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Author(s): Patrick T. Gregory and Karl W. Larsen

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Geographic Variation in Reproductive Characteristics among Canadian Populations of the Common Garter Snake (*Thamnophis sirtalis*)

PATRICK T. GREGORY AND KARL W. LARSEN

We studied geographic variation in reproductive characteristics, especially litter size and neonate size, among several populations across Canada of the wide-ranging garter snake, *Thamnophis sirtalis*. Gravid females differed significantly in body size among sites. However, even after we corrected for intersite differences in maternal body size, there were highly significant differences among populations in litter size and neonate size. Populations with large litters tended to have small progeny, but we found only weak evidence of a “tradeoff” between neonate size and litter size within populations. There was a conspicuous east–west difference in reproductive characteristics of snakes: snakes from eastern Canada were relatively small at maturity and produced large litters of very small young, whereas those from western Canada generally were large and produced smaller litters (for a given body size) of larger young. Although litter size and neonate size are both phenotypically plastic traits, the differences observed among populations in this study were often much larger than those expected from simple environmental influences. We, therefore, hypothesize that reproductive traits differ genetically among populations of *T. sirtalis*, at least between eastern and western Canada.

PATTERNS of variation of life histories of organisms depend on the taxonomic level at which comparisons are made (e.g., Brown, 1973) and predictions from one level may not apply at another. Much of life-history theory is derived from broad comparisons between species; it is, therefore, not surprising that intraspecific patterns of life-history variation are not very predictable from current theory (Stearns, 1980; Dunham et al., 1988a). However, comparisons among populations of a species may be very valuable in the study of life-history evolution because phylogenetic “noise” is reduced and because genetic and nongenetic factors potentially can be separated (Brown, 1973; Dunham et al., 1988a). Geographically widespread species should be particularly rewarding in this respect because they often occur in sufficiently diverse environments that we can expect significant diversity in life histories.

The common garter snake, *Thamnophis sirtalis*, is the most northerly and widely distributed of North American reptiles. Although absent from most of the southwestern United States, it occurs from the Atlantic to the Pacific oceans and from the southern Northwest Territories to Florida, thereby encompassing a wide array of environments. This species is geographically variable in color and other characteristics, and 12 subspecies are recognized (Fitch, 1980).

In addition to the usual systematic characters,

T. sirtalis also exhibits considerable geographic variation in litter (=clutch) size. Fitch (1985), in his review of geographic variation in clutch size of North American reptiles, showed that litter size of *T. sirtalis* declined from east to west but that there was little latitudinal variation. However, clutch size can be influenced by many factors, including body size of mother (Seigel and Ford, 1987; Barbault, 1988), and Fitch’s data set, as he acknowledged, did not include body size or other important measurements such as size of progeny. Life histories are suites of coevolved (and often correlated) traits (Stearns, 1976). Any analysis of geographic variation in life histories, therefore, must necessarily be multivariate.

The ideal analysis would include data on age-specific patterns of mortality and fecundity, but such details are available for very few populations of snakes (Parker and Plummer, 1987). By contrast, a relative wealth of data is available on body size, litter size, and size of offspring for many species, including *T. sirtalis*. In this paper, we analyze geographic variation in reproductive characteristics of *T. sirtalis* from several locations across Canada and compare our findings with published data on this species from elsewhere in its range. We address three main questions: (1) Are there identifiable geographic patterns in reproductive traits overall of *T. sirtalis* not just in litter size? Given the important demographic consequences of variation in litter

size, one would expect that variation in that trait would be accompanied by variation in other traits. Potentially, different combinations of trait values represent different life-history "strategies." (2) Is geographic variation in reproductive traits such as litter size and offspring size largely a consequence of geographic variation in adult body size? This is a plausible and parsimonious hypothesis, although it leaves open the question of why body size itself should vary. (3) Can reproductive traits in *T. sirtalis* be viewed as "tradeoffs" (Reznick, 1985) against one another? Organisms have finite resources with which to produce progeny. Therefore, individual snakes, for a given "investment," can produce either a few large young or a larger number of smaller young; that is, litter size and offspring size should be negatively correlated.

METHODS

We obtained data on reproductive characteristics for 11 Canadian populations of *T. sirtalis* (Fig. 1, Table 1), although we lacked data on some characters for some populations and for some litters within populations. The characters that we measured were size of gravid female [snout-vent length (SVL) and mass (both pre- and postpartum)], clutch size, neonate size (SVL and mass), and relative mass loss by female at parturition [$RML = (\text{prepartum mass} - \text{postpartum mass}) / \text{postpartum mass}$]. We chose RML as an index of reproductive investment over the more commonly used relative clutch mass (RCM; Seigel and Ford, 1987) because the mass of material lost at parturition, and therefore reproductive investment, is more than just the mass of the clutch. However, pre- and postpartum mass were not measured at consistent intervals before and after birth.

We also had a small number of miscellaneous litters from various locations in Canada and the United States. These miscellaneous litters were not used in most of our analyses, except to classify them, using discriminant analysis (see below), with respect to litters from our 11 main sites.

