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Volume 34 Number 4 May 2009 ISSN 0306-4565

ELSEVIER

Journal of
THERMAL BIOLOGY

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CONTENTS

Review article
Thomas Reilly and Jim Waterhouse 161 Circadian aspects of body temperature regulation in exercise

General papers
Giuseppe Piccione, Francesco Fazio, Elisabetta Giudice and Roberto Refinetti 171 Body size and the daily rhythm of body temperature in dogs
Jonathan D. Scudder, Robert V. Blystone and Daniel A. Pulliam 176 Control of anesthesia-induced hypothermia by ambient temperature regulation in rats
Glenn D. Wylie, Michael L. Casazza, Brian J. Halstead and Christopher J. Gregory 183 Sex, season, and time of day interact to affect body temperatures of the Giant Gartersnake
Claire Lindsay, Colleen Downs and Mark Brown 190 Physiological variation in Amethyst Sunbirds (*Chalcomitra amethystina*) over an altitudinal gradient in summer
Suzana Dinevska-Kjovkarovska, Teuta Guladin, Biljana Miova, Slavco Mitev and Katerina Gerazova 200 Changes in the hypothalamo-pituitary-adrenocortical and hypothalamo-pituitary-thyroid axes in diabetic rats acclimated to moderate hyperthermic environment
Clark J. Cotton and Henry J. Harlow 206 Do hypothermic tissue tolerances limit torpor expression?

J. Therm. Biol. is Indexed/Abstracted in: Biosis. Data., CAB Int., Cam. Sci. Abstr., Curr. Cont./Agri. Bio. Env. Sci., Elsevier BIOBASE/Current Awareness in Biological Sciences, EMBASE, EMBiology Excerp. Med., INSPEC Data., Curr. Cont. Thomson Scientific BIOMED Data, PASCAL-CNRS Data., Res. Alert, Curr. Cont. Sci. Cit. Ind., Curr. Cont. SCISEARCH Data., Curr. Cont./Life Sci. Also covered in the abstract and citation database SCOPUS®. Full text available on ScienceDirect®

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Journal of Thermal Biology 34 (2009) 183–189

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Sex, season, and time of day interact to affect body temperatures of the Giant Gartersnake

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ARTICLE INFO

Article history:
Received 21 November 2008
Accepted 27 January 2009

Keywords:
Radio telemetry
Seasonal variation
Sexual dimorphism
Thamnophis gigas
Thermal ecology

ABSTRACT

1. We examined multiple hypotheses regarding differences in body temperatures of the Giant Gartersnake using temperature-sensitive radio telemetry and an information-theoretic analytical approach.
2. Giant Gartersnakes selected body temperatures near 30 °C, and males and females had similar body temperatures most of the year, except during the midsummer gestation period.
3. Seasonal differences in the body temperatures of males and females may relate to both the costs associated with thermoregulatory behavior, such as predation, and the benefits associated with maintaining optimal body temperatures, such as successful incubation.

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1. Introduction

Appropriate use and exploitation of the thermal landscape by individual ectotherms has important consequences for individual performance (Scott et al., 1982; Lillywhite, 1987). Snakes are particularly appropriate subjects for thermal ecology because their long, slender bodies allow them to simultaneously expose different parts of their body to different thermal environments (Gregory, 1990; Peterson et al., 1993) and manipulate their surface area to modify rates of heat gain and loss (Peterson et al., 1993). In addition to shape, the legless form of snakes usually results in direct contact with their substrate, resulting in high rates of conductive heat transfer relative to limbed animals (Peterson et al., 1993). Although many investigators have studied snake thermal ecology (Peterson et al., 1993), many questions regarding the interaction of snakes with their thermal environments remain. In particular, the thermal ecology of species in thermally benign environments is underrepresented in the literature (Rosen, 1991).

