Factors affecting litter size in Western Gartersnake (*Thamnophis elegans*) in British Columbia: place, time, and size of mother

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Abstract

Life-history traits of organisms are influenced by both genetic and environmental factors. We used counts of offspring in captive-born litters to determine how geographic location, year-to-year variation, and body size of mother affected litter size of Western Gartersnake (*Thamnophis elegans*) in four widely separated populations in British Columbia. Litter size varied significantly among populations, but that variation was largely explained by differences in maternal body size among populations; that is, larger females had larger litters. With maternal size treated as a covariate, there was no further significant effect of location or of different years within sites on litter size. The overall regression, pooled over sites and years, between litter size and size of mother accounted for 55% of the total variation in litter size. Nonetheless, the significant variation in body size among locations calls for explanation and the consequent differences in litter size could be important demographically. Presumably, the large amount of unexplained residual variation reflects other differences, beyond body size, between individual mothers. Such differences among individuals might be determined by genetics or by environmental effects such as foraging success, but our data cannot address this question.

Key words: Gartersnake; *Thamnophis elegans*; British Columbia; litter size; body size

Introduction

Life histories are suites of co-varying traits that influence the dynamics of a population and therefore its potential rate of increase in numbers. Key life-history traits of animals include clutch/litter size and frequency, offspring size at hatching/birth, individual growth rate, body size, age at reproductive maturity, and mortality rate (Stearns 1992). Thus, the individual organism's life history is a measure of its relative fitness. To the extent that they are heritable, life histories, and the traits that comprise them, are subject to natural selection; different life histories may be advantageous in different situations (e.g., high versus low risk of predation; Reznick and Endler 1982; more versus less variable environments; Bronikowski and Arnold 1999).

Life histories vary among taxa at all taxonomic levels, including lineage-specific effects. For example, most lizards can vary their clutch size, but two unrelated lineages of lizards, geckos and anoles, have fixed clutch size of one or two eggs (Selcer 1990). Small fixed clutches appear to be adaptations to arboreal habitats in the tropics in which these two groups originated, but they may now constrain these lizards from colonizing temperate-zone environments (Ballinger 1983). Most life-history traits, however, are not constant, but vary among populations within species, between individuals within populations, and within individuals during their lifetime. Some of this variation is genetic, but life-history traits typically exhibit low heritability (Stearns 1992), so other factors, including phenotypic plasticity, play an important role in the expression of these traits. Understanding patterns of variation in life-history traits is relevant not only to testing evolutionary theory, but also for wildlife management and conservation.

Successful reproduction is fundamental to an organism's fitness. The simplest measure of reproductive output is clutch or litter size, the number of offspring produced on a given occasion. In snakes, clutch or litter size is the most frequently recorded measure of reproductive output and has been the focus of numerous studies of life-history variation within and among species (Seigel and Ford 1987). Here, we focus on inter-population comparisons of a widely distributed species of snake in western North America, Western Gartersnake (*Thamnophis elegans*), which ranges latitudinally from southern Arizona to central British Columbia (Rossman *et al.* 1996). Throughout this range, *T. elegans* occupies a diversity of environments that differ in climate, biophysical characteristics, and other attributes that could influence the expression of life-history traits, including litter size. Other wide-ranging species of gartersnakes show considerable geographic variation in litter size (Gregory and Larsen 1993, 1996; Tuttle and Gregory 2014).

Because litter size in gartersnakes is often strongly correlated with body size of mother (Seigel and Ford 1987), litter size could vary geographically simply because of geographic variation in body size. However,

in Common Gartersnake (*T. sirtalis*), variation among sites in litter size was not explained solely by maternal size (Gregory and Larsen 1993); both slopes and elevations of the linear relationships between litter size and maternal size varied among populations. Similar variation in litter size-maternal size relationships was observed between two ecotypes of *T. elegans* in California (Bronikowski and Arnold 1999). Unfortunately, Fitch's (1985) early exploration of geographic variation in litter size of *T. elegans* did not incorporate data on maternal body size.