Most of the data were collected by us, but several data were extracted from records of colleagues. In general, these data have not been previously published, although Gregory et al. (1992) used the same snakes in their analysis. In addition, much of the Manitoba data set was summarized by Gregory (1977) and the Wood Buffalo data are presented by Larsen et al. (1993). Gregory's (1977) data were augmented for this paper by one additional captive-born litter that he had failed to record and by dis-

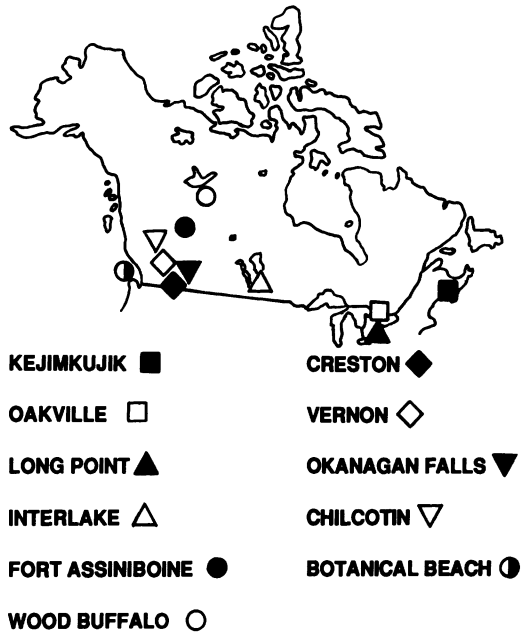


Fig. 1. Map of Canada showing locations of study sites.

sections of freshly killed gravid females that had not been considered in his analysis of litter size. For the most part, litters of snakes were obtained by bringing gravid females into the laboratory and maintaining them at room temperature (23–28 C) until parturition; water was provided ad libitum, but food was rarely offered. Gregory's (1977) gravid females were maintained in an outdoor enclosure until near the time of parturition.

For the purposes of our analyses, litter size was defined as the sum of live young, dead young, and undeveloped eggs (approximately equivalent to secondary clutch size of Dunham et al., 1988b). This decision was based on previous studies (Farr and Gregory, 1991; Gregory et al., 1992) that showed that this was the least variable way of estimating litter size. In addition, it was the only reasonable way of comparing data from captive births with those derived from dissections of females in early stages of pregnancy. In any case, the overall conclusions of our study remain the same whether or not we include undeveloped eggs in our estimates of litter size.

Our analyses focused on correlations among variables and on intersite differences in reproductive characteristics. Because data sets were incomplete for several characters, we concentrated on relationships among female SVL, litter size, and neonate SVL. However, summary statistics of all features that we measured are presented in the Results.

TABLE 1. SUMMARY OF ENVIRONMENTAL DATA FOR SITES FROM WHICH SNAKES WERE OBTAINED IN THIS STUDY. Weather data were obtained from Atmospheric Environment Service (1982). Temp. = mean daily temperature, 1 May–31 Aug.; C. V. = coefficient of variation of daily temperature, 1 May–31 Aug. Source = source of data on snakes.

Location	Lat. and Long.	Alt. (m)	Closest community	Temp. (C)	C.V.	Source
Kejmkujuk National Park, Nova Scotia	44°25'N 66°12'W	127	Jake's Landing	15.5	8.08	W. F. Weller, pers. comm.
Oakville, Ontario	43°25'N 79°41'W	85	Oakville	17.1	8.89	P. T. Gregory, unpubl.
Long Point, Ontario	42°33'N 80°03'W	177	Long Point	17.8	7.40	P. T. Gregory, unpubl.
Interlake region, Manitoba	50°30'N 97°53'W	267	Stonewall	16.0	12.50	Gregory, 1977, and unpubl.
Fort Assiniboine, Alberta	54°22'N 114°55'W	670	Fort Assiniboine	14.4	9.23	K. W. Larsen, unpubl.
Wood Buffalo National Park, Alberta/Northwest Terri- tories	60°00'N 111°53'W	202	Fort Smith, NWT	12.9	13.10	Larsen et al., 1993
Creston, British Columbia	49°06'N 116°31'W	613	Creston	16.8	9.47	Farr, 1988; P. T. Gregory, un- publ.
Vernon, British Columbia	50°14'N 119°33'W	400	Vernon	17.2	8.55	J. M. Macartney and K. W. Lar- sen, unpubl.
Okanagan Falls, British Co- lumbia	49°19'N 119°12'W	335	Penticton	17.6	8.10	P. T. Gregory and K. W. Lar- sen, unpubl.
Chilcotin region, British Co- lumbia	52°01'N 112°31'W	1005	Williams Lake	15.0	9.43	P. T. Gregory, unpubl.
Botanical Beach, British Co- lumbia	48°34'N 124°24'W	6	Port Renfrew	12.9	7.28	C. M. Carr, unpubl.

TABLE 2. SUMMARY OF REPRODUCTIVE DATA FOR SNAKES FROM SITES EXAMINED IN THIS STUDY. RML = relative mass loss (see text for explanation). Data in each case are mean (top row), sample size and standard deviation (middle row), and range (bottom row).

