,87$, $P = 0.48$). Thus, contrary to our prediction, there was no evidence of a bias toward capturing sexually mature males. We removed the sex \times SVL interaction term from the final model and assessed the significance of the main effects. As predicted, recapture intervals were significantly longer for smaller snakes ($F = 4.21$, $df = 1,88$, $P = 0.04$; Fig. 2). Recapture intervals did not differ significantly between males and females ($F = 1.34$, $df = 1,88$, $P = 0.25$; Fig. 2).

At Curtis hibernaculum, the interaction between size and sex was not significant (F

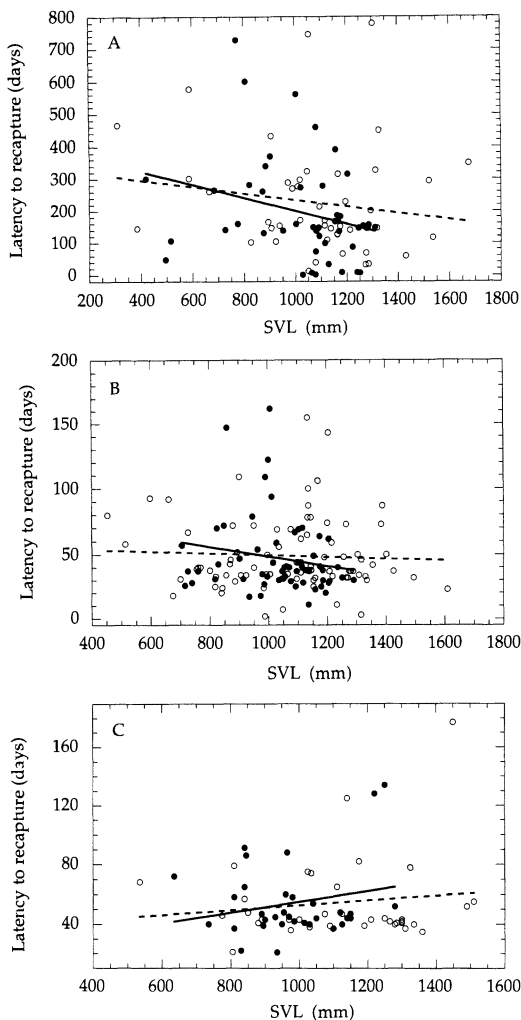


FIG. 2.—Latency to recapture as a function of size for female (filled circles, solid line) and male (open circles, dashed line) black rat snakes in the (A) opportunistic samples at QUBS, (B) hibernacula samples at QUBS, and (C) hibernacula samples at Hill Island.

$= 0.49$, $df = 1,136$, $P = 0.49$). In the reduced model, latency to recapture did not differ significantly between the sexes ($F = 0.01$, $df = 1,137$, $P = 0.91$; Fig. 2) or differ with size ($F = 1.23$, $df = 1,137$, $P = 0.27$; Fig. 2). Similarly, among samples from the Lower Hill hibernaculum, the interaction between sex and size was not significant ($F = 0.30$, $df = 1,66$, $P = 0.59$). In the reduced model, recapture intervals did not differ between males and females ($F = 0.08$, $df = 1,67$, $P = 0.78$; Fig. 2) or by

size ($F = 0.89$, $df = 1,67$, $P = 0.35$; Fig. 2).

Variation among Hibernacula

The population over all the hibernacula was predominantly sexually mature adults (overall mean = $62.8 \pm 13.1\%$ mature), although the range in the proportion of adults at each hibernaculum was quite broad (42–86%; Tables 1, 2). The sex-composition of all hibernacula populations varied from 31–64% females, with an overall mean of $46.7 \pm 10.5\%$ females (Table 1). Among the seven widely spaced hibernacula sampled from 1992–1994, we found significant differences in the distribution of snakes among size classes ($n = 430$, $\chi^2 = 73.76$, $df = 18$, $P < 0.001$) but no significant differences in sex composition ($n = 434$, $\chi^2 = 10.92$, $df = 6$, $P = 0.09$). Among the six neighboring hibernacula sampled from 1996–1998 at QUBS, distribution among size classes differed significantly ($n = 363$, $\chi^2 = 27.84$, $df = 15$, $P = 0.02$), as did sex composition ($n = 363$, $\chi^2 = 17.86$, $df = 5$, $P = 0.003$).