In addition to geographic variation, litter size in snakes also may vary from year to year, depending on weather, either in the current or previous year (Seigel and Fitch 1985; Brown and Shine 2007; Tuttle and Gregory 2014). Variation in weather within and among years affects prey productivity, and therefore availability of resources to snakes for reproduction. As snakes are ectotherms, their activity and ability to acquire resources also could be affected by weather, independently of resource availability, thereby indirectly influencing reproduction.

Here, we revisit a previous study on reproductive characteristics of *T. elegans* at four widely separated sites in British Columbia (BC; Farr and Gregory 1991), to which we have since added substantially more data. Analysis of litter size in our earlier study was confined to comparisons of different ways of estimating litter size within each site. Here, we test the influences of size of mother, location, and year on litter size across all four populations.

Methods

The four study sites were located, respectively, near Creston in the Kootenay region (KOOT, southeastern BC: 49.12°N, 116.64°W); near Williams Lake in the Chilcotin region (CHIL, central BC: 51.97°N, 122.53°W); at Okanagan Falls in the Okanagan Valley (OKAN, south central BC: 49.34°N, 119.57°W); and near Victoria on Vancouver Island (VANI, southwestern BC: 48.48°N, 123.55°W). These four sites represent distinctly different habitat types. The KOOT site is a complex of extensive marshes bordered by forested slopes, with additional riverside habitat. The CHIL site is a dry, sparsely vegetated grassland with scattered small, isolated ponds. The OKAN site is mainly riverside habitat. Finally, the VANI site is an estuary. All of these sites, except for VANI, were also included in Gregory and Larsen's (1993, 1996) analyses of geographic variation in reproductive characteristics of *T. sirtalis*.

In this study, we recorded litter size through exact counts of offspring borne by gravid females held in captivity until parturition. Our 1991 study consisted of 78 litters collected between 1975 and 1988, albeit not in all years and in different years for each location. For this new analysis, we have added 18 litters from KOOT collected in 1996 for laboratory experiments (Gregory and Skebo 1998; Gregory *et al.* 1999) and 20 from

OKAN collected between 1990 and 2000 (P.T.G. unpubl. data). Conditions under which snakes were maintained in captivity are detailed in Farr and Gregory (1991) and Gregory and Skebo (1998). The additional snakes from OKAN were housed and maintained at University of Victoria as described in Farr and Gregory (1991).

Although most young were born alive, some litters contained dead young and/or undeveloped eggs. From a strictly demographic perspective, only live births matter. However, from an energetic perspective, dead and undeveloped young still represent an investment in reproduction and, together with live young, comprise potential litter size. Furthermore, as it is unclear to what extent the occurrence of dead or undeveloped young is due to stresses experienced by gravid females in captivity (Gregory 2001), excluding these classes of offspring might artificially deflate litter size estimates. Our previous studies suggest that litter size, relative to maternal body size, in a given population is less variable when all components are included (Farr and Gregory 1991; Gregory *et al.* 1992). Finally, counting all litter elements enables comparison with other studies based on estimates of litter size from abdominal palpations in the field or dissections of females in early pregnancy. That is the approach that we have taken here.

In the analyses of variance (ANOVA) and covariance (ANCOVA) that follow, we treat location and year as random factors. Location is a random factor because we did not choose these four study sites for any particular features relevant to life-history variation, but simply because they had populations of *T. elegans*. Similarly, we did not choose years based on weather or any other factors. The years in which we collected data differed for each site, so location and year are not crossed in an orthogonal factorial design; rather, year nested within location is the appropriate model for combined analysis of these two factors. We did all analyses using SAS 9.3 software (SAS Institute Inc. 2011) and a conventional alpha level of 0.05 for rejection of null hypotheses; F-tests were based on Type III sums of squares.

