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Using time-dependent models to investigate body condition and growth rate of the giant gartersnake

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Abstract

Identifying links between phenotypic attributes and fitness is a primary goal of reproductive ecology. Differences in within-year patterns of body condition between sexes of gartersnakes in relation to reproduction and growth are not fully understood. We conducted an 11-year field study of body condition and growth rate of the giant gartersnake *Thamnophis gigas* across 13 study areas in the Central Valley of California, USA. We developed *a priori* mixed effects models of body condition index (BCI), which included covariates of time, sex and snout–vent length and reported the best-approximating models using an information theoretic approach. Also, we developed models of growth rate index (GRI) using covariates of sex and periods based on reproductive behavior. The largest difference in BCI between sexes, as predicted by a non-linear (cubic) time model, occurred during the mating period when female body condition (0.014 ± 0.001 SE) was substantially greater than males (-0.027 ± 0.002 SE). Males likely allocated energy to search for mates, while females likely stored energy for embryonic development. We also provided evidence that males use more body energy reserves than females during hibernation, perhaps because of different body temperatures between sexes. We found GRI of male snakes was substantially lower during the mating period than during a non-mating period, which indicated that a trade-off existed between searching for mates and growth. These findings contribute to our understanding of snake ecology in a Mediterranean climate.

An important aspect of physiological ecology is to identify costs and benefits among linked life history attributes (Sterns, 1989, 1992; Lessells, 1991). One major goal is to understand the relationship between phenotypic traits and fitness (Sibly & Calow, 1986; Seigel & Ford, 1987). Because snakes use time and energy to acquire resources in their environment, they balance the costs of using stored energy in body reserves with the benefits of optimized reproduction, survival and growth (Bronikowski & Arnold, 1999; Naulleau & Bonnet, 1996). Information of how snakes use energy for reproduction and growth throughout their annual cycle is essential to understand their ecological requirements.

Reproduction is critical to population viability, and although both sexes rely on body reserves for reproduction, the sexes fundamentally differ on how they allocate their respective reserves (Bonnet & Naulleau, 1996; Aubret *et al*., 2002). For example, males contribute relatively little to gamete production but allocate energy to find mates, whereas females use energy for embryonic development. Time-dependent differences between sexes in body condition as an index of energy allocation are not fully understood. This type of information, however, is essential to understanding the reproductive ecology of snakes.

Most of our current knowledge of gartersnake ecology is derived from the common gartersnake *Thamnophis sirtalis* studied at relatively few locations (Shine *et al*., 2001; Shine & Mason, 2005). Furthermore, a disproportionate amount of scientific investigation has focused on the Manitoba populations, which are at the northern fringe of the species range in a cool climate (Shine *et al*., 2001; Shine & Mason, 2005) where the necessity of communal hibernacula might influence life history strategies. Information derived from studies of other gartersnake species is lacking, particularly for those species inhabiting benign climates.

The giant gartersnake *Thamnophis gigas* is a rare, relatively large snake endemic to wetlands of the Central Valley of California, USA. Although listed as threatened (US Fish and Wildlife Service, 1993), relatively little is known about this species. The principal objective of this study was to measure physical attributes of giant gartersnakes that were marked and recaptured over an 11-year period to identify time-dependent patterns in body condition and growth rates among sexes using an information theoretic approach. We developed *a priori* models (hypotheses) that were supported by observations or biological rationale from the literature. Specifically, we hypothesized that body condition and growth rate were relatively lower in males than females

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during the mating period because they allocate energy to mate searching. Additionally, we compared body condition before and after hibernation to test the hypothesis that males use more endogenous reserves while inactive than do females. The relationships between body condition, growth and reproduction contribute to a greater understanding of gartersnake ecology in a Mediterranean environment.

Methods

Field methods

We captured giant gartersnakes within the Central Valley of California [UTM (ranges) 582953–641709 Easting, 4333861–4237260 Northing, NAD 27, Zone 10N]. The majority of giant gartersnake captures (83%) occurred at four study areas: Badger Creek, Colusa National Wildlife Refuge (NWR), Gilsizer Slough and the Natomas Basin (Fig. 1). Snakes were associated with irrigation and drainage canals, rice croplands, sloughs, ponds, small lakes, low gradient streams and adjacent uplands. Badger Creek (321 ha) in southern Sacramento County was characterized primarily by wetland with permanent water (61%) and upland vegetation (33%). These shallow wetlands were at the confluence of Badger Creek and Willow Creek, tributaries of the Cosumnes River. Colusa NWR and the adjacent habitat that was used by snakes (9676 ha) in eastern Colusa County consisted of seasonal (3%) and permanent (3%) wetlands intersected by a network of irrigation canals. Surrounding habitat consisted of rice croplands (90%). Gilsizer Slough (2645 ha) in central Sutter county is a remnant drainage feature of the Yuba River. The slough is adjacent to rice (53%) and non-rice (27%) croplands and was used as both a drain and a water source for surrounding agriculture. The Natomas Basin (3007 ha) in northern Sacramento and southern Sutter Counties consisted primarily of a network of irrigation canals intersecting rice croplands (77%) with adjacent upland (23%) habitat.