Location and year(s)	Female SVL (mm)	Litter size	Neonate SVL (mm)	Neonate mass (g)	RML
Kejimikujik (1971)	532.25 (4, 56.41) (464–601)	23.00 (4, 7.35) (17–33)	130.42 (88, 6.04) (116–147)	—	—
Oakville (1988–1989)	530.00 (4, 12.25) (520–545)	14.50 (4, 6.56) (9–24)	161.11 (36, 16.35) (125–186)	1.40 (53, 0.45) (0.64–2.28)	0.52 (4, 0.30) (0.17–0.89)
Long Point (1970–1975)	590.00 (5, 79.09) (505–680)	19.00 (5, 6.28) (14–30)	142.54 (100, 9.96) (119–160)	1.80 (48, 0.12) (1.30–2.00)	—
Interlake (1970–1972)	578.37 (30, 62.01) (514–800)	18.83 (30, 8.11) (7–50)	154.43 (207, 9.86) (117–175)	—	—
Fort Assiniboine (1988–1989)	621.62 (21, 53.08) (540–735)	13.81 (21, 6.01) (5–25)	175.47 (203, 6.70) (154–195)	1.66 (203, 0.23) (0.84–3.00)	0.67 (21, 0.27) (0.17–1.13)
Wood Buffalo (1983–1986)	744.57 (23, 75.90) (640–915)	12.48 (23, 4.85) (5–25)	191.41 (188, 9.28) (146–214)	2.61 (182, 0.39) (0.95–3.80)	0.58 (18, 0.20) (0.31–1.13)
Creston (1982–1987)	560.07 (15, 64.89) (492–749)	7.60 (15, 4.24) (2–21)	180.71 (94, 14.86) (112–200)	2.49 (96, 0.51) (0.50–3.30)	0.49 (15, 0.17) (0.25–0.78)
Vernon (1980–1983)	568.27 (26, 41.54) (500–655)	10.73 (26, 2.52) (6–18)	182.33 (216, 10.7) (155–210)	2.37 (218, 0.43) (1.38–3.74)	0.82 (17, 0.22) (0.45–1.21)
Okanagan Falls (1983–1989)	620.50 (10, 38.83) (535–665)	9.70 (10, 4.22) (2–19)	201.32 (87, 13.26) (145–220)	2.99 (87, 0.58) (1.70–4.24)	0.83 (6, 0.38) (0.19–1.28)
Chilcotin (1982–1983)	679.29 (7, 81.36) (605–785)	13.00 (7, 5.03) (9–21)	197.76 (84, 8.03) (180–215)	3.00 (85, 0.46) (1.89–4.01)	0.48 (2, 0.12) (0.40–0.57)
Botanical Beach (1975)	603.33 (15, 61.20) (500–695)	13.27 (15, 4.59) (7–22)	172.28 (202, 9.71) (130–190)	—	—

We tested simple correlations among female SVL, litter size, and mean neonate SVL for each population separately. We also tested the correlation between neonate SVL and neonate mass for all populations combined. Life-history theory predicts that, all other things being equal, litter size and neonate size should be negatively correlated (e.g., Smith and Fretwell, 1974); however, because both may be correlated with size of mother, simple correlations between these two traits may be nonsignificant or significantly positive, even if there actually is a tradeoff, just because of differences in sizes of mothers (Ford and Seigel, 1989). To adjust for differences in

SVL among mothers, we regressed litter size on female SVL and mean SVL of littermates (live plus normally developed dead young) on female SVL and then tested the correlation between the residuals from each regression line. This was done for each population separately to detect any differences in the nature of the relationship from one population to another. Correlation of litter size and neonate size among populations was tested using mean litter size and mean neonate SVL for each population.

We compared female SVL, litter size, neonate SVL, and RML among sites by separate ANOVAs. The first two were simple one-way

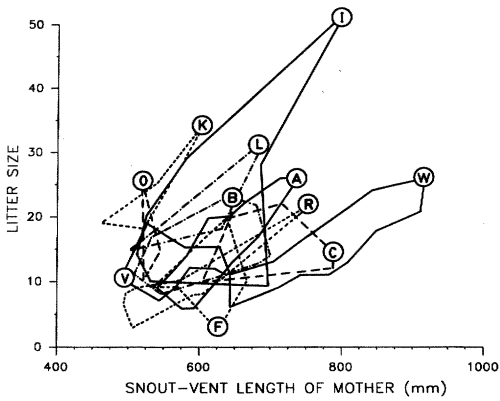


Fig. 2. Plot of litter size vs SVL of mother for all sites combined (K = Kejimikujik, O = Oakville, L = Long Point, I = Interlake, A = Fort Assiniboine, W = Wood Buffalo, R = Creston, V = Vernon, F = Okanagan Falls, C = Chilcotin, B = Botanical Beach). Lines enclose outermost set of points for each site. Overall $r^2 = 0.08$, $P = 0.002$, $n = 160$.

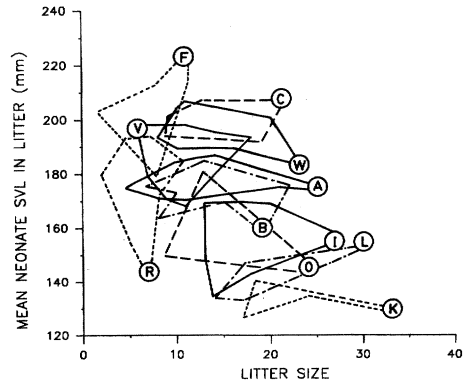


Fig. 4. Plot of mean neonate SVL vs litter size for all sites combined. Symbols as in Figures 2 and 3. Overall $r^2 = 0.17$, $P = 0.0001$, $n = 129$.