Despite the large body of literature on the thermal ecology of the gartersnakes (Peterson, 1987; Rosen, 1991; Rossman et al., 1996), the thermal ecology of the Giant Gartersnake (*Thamnophis gigas*) has not been studied. The Giant Gartersnake is the largest of the gartersnakes, is precinctive to wetlands in the Central Valley of California, USA, and has suffered a dramatic decrease in its extent of occurrence caused by destruction and degradation of its wetland habitat (U.S. Fish and Wildlife Service, 1993; Noss et al., 1995). The current distribution of the species is almost entirely restricted to a few remnant and restored wetlands and drainage features associated with rice agriculture. It has therefore been state and federally listed as a threatened species (U.S. Fish and Wildlife Service, 1993). The thermal ecology of the Giant Gartersnake is likely influenced by its large size, predominantly aquatic habits, and restriction to a relatively benign Mediterranean climate.

In this study, we investigated the thermal ecology of the Giant Gartersnake. We describe body temperatures (T_b) and examine several hypotheses that explain variation in T_b, including the effects of sex and time of year on an annual scale. We also examine these hypotheses and include additional hypotheses for the effects of time of day on T_b during the active season. We then use the most strongly supported hypotheses to explore the relationship of Giant Gartersnake T_b with the thermal environment.

2. Materials and methods

2.1. Study sites and field methods

We studied the Giant Gartersnake in 1996, 1997, and 2006 at four sites in the Sacramento Valley, California: Gilsizer Slough (1996–1997), Colusa National Wildlife Refuge (1996–1997),

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0306-4565/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.jtherbio.2009.01.006

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Badger Creek Wetlands (1996–1997), and the Colusa Drain (2006). All sites consisted of various combinations of wetlands, agricultural fields (predominantly rice), and associated drainage features (ditches, canals, and drains).

We monitored the location, behavior, and body temperatures of individual Giant Gartersnakes using radio telemetry. We captured individuals by hand or in floating modified minnow traps (Casazza et al., 2000), and measured, sexed, and uniquely marked each individual with passive integrated transponder (PIT) tags. We retained individuals with a mass greater than 110 g for radio telemetry, and immediately released all other individuals following processing. We implanted individuals with a mass greater than 172 g with 8.6 g Model SI-2T temperature-sensitive radio transmitters (Holohil Systems, Ltd., Carp, Ontario, Canada), and we implanted smaller individuals with 3.2 g Model BD-G2 temperature-sensitive transmitters (Holohil Systems, Ltd., Carp, Ontario, Canada). Prior to implantation, we calibrated each transmitter in a water bath with a mercury thermometer. Our results were always within 0.5 °C of the calibration curve provided by the manufacturer, so we used temperatures derived from these calibration curves for analysis. Veterinarians at the University of California Wildlife Health Center, Davis, California, surgically implanted a cold-sterilized radio transmitter into the coelom of each selected individual using standard techniques (Reinert and Cundall, 1982) under aseptic conditions and isoflurane anesthesia. We allowed individuals to recover in the laboratory for 1–2 weeks until the surgical site healed and they ate small fish and tadpoles. After the recovery period, each individual was released at its capture location.

We located individuals daily following their release. We used Advanced Telemetry Systems R4000 receivers (ATS; Isanti, Minnesota, USA) with handheld three-element Yagi antennae for most of our telemetry. We determined the pulse rate of each transmitter at each observation with a stopwatch prior to approaching the individual for collection of additional data. We recorded the location of the individual with GPS (3–5 m accuracy). For each observation, we measured shaded air temperature, surface water temperature, and substrate temperature near the individual's location. We varied the time at which we located individuals each day within each week, but all locations were diurnal.

2.2. Analytical methods

To examine the "preferred" body temperature of the Giant Gartersnake, we calculated field preferred body temperature (FPBT; Rosen, 1991) as the median temperature obtained from the mean T_b of 99 individual snakes during the active season when at least one microhabitat exceeded 30 °C. These 99 individuals included observations from additional sites for which we did not have any observations of male snakes. The FPBT range was delimited as the 12.5% and 87.5% quantiles of these mean T_bs.

We used linear mixed models to evaluate hypotheses for patterns in the variation of T_b at two temporal scales (see below). We tested these hypotheses by examining the fit of the corresponding models using AIC_c (Burnham and Anderson, 2002). Site and individual nested within site were incorporated into each model as random effects to account for non-independence of observations at the same site and upon the same individual using the package lme4 in R (Bates, 2007). For each model, we averaged air and water temperature (hereafter referred to as environmental temperature), centered environmental temperature about its mean, and included it as a linear covariate to correct T_b for variation in environmental temperature. We did not include substrate temperature in the calculation of environmental temperature because of a high proportion of missing values.

