



Are There Any Meaningful Correlates of Geographic Life-History Variation in the Garter Snake, *Thamnophis sirtalis*?

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ARE THERE ANY MEANINGFUL CORRELATES OF GEOGRAPHIC LIFE-HISTORY VARIATION IN THE GARTER SNAKE, *THAMNOPHIS SIRTALIS*?—Many species of organisms vary markedly in demographic char-

acteristics across their range, but identification of causative variables is usually difficult. In a recent paper (Gregory and Larsen, 1993), we described geographic variation in reproductive traits among 11 Canadian populations of the common garter snake, *Thamnophis sirtalis*, but did not examine the relationships between these traits and environmental or other potentially influential variables. Such an examination, largely based on the same data set, is the aim of this note.

To begin, we correct three minor errors in our original paper. First, in figure 1 of Gregory and Larsen (1993), the symbols for two of the study sites, Creston and Okanagan Falls, are reversed. Second, in our earlier table 1, the longitude given for Chilcotin should be 122°31'W. Third, we inadvertently used the wrong average size of neonates for one of our litters and left out that variable for another litter; correcting this resulted in extremely small changes to the values in our discriminant analysis and in our figures 2–5 but did not affect our conclusions at all. Our earlier paper also included some fairly small samples, especially from eastern Canada. To add confidence to our estimates of values of reproductive traits in that paper, we have since added counts of litter size by palpation for nine gravid snakes from Oakville in 1992, raising the sample size for that site to 13. Palpation of females in the field has been shown to be a reasonable method for estimating litter size in garter snakes (Farr and Gregory, 1991). Inclusion of the new data changed the mean snout–vent length (SVL) of Oakville gravid females from 530 mm to 526.1 and mean litter size from 14.5 to 15.7, making scarcely any difference. In the analyses that follow, which mainly involve canonical variable 1, we do not use these revised values for Oakville (except in Fig. 1 below), because the canonical variables are based on neonate SVL as well as female SVL and litter size; we did not obtain neonates from the 1992 snakes. All analyses were done with Statistical Analysis Systems Version 6.03 (SAS Institute, Inc., 1988), using $\alpha = 0.05$ as the significance level. The figure was produced using SYGRAPH (Wilkinson, 1990). Except where otherwise indicated, $n = 11$ in all correlations discussed below.

In our 1993 paper, we found that there was significant variation among sites in female SVL, litter size, and neonate SVL. Figure 1 summarizes mean values of traits for each population (including the additional data from Oakville) and relationships among them. Within most sites and for all sites combined, size of female was positively correlated with litter size (not al-