ANOVAs, but neonate SVL (using live plus normally developed dead neonates) was analyzed as a nested ANOVA with individual litters treated as random subgroups within sites. Because litter size was strongly correlated with female SVL in some populations, we recompared litter size among sites, after making adjustments for differences in female SVL, using analysis of covariance (ANCOVA), with female SVL as covariate. We also calculated the least-squares mean (LSM; Searle et al., 1980) for each site.

To avoid statistical problems associated with the analysis of ratios (Sokal and Rohlf, 1981; Brodie, 1989), we analyzed intersite variation in RML by first regressing mass loss at parturition on postpartum mass and then performing

an ANOVA among locations on the residuals from the regression.

Finally, to determine what characteristic or combination of characteristics best distinguished the various populations from one another, we performed a discriminant analysis (DA) among sites, using female SVL, litter size, and mean SVL of littermates as variables. The resulting discriminant functions also were used to classify a small number of unassigned or miscellaneous litters that represented either single records from a site or records that were known only by general geographic area.

All statistical analyses were performed using PC Statistical Analysis System Version 6.03 (SAS Institute, Inc., 1988). We considered results to be significant at $\alpha = 0.05$. When more than one correlation was tested from the same set of multiple variables, α -level was adjusted using the Bonferroni procedure (Larzelere and Mulaik, 1977); that is, the α -level per test was 0.05 divided by the number of correlations tested from the same data set. Type III sums of squares were used in assessing the results of all ANOVAs and the ANCOVA.

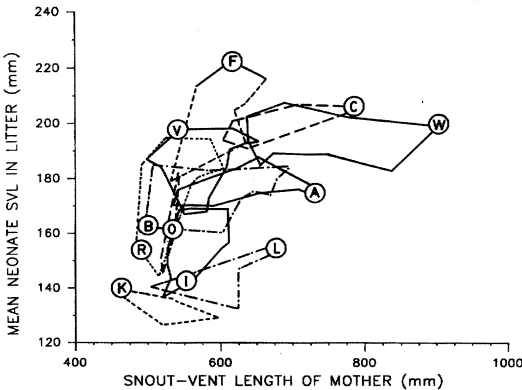


Fig. 3. Plot of mean neonate SVL vs SVL of mother for all sites combined. Symbols as in Figure 2. Overall $r^2 = 0.22$, $P = 0.0001$, $n = 129$.

RESULTS

Of 162 captive-born litters, 83 consisted entirely of living young. The remaining 79 litters also included a variable number of dead young or undeveloped yolky eggs; additional details on composition of these litters are given by Gregory et al. (1992).

There was considerable intersite variation in all reproductive characters that we measured (Table 2, Figs. 2-4). For several sites with large samples, there was a significant positive correlation between female SVL and litter size, but

TABLE 3. SUMMARY OF CORRELATIONS AMONG FEMALE SVL, LITTER SIZE, AND MEAN NEONATE SVL. Significant correlations are indicated by *, and sample sizes (=number of litters) are given in parentheses. Significance levels for each test are $0.05/3 = 0.017$, given three tests for each location (Larzelere and Mulaik, 1977); however, tests for different locations are considered to be independent.

Location	Female SVL– litter size	Litter size– neonate SVL	Female SVL– neonate SVL
Kejimkujik	0.88 (4)	–0.22 (4)	–0.63 (4)
Oakville	–0.31 (4)	–0.37 (5)	0.97 (4)
Long Point	0.72 (5)	0.83 (5)	0.60 (5)
Interlake	*0.64 (30)	0.12 (12)	0.50 (12)
Fort Assiniboine	*0.80 (21)	0.14 (15)	0.41 (15)
Wood Buffalo	*0.84 (23)	–0.22 (17)	–0.04 (17)
Creston	*0.86 (15)	0.28 (14)	0.51 (14)
Vernon	0.38 (26)	0.14 (26)	0.26 (26)
Okanagan Falls	0.25 (10)	–0.12 (10)	0.55 (10)
Chilcotin	0.27 (7)	0.17 (7)	0.84 (7)
Botanical Beach	0.43 (15)	–0.22 (15)	0.31 (15)

mean neonate SVL was never significantly correlated with either female SVL or litter size, at least following correction of α -level for multiple tests (Table 3). Even after we adjusted both litter size and mean neonate SVL for differences in female SVL, there was no significant correlation between these two variables for any site, although several correlations that were positive in the unadjusted form became negative after adjustment for female SVL. To make a more powerful test of within-population correlation between litter size and mean SVL of littermates, we increased sample size by pooling the residuals from the various locations (analogous to pooled “within groups” sum of squares in ANOVA). Before pooling, however, we eliminated the effects of different population variances by expressing the residuals as standard normal deviates from their corresponding regression lines. This approach obscures variation

among populations but gives an indication of overall within-population correlation. The result was a weak but significant relationship between litter size and neonate size ($r = -0.19$, $n = 130$, $P = 0.03$). The correlation between mean litter size and mean neonate size among populations was highly significant even without adjustments for mean body size of mothers ($r = -0.87$, $n = 11$, $P < 0.001$). Neonate SVL and neonate mass were strongly correlated ($r = 0.73$, $n = 1025$, $P = 0.0001$, log-transformed data) for all neonates pooled.