Deviation in mean SVL for individual hibernacula from the overall mean value across hibernacula did not vary significantly with the number of snakes sampled at a hibernaculum ($F = 4.05$, $df = 1,10$, $P = 0.07$, $r = 0.539$). Similarly, we found no significant variation between the deviation in sex ratio from the overall mean and the number of snakes sampled at a hibernaculum ($F = 0.98$, $df = 1,10$, $P = 0.34$, $r = -0.300$).

Site Fidelity

We recaptured 375 individuals 663 times at two pairs of hibernacula. Six individuals (1.6%), which accounted for 14 recaptures (2.1%), were captured at two hibernacula each. All of these movements between hibernacula occurred between Lower Hill and Upper Hill. Five of the six snakes were sexually mature, and all but one (including the immature individual) were males. Among all the other hibernacula that we sampled, we have no other instance of an individual moving between sites. Thus, rat snakes in our study population appear very faithful to hibernacula,

TABLE 1.—Number of individuals per size class (mm SVL) and number of females (percent of total in parentheses) in seven black rat snake hibernacula sampled from 1992–1994 in Ontario (maximum distance between two hibernacula approximately 50 km).

Locality Hibernaculum	Size class (mm)				Females	Total
	250–799	800–1049	1050–1299	1300–1800		
Murphy's Point						
Hydro	6 (4.6)	13 (9.9)	59 (44.7)	54 (40.9)	73 (55.3)	132
Silver Queen	3 (7.3)	7 (17.1)	17 (41.5)	14 (34.1)	19 (46.3)	41
Station Point						
Cow Island	1 (3.6)	5 (17.9)	20 (71.4)	2 (7.1)	15 (53.6)	28
Curtis	9 (11.1)	21 (25.9)	43 (53.1)	8 (9.9)	41 (50.6)	81
Hill Island						
Upper Hill	3 (12.5)	10 (41.7)	9 (37.5)	2 (8.3)	6 (25.0)	24
Lower Hill	4 (6.9)	18 (31.0)	31 (53.5)	5 (8.6)	31 (53.4)	58
La Rue Mills						
La Rue Mills	3 (4.6)	25 (37.9)	20 (30.3)	18 (27.3)	26 (39.4)	66

although on rare occasions individuals move between nearby sites.

Variation among Populations

The distribution of black rat snakes in the four size classes differed significantly between our population (i.e., hibernacula samples plus additional opportunistic captures from Station Point) and the population in Maryland ($n = 836$, $\chi^2 = 134.75$, $df = 3$, $P < 0.001$). The Station Point population was characterized by an increase in the percentage of individuals in size-classes one through three (up to 1300 mm SVL), followed by a sharp decline in the percentage in size-class four (≥ 1300 mm SVL). The Maryland population was characterized by a strong bias toward large snakes (Fig. 3). Sex ratios also varied among populations. At Station Point, the sex ratio was almost 1:1 (49.6% females), while there was a pronounced male bias in the Maryland (36.4% females) population.

DISCUSSION

Knowledge of the demographic composition of a population is fundamental to understanding the ecology of this population. However, total counts of animal populations (that would yield a "true" demographic composition) are rarely possible and researchers usually have to rely on statistical estimates of population parameters (Lancia et al., 1994). These estimates are approximations and are based on population models that require a certain set of assumptions. Departure from these assumptions will bias the parameter estimates, often in unknown ways, depending on which assumptions are violated and on how they are violated (Minta and Mangel, 1989). One assumption common to most population models is that capture probabilities should be homogeneous both for different individuals and for different capture periods (Pollock et al., 1990). To help

TABLE 2.—Number of individuals per size class (mm SVL) and number of females (percent of total in parentheses) in six black rat snake hibernacula sampled from 1996–1998 at QUBS (maximum distance between two hibernacula approximately 6 km).