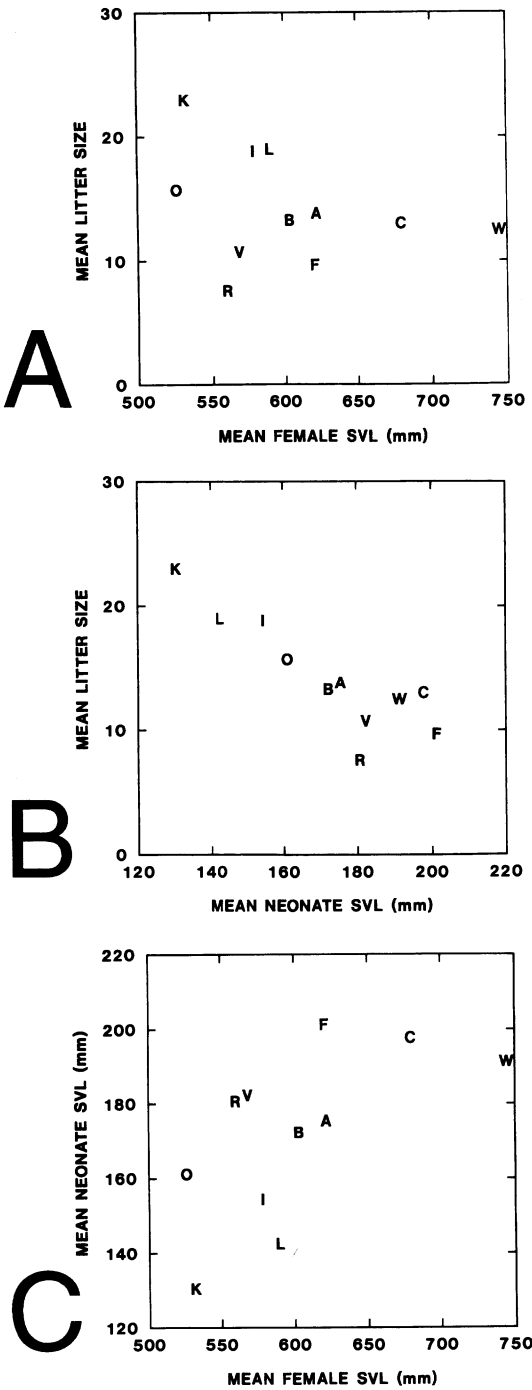


Fig. 1 Plots of relationships among life-history traits, using means for 11 populations (including data from nine Oakville females added to data from Gregory and Larsen, 1993): (A) litter size vs SVL of mother ($r = -0.32, P = 0.34$); (B) litter size vs SVL of neonates ($r = -0.87, P = 0.0004$); (C) SVL of neonates vs SVL of mother ($r = 0.63, P = 0.04$). Letters indicate locations: O = Oakville, I = Interlake, L = Long Point, K = Kejimikujik, B = Botanical Beach, A = Fort As-

ways significantly; Gregory and Larsen, 1993), but these variables were negatively correlated among sites (Fig. 1A). However, when we removed the effect of neonate size by partial correlation, litter size became positively related to female SVL among sites ($r = 0.61, P = 0.06$). This is because litter size was significantly negatively correlated with neonate size, both within and among populations (although weakly in the former; Gregory and Larsen, 1993), indicating a possible trade-off between these two traits (Fig. 1B). This partial correlation was strengthened when we calculated mean values using only snakes for which we had measured all three traits, weighting each population (as below) by the number of litters used ($r = 0.66, P = 0.04$). In short, populations producing larger litters tended to produce smaller babies. Overall, using canonical discriminant analysis on three life-history variables (with mean SVL of littermates = neonate SVL), we found a distinct geographic trend, with eastern Canadian snakes tending to be smaller at maturity (but not necessarily at maximum size) than western snakes and to produce larger litters of smaller young (Gregory and Larsen, 1993).

In calculating the interpopulation correlations that follow, we had three options: (1) to treat each litter as an individual observation; (2) to treat each population as an observation, using means for the three life-history traits; or (3) to proceed as in method 2, but to weight each observation by the sample size (= number of litters) in each population (Freund et al., 1986). The first approach is inappropriate here because the sample size varies drastically among populations, especially between our three most easterly populations and the remainder. On the other hand, the second approach gives each population equal weight even though they are based on samples of different sizes. The third approach is best because it maintains the same number of observations as method 2 but gives each observation a weight corresponding to the number of data used to derive it. We use approach 3 here, with average neonate SVL for each site represented by the weighted (by number of neonates measured), rather than the simple, average of mean SVLs of littermates from that site. A further consideration was whether or not to use all the observations in our data set or restrict ourselves to the subset of 130

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siniboine, R = Creston, V = Vernon, C = Chilcotin, F = Okanagan Falls, W = Wood Buffalo (see Gregory and Larsen, 1993, for descriptions of localities).

litters on which we had measurements for all traits and could therefore calculate canonical variables. We chose the latter for presentation here. In practice, it made no great difference to our conclusions whether we used individual observations or population means or whether we used all data available, including the additional snakes from Oakville, or just the litters used in our discriminant analysis. Except for the relationship between female SVL and litter size, which was positive overall and within sites but negative among sites (see above), only a few borderline correlations changed from significant to nonsignificant or vice versa depending on the particular approach.

In our canonical discriminant analysis, canonical variable 1 was highly correlated with average SVL of littermates and somewhat less so with litter size and SVL of mother ($r = 0.97$, -0.55 , and 0.53 , respectively; $n = 130$, $P = 0.0001$ in each case); these relationships were even stronger when we used the weighted population means (respectively: $r = 0.99$, $P = 0.0001$; $r = -0.79$, $P = 0.004$; $r = 0.65$, $P = 0.03$). As a result of these strong relationships between canonical variable 1 and the traits we measured, we focus mainly on the former in our analyses. Because this is a purely exploratory exercise to seek potentially interesting hypotheses for further study, we make no attempt to control the rejection level for multiple correlations calculated on the same data set (Larzelere and Mulaik, 1977).