ANOVAs indicated that there were significant differences among sites in female SVL, litter size, and neonate SVL (Table 4). However, because of correlations between female SVL and litter size (Table 3), it was also important to compare litter size among populations after adjusting for differences in female SVL by ANCOVA. There was marginally significant het-

TABLE 4. SUMMARIES OF ANALYSES OF VARIANCE OF INTERSITE DIFFERENCES IN FEMALE SVL, LITTER SIZE, AND NEONATE SVL. All sums of squares (SS) are Type III.

	df	SS	F	P
Female SVL				
Location	10	610,898.81	16.79	0.0001
Remainder	151	549,497.54		
Litter size				
Location	10	2263.80	7.31	0.0001
Remainder	149	4613.89		
Neonate SVL				
Location	10	456,691.38	59.86*	0.0001
Litters within locations	121	102,666.60	23.56	0.0001
Remainder	1373	494,446.24		

* Approximate F-test based on 10 and 122.17 df, using RANDOM/TEST option in PROC GLM (SAS Institute, Inc., 1988).

TABLE 5. SUMMARY OF ANALYSIS OF COVARIANCE OF INTERSITE DIFFERENCES IN LITTER SIZE, ADJUSTING FOR DIFFERENCES IN FEMALE SVL (=COVARIATE). All sums of squares (SS) are Type III. LSM = least-squares mean.

	Analysis of covariance			
	df	SS	F	P
Location	10	3457.79	17.93	0.0001
Female SVL	1	1759.66	91.24	0.0001
Remainder	148	6877.69		

Location (n)	LSMs	
	Unadjusted (ANOVA)	Adjusted (ANCOVA)
Kejimkujik (4)	23.00	27.56
Oakville (4)	14.50	19.19
Long Point (5)	19.00	27.56
Interlake (30)	18.83	20.76
Fort Assiniboine (21)	13.81	13.26
Wood Buffalo (23)	12.48	4.89
Creston (15)	7.60	10.57
Vernon (26)	10.73	13.23
Okanagan Falls (10)	9.70	9.21
Chilcotin (7)	13.00	9.15
Botanical Beach (15)	13.27	13.76

erogeneity among slopes (litter size on female SVL, from "homogeneity-of-slopes" model, PROC GLM; SAS Institute, Inc., 1988; Freund et al., 1986) for the various locations ($F = 354.51$, $df = 10, 138$, $P = 0.043$), a violation of an assumption of ANCOVA; therefore, the results of this analysis should be considered circumspectly. After adjustments for differences in SVL of females, differences among populations were even larger than before adjustment and were highly significant (Table 5); Figure 2, in fact, shows that there was no overlap between data sets for some populations with clearly different relationships between female SVL and litter size (e.g., Kejimkujik and Wood Buffalo). In contrast, analysis of litter size using just the homogeneity-of-slopes model to adjust for female SVL revealed no significant differences among populations ($F = 1.47$, $df = 10, 138$, $P = 0.16$); however, validity of this test in such a model is questionable when slopes are heterogeneous (Freund et al., 1986). Because neonate size was not correlated with female SVL within populations (Table 3), adjusting these values for differences in SVL of mother did not influence our conclusions.

There was significant variation in RML ($F = 2773.01$, $df = 6, 76$, $P = 0.036$) among locations. Snakes from Vernon, Fort Assiniboine, Wood Buffalo, and Okanagan Falls lost more mass than would be predicted by the regression, whereas

snakes from Chilcotin, Creston, and Oakville lost less than predicted, on average. There was no obvious geographic pattern in RML.

We initially restricted the DA to the eight populations from western Canada (Interlake and all points west) because we generally had larger samples from those sites. The exception was Chilcotin, for which we had only seven litters, but the results were not strongly affected by inclusion or exclusion of data from this site. The analysis revealed highly significant differences among populations (Wilks' lambda = 0.105, $P = 0.0001$). Our conclusions also were not substantially different whether or not we used equal or proportional prior probabilities in the analysis; the results presented here are based on equal priors. Reclassification of the cases used to do the DA resulted in an overall error rate of 0.44, with error rate varying widely among populations (Table 6); it was particularly high for Botanical Beach (west coast) but very low for Interlake (easternmost of western populations). When we attempted to classify observations from our three eastern populations, plus an additional three miscellaneous litters from eastern North America, into this scheme, most were categorized with Interlake snakes (Table 6). Miscellaneous litters from the southwestern coast of British Columbia, like those from Botanical Beach, did not fall into clear categories (Table 6).

We then redid the DA with all 11 study sites included; the results were not markedly different. Figure 5 shows canonical variable 1 plotted against canonical variable 2; although there is much overlap among sites, there is a marked trend toward separation of eastern (now including Interlake) and western populations along canonical variable 1. This trend is even reflected somewhat within the eastern group, the Kejimkujik snakes being the most extreme. In general, eastern *T. sirtalis* were smaller and produced larger litters of smaller young than did western conspecifics.

DISCUSSION

Latitudinal clines in reproductive characters, especially clutch size, have been studied in a variety of vertebrates. In some cases, clutch size increases with latitude (e.g., Cody, 1966; Healey and Heard, 1984; Fleming and Gross, 1990); in other cases, it declines (e.g., Leggett and Carscadden, 1978) or shows no relationship (e.g., Ritke, 1990). Explanations for the observed patterns vary greatly. Our data reveal no evidence of latitudinal clines in litter size of *T. sirtalis*. Fitch (1985) hedged somewhat on this point,

TABLE 6. SUMMARY OF CLASSIFICATIONS AND MISCLASSIFICATIONS OF OBSERVED CASES INTO STUDY SITES, BASED ON DISCRIMINANT ANALYSIS OF FEMALE SVL, LITTER SIZE, AND MEAN NEONATE SVL. Data are percentages; underlined figures are correct classifications. Discriminant analysis was done on the first eight sites, then all observations from those sites and other sites were classified; last four categories are miscellaneous litters known only by general geographic location. Abbreviations as in Figures 2–5.