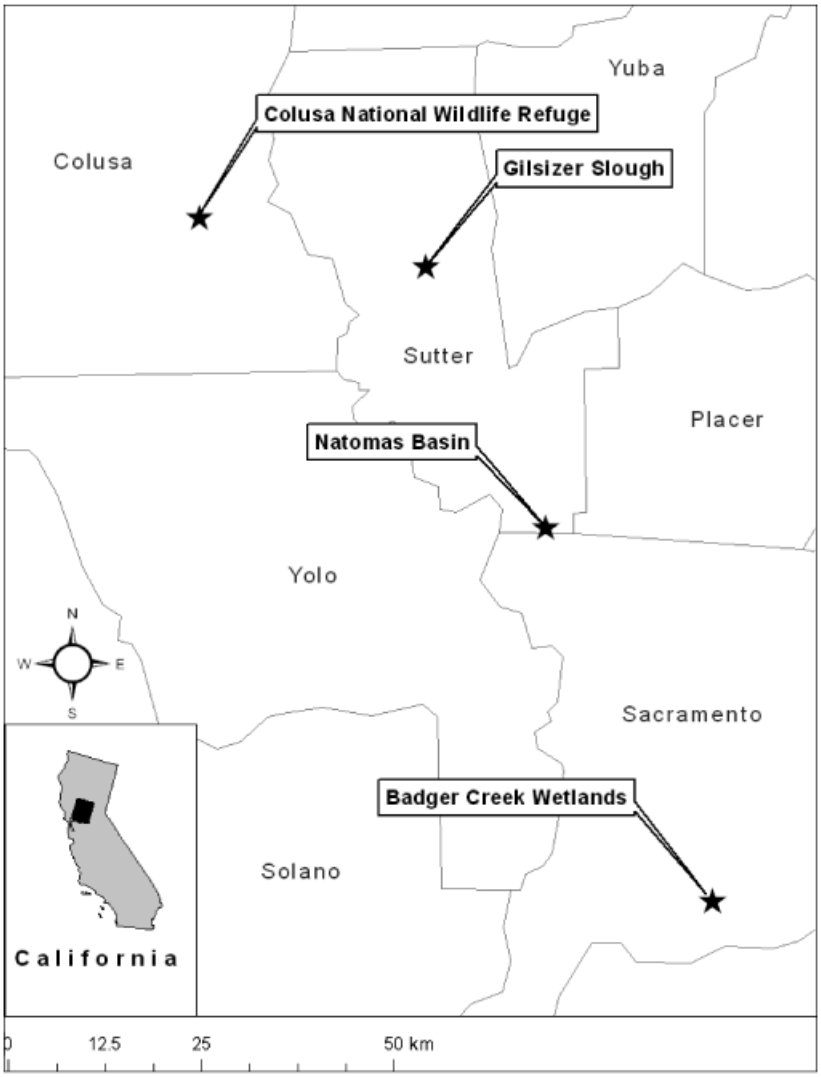

Figure 1 The four major study sites at which giant gartersnakes *Thamnophis gigas* were captured and measured in the Central Valley of California during 1995–2006.

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We captured and marked 1538 giant gartersnakes from 1995 to 2006 (Table 1). The majority of captures (79%) were in modified minnow traps deployed at the edge of canal and wetland habitats (Casazza, Wylie & Gregory, 2000). We also captured snakes by hand and with tongs during visual searches of the study areas. We measured snout–vent length (SVL; mm) and mass (g) of each snake. We determined sex by probing to detect hemipenes (Schaefer, 1934). Snakes were palpated to record food items and visually searched for abnormalities. Snakes were marked with passive integrated transponder tags (Gibbons & Andrews, 2004) for unique identification. After processing, snakes were released at the location of capture.

Statistical analyses

Body condition

We quantified body condition using a weight–length relationship, or body condition index (BCI), which is a reliable indicator of body reserves for snakes (Bonnet & Naulleau, 1994). First, we used log-transformed mass and SVL to estimate the parameters of a linear model. To avoid psuedoreplication, we randomly selected one set of concurrent mass and length measurements from all captures for each snake. Second, we used the model parameters to calculate residuals of measurements for all captures of all snakes. Third, we divided the residuals by the predicted mass to obtain a BCI (% above or below the predicted mass) (Blouin-Demers, Gibbs & Weatherhead, 2005). To avoid confounding effects between mass caused by developing embryos with mass caused by energy reserves (i.e. lipid and protein storage), we omitted all female snakes during the gestation period (15 June–7 September). Gestation period was determined based on 38 confirmed parturition dates. Also, snakes with abnormal growths (usually caused by encysted parasitic nematodes) and discernible food items were noted in the field and not included in the analyses. Means of BCI were reported with SE.

We developed a candidate set of predictive models (hypotheses) for BCI using multiple covariates (Table 2) and evaluated models in two steps. Only biologically feasible

Table 1 Number of new captures (CP), recaptures (RCP) and individuals (IND) by sex that were measured in an 11-year study of body condition and growth rates of the giant gartersnake *Thamnophis gigas*

	Female (*n*)			Male (*n*)			Total (*n*)		
Year	CP	RCP	IND[a]	CP	RCP	IND[a]	CP	RCP	IND[a]
1995	33	0	33	39	2	39	72	2	72
1996	63	12	68	68	23	77	131	35	145
1997	84	20	94	77	21	92	161	41	186
1998	74	17	85	55	14	67	129	31	152
1999	70	18	81	85	18	92	155	36	173
2000	51	11	59	44	12	51	95	23	110
2001	45	21	57	53	19	61	98	40	118
2002	92	36	108	102	40	116	194	76	224
2003	90	29	105	119	39	132	209	68	237
2004	73	29	84	90	45	106	163	74	190
2005	34	18	47	40	17	53	74	35	100
2006	25	4	27	32	1	32	57	5	59

Data were collected in the Central Valley of California.
[a]Some individual snakes were captured in multiple years.