We analyzed the data in stages. First, we combined data for all years for each site and did separate one-way ANOVAs among sites of both size of mother (snout-vent length, SVL) and litter size. Second, to separate the effects of maternal SVL and location on litter size, we ran an ANCOVA of litter size among locations (again combining years for each location), with maternal SVL as a covariate. We first ran the analysis with the interaction of SVL × location included (as a test of homogeneity of slopes), then re-ran it with the interaction removed if that effect was non-significant. Third, for each location, we performed an ANCOVA of litter size among years, again with maternal SVL as a covariate and the same considerations concerning the interaction SVL × year. Fourth, we combined the data across all locations and years for an overall ANCOVA of litter

size, with maternal SVL as covariate and location and year as factors (year nested within location).

Although litter size is a fundamental life-history trait, it is not the only measure of a female's reproductive output. For example, in snakes, offspring size also often varies with maternal size (Seigel and Ford 1987). Because the variable litter mass incorporates both litter size and offspring size, we repeated the analyses described above with litter mass, rather than litter size, as a dependent variable.

Results

We analyzed data from 118 litters (KOOT: 49 litters over five different years; CHIL: 29 over four; OKAN: 31 over seven; VANI: nine over four). Samples in some years were very small, especially for VANI.

Mean litter size was significantly different among locations (ANOVA, $F_{3,114} = 14.74$, $P < 0.0001$; Figure 1), but the pattern of variation was mirrored by significant differences in mean size of mother among locations ($F_{3,114} = 27.23$, $P < 0.0001$; Figure 2). The test of slope heterogeneity of litter size on maternal SVL among locations was non-significant (interaction between location and SVL, $F_{3,110} = 1.90$, $P = 0.13$), so we dropped the interaction term and proceeded with the ANCOVA, which revealed a highly significant effect of maternal SVL on litter size ($F_{1,113} = 138.66$, $P < 0.0001$), but no difference among locations ($F_{3,113} = 0.41$, $P = 0.75$). Thus, the relationship between litter

FIGURE 2. Boxplots of body size (snout-vent length, SVL) of gravid female Western Gartersnake (*Thamnophis elegans*) at four sites in British Columbia. See Figure 1 caption for sample sizes and explanation of boxplots. Locations defined as in Figure 1.

size and maternal body size for the four populations was best described by a common linear regression (Litter Size = 0.048 × Female SVL − 16.56, $r^2 = 0.55$, $F_{1,116} = 140.80$, $P < 0.0001$; Figure 3).
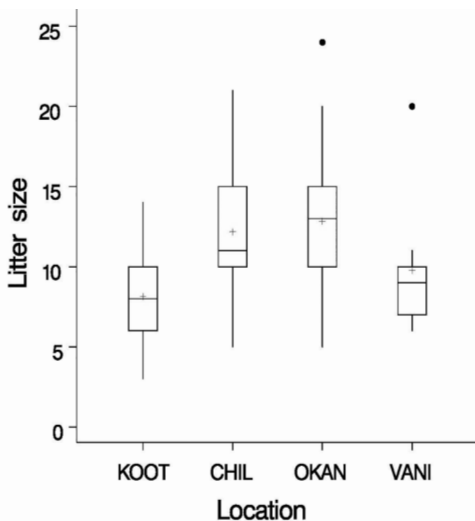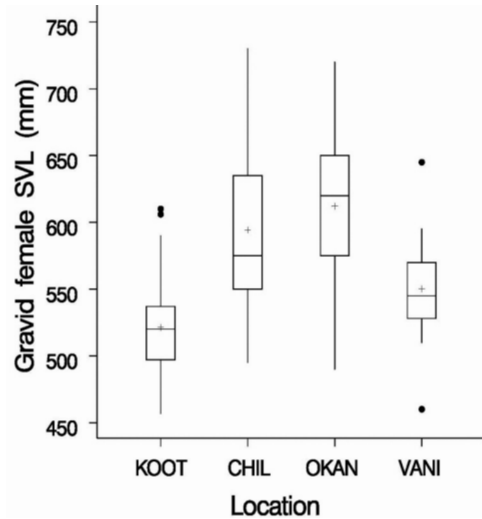