What might explain the observed differences in life-history traits among populations? At the outset, it is important to remember that we have no idea to what extent the differences among these populations are genetically vs environmentally determined. This is not a trivial question because numerous studies have shown that these kinds of traits are extremely plastic phenotypically in animals. For example, Ford and Seigel (1989) showed that litter size in the garter snake, *T. marci*, varied significantly with food intake by the mother. We need to test the heritability of traits such as body size and litter size, and we are planning cross-breeding experiments to do this. However, for now, we simply note that the differences we have observed in litter size and neonate SVL among populations are much greater than those seen in any experiments concerning plasticity of those traits.

Why should western snakes be bigger, both at birth and as adult, and have smaller litters? Not only do we not know what external factors are involved, but causal relationships among these variables are unknown. Various models could be invoked and then analyzed using an

appropriate approach such as path analysis (King, 1993). For example, the key variable here might be size at birth because finding appropriate prey is critical to early survivorship, and we might expect size at birth to vary with availability of prey of different sizes. Size at birth might then partly determine the values of the other two variables. We have evidence from *T. elegans* that, all else being equal, larger neonates grow faster in their first year (Gregory and Prelypchan, 1994), and there is certainly a positive correlation between neonate SVL and adult female SVL among populations in our data (Fig. 1C). Under this model, larger neonates also would mean fewer neonates, given a finite amount of energy available for reproduction. We have too few sites to do a meaningful path analysis among sites for this data set, but such an analysis potentially would be useful.

In the field, *T. sirtalis* feeds mainly on amphibians, especially anurans, and earthworms; furthermore, there is a tendency for eastern populations to feed more heavily on earthworms and western populations on amphibians (Fitch, 1965; Gregory, 1978). Even where amphibians are eaten more frequently, earthworms seem to be more important food for the younger (smaller) age groups (Farr, 1988; PTC, unpubl. data). Thus, there is an association between smaller size and feeding on earthworms. We have no data on earthworm abundance for any of our sites, but earthworms seem rare or absent at the three sites with very large neonates (Wood Buffalo, Chilcotin, Okanagan Falls). However, common species of earthworms, although now widespread, are probably not native to Canada (Reynolds, 1977) and are therefore not "traditional" prey. With respect to other prey, canonical variable 1 was strongly correlated with the number of anuran species present in the areas of the various sites ($r = -0.73$, $P = 0.01$), as was only neonate SVL among the individual life-history traits; number of frog species is based on field guides (Conant, 1975; Stebbins, 1985) but confirmed by direct observation at most sites. However, from data in Wright and Wright (1949), most of these species of frogs are too big even at metamorphosis for neonate garter snakes to eat. When we restricted the analysis to "small" frogs (< 15 mm at metamorphosis), the correlation with canonical variable 1 (and neonate SVL) was weaker, although still significant ($r = -0.65$, $P = 0.03$). Furthermore, even small frogs at some sites may not be suitable as food for neonate garter snakes. For example, at Wood Buffalo, Larsen (1986) found that neonate *T. sirtalis* were unable to swallow live or dead newly metamor-

phosed wood frogs (*Rana sylvatica*), easily the most abundant anuran species at the site. This analysis also ignores variation among sites in size of frogs at metamorphosis and anuran abundance at most sites, on which we have no data. Whether there is a causal connection between occurrence of different types of prey and values of life-history traits or whether it is simply a coincidence of geographic variation is unknown, but the hypothesis that body size at birth is partly determined by prey availability remains an idea worthy of further investigation. Other authors have linked size or availability of prey with body or head size of both adult (Shine, 1987; Hasegura and Moriguchi, 1989; Forsman, 1991) and young (Völkl, 1989) snakes.