Table 2 Description of variables that were used to model body condition (BC) and growth rate (GR) of the giant gartersnake *Thamnophis gigas* within the Central Valley of California

Abbreviations	Description	Effect	Model
mSVL	Mean snout–vent length (mm)	Fixed	GR
SEX	Sex of snake	Fixed	BC, GR
JUD	Julian date	Fixed	BC
SEAS	Season (Spring, Summer and Fall)	Fixed	BC
SA	Study area (13 study areas throughout the Central Valley)	Random	BC, GR
ORD	Ordinal date (days elapsed from 1 January)	Fixed	BC
YR	Year of capture	Random	BC, GR
IND	Repeated-measures on individual snakes	Random	BC, GR
RBP	Reproductively based period (mating = 3 March–14 June, post-mating = 15 June–30 October)	Fixed	GR

Data were collected during 1995–2006.

models were included in our model sets. We divided the variables into random and fixed effect categories. A two-step variable selection procedure allowed us to objectively reduce the number of considered models in each candidate set. In step 1, we evaluated models of random terms only (e.g. study site and repeated measurements per individual). This was necessary because the response variables can only be partly explained by fixed effects (e.g. date and sex). We selected the best-fit models of the random effects using conditional Akaike's information criterion (cAIC; Vaida & Blanchard, 2005) and reported the random variance estimates. Our goal in this step was to select the most parsimonious model that consisted only of random effects terms that accounted for 'nuisance' variation.

In step 2, we compared evidence for *a priori* models that consisted of the best-fit random structure (derived from step 1) and different fixed effects. To examine temporal patterns, we included the covariates ordinal date (three-digit number indicating the day of year, i.e. 001–365) and Julian date (number of days since 1 January 4713 BC) as fixed effects. We also used quadratic and cubic functions of ordinal date as fixed effects. Ordinal date represented within-year variation, whereas Julian date represented variation throughout the duration of the study. We investigated the categorical variable of calendar season to evaluate effects of spring, summer and fall. We also included sex and SVL to examine differences in BCI with sex and length. Interactions between ordinal date and sex were considered to evaluate within-year patterns in BCI by sex (Naulleau & Bonnet, 1996). We did not include covariates in the same model that were correlated (Pearson's $R \geq 0.65$) to avoid effects of multicollinearity. Parameter estimation and model fit were performed using mixed models in the package lme4 (Bates, Maechler & Dai, 2008) for Program R (R Development Core Team, 2008). AIC (Akaike, 1973) was used to calculate differences between models (ΔAIC) and to calculate model probabilities (Anderson, 2008).

To investigate the relationship between hibernation and body condition, we estimated the differences between snakes ($n = 29$) that were captured during the fall and recaptured during the spring and calculated mean differences and confidence intervals for each sex (males = 9, females = 20). We used measurements from the earliest and latest captures during spring (10 March–31 May) and fall (2 August–10 October), respectively. We also tested differences in the number of days elapsed from measurements of pre-hibernation and post-hibernation between males and females to ensure that differences in time between measurements did not introduce bias into comparison of male and female body condition.

Growth rate

To calculate growth rate, we measured the change in SVL between two capture occasions and divided this number by the number of days elapsed (ΔSVL/Δdays). Growth rate under this model was expressed as a function of body length (Van Devender, 1978). We calculated daily growth rate (hereafter referred to as growth rate) only for snakes that were captured more than once within an active period of 1 year ($n = 100$; males, $n = 51$; females, $n = 49$). We did not calculate growth rate for snakes that extended through hibernation because we sought to reduce biases in slower growth associated with inactive periods and were uncertain of precise dates of hibernation for each individual. Means of growth rate were reported with SE.

We modeled growth rate in multiple steps. First, we modeled growth rate as a function of the mean SVL (initial and final) (Van Devender, 1978) using a von Bertalanffy differential equation growth model (Fabens, 1965) only on snakes captured more than once in one active season. This allowed us to test the hypothesis that an increase in snake length is related to a decrease in the growth rate (Andrews, 1982). Similar to our analysis of BCI, we first evaluated different random structures, and then compared the best-approximating random effects structure with a model that also included a fixed effect of mean SVL.

Second, we developed a growth rate index (GRI) as a response variable to investigate the effects of sex on growth rate, which allowed us to account for a growth–size relationship. To develop GRI we used a similar process as that described for BCI. We conducted a linear regression on log-transformed growth rate and mean SVL. We then divided the residuals of this regression by the predicted growth rate to obtain a GRI (% above or below the predicted growth rate).

Third, we restricted the dataset to evaluate evidence for the hypothesis that the growth rates of males and females differed between two reproductively based periods (RBP): an early period of mating (03 March–14 June) and a later period of parturition and post-parturition (15 June–30 October). This restricted dataset consisted of calculating GRI from two consecutive measurements of an individual snake taken during a RBP (males, $n = 32$; females, $n = 24$). We used the same two-step process described above for BCI to evaluate growth rate models for each dataset.