FIGURE 1. Boxplots of litter size of Western Gartersnake (*Thamnophis elegans*) at four sites in British Columbia. Upper and lower ends of boxes represent 75th and 25th percentiles (quartiles), respectively; horizontal line in each box is the median and the mean is indicated by +. Whiskers extend to the most extreme value not exceeding 1.5 times the interquartile distance; individual points represent more extreme observations. KOOT = Kootenay, CHIL = Chilcotin, OKAN = Okanagan, VANI = Vancouver Island. Sample sizes are: KOOT $n = 49$; CHIL $n = 29$; OKAN $n = 31$; VANI $n = 9$.
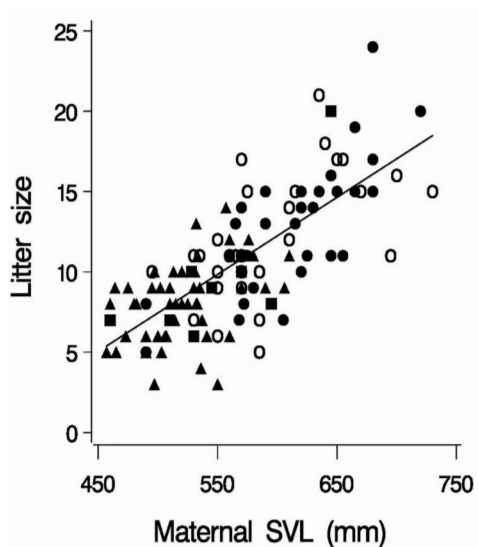

FIGURE 3. Plot of litter size against body size (snout-vent length, SVL) of maternal Western Gartersnake (*Thamnophis elegans*) for four sites in British Columbia. Line represents linear regression of litter size on maternal body size for all locations combined (Litter Size = 0.048 × Female SVL − 16.56). KOOT snakes: triangles ($n = 49$); CHIL snakes: open circles ($n = 29$); OKAN snakes: filled circles ($n = 31$); VANI snakes: squares ($n = 9$). Locations defined as in Figure 1.

When we compared litter size among years for each location, with maternal SVL as a covariate, the interaction between year and maternal SVL was non-significant in each case (Table 1). With no evidence of heterogeneity of slopes, we performed the ANCOVA for each location with the interaction term omitted from the model and found that for each location, there was again a significant positive relationship between litter size and maternal SVL, but no significant variation in litter size among years (Table 2).

The final analysis including all factors again showed that maternal size had a highly significant effect on litter size ($F_{1,97} = 49.51$, $P < 0.0001$), but that neither location ($F_{3,97} = 0.45$, $P = 0.72$) nor year (nested within location; $F_{16,97} = 0.76$, $P = 0.73$) significantly influenced litter size. Overall r^2 for this analysis was 0.60, leaving 0.40 of the total variation in litter size as residual or unattributed.

Litter mass was highly correlated with litter size ($r = 0.87$, $n = 107$, $P < 0.0001$) and the analysis of litter mass essentially duplicated that of litter size, so we omit those additional results here.

TABLE 1. Tests of heterogeneity of slopes of litter size against maternal snout-vent length (SVL) among years (SVL × year interaction) for Western Gartersnake (*Thamnophis elegans*) at each study site. Main effects (SVL, year) also were included in the model, but results are not shown (see Table 2 for these effects in reduced ANCOVA model). KOOT = Kootenay, CHIL = Chilcotin, OKAN = Okanagan, VANI = Vancouver Island.

Location	F_{df}	P
KOOT	$1.14_{4,39}$	0.35
CHIL	$1.21_{2,22}$	0.32
OKAN	$1.65_{5,18}$	0.20
VANI	$3.90_{1,3}$	0.14

TABLE 2. Analyses of covariance (ANCOVA) of litter size among years, with maternal snout-vent length (SVL) as covariate, for Western Gartersnake (*Thamnophis elegans*) at each study site. Slopes of regression of litter size on maternal SVL were homogeneous among years in each case (see Table 1). Locations defined as in Table 1.