Locality Hibernaculum	Size class (mm)				Females	Total
	250–799	800–1049	1050–1299	1300–1800		
Bedford	4 (16.0)	7 (28.0)	13 (52.0)	1 (4.0)	16 (64.0)	25
Curtis	7 (12.7)	10 (18.2)	30 (54.6)	8 (14.6)	19 (34.5)	55
Dowsley	26 (24.1)	37 (34.3)	39 (36.1)	6 (5.6)	47 (43.5)	108
Garter Lake	7 (17.1)	11 (26.8)	20 (48.8)	3 (7.3)	24 (58.5)	41
Old Rideau Trail	5 (13.2)	12 (31.6)	15 (39.5)	6 (15.8)	21 (55.3)	38
Two Island Lake	6 (6.3)	24 (25.0)	51 (53.1)	15 (15.6)	30 (31.3)	96

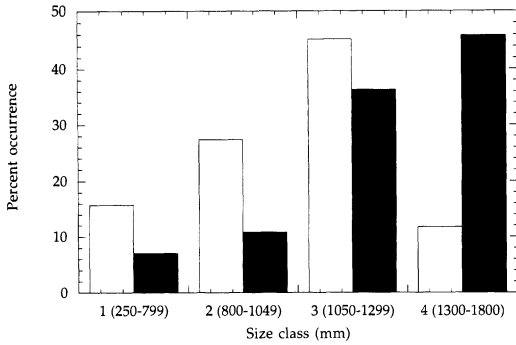


FIG. 3.—Size structure of captures in Ontario (intensive field work, open) and Maryland (incidental encounters, filled).

relax or satisfy this assumption, it has been recommended to use more than one capture method (Minta and Mangel, 1989). For especially secretive animals like snakes, obtaining accurate estimates of basic population parameters is often difficult (Parker and Plummer, 1987) because capture probabilities are very low and probably heterogeneous. Potentially even more problematic is that the estimates of these parameters that are obtained may be biased in ways that are unknown because few quantitative data are available on sampling biases for snakes. Unknown biases can result in incorrect inferences about the population. In this study, we showed that different sampling methods produced different demographic profiles of the same population of black rat snakes, and probably produced incorrect profiles of different rat snake populations. We first discuss our specific results and then consider how these problems should be addressed in the future.

We predicted that larger snakes should be over-represented in opportunistic samples simply because they are more likely to be seen and that large males should be more visible than large females because they are more active than large females (Weatherhead and Hoysak, 1989). Larger snakes were recaptured more frequently than smaller snakes, confirming the first prediction, but contrary to the second prediction, recapture intervals did not differ between males and females. Furthermore, because the interaction between size and

sex was not significant, our expectation that large, reproductive males should be recaptured more because they are more active was not supported. Thus, our opportunistic captures were representative in terms of sex, but disproportionately sampled larger snakes. One apparent bias associated with opportunistic samples that we had not anticipated was the greater representation of large snakes in the short-term QUBS samples compared to the long-term samples from Station Point. The fact that nearly twice as many snakes in the former sample were encountered by researchers driving on roads suggests two possibilities. Either small rat snakes cross roads less often than large rat snakes, or small snakes are more difficult to see by someone driving. Whatever the explanation, these results indicate that opportunistic samples are not only biased, but that different kinds of opportunistic samples (i.e., snakes seen while walking versus driving) may have substantially different biases.