Results

We found a distinct difference in annual patterns of body condition between male and female gartersnakes. The most parsimonious model for the random structure consisted of year (standard deviation = 0.004) and multiple measures of the same individuals (standard deviation = 0.033; Table 3). The two most parsimonious models ($w_5 = 0.92$, $w_6 = 0.08$; Table 3) for predicting body condition contained an interaction between sex and a polynomial function of ordinal date, meaning that the within-year pattern of BCI change was different between the sexes. We did not find support for a model without the interaction that contained the same covariates. Additionally, our two best models predicted that body condition had a non-linear relationship with time. The cubic model was 12 times more likely to predict BCI than the quadratic model (w_5/w_6). Models that contained a categorical season effect lacked support from these data (Table 3).

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Table 3 Analysis of information criteria table for assessing mixed models fitted to the body condition index data for the giant gartersnake *Thamnophis gigas* in the Central Valley of California

Structure	Model	Specification[a]	DF	*K*	LL[b]	ΔAIC[c]	*w*
Random	1	YR, IND	964	3	3613	0	1.00
	2	YR, SA (IND)	942	4	3628	14	0.00
	3	IND	958	2	3609	22	0.00
	4	SA (IND)	938	3	3626	26	0.00
Mixed	5	$ORD^3 \times SEX$	–	10	3720	0	0.92
	6	$ORD^2 \times SEX$	–	8	3715	5	0.08
	7	ORD × SEX	–	6	3706	20	0.00
	8	ORD^3, SEX	–	7	3705	24	0.00
	9	SEAS × SEX	–	6	3704	27	0.00
	10	SEX	–	4	3681	66	0.00
	11	ORD^2	–	5	3631	158	0.00
	12	ORD^3	–	6	3631	170	0.00
	13	ORD	–	4	3625	179	0.00
	14	SEAS	–	5	3623	184	0.00
	Null	Intercept	–	3	3613	199	0.00
	15	JUD	–	4	3614	199	0.00

[a]Random components in model 1 were incorporated in models 5–15 based on evidence as measured by Akaike'ss information criterion.
[b]LL for the random models (models 1–4) is the conditional log-likelihood, LL for the mixed models is the marginal likelihood (Vaida & Blanchard, 2005).
[c]ΔAIC for the random models (models 1–4) is ΔcAIC (see equation 10 in Vaida & Blanchard, 2005).
DF, effective degrees of freedom for random effect models (Vaida & Blanchard, 2005); *K*, number of model parameters; LL, model log-likelihood; ΔAIC, difference in AIC units between the model of interest and the most parsimonious model; *w*, model probability (Anderson, 2008); YR, year of capture; SA(IND), individual snakes nested within study areas; IND, repeated-measures from individual snakes; ORD^3, ordinal date (cubic); ORD^2, ordinal date (quadratic); ORD, ordinal date (linear); SEAS, season (spring, summer and fall); JUD, Julian date.

Also, we did not find evidence of a linear relationship with Julian date.

The greatest difference in body condition between males and females occurred during 25 April–15 May, when female body condition (0.014 ± 0.001) was substantially greater than male body condition (-0.027 ± 0.002, Fig. 2). Also, we found female body condition (0.022 ± 0.005) to be similar to male condition (0.020 ± 0.007) during a 30-day period before hibernation (1–30 October), but female condition was greater (0.017 ± 0.007) than that of males (0.001 ± 0.003) during the first 20 days of capture following hibernation (8–28 March).

Males lost more body mass than females during hibernation (Fig. 3). Male BCI of snakes captured before hibernation (0.011 ± 0.013) was substantially greater than when they were recaptured after hibernation (-0.036 ± 0.010). The confidence interval of the estimated mean difference (0.047) did not include zero (CI = 0.015–0.080). In females, we did not detect a strong difference in BCI between those captured before (0.009 ± 0.005) and then recaptured after (0.002 ± 0.006) hibernation (mean difference = −0.007, 95% CI = −0.024–0.010). Additionally, we did not detect any difference between days elapsed from capture before hibernation to capture following hibernation between sexes (mean difference = 11.4, 95% CI = −52.3–29.5).

When measuring snakes throughout the active period, we found growth rate decreased as snake length increased (Table 4, Fig. 4). Year (standard deviation = 0.24) and multiple measures of the same individual nested within study site (standard deviation = 0.28; Table 4) had the greatest support as random effects. The mean growth rate (0.54 ± 0.04 mm SVL day^{-1}) decreased by 3.1 ± 0.7% with a 1 mm increase in SVL.