Location	Test	F_{df}	P
KOOT	SVL	$7.46_{1,43}$	0.0091
	Year	$0.61_{4,43}$	0.6549
CHIL	SVL	$11.78_{1,24}$	0.0022
	Year	$0.11_{3,24}$	0.9546
OKAN	SVL	$23.41_{1,23}$	< 0.0001
	Year	$0.70_{6,23}$	0.6536
VANI	SVL	$5.90_{1,4}$	0.0720
	Year	$1.33_{3,4}$	0.3811

Discussion

It is worth considering at the outset the degree to which our conclusions were influenced by the methods we used. Holding gravid females in captivity may have a number of effects on litter characteristics because the gravid snake is not usually free to feed or thermoregulate in the same manner as a wild snake (Farr and Gregory 1991). The overall ANCOVA model that we used has practical limitations (Ballinger 1983) and our data set represents an imperfect nested design (e.g., the data are non-orthogonal, years within location were not chosen strictly at random). Nevertheless, our analysis contributes to a broader understanding of geographic and temporal variation in litter size of *T. elegans* and suggests directions for future studies.

Our study has three major findings: litter size of *T. elegans* varies significantly among populations, significant differences in maternal body size among populations account for much of the observed variation in litter size, and little geographic or temporal variation in litter size remains after effects of maternal body size are taken into account. Thus, most of the residual variation in litter size (after maternal size effects have been removed) is due to further differences among individual mothers and/or other unmeasured factors.

Two important issues emerge from this analysis. First, because litter size varies with maternal body size, which varies significantly among populations, we need to explain geographic variation in body size. Second, we need to determine the extent to which variation in litter size among individual females is determined by genetic or environmental factors (e.g., differences in foraging success).

Significant body-size variation among populations has been observed for numerous snake species (e.g., Semlitsch and Moran 1984; Schwaner 1985; Plummer 1987; King 1989; Gregory and Larsen 1993, 1996; Madsen and Shine 1993; Tuttle and Gregory 2012), but explanations vary. For example, body size often increases with size and/or availability of prey (Schwaner 1985; Shine 1987; Madsen and Shine 1993; Boback 2003; Filippakopoulou *et al.* 2014). Smaller size might also be partly attributable to higher mortality from various causes, including predation (King 1989; Filippakopoulou *et al.* 2014). Climate may also play a role. The temperature-size rule predicts that ectotherms should grow more slowly, but reach larger sizes, in colder environments (Angilletta and Dunham 2003). However, departure from the temperature-size rule is common (Tuttle and Gregory 2012) and most species of snakes are actually smaller at higher latitudes and elevations (Ashton and Feldman 2003).

At present, we can offer no explanation for the pattern of body size variation that we observed in *T. elegans* in British Columbia. However, the two sites with relatively large *T. elegans* in our study (CHIL and OKAN) also had larger *T. sirtalis* than most other sites in Gregory and Larsen's (1993) comparative study of that species, suggesting that similar environmental factors may explain at least some variation in body size within these two closely related species.

Thamnophis elegans is a wide-ranging species, but there has been little documentation of geographic variation in its reproductive characteristics. Based on data

from several subspecies combined, Fitch (1985) showed that litter size generally declined from the southern part of the range to the north. Although our data for KOOT and VANI are consistent with this trend, litter sizes of *T. elegans* from CHIL and OKAN are much larger than those from farther south. In fact, the mean litter size (12.8) and maximum litter size (24) that we recorded for OKAN snakes are larger than any reported by Fitch (1985). However, Bronikowski and Arnold (1999) reported similar maximum litter size for large *T. elegans* in northern California. Unfortunately, Fitch's (1985) analysis did not include body sizes of snakes, limiting its comparative value here.

The consistent relationship between litter and maternal body size that we observed for *T. elegans* in British Columbia contrasts observations for populations in northern California. There, lakeshore and meadow ecotypes of *T. elegans* occur in contrasting environments and exhibit differences in numerous life-history traits, including the relationship between litter size and maternal size (Bronikowski and Arnold 1999). The overall relationship that we observed is very similar to that seen for the meadow ecotype; in contrast, lakeshore snakes have a steeper relationship (Bronikowski and Arnold 1999). It would be informative to determine whether British Columbia populations also match the California meadow ecotype in other life-history traits.