As indicated above, canonical variable 1 was strongly correlated with longitude ($r = 0.77$, $P = 0.01$), but it was also, somewhat more weakly, correlated with latitude ($r = 0.63$, $P = 0.04$). This reflects the fact that our eastern samples also were all more southerly than our western samples. These correlations were weakened somewhat, the latter becoming nonsignificant, when we used partial correlation to control the effect of latitude on longitude and vice versa. Female SVL was positively related to latitude, litter size negatively to longitude, and neonate SVL positively to longitude. None of the life-history variables was significantly correlated with altitude (data in Table 1 of Gregory and Larsen, 1993), even when latitude and longitude were controlled by partial correlation. In sum, there is a trend in our samples, from southeast to northwest, of increasing body size (both at birth and at maturity) and decreasing litter size, but we lack samples from key areas (e.g., northern Ontario, more southerly populations in the United States).

Despite the correlation with latitude, canonical variable 1 was not significantly correlated with climatic variables (mean daily summer temperature: $r = -0.20$, $P = 0.55$; coefficient of variation of daily summer temperature: $r = 0.17$, $P = 0.63$; climate data in Table 1 of Gregory and Larsen, 1993). However, female SVL was significantly correlated with mean summer temperature ($r = -0.67$, $P = 0.02$). In a recent review, Atkinson (1994) concluded that, for many ectotherms, increased rearing temperature results in smaller eventual body size (even with faster growth rates), although it is generally not clear what proximate or ultimate factors are responsible. Thus, snakes at northern latitudes might be larger because they grew up at lower temperatures. However, among other things, this hypothesis ignores genetic differences between the populations. It also relies on

a simplistic explanation of the relationship between environmental temperature and the actual body temperature of the snake; the latter seems more likely to be the critical variable.

Finally, it is possible that the differences that we have observed in life-history characteristics among populations are mainly phylogenetic in origin. As recently as 14–16,000 years ago, Canada was covered by ice (Rutter, 1988), and it is probable that widespread forms like *T. sirtalis* reinvaded the country via multiple routes, as is the case for other species (Todd and Hatcher, 1993). If so, the differences between eastern and western snakes largely could be a result of different histories.

Unfortunately, we do not have a phylogeny for these populations, but we do have a taxonomy in their subspecific status. Following Fitch (1980), the populations we studied encompass five recognized subspecies, from east to west: *pallidula* (Kejimikujik), *sirtalis* (Oakville, Long Point), *parietalis* (Interlake, Fort Assiniboine, Wood Buffalo), *fitchi* (Creston, Vernon, Okanagan Falls, Chilcotin), and *pickeringi* (Botanical Beach). Table 1 provides a statistical summary, by subspecies, of the values of the life-history traits we measured in these 11 populations. One-way analysis of variance of canonical variable 1 among subspecies revealed significant variation among nearly all putative taxa ($F_{4,125} = 23.37$, $P = 0.0001$, with variation among subspecies accounting for 50.7% of total variance; Bonferroni test showed that only *pickeringi* and *parietalis* were not significantly different). However, because three of the subspecies were represented by multiple populations, a better analysis in this case would be a nested ANOVA, which showed that, although there was much variation among subspecies, it was not significant, and there was even more variation among sites within subspecies (Table 2).

Of particular interest here is the observation that *parietalis* was generally more variable than any of the other subspecies (Table 1). In an earlier study, Larsen et al. (1993) compared two of these populations of *parietalis* (Wood Buffalo and Interlake) and showed how greatly different they were in life-history traits, despite otherwise similar ecologies (e.g., communal overwintering, long-distance migration); Fort Assiniboine snakes are intermediate between these two extremes. When we did cluster analyses among populations on mean values of canonical variables or individual life-history traits using a variety of methods available in Statistical Analysis Systems, we found a variety of clustering patterns, but in virtually all cases, Interlake snakes clustered with Ontario snakes. This

TABLE 1. STATISTICAL SUMMARY OF LIFE-HISTORY DIFFERENCES AMONG SUBSPECIES OF *Thamnophis sirtalis* BASED ON DATA COLLECTED FOR 11 POPULATIONS ACROSS CANADA. n = number of litters. Shown are mean (standard deviation) in upper line and (minimum-maximum) in lower line. Only litters on which all variables were measured were used, so that values presented differ somewhat from those that would be calculated from Table 1 of Gregory and Larsen (1993) or from Figure 1 of this paper. Also, each value of SVL of neonates is represented by mean SVL of littermates, so that range is smaller than seen in Table 1 of Gregory and Larsen (1993), which was based on individual SVLs. The subspecies means for neonate SVL are weighted by number of neonates measured in each litter and the standard deviation is calculated from similarly weighted estimates of variance among litter means. Canonical variable 1 is recalculated from Gregory and Larsen (1993) and is based on an analysis among populations, not subspecies.