From location (n)	Percentage of observations classified into locations							
	I	A	W	R	V	F	C	B
I (12)	<u>91.67</u>							8.33
A (15)		<u>46.67</u>		20.00	6.67			26.67
W (17)			<u>88.24</u>			5.88		5.88
R (14)	7.14			<u>57.14</u>	14.29	14.29	7.14	
V (26)				11.54	<u>57.69</u>	7.69	7.69	15.38
F (10)				10.00	10.00	<u>80.00</u>		
C (7)			28.57		14.29	42.86	<u>14.29</u>	
B (15)	6.67	33.33	13.33	20.00	13.33			<u>13.33</u>
K (4)	100.00							
O (5)	40.00	20.00			20.00			20.00
L (5)	100.00							
New York (1)	100.00							
Southern Ontario (1)				100.00				
Iowa (1)	100.00							
Southwestern B.C. (13)		30.77	7.69	30.77				30.77

concluding that litter size of *T. sirtalis* increased weakly northward in the east and weakly southward in the central and western parts of the range, but he had few data from the northern populations. This ambiguous result actually reflects a strong east–west trend in litter size that is seen in Fitch’s data and supported by ours: eastern *T. sirtalis* have larger litters than do western conspecifics.

Because some of our samples were small, especially for eastern sites, analyses such as DA should be considered exploratory and descriptive only. Nonetheless, the strong trends seen in our data make us confident of the generality of our conclusions. Fitch’s (1985) analysis was limited by an absence of data on characters such as adult and neonate size for many of the populations he summarized. When we include such data, it is clear that geographic variation in reproductive characteristics of *T. sirtalis* involves more than simply variation in litter size.

Perhaps the most obvious character that varies geographically in this species is adult body size. In this study, there was highly significant variation in SVL of gravid females among sites. In particular, several of our samples from western Canada included much larger females than did those from eastern Canada (Table 2). However, very large females also are known from eastern parts of the range of *T. sirtalis* (e.g., Wallace, 1938; Wood, 1948; Martof, 1954). Thus, the important distinction between pop-

ulations such as, for example, Oakville (“small” snakes) and Wood Buffalo (“large” snakes), is probably not the maximum size possible in each but the average size (age) at which they reach maturity. Parallel variations in body size among sites are seen for adult males and nongravid

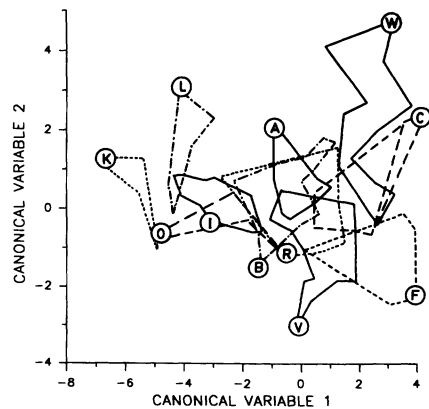


Fig. 5. Plot of litter scores on canonical variable 2 vs scores on canonical variable 1 for all sites combined. Analysis was done on female SVL, mean neonate SVL, and litter size. Symbols as in Figures 2–4; n = 129. Canonical variable 1 is positively correlated with female SVL and neonate SVL but negatively correlated with litter size, whereas canonical variable 2 is positively correlated with female SVL and litter size but negatively correlated with neonate SVL. However, the (partial) coefficient for litter size on canonical variable 2 is negative.

adult females (P. T. Gregory, K. W. Larsen, and D. R. Farr, unpubl.). The factors influencing geographic variation in body size of *T. sirtalis* are not known, but students of island populations of various snakes have suggested that body size variation might be attributable to variations in food availability (Shine, 1987; Hasegawa and Moriguchi, 1989; Forsman, 1991) or differential mortality (King, 1989).

Body size of female might be expected to account for much interpopulation variation in characters such as litter size (Ritke, 1990). However, in this study, SVL "explains" very little of such variation (Fig. 2). Although female SVL is a good predictor of litter size within several populations, the relationship between female SVL and litter size varies too much among populations for it to be of general utility. This seems similar to the situation in *Storeria occipitomaculata* (Semlitsch and Moran, 1984; Brodie and Ducey, 1989) and *Bothrops asper* (Solorzano and Cerdas, 1989) but contrasts strongly with that in *T. elegans* (P. T. Gregory and D. R. Farr, unpubl.), in which geographically distinct populations share a common relationship between female SVL and litter size. In that case, variation in female SVL accounts for 58% of the variation in litter size overall (P. T. Gregory and D. R. Farr, unpubl.). Our data also suggest that interpopulation variation in female body size of *T. sirtalis* only partly accounts for geographic differences in neonate size (Fig. 3).