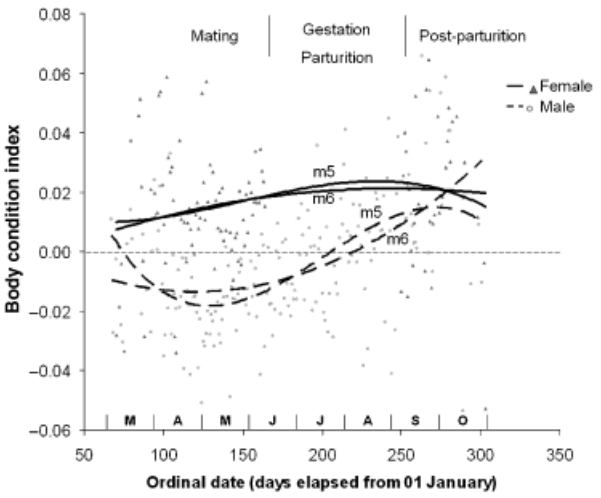

Figure 2 Temporal patterns of body condition index in relation to ordinal date between male and female giant gartersnakes *Thamnophis gigas*. The evidence for a cubic model (m5) was supported more by these data than evidence of a quadratic model (m6). These data were collected in the Central Valley of California during 1995–2006.

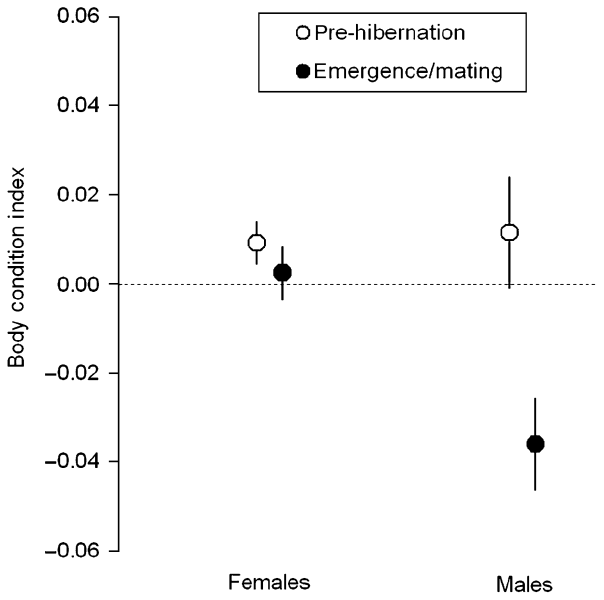

Figure 3 Differences in body condition between periods of pre-hibernation (2 August–10 October) and emergence (10 March–31 May) among sexes of giant gartersnakes *Thamnophis gigas* in the Central Valley of California during 1995–2006. Average (circle) ± SE (line).

When we used measurements throughout the active season to model GRI, the random structure that included repeated measurements of individuals had the greatest support ($w_6 = 0.30$) (standard deviation = 0.98) and was therefore used in the mixed effect models (Table 4). No evidence existed for an effect of sex on GRI ($w_{10} = 0.50$) compared with the intercept and random term model ($w_{null} = 0.50$).

The most parsimonious random structure for models of reproductive seasonal differences in GRI consisted of year ($w_{11} = 0.72$) (standard deviation = 0.53; Table 4). The best-fit mixed effects model included an interaction between reproductively based period and sex ($w_{13} = 0.63$; Table 4, Fig. 5). This model was 2.3 times more likely to describe these data than reproductively based period as the only fixed effect (w_{13}/w_{14}) and 12.6 times more likely than the null (w_{13}/w_{null}). The average growth rate of males in the mating/early gestation period (0.27 ± 0.06 mm SVL/day) was significantly lower than the post-parturition period (0.85 ± 0.12 mm SVL/day). The average growth rate of females, however, was similar in both periods (mating/early gestation = 0.61 ± 0.14 mm SVL/day, post-parturition = 0.82 ± 0.13 mm SVL/day).

Discussion

We identified distinct differences in within-year patterns of body condition between the sexes, likely caused by differences in reproductive strategies. The strong evidence of the approximating models that contain a polynomial effect of time indicated a predictable annual cyclic pattern, especially for male snakes. The difference in the annual pattern that we observed between sexes was likely caused by energetic balances that support different reproductive strategies, which was evidenced by the greatest difference in body condition occurring during the mating period, a time when sexes show distinct differences in reproductive behavior (Shine, 2003). During the mating period, males of many snake species search intensively for mates (Naulleau, Fleury & Boissin, 1987; Shine *et al.*, 2001). For example, male red-sided gartersnakes *Thamnophis sirtalis parietalis* often travel long distances to search out potential mates (Shine *et al.*, 2001). Body condition is strongly correlated with main body reserves and fat bodies (Bonnet & Naulleau, 1996). Perhaps males relied on endogenous lipids and proteins during the mating period, saving on the time and energy that was needed to find, capture and digest prey. Other species of snakes often decrease their feeding rates during the mating season (Naulleau *et al.*, 1987; Madsen & Shine, 2000) and lose substantial amounts of mass (Shine *et al.*, 2001). Authors have reported observations of aphagia in red-sided gartersnake during the mating period (O'Donnell, Shine & Mason, 2004). Therefore, a trade-off between maintaining or replenishing endogenous reserves and searching for mates may be critical to the mating success of male giant gartersnakes.

The lack of support for a linear time model demonstrates that body reserves of male snakes are largely invested in reproduction, corroborating the 'capital breeder' hypothesis (Gregory, 2006). In male snakes, body condition decreased substantially from March to mid-May. During late May, we observed the first sign of a body condition increase for males. In June, male body condition increased substantially, which suggested that males acquired food resources to replenish energy reserves. Giant gartersnakes are more widely dispersed during hibernation than well-studied populations of the red-sided gartersnake in Manitoba (Shine *et al.*, 2001; Shine & Mason, 2005). Male giant gartersnakes in our study might have had to invest more time and energy into searching for females from March to May.

In contrast to males, we observed a slight increase in body condition from March to May in female snakes. The difference in temporal patterns between the sexes does not obviate females also being capital breeders. Sexes appear to show dissimilar patterns in body condition through time based on reproductive strategies. Perhaps females foraged more often than males to provide additional reserves to support embryonic development. In dark green snakes *Hierophis viridiflavus*, BCI is strongly correlated to the mass of the liver (Bonnet, Naulleau, 1996), which serves as a reserve for amino acids and lipids necessary for the production of vitellogenin (Bonnet, Naulleau, & Mauget, 1994). Also, a threshold of body condition was identified as necessary for the production of vitellogenins in other viviparous snakes (Naulleau & Bonnet, 1996).

The greater loss in body condition of male snakes compared with females during hibernation is possibly caused by differences in body temperature between the sexes during hibernation. Male giant gartersnakes have elevated body temperatures relative to females during hibernation,

Table 4 Analysis of information criteria assessing mixed models for growth rate of the giant gartersnake *Thamnophis gigas* in the Central Valley of California

Period[a]	Response	Structure	Model	Specification[b]	DF	*K*	LL	ΔAIC[c]	*w*
Active	Log(GR)	Random	1	YR, SA (IND)	26	4	−499	0.0	0.96
			2	SA (IND)	23	3	−501	7.0	0.03
			3	YR, IND	29	3	−502	8.8	0.01
			4	IND	23	2	−503	14.9	0.00
		Mixed	5	Log(mSVL)	–	5	−485	0.0	1.00
			Null	Intercept	–	4	−499	27.7	0.00
Active	GRI	Random	6	IND	66	2	−96	0.0	0.30
			7	YR	65	2	−96	0.0	0.29
			8	SA (IND)	65	3	−97	0.6	0.23
			9	YR, SA (IND)	65	4	−97	1.0	0.18
		Mixed	Null	Intercept	–	2	−179	0.0	0.50
			10	SEX	–	3	−178	0.0	0.50
Reproductive	GRI	Random	11	YR	7	2	−96	0.0	0.72
			12	SA	4	2	−99	1.9	0.28
		Mixed	13	RBP × SEX	–	5	−96	0.0	0.63
			14	RBP	–	3	−99	1.7	0.27
			15	SEX	–	3	−100	5.1	0.05
			Null	Intercept	–	2	−101	5.2	0.05

[a]Active period consisted of using data of growth rate between two measurements within the active period. Reproductive periods consisted of growth rates between two consecutive measurements within a mating/early gestation period (3 March–14 June) and parturition and post parturition period (15 June–30 October) by using a restricted dataset.
[b]The best-approximating random structure model of those considered in each dataset was used in the mixed effects models. We considered the intercept with random covariates as the null case. In the reproductive season model set, we did not use a random effect of IND because there were no repeated measurements per individual snake.
[c]ΔAIC for the random models (models 1–4) is ΔcAIC (see equation 10 in Vaida & Blanchard, 2005).
DF, effective degrees of freedom for random effect models (Vaida & Blanchard, 2005); *K*, number of model parameters; LL, model log-likelihood; ΔAIC, difference in AIC units between model of interest and the most parsimonious model; *w*, model probability (Anderson, 2008); log(GR), log-transformed instantaneous growth rate, (log[ΔSVL/Δdays]); GRI, growth rate index; YR, year of capture; IND, repeated-measures from individual snakes; SA, study areas; log(mSVL), log-transformed mean snout–vent length; SA(IND), individual snakes nested within study areas; RBP, reproductively based period.

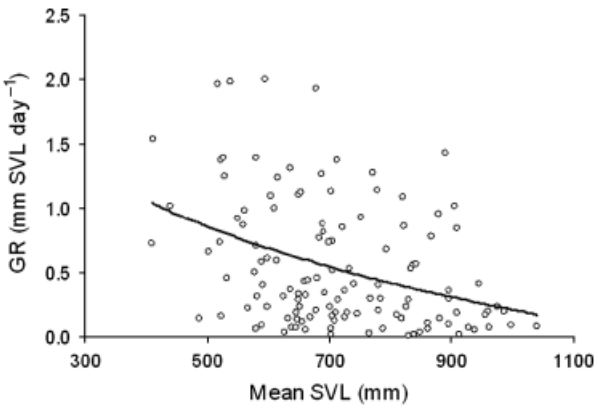

Figure 4 Relationship between growth rate and the mean snout–vent length (SVL) of giant gartersnakes *Thamnophis gigas*. Growth rate was calculated as a change in length between two capture occasions and divided by days elapsed (ΔSVL/Δdays). The solid line represents the logarithmic best-fit. These data were collected in the Central Valley of California during 1995–2006.

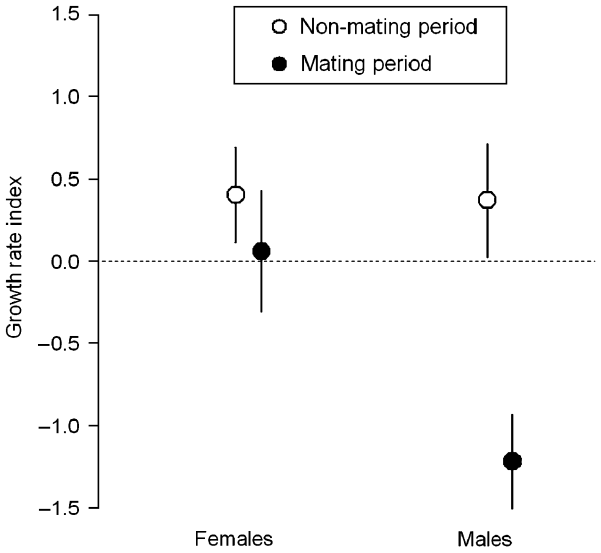

Figure 5 Differences in growth rates between periods of mating (3 March–14 June) and non-mating (15 June–30 October) among sexes of giant gartersnakes *Thamnophis gigas* in the Central Valley of California during 1995–2006. Average (circle) ± SE (line).

particularly in the months just before emergence (Wylie *et al.*, 2009). The positive correlation between body temperature and resting oxygen consumption (Al-Johany & Al-Sadoon, 1996) coupled with a negative correlation between body mass and metabolic activity in snakes (Calder, 1996) indicate that males use relatively more reserves than females during hibernation. Perhaps a less dormant hibernation for males allows them to emerge earlier at the onset of the mating period, which may increase their probability of finding mates. Additional studies of den site selection in relation to microclimates, body condition and dormancy would be informative.

We offer further support for the hypothesis that SVL has a negative relationship with growth rate (Naulleau & Bonnet, 1996). Shorter snakes appeared to have the greatest growth rates. A possible explanation for this relationship is related to size-dependent reproductive success. If larger females produce larger litters, as suggested elsewhere (Seigel & Ford, 1987), smaller snakes should allocate relatively less energy into reproduction and more into growth. Reproductively mature individuals face an energetic trade-off between growth and reproduction (Shine, 1980) and less energy is likely allocated to growth among these individuals. Taken together, the positive relationship of litter size with female size and energetic trade-offs between reproduction and growth likely result in greater growth rates of pre-reproductive individuals. Furthermore, if body length increases the distance moved by snakes, as suggested for the Western ribbonsnake *Thamnophis proximus* in a warm-temperate climate (Clark Jr, 1974), then relatively short young males may allocate more stored energy to growth rather than immediate mate searching. Regardless of sex, trade-offs between reproduction and growth help us understand why growth rates were greater for shorter (younger) individuals.

The findings of this study are unique in that we found substantial differences in growth rates of males between mating and non-mating periods, which was not observed in females. During March, a period of movement and breeding, the low growth rate of males coupled with a declining BCI suggested that males allocated energy to mate searching rather than obtaining food for growth, which has been documented elsewhere as an important factor that influences growth rate (Ford & Seigel, 1994). Conversely, females may face strong selective pressures for larger size to produce larger litters (Madsen & Shine, 1996; Shine, 2003).

An alternative explanation for the observed increased growth rate of males during the non-mating period is food availability. Giant gartersnakes feed on aquatic prey, primarily fish, frogs and tadpoles (U. S. Fish and Wildlife Service, 1999). Earlier in the year, when snakes are less likely to use open water sources, less food may have been available limiting consumption and growth. Although this explanation is possible, the mate-searching hypothesis offers stronger support because of the relative importance of an interaction between sex and mating period indicated by the best-fit model for growth rate. If prey availability was the exclusive cause of reduced growth rates, then we might have expected similar changes in growth rates between sexes. An investigation of links between habitat use, body condition, and growth patterns of giant gartersnakes would be largely beneficial.

In conclusion, we developed a robust time-dependent model that predicted distinct annual patterns in body condition of males and female giant gartersnakes. Also, we provided important evidence that the growth rate of male snakes was reduced during the mating period, a time when male body condition was lower than females and lower than males at later dates, and we related these findings to distinct differences in reproductive strategies between sexes. This fundamental knowledge that links life history attributes of the giant gartersnake to snake reproductive behavior contributes to our understanding of snake ecology in Mediterranean climates.

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References

Al-Johany, A.M. & Al-Sadoon, M.K. (1996). Selected body temperature and metabolic rate–temperature curves of three species of desert snakes. *J. Arid Environ.* **34**, 363–370.

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory*: 267–281. Petrov and B.N. & Csaki, F. (Eds). Budepest: Akademiai Kiado.

Anderson, D.R. (2008). *Model based inference in the life sciences: a primer on evidence*. New York: Springer.

Andrews, R.M. (1982). Patterns of growth in reptiles. In *Biology of the Reptilia*, Vol. 13: 273–320. Gans, C. & Pough, F.H. (Eds). New York: Academic Press.

Aubret, F., Bonnet, X., Shine, R. & Lourdais, O. (2002). Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (*Vipera aspis*). *Horm. Behav.* **42**, 135–147.

Bates, D., Maechler, M. & Dai, B. (2008). lme4: linear mixed-effects models using S4 classes. R package version 0.999375-27. Available at http://lme4.r-forge.r-project.org/ (accessed 20 August 2008).

Blouin-Demers, G., Gibbs, H.L. & Weatherhead, P.J. (2005). Genetic evidence for sexual selection in black ratsnakes, *Elaphe obsoleta*. *Anim. Behav.* **69**, 225–234.

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Bonnet, X. & Naulleau, G. (1994). A body condition index (BCI) in snakes to study reproduction. *C. R. Acad. Sci.* **317**, 34–41.

Bonnet, X. & Naulleau, G. (1996). Are body reserves important for reproduction in male dark green snakes (Colubridae: *Coluber Viridiflavus*)? *Herpetologica* **52**, 137–146.

Bonnet, X., Naulleau, G. & Mauget, R. (1994). The influence of body condition on 17-beta estradiol levels in relation to vitellogenesis in female *Vipera aspis* (Reptilia, Viperidae) *Gen. Comp. Enodocrinol.* **93**, 424–427.

Bronikowski, A.M. & Arnold, S.J. (1999). The evolutionary ecology of life history variation in the Garter Snake *Thamnophis elegans*. *Ecology* **80**, 2314–2325.

Calder, W.A. (1996). *Size, function and life history*. New York: Dover Publications.

Casazza, M.L., Wylie, G.D. & Gregory, C.J. (2000). A funnel trap modification for surface collection of aquatic amphibians and reptiles. *Herpetologica* **31**, 91–92.

Clark, D.R. Jr. (1974). The western ribbon snake (*Thamnophis proximus*): ecology of a Texas population. *Herpetologica* **30**, 372–379.

Fabens, A.J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–289.

Ford, N.B. & Seigel, R.A. (1994). An experimental study of the trade-offs between age and size at maturity: effects of energy availability. *Funct. Ecol.* **8**, 91–96.

Gibbons, J.W. & Andrews, K.M. (2004). PIT tagging: simple technology at its best. *Bioscience* **54**, 447–454.

Gregory, P.T. (2006). Influence of income and capital on reproduction in a viviparous snake: direct and indirect effects. *J. Zool. (Lond.)* **270**, 414–419.

Lessells, C. (1991). The evolution of life-histories. In *Behavioural ecology*: 32–68. Krebs, J.R. & Davies, N.B. (Eds). Oxford: Blackwell.

Madsen, T. & Shine, R. (1992). Determinants of reproductive success in female adders, *Vipera berus*. *Oecologia* **92**, 40–47.

Madsen, T. & Shine, R. (2000). Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. *Aust. J. Ecol.* **25**, 670–675.

Naulleau, G. & Bonnet, X. (1996). Body condition threshold for breeding in a viviparous snake. *Oecologia* **107**, 301–306.

Naulleau, G., Fleury, F. & Boissin, J. (1987). Annual cycles in plasma testosterone and thyroxine for the male aspic viper *Vipera aspis L.* (Reptilia, Viperidae), in relation to the sexual cycle and hibernation. *Gen. Comp. Endocrinol.* **65**, 254–263.

O'Donnell, R.P., Shine, R. & Mason, R.T. (2004). Seasonal anorexia in the male red-sided garter snake, *Thamnophis sirtalis parietalis*. *Behav. Ecol. Sociobiol.* **56**, 413–419.

R Development Core Team. (2008). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Schaefer, W.H. (1934). Diagnosis of sex in snakes. *Copeia* **1934**, 181.

Seigel, R.A. & Ford, N.B. (1987). Reproductive ecology. In *Snakes: ecology and evolutionary biology*: 210–252. Seigel, R.A., Collins, J.T. & Novak, S.S. (Eds). New York: Macmillan.

Shine, R. (1980). "Costs" of reproduction in reptiles. *Oecologia* **46**, 92–100.

Shine, R. (2003). Reproductive strategies in snakes. *Proc. Roy. Soc. Lond. Ser. B* **270**, 995–1004.

Shine, R., Elphick, M.J., Harlow, P.S., Moore, I.T., LeMaster, M.P. & Mason, R.T. (2001). Movements, mating, and dispersal of red-sided gartersnakes (*Thamnophis sirtalis parietalis*) from a communal den in Manitoba. *Copeia* **2001**, 82–91.

Shine, R. & Mason, R.T. (2005). Does large body size in males evolve to facilitate forcible insemination? A study of garter snakes. *Evolution* **59**, 2426–2432.

Sibly, R.M. & Calow, P. (1986). *Physiological ecology of animals: an evolutionary approach*. Oxford: Blackwell.

Sterns, S.C. (1989). Trade-offs in life history evolution. *Funct. Ecol.* **3**, 259–268.

Sterns, S.C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.

US Fish and Wildlife Service. (1993). Endangered and threatened wildlife and plants: determination of threatened status for the giant garter snake. *Federal Register* **58**, 54053–54066.

US Fish and Wildlife Service. (1999). *Draft Recovery Plan for the giant garter snake (Thamnopsis gigas)*. Oregon: US Fish and Wildlife Service.

Vaida, F. & Blanchard, S. (2005). Conditional Akaike information for mixed-effects models. *Biometrika* **92**, 351–370.

Van Devender, R.W. (1978). Growth ecology of a tropical lizard, *Basiliscus basiliscus*. *Ecology* **59**, 1031–1038.

Wylie, G.D., Casazza, M.L., Halstead, B.J. & Gregory, C.J. (2009). Sex, season, and time of day interact to affect body temperatures of the giant gartersnake. *J. Therm. Biol.* **34**, 183–189.