2.2.1. Annual T_b analysis

We hypothesized that the annual T_b of tracked snakes would differ by sex and month of year. In particular, our five hypotheses included T_b explained by environmental temperature only (null model), a constant difference in T_b between the sexes, monthly differences in T_b, monthly differences in T_b with a constant difference between the sexes, and differences in T_b between the sexes that vary from month to month. We limited these analyses to months and sites in which we observed T_b for both males and females ($n = 14$ males and 50 females; May through February). We did not subdivide females into gravid vs. non-gravid because nearly all females large enough for a transmitter are mated each year; effects of reproductive status of females are therefore subsumed into month. After selecting a best-fit model, we graphically explored the differences in T_b between sexes and among months by using parameter estimates from the best-fit model to predict body temperatures of males and females in each month while holding temperature constant at the mean environmental temperature. This comparison demonstrates sexual differences in the behavioral response to environmental temperature among months.

2.2.2. Active season T_b analysis

To remove the influence of low T_b during hibernation, we also examined T_b during the active season (May through September; no data were available for males in April) only. We hypothesized that the active season T_b of tracked snakes would vary by sex, month, and time of day. We identified time of day as early morning (EM, 0530–0830 PST), late morning (LM, 0830–1130 PST), early afternoon (EA, 1130–1430 PST), and late afternoon (LA, 1430–1730 PST). Analysis proceeded exactly as for the annual timescale, except that we included 11 additional models that incorporated the effects of time of day (TOD; Table 1). We used the program R 2.6.2 for Windows (R Development Core Team, 2008) for all analyses.

3. Results

3.1. Description of the thermal environment and T_b

We recorded the body temperature of 64 individuals (14 male, 50 female) a total of 3805 times. Of these temperatures, 2927 observations of 58 individuals (14 male, 44 female) occurred during the active season. Females in our study measured 817 ± 13 mm SVL and 333 ± 17 g (mean $\pm$ 1 standard error of the mean). Males measured 706 ± 9 mm SVL and 173 ± 6 g. Mean T_b during the active season was well within the range of temperatures available in selected microhabitats (Table 2). The annual distribution of T_b was negatively skewed compared to environmental temperature (Fig. 1), but mean T_b and mean environmental temperature were similar (mean $T_b = 25.0 \pm 0.48$ °C; mean environmental temperature $= 23.7 \pm 1.03$ °C). The FPBT of the Giant Gartersnake was 29.8 °C, with a FPBT range 27.6–31.7 °C.

3.2. Annual T_b

On an annual timescale, variation in T_b reflected the activity cycle of the Giant Gartersnake. Monthly mean T_b was greatest from April through September, and varied substantially among months when most individuals were inactive (Fig. 2). The hypothesis that differences in T_b between the sexes varied from

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Table 1
Hypotheses for active season body temperature of the Giant Gartersnake and the model specification for each.

Hypothesis	Model specification
T_b varies only with environmental temperature	T_b = cTe
T_b varies between sexes	T_b = sex+cTe
T_b varies among months	T_b = month+cTe
T_b varies among time of day (TOD)	T_b = TOD+cTe
T_b varies among months with constant difference between sexes	T_b = sex+month+cTe
T_b difference between sexes varies among months	T_b = sex*month+cTe
T_b varies among TOD with constant difference between sexes	T_b = sex+TOD+cTe
T_b difference between sexes varies among TOD	T_b = sex*TOD+cTe
T_b varies among TOD with constant difference among months	T_b = month+TOD+cTe
T_b differences among TOD varies among months	T_b = month*TOD+cTe
T_b varies among months with constant difference among TOD and sexes	T_b = sex+month+TOD+cTe
T_b difference between sexes varies among months, with additional constant difference among TOD	T_b = sex*month+TOD+cTe
T_b difference between sexes varies among TOD, with additional constant difference among months	T_b = sex*TOD+month+cTe
T_b differences among TOD varies among months, with additional constant difference between sexes	T_b = month*TOD+sex+cTe
T_b difference between sexes varies by month and differences among TOD vary by month	T_b = sex*month+month*TOD+cTe
T_b difference between sexes varies by month and TOD, and differences among TOD vary by month	T_b = sex*month+month*TOD+sex*TOD+cTe

Each model includes site and individual nested within site as random effects. All models with interaction terms include underlying main effects. All models include an intercept term. cTe = centered environmental temperature.