Other species also show geographic variation in the litter size-maternal size relationship. For example, in *T. sirtalis*, the relationship between litter size and maternal SVL varies strongly among populations, in both slope and intercept (Larsen and Gregory 1993), especially between eastern and western Canada (Gregory and Larsen 1996). Populations of *T. sirtalis* range from those comprised of small females that produce large numbers of young to those consisting of large females that produce small litters. Correlated with this is variation in neonate size, large litter size usually being accompanied by small offspring (Larsen and Gregory 1993). However, offspring size of *T. elegans* varies relatively little among our study sites (Farr and Gregory 1991). Geographic differences in the relationship between litter size and maternal size also have been observed in Red-bellied Snake (*Storeria occipitomaculata*; Semlitsch and Moran 1984; Brodie and Ducey 1989). In all of these studies, geographic variation in body size accounts for only a small fraction of the variation in litter size.

A perhaps surprising result of our study is the lack of variation among years in litter size, but our samples were small. That said, Brodie and Ducey (1989) also found no significant variation between years in maternal size-adjusted litter size of *S. occipitomaculata*. In Rough Greensnake (*Opheodrys aestivus*) clutch size did not vary among years at one site (Plummer 1983) but did at a second site (Plummer 1997). Seigel and Fitch (1985) determined that, even after correcting for differences in maternal body size, clutch size varied significantly among years in four populations (different species) of snakes, and that this variation was related to rainfall (larger litter sizes in wetter years). This finding prompted Seigel and Fitch (1985) to caution researchers about the limitations of data from short-term (especially from just one year) studies to characterize reproductive habits, an admonition with which we concur. The temporal variations in clutch size reported by Seigel and Fitch (1985) far exceed those that we observed, and it is possible that the environment in their study area (Kansas) is more variable than any of ours. In most cases, their samples extended over a greater number of years than did ours, increasing the likelihood of observing extreme values. Litter size of Plains Gartersnake (*Thamnophis radix*) in Alberta also varies among years in relation to the previous year's rainfall and temperature (Tuttle and Gregory 2014). In addition to the temperate-zone snakes cited above, weather-related annual variation in clutch or litter sizes have been reported in tropical snakes (Brown and Shine 2007) and in other reptilian taxa (e.g., Bleu *et al.* 2013; Hedrick *et al.* 2018).

Weather per se presumably has an indirect effect on clutch size through resource acquisition, possibly by limiting activity and foraging opportunities (e.g., in cool conditions; Tuttle and Gregory 2014) or by influencing prey abundance and availability. For example, Seigel and Fitch (1985) attributed higher clutch size of Ring-necked Snake (*Diadophis punctatus*) in wet years to increased prey availability. Other studies have explicitly demonstrated the link between year-to-year variation in litter size and prey availability, whether driven by weather or other factors (Andrén and Nilson 1983; Brown and Shine 2007; King *et al.* 2008). However, in Brown Water Python (*Liasis fuscus*) changes in prey availability influenced clutch size only slightly, instead affecting the post-oviposition body condition of females (Madsen and Shine 1999).

The search for general patterns among diverse groups of organisms is a central aim of life-history research. But comparative studies also are needed at the intraspecific level, because potentially confounding phylogenetic factors are reduced in such studies and because they should allow us to distinguish proximal from evolutionary causes of variation (Brown 1983). The issue of genetic versus non-genetic sources of variation will not be a simple one to resolve (Ballinger 1983; Stearns 1992). But we believe that it is essential to understand the degree to which important traits vary naturally in the field, both spatially and temporally, to provide the background against which to interpret eventual experimental results.

Council of Canada. All necessary British Columbia government permits were obtained for fieldwork, as were approvals from the University of Victoria Animal Care Committee.

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