Subspecies	n	Female SVL (mm)	Litter size	Neonate SVL (mm)	Canonical variable 1
<i>pickeringi</i>	15	603.33 (61.20) (500–695)	13.27 (4.59) (7–22)	172.28 (23.23) (159.41–182.50)	0.043 (0.94) (–2.23–1.09)
<i>fitchi</i>	57	588.70 (66.28) (492–785)	10.05 (3.97) (2–21)	188.15 (38.44) (143.80–213.67)	1.00 (1.40) (–2.61–3.90)
<i>parietalis</i>	45	651.31 (92.36) (525–905)	14.27 (5.45) (5–27)	174.05 (59.56) (133.71–204.82)	0.04 (2.33) (–4.40–3.73)
<i>sirtalis</i>	9	563.33 (64.68) (505–680)	17.00 (6.44) (9–30)	147.46 (55.87) (130.77–179.00)	–3.30 (1.55) (–5.34––0.34)
<i>pallidula</i>	4	532.25 (56.41) (464–601)	23.00 (7.35) (17–33)	130.42 (25.50) (124.15–137.72)	–5.64 (0.74) (–6.68––4.94)

matches our original discriminant analysis (Gregory and Larsen, 1993), in which we found that Interlake snakes, the easternmost of our western populations, were actually more similar in reproductive traits to Ontario and other eastern snakes than they were to western snakes. Therefore, we removed Interlake snakes from the nested analysis and found that a greater amount of variance was accounted for by differences among subspecies (although still not significantly so, Table 2). However, reclassifying *parietalis* as *sirtalis* or leaving out *parietalis* altogether revealed highly significant variations among subspecies that accounted for much of the variance in canonical variable 1 (Table 2). At the other extreme, reclassifying Wood Buffalo snakes as *fitchi* had a similar effect.

Therefore, the subspecies *parietalis* is some-

what of an anomaly in this analysis. Taxonomically, and certainly in terms of general appearance, Interlake snakes are western snakes, but they more closely resemble eastern snakes in life-history characteristics. If we imagine, for example, two main lineages of common garter snakes in Canada, one eastern and one western, then the Interlake snakes might be either western snakes convergent on eastern snakes in life history or eastern snakes convergent on western snakes in morphology and coloration. Which ever is the case, it opens up an interesting avenue for future research.

So far, we are unable to point to any pattern of variation in life-history traits of *T. sirtalis* that is clearly explained, other than in a purely statistical sense, by any of the environmental or other factors for which we have measurements.

TABLE 2. COMPONENTS OF VARIANCE (% VARIANCE EXPLAINED), CALCULATED AS DESCRIBED BY GREGORY AND PRELYPCHAN (1994), FROM NESTED ANALYSES OF VARIANCE OF CANONICAL VARIABLE 1 (RECALCULATED FROM GREGORY AND LARSEN, 1993) AMONG SUBSPECIES AND LOCATIONS WITHIN SUBSPECIES, WITH VARIOUS POPULATIONS OF *parietalis* EITHER REMOVED OR RECLASSIFIED. Both subspecies and location were treated as random factors. Because of nonorthogonality, F-tests were approximated using RANDOM/TEST option in PROC GLM (SAS, 1988) and Type III mean squares. * = significant at $P = 0.05$.

Source of variation	All data	Interlake removed	Interlake reclassified as <i>sirtalis</i>	<i>parietalis</i> removed	Wood buffalo reclassified as <i>fitchi</i>
Subspecies	33.0	57.9	64.5*	75.1*	65.3*
Locations within subspecies	52.1*	26.1*	20.9*	12.0*	21.8*
Remainder	14.9	16.0	14.6	12.9	12.9
n	13.0	118	130	85	130

This is similar to the situation in the lizard, *Sceloporus undulatus*, reviewed by Niewiarowski (1994), in which life histories of different populations were not readily grouped by either habitat or subspecies. Clustering pattern was also sensitive to the clustering algorithm used.