Table 2
Giant Gartersnake body temperatures (T_b) and environmental temperatures for three microhabitats during the active season (May–September).

Measure	Mean ± 1 standard error	Range
Body temperature, T_b (°C)	26.7 ± 0.48	7.2–36.9
Environmental temperatures (°C)		
Air	26.6 ± 0.95	9.0–43.0
Water	23.7 ± 0.91	9.0–41.0
Substrate	26.2 ± 0.81	0.0–49.0
Mean Env. Temp.	25.1 ± 0.91	9.0–38.5

n = 2927 observations of N = 58 individuals.

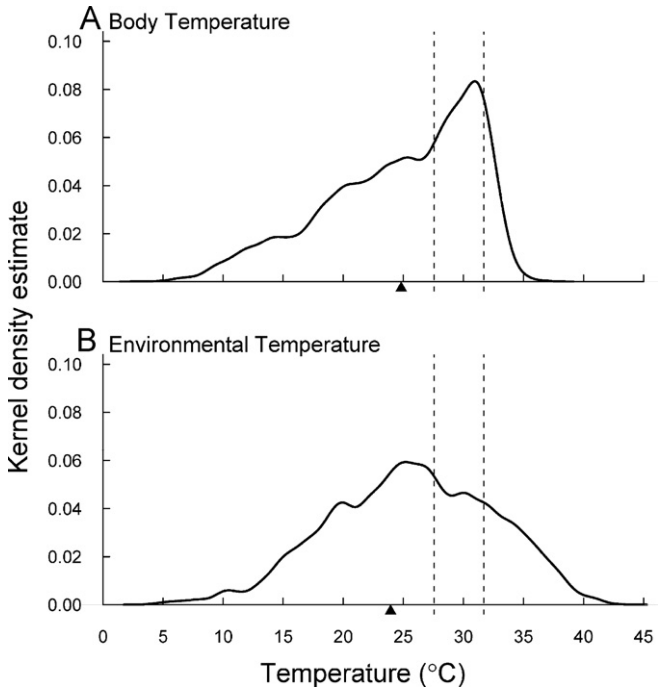

Fig. 1. Kernel density estimates for (A) Giant Gartersnake body temperature (T_b) and (B) environmental temperature. Vertical dashed lines indicate the upper and lower field preferred body temperature (FPBT) range boundaries, and triangles on the x-axis indicate mean T_b and mean environmental temperature.

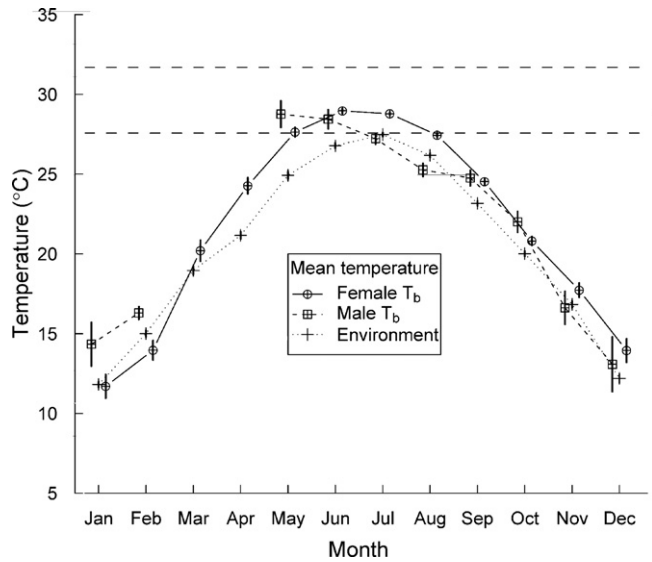

Fig. 2. Mean monthly body temperature (T_b) and mean monthly environmental temperature of male and female Giant Gartersnakes. Error bars are ±1 standard error of the mean. Horizontal dashed lines indicate the upper and lower field preferred body temperature (FPBT) range boundaries. Data points for males, females, and environmental temperature are offset for ease of interpretation.

month to month was strongly supported (Table 3). Females had greater T_b than males during July and August, but the sexes had similar T_b during the rest of the year (Fig. 2). The best-fit model indicated that females maintained higher T_b than males during the summer, but males maintained higher T_b than females during the late winter and spring (Fig. 3). Giant Gartersnake T_b was depressed relative to environmental temperature during the late fall and winter (Fig. 3).