We expected that our samples of snakes captured emerging from a given hibernaculum would not be biased by size or sex but, rather, would be representative of that hibernaculum's population. Consistent with this expectation, our analysis of recapture intervals for hibernacula samples revealed no effect of size or sex. Nevertheless, while we found that hibernacula samples were representative of hibernacula populations, we did not expect them to be a true reflection of local populations. Rat snakes lay their eggs remote from communal hibernacula, and young rat snakes often take many years before they hibernate in these sites (G. Blouin-Demers, unpublished data). We had no independent way to test the prediction that large snakes should be over-represented in hibernacula samples relative to the local population. However, long-term samples from Station Point indicated that there were proportionately more large snakes in hibernacula samples than in opportunistic samples. Because we demonstrated that opportunistic captures disproportionately sampled large snakes, it follows that hibernacula populations must also be biased

toward large snakes, relative to the local population.

Our evidence that hibernacula samples were unbiased relative to hibernacula populations, and that individuals were very faithful to a hibernaculum, supports the contention that sampling at hibernacula might be the best way to sample rat snake populations. However, in addition to the under-representation of small snakes in hibernacula discussed above, we also found substantial variation in the demographic profiles of different hibernacula. Sampling at a single hibernaculum, regardless of size, could result in unreliable estimates of the age or sex composition of the local population.

Our comparison of rat snakes in Ontario with a population in Maryland (Stickel et al., 1980) produced two very different profiles. This difference could be a consequence of real demographic differences among the populations, differences in sampling techniques, or both. Without knowing the true profiles of each population, we cannot determine which explanation is correct. However, there is some basis for concluding that sampling biases were likely to have been important. The profile for the Ontario population was based on hibernacula samples plus additional snakes captured opportunistically. Even though opportunistic captures are biased toward larger snakes, small snakes are captured, and these are the individuals that were under-represented in the hibernacula samples. Therefore, because our Ontario sample was obtained by two methods, it should have been more representative than a profile based on only one sampling technique (Minta and Mangel, 1989). The Maryland population was only sampled opportunistically. Consistent with the bias of opportunistic captures toward larger snakes, the Maryland population was very strongly biased toward large individuals. Demographic information is also available for one additional black rat snake population. Fitch (1961, 1963) studied black rat snakes in Kansas and the majority of captures were obtained by "funnel traps primarily made and set for small snakes (which) were not highly effective for the

capture of large adult rat snakes" (Fitch 1963:650). Consistent with this recognized bias, the samples were strongly biased toward small snakes (Fitch, 1961).

Given the likelihood that sampling biases contributed to the demographic differences between the three populations, uncritical use of these data could produce misleading outcomes. Parker and Plummer (1987) reviewed the available data on size and age composition of snake populations from a survey of the literature. They included the data from Kansas and Maryland for black rat snakes in that review. If other studies in Parker and Plummer's (1987) review were as prone to sampling biases as the black rat snake studies, then attempts to derive general insights into snake demography from this review are likely to fail. Our point here is not to criticize Parker and Plummer's review, but rather to urge caution in how those data are used.

Our results suggest several considerations for future population sampling and monitoring. In the specific case of black rat snakes, sampling at hibernacula is the easiest way to capture a reasonable number of snakes in a relatively short time, and one can resample the same site and safely assume that the same population is being re-sampled. However, the fewer hibernacula that are sampled, the less representative of the local population the samples are likely to be. Opportunistic samples of the same population can complement hibernacula samples, but on their own these samples may be unreliable, particularly if different ways of encountering snakes (e.g., walking versus driving) are used with varying emphasis. Finally, one must remain aware that young snakes are under-represented in both hibernacula and opportunistic samples, a problem of long standing in snake population biology (Parker and Plummer, 1987).

Our results have implications for sampling other snake species, in addition to reinforcing the general caveat that one needs to be aware of potential biases. Black rat snakes are typical of the majority of species that over-winter communally, in that hibernacula populations were com-

prised largely of adults (Gregory, 1984). Thus, sampling similar snake species at hibernacula is likely to offer the same problems and benefits. Even better for accurate sampling at hibernacula will be species such as those rattlesnakes for which gestation and over-wintering sites are relatively close (0–100 m apart: e.g., Duvall et al., 1985; Gannon and Secoy, 1985). Because this allows neonates to attend communal hibernacula (Charland, 1989; Galligan and Dunson, 1979), hibernacula samples will include younger snakes.

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