There is a marked tendency for litters of *T. sirtalis* to be larger in the east than in the west, even when differences in SVLs of mothers are taken into account. This is not simply a function of the small sizes of our samples from eastern populations. Large females from eastern North America can produce huge litters (Wood, 1945; Mattlin, 1948; T. J. Guenther and P. T. Gregory, unpubl.), comparable to that of the single large Interlake female reported in this study (Fig. 2). Wallace (1938) recorded a litter of 73 young (plus one fetus) from a female 940 mm total length, and Martof (1954) reported a litter of 85 from a female 110.5 cm total length (SVL not given in either case). Data from other studies offer some support for our conclusion that litter sizes are greater in eastern than western populations (Table 7), but the data sets are incomplete in most cases. The large litters produced by California captive-reared *T. sirtalis* in the study by Cover and Boyer (1988; Table 7) are a notable exception to this trend (but see below).

In addition to larger litters, eastern *T. sirtalis* produce markedly smaller young than do western *T. sirtalis*, in general (Tables 2, 7), although

Hebard's (1950) data (Table 7) stand out from other western populations. Thus, there is an apparent tradeoff between litter size and offspring size overall. However, offspring size tends to be relatively constant within populations, as would be predicted from models of optimal offspring size (Smith and Fretwell, 1974), and there is only weak evidence of tradeoffs between litter size and offspring size within populations, even after we make adjustments for differences in body sizes of mothers. King (1993), in a careful study of *Storeria dekayi* using path analysis, demonstrated a clear tradeoff between offspring size and litter size but found the conclusions from studies of other snake species to be variable. Plummer (1992) found no evidence of such a tradeoff in *Nerodia rhombifer*. Tradeoffs are difficult to measure, and correlations among different individuals, such as those presented here, are probably the least desirable kind of evidence (Reznick, 1985). Ultimately, tradeoff occurs at the level of the individual, regardless of the relationship among different individuals.

The continentwide pattern of variation in reproductive characteristics of *T. sirtalis* is superimposed on smaller-scale variation, which occurs even locally. For example, our two study sites in the Okanagan Valley of British Columbia (Vernon and Okanagan Falls) are separated by only 140 km, yet neonates at one site were much bigger than at the other. Several authors have found differences in litter size of *T. sirtalis* between nearby sites (e.g., Kephart, 1981; Greenwell et al., 1984; Seigel and Fitch, 1985), although in some cases the difference was either not significant or insufficient information was provided for it to be tested. These studies and ours emphasize the notion that any characterization of a species must be site specific. It probably also should be time specific.

One of the problems in comparing litter size between sites is that litter size also may vary significantly between years at a given site, as Seigel and Fitch (1985) showed for three species of snakes, including *T. sirtalis*. If reproductive characteristics change from year to year, then comparisons between sites may be biased, depending on the year in which data were collected. This is a potential problem in the interpretation of our analysis because we had insufficient samples to study interyear variation. However, P. T. Gregory and D. R. Farr (unpubl.) studied several of the same sites used here and found that year-to-year variation in litter size (corrected for female SVL) of *T. elegans* was not significant. By contrast, annual variation in neonate size in that study, although modest, was significant.

TABLE 7. REPRODUCTIVE DATA FROM SELECTED STUDIES OF *Thamnophis sirtalis*. Headings and values as in Table 2. See Fitch (1985) and Farr (1988) for other sources.

Location	Female SVL (mm)	Litter size	Neonate SVL (mm)	Neonate mass (g)	RML	Source
New Hampshire	—	12.90 (104, —)	—	—	—	Zehr, 1962
Ohio	—	—	—	2.14 (10, —) (2–2.5)	—	Mattlin, 1948
Ontario ^a	558.88 (25, 75.47) (414–746)	18.32 (25, 7.40) (6–36)	—	—	—	T. J. Guenther and P. T. Gregory, un- publ.
Michigan	—	18.00 (20, —)	—	—	—	Carpenter, 1952
Michigan	—	85 (1, —)	140.37 (78, —) (117–151)	—	—	Martof, 1954
Minnesota	497.8 (35, 31.0) (422–452)	13.7 ^b (35, 3.8) (6–22)	—	—	—	Dunlap and Lang, 1990
Kansas ^c	660 (approx.) (504–950)	14.5 ^d (132, —) (4–29)	167.90 (151, —)	1.88 (151, —)	—	Fitch, 1965
California ^e	542.59 (29, 70.81) (470–775)	7.59 ^e (29, 3.99) (1–22)	—	—	—	Kephart, 1981
California ^f	658.17 (6, 63.12) (581–755)	17.00 (6, 9.27) (9–35)	167.58 (93, —) (147–185)	2.94 (102, —) (1.7–4.0)	0.45 (2, 0.02) (0.44–0.46)	Cover and Boyer, 1988
Washington ^g	—	—	159.23 (68, 5.07) (148–170)	—	—	Hebard, 1950

^a Based on dissections of *preserved* specimens (therefore, SVL measurements may differ from those on fresh specimens).

^b Based on advanced-stage embryos.

^c Estimates made from figures in source.

^d Based on both captive births and hand palpations in field.

^e Based on hand palpation in field.

^f From captive breeding of zoo specimens; statistics calculated from figures in source, which included repeated measurements from same females in different years.

^g Methods not given.

Why do reproductive traits differ in value from year to year and from place to place? Andrén (1982) and Andrén and Nilson (1983) concluded that changes in prey availability were responsible for yearly variations in reproductive characteristics of *Vipera berus*. Seigel and Fitch (1985) proposed a similar hypothesis after showing that annual changes in clutch size of snakes were correlated with rainfall. Differences in prey availability obviously could explain spatial differences in reproductive output as well as temporal.