Determination of which factors explain geographic variation in life histories of the common garter snake will require much further work beyond what we have reported here. In particular, we suggest that we need to examine the genetics of these traits, to look at fitness differences in various environments and, most important, to construct phylogenies.

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 Ichthyologists and Herpetologists

LONGEVITY OF SOME CORAL REEF FISH SPAWNING AGGREGATIONS.—Many species of coral reef fishes that spawn planktonic eggs aggregate at discrete sites for spawning. These range from predatory groupers (Smith, 1972; Colin, 1992, Samoils and Squire, 1994) and snappers (Carter and Perrine, 1994) to herbivorous parrotfishes and surgeonfishes (Randall and Randall, 1963; Colin and Clavijo, 1988; Myrberg, et al., 1989). Little is known, though, of the long-term use of aggregation and spawning sites by reef fishes. Observations at three sites, reported here, extend the known use of discrete aggregation and spawning sites, for which excellent records exist, to periods of 12–28 years. One, an aggregation site of redbtail parrotfish, *Sparisoma rubripinne*, was first discovered in 1960 by Randall and Randall (1963). A second site had spawning aggregations of two species of surgeonfishes, *Acanthurus bahianus* and *A. coeruleus*, first observed in 1976 (Colin and Clavijo 1988), and the third had an aggregation of striped parrotfish, *Scarus iserti* (= *S. croicensis*), in 1971 (Colin, 1978). Anecdotal records exist for several decades of occurrence of grouper spawning aggregations at specific sites, but no long-term detailed information on site usage is available for any of these species (Colin, 1992; Sadovy, 1994).

Virtually all of the larger fishes found on coral reefs produce planktonic eggs (Colin and Clavijo, 1988; Leis, 1991), rather than demersal eggs, and potentially may have spawning aggregations. It is these species that are targeted by fishing activity, but these are also the species about which we know the least regarding the effect of fishing on their populations and resultant effects in the reef community (Russ, 1991). Most reef fish population monitoring studies over a year or two in duration (Sale,

1991) have largely dealt with relatively small, benthic spawning fishes, principally pomacentrids, which do not aggregate to spawn and are insignificant in reef fisheries. Spawning aggregations, as shown here, present a unique opportunity for managers and ecologists to assess and monitor the population size and reproductive potential of numerous species of larger reef fishes, many of which are normally widely dispersed. Larger fishes are often cryptic or difficult to approach, behaviors which tend to break down during aggregations. Once the relationship of aggregation occurrence and size with spawning occurrence has been documented (Colin, 1992), an estimation of eggs spawned is also possible, data which are difficult to obtain by other methods.

Methods.—Observations were made while SCUBA diving with notes recorded on underwater slates. Sites were located using information provided in earlier publications or by using known landmarks on shore. There is no doubt that the same areas of reef that were previously examined were revisited because reef topography and features were very distinctive in the study areas.

Results.—Virgin Islands: Randall and Randall (1963) described the first known spawning aggregation of a parrotfish, *S. rubripinne*, near Reef Bay, Saint John, US Virgin Islands. The site was at the most seaward (southern) projection of a fringing reef which terminated in a sandy bottom at 20 m depth. Approximately 200 initial phase individuals occurred in the group. Spawning occurred over a long season, possibly year round, during the afternoon.

This site was revisited in 1977 and 1988. On 3–4 March 1977, in late afternoon, approximately 200 *S. rubripinne* were engaged in group spawning an estimated 20 m from the 1977 site. Additionally, a spawning group of about 300–400 spotted goatfish, *Pseudupeneus maculatus*, was about 50 m away (Colin and Clavijo, 1978). It is unlikely that a spawning group of goatfish occurred at the site during Randall and Randall's work (1960–1962), because they certainly would have described such a group.

On 19–20 April 1988, a group of about 50 *S. rubripinne* were found spawning in the afternoon about 20 m from the 1977 site, in a direction believed closer (than the 1977 site) to the exact site reported by Randall and Randall (1963). The *P. maculatus* found in 1977 were not observed in 1988. D. Fagen (pers. comm.), who visited the site with us in April 1988, returned to it again on 29 June 1988 and found