3.3. Active season T_b

During the active season, Giant Gartersnake T_b varied as a function of sex, month, and time of day. The hypothesis that sexual differences in T_b varied by month and time of day, and diel differences in T_b varied by month, was strongly supported

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(Table 4). Diel variation in T_b depended upon the month in which snakes were located during the active season. For example, when environmental temperatures were controlled for during analyses, snake T_b was highest throughout the morning in May and lowest throughout the morning in September (Figs. 4 and 5). Females had a greater T_b than males in the morning, particularly during June, July, and August (Fig. 5).

Table 3
Evaluation of hypotheses for annual body temperature (T_b) variation in the Giant Gartersnake.

Hypothesis	Deviance	Log-likelihood	K	AIC_c	ΔAIC_c	w_i
T_b = sex*month+cTe	20,814	−10,407	24	20,862	0.00	1.00
T_b = month+cTe	20,867	−10,433	14	20,894	31.79	0.00
T_b = sex+month+cTe	20,866	−10,433	15	20,896	33.81	0.00
T_b = cTe	21,344	−10,672	5	21,354	491.70	0.00
T_b = sex+cTe	21,344	−10,672	6	21,356	493.70	0.00

Models are presented in order of decreasing support. K = number of model parameters, w_i = model probability. n = 3805 observations of N = 64 individuals.

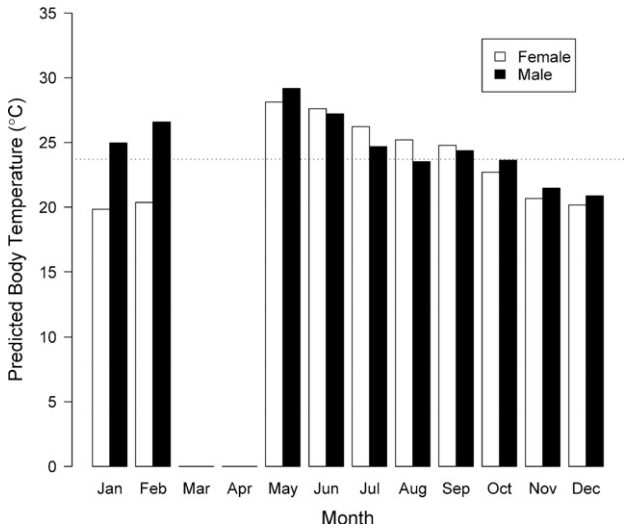

Fig. 3. Annual monthly predicted body temperatures for male and female Giant Gartersnakes based upon the best-fit model (T_b = sex*month+cTe). The horizontal dotted line indicates the mean environmental temperature.

4. Discussion

As we hypothesized, body temperatures of the Giant Gartersnake varied at multiple temporal scales and between the sexes. The best-fit models for both annual and active season time scales indicated that sexual differences in T_b varied by month. The greatest differences in T_b were during late winter and spring, when males had greater T_b, and during July and August, when females maintained greater T_b.

A number of different mechanisms may account for seasonal differences in T_b between the sexes. The link between T_b and physiological performance of ectotherms is well established (Lillywhite, 1987), and if males and females have different physiological requirements during different seasons, they may regulate T_b at different levels accordingly. Thus, males may thermoregulate to achieve higher T_b during spring, when they are searching for and courting females (but see Shine et al., 2000). It would therefore be informative to examine intersexual differences in T_b in March and April to further examine this hypothesis. In a similar manner, normal embryonic development is dependent on temperature (Lillywhite, 1987), and females may thermoregulate to achieve high T_b to aid embryonic development during the summer gestation period (Charland, 1995; Gregory et al., 1999; Isaac and Gregory, 2004; Kapfer et al., 2008). Thermoregulatory behavior has a strong influence on the duration of gestation and fitness of offspring in viviparous squamates (Shine and Harlow, 1993; Lourdais et al., 2004); therefore, natural selection may act upon females to thermoregulate precisely while gravid (Shine and Harlow, 1993). For example, maternal temperature during different stages of development affects the number of body segments, developmental rate, and the incidence of stillbirths in the Aspic Viper (*Vipera aspis*; Lourdais et al., 2004). If thermoregulation to high T_b has associated costs, such as increased predation risk (Huey and Slatkin, 1976; Peterson, 1987; Charland, 1995; Isaac and Gregory, 2004), reduced T_b may be an adaptive response when fitness benefits of reproductive activity are not imperative. Alternatively, differing T_b may be a consequence of differences in behavior, rather than causing differences in behavior. For example, the high T_b of males in May might be a consequence of

Table 4
Evaluation of hypotheses for active season (May–September) body temperature (T_b) variation in the Giant Gartersnake.

Hypothesis	Deviance	Log-likelihood	K	AIC_c	ΔAIC_c	w_i
T_b = sex*month+month*TOD+sex*TOD+cTe	15,139	−7569	32	15,203	0.00	1.00
T_b = sex*month+month*TOD+cTe	15,175	−7587	29	15,233	29.87	0.00
T_b = month*TOD+cTe	15,198	−7599	24	15,246	43.68	0.00
T_b = month*TOD+sex+cTe	15,196	−7598	25	15,246	43.72	0.00
T_b = sex*TOD+month+cTe	15,269	−7635	16	15,302	99.46	0.00
T_b = sex*month+TOD+cTe	15,291	−7645	17	15,324	121.48	0.00
T_b = sex+month+TOD+cTe	15,307	−7653	13	15,332	129.40	0.00
T_b = month+TOD+cTe	15,309	−7655	12	15,334	131.38	0.00
T_b = sex*month+cTe	15,476	−7738	14	15,504	301.41	0.00
T_b = month+cTe	15,497	−7748	9	15,514	311.33	0.00
T_b = sex+month+cTe	15,493	−7747	10	15,514	311.35	0.00
T_b = sex*TOD+cTe	15,499	−7749	12	15,522	319.38	0.00
T_b = TOD+cTe	15,539	−7769	8	15,554	351.32	0.00
T_b = sex+TOD+cTe	15,535	−7768	9	15,554	351.33	0.00
T_b = sex+cTe	15,702	−7851	6	15,714	511.30	0.00
T_b = cTe	15,706	−7853	5	15,716	513.29	0.00

Models are presented in order of decreasing support. K = number of model parameters, w_i = model probability. n = 2927 observations of N = 58 individuals.

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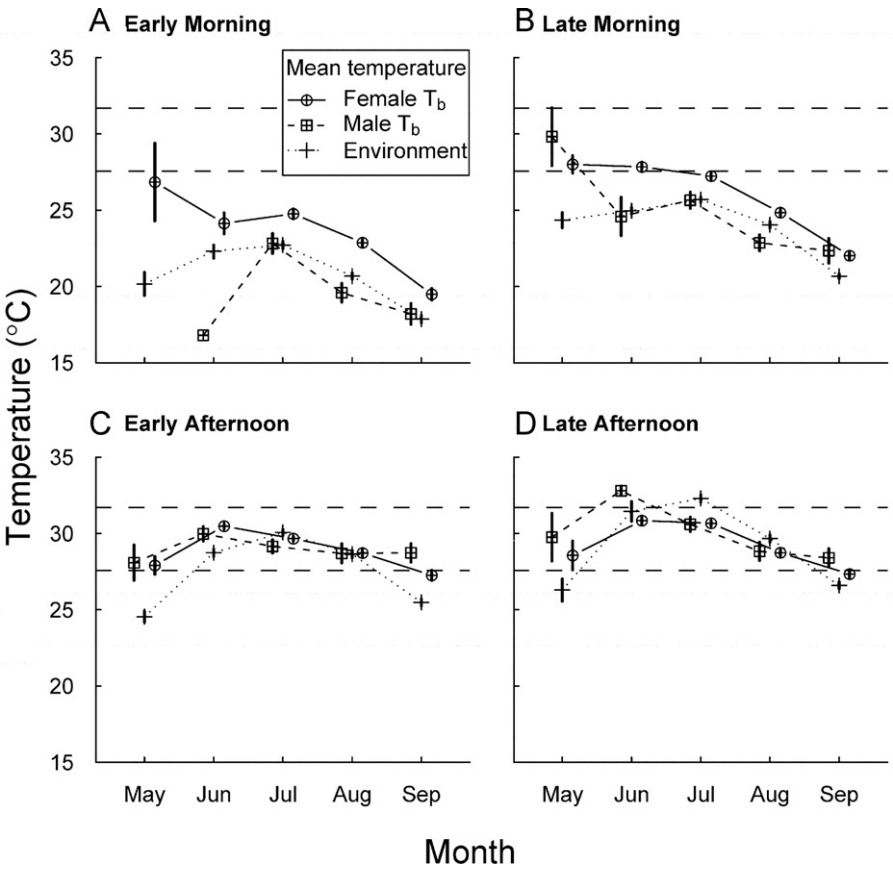

Fig. 4. Mean monthly body temperature (T_b) and mean monthly environmental temperature of male and female Giant Gartersnakes at different times of day. Error bars are ± 1 standard error of the mean. Horizontal long dashed lines indicate the upper and lower field preferred body temperature (FPBT) range boundaries. Data points for males, females, and environmental temperature are offset for ease of interpretation. (A) Early morning, (B) late morning, (C) early afternoon and (C) late afternoon.

extensive overland searching movements in warmer microenvironments. Similarly, greater female T_b during the summer gestation period may be a consequence of female anorexia while gravid (Gregory et al., 1999), resulting in higher T_b because of the lack of aquatic foraging behavior. A post-mating season increase in foraging activity may also explain male T_b decreasing below the FPBT range during July and August. Carefully designed experiments will be necessary to resolve these potentially interacting hypotheses.

Individuals seldom attained FPBT in the early morning, but were able to maintain FPBT during the afternoon throughout the active season. Low T_b in the early morning might simply be the result of low environmental temperatures at this time of day. Low humidity and little cloud cover in the Central Valley of California during the active season of the Giant Gartersnake result in large differences between diurnal high and nocturnal low temperatures. Therefore, environmental temperatures may simply be too low for individuals to attain FPBT. Alternatively, morning operative temperatures may be high enough that individuals could achieve FPBT, but they may remain in overnight shelters because of an insufficient thermal gradient to initiate a behavioral response or because of predation risk while thermoregulating under marginal conditions (Huey and latkin, 1976; Peterson, 1987). The elevated T_b of females relative to males in the early morning, particularly from June through August, might be caused by more careful thermoregulation of gravid females. Alternatively, the greater mass of females might result in enough thermal inertia to maintain greater temperatures overnight without overt thermoregulatory behavior. Assessment of these hypotheses will require detailed description of the thermal environment with an array of operative temperature models.

The thermal ecology of gartersnakes is remarkably consistent given the variety of body sizes and habitats occupied by this genus. The mean FPBT of the Giant Gartersnake during the active season, given at least one microhabitat with a minimum temperature of 30 °C, was 29.8 °C. This is within the range of values observed for gartersnakes in other studies throughout North America (Rosen, 1991). Thus, our data support the hypothesis of phylogenetically conservative FPBT (Rosen, 1991).

Despite the impact of the thermal environment on most biological processes of ectotherms (Peterson et al., 1993), we do not expect conservation measures to impact the thermal ecology of the Giant Gartersnake. The Giant Gartersnake primarily uses the edges of aquatic habitats and wetlands, and it occurs in a climate with abundant radiant energy and high ambient temperatures during the active season. Therefore, the occurrence of permanent wetlands containing emergent vegetation with adjacent vegetated shoreline habitats likely constitutes an environment with readily accessible thermoregulatory opportunities for this rare snake. Future studies should focus on interactions among thermoregulatory, foraging, and reproductive behaviors in relation to individual survival. Such information would be integral to the design of habitat restoration projects to support recovery efforts for this listed species.

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