This hypothesis recently received support from an experimental study by Ford and Seigel (1989), who showed that litter size in *T. marci-*

anus increases with food intake (before ovulation; R. A. Seigel, pers. comm.) by the mother. Further work by Seigel and Ford (1991) has yielded similar results for an oviparous snake, *Elaphe guttata*. It is, therefore, possible that the large litters produced by California *T. sirtalis* in the study by Cover and Boyer (1988; Table 7) might partly reflect high food intake in captivity. Their data indicate a steep increase in litter size with increasing SVL, similar to, but much more marked than, that seen in the high-intake group in Ford and Seigel's (1989) study. However, Cover and Boyer's study included only six litters from just three individual females.

Temporal and spatial variations in weather

or climate also could influence other reproductive characteristics of snakes. For example, experimental work has shown that developmental temperature can affect size of hatchling lizards and snakes (see review in Farr and Gregory, 1991).

Because of studies such as those cited above, we cannot reject the hypothesis that differences in conditions under which we held snakes were responsible for the differences we found among populations. However, most of our snakes were held under similar conditions. Only Interlake snakes were held under markedly different conditions, yet these snakes and wild-caught Interlake snakes that were dissected showed the same relationship between female SVL and litter size, suggesting that captive conditions were not a significant influence on litter size. On the other hand, small differences in captive conditions might have significantly affected RML by influencing the mass of the mother but not her brood; this perhaps might account for the virtual lack of pattern in variation of RML among populations. However, the inconsistent timing of our measurements of pre- and postpartum mass also may have had an influence. It would be worthwhile to determine what proximate factors influence RML (or the more commonly used RCM) because it is a potentially important life-history trait.

Even if captive conditions influenced some of our measurements, the magnitude of interpopulation variation in litter size and neonate SVL that we observed was much greater than has previously been reported among years at a site or in experimental situations. It seems unlikely that such a marked longitudinal cline in litter size, for example, could be explained simply by differences in feeding level. A more likely hypothesis, therefore, is that there are genetic differences in life-history traits among some of these populations. Such differences could represent adaptive responses to differing environmental pressures. Clearly, however, we need experiments to determine the relative contributions of environment and genetics to these traits before we can say much about the adaptive significance or lack thereof of any particular trait or combination of traits (Stearns, 1980).

We also need data on other important demographic traits, especially lifetime patterns of mortality. Larsen and Gregory (1989) and Larsen et al. (1993) compared the known life-history features of two of the populations considered here, Interlake and Wood Buffalo. At both sites, summers are fairly short and winters long and cold. Although these two populations

are regarded as belonging to the same subspecies and are ecologically similar in several respects, it is difficult to imagine how they could be more different demographically. Wood Buffalo snakes are much larger on average, have higher adult (male) survivorship, and produce smaller litters of larger young than do Interlake snakes. We have no data on mortality rates of young snakes or adult females in either case, but the above data are consistent with a "bet-hedging" life history (Stearns, 1976); that is, if adult mortality is high relative to that of juveniles, the best strategy is to flood the environment with young (Interlake snakes), but if adult mortality is low, it is more advantageous to produce just a few young each time, spreading the risk of losing a litter over more reproductive opportunities in a lifetime (Wood Buffalo snakes). However, there is no evidence, from our small samples, of east-west differences in reproductive investment (crudely indexed by RML), which would be expected to accompany variations in litter size in such a situation (e.g., Leggett and Carscadden, 1978). Furthermore, lifetime mortality patterns will be partly dependent on offspring size, which is itself likely subject to direct selection in response to other factors. For example, Völkl (1989) suggested that small neonate *Vipera berus* would be favored where prey density is low, because small neonates would be more likely than large neonates to achieve the 25% gain in mass necessary for successful hibernation. Size of available prey species also might influence the evolution of neonate size, but we have no data on such factors for any of our study populations.

The comparison of Interlake and Wood Buffalo snakes is somewhat reminiscent of Dunham et al.'s (1988a) finding of little concordance between variation in life histories of populations of *Sceloporus undulatus* and environments in which they occurred. They also found no clustering of apparently closely related populations (same subspecies) on the basis of life histories.

Finally, even if the reproductive differences between eastern and western *T. sirtalis* are genetically based, it is possible that they have little to do with adaptive responses to their present environments. There are probably multiple possible "solutions" to any given environmental "problem," and two or more suites of characteristics might be equally adaptive [or "expansive" (Gould and Vrba, 1982)] in a particular situation. Present-day differences between the life histories of eastern and western *T. sirtalis*, therefore, might just reflect different origins, perhaps resulting from geographic isolation during glacial periods (Blair, 1965) prior to

reinvasion of northern latitudes in the last 12,000 years. Understanding of phylogeny is critical to interpretation of adaptation (Brooks and McLennan, 1991).

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- (PTG) DEPARTMENT OF BIOLOGY, UNIVERSITY OF VICTORIA, VICTORIA, BRITISH COLUMBIA, V8W 2Y2 CANADA; AND (KWS) DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ALBERTA, EDMONTON, ALBERTA T6G 2E9 CANADA. Submitted 8 June 1992. Accepted 16 Nov. 1992. Section editors: D. Cundall and F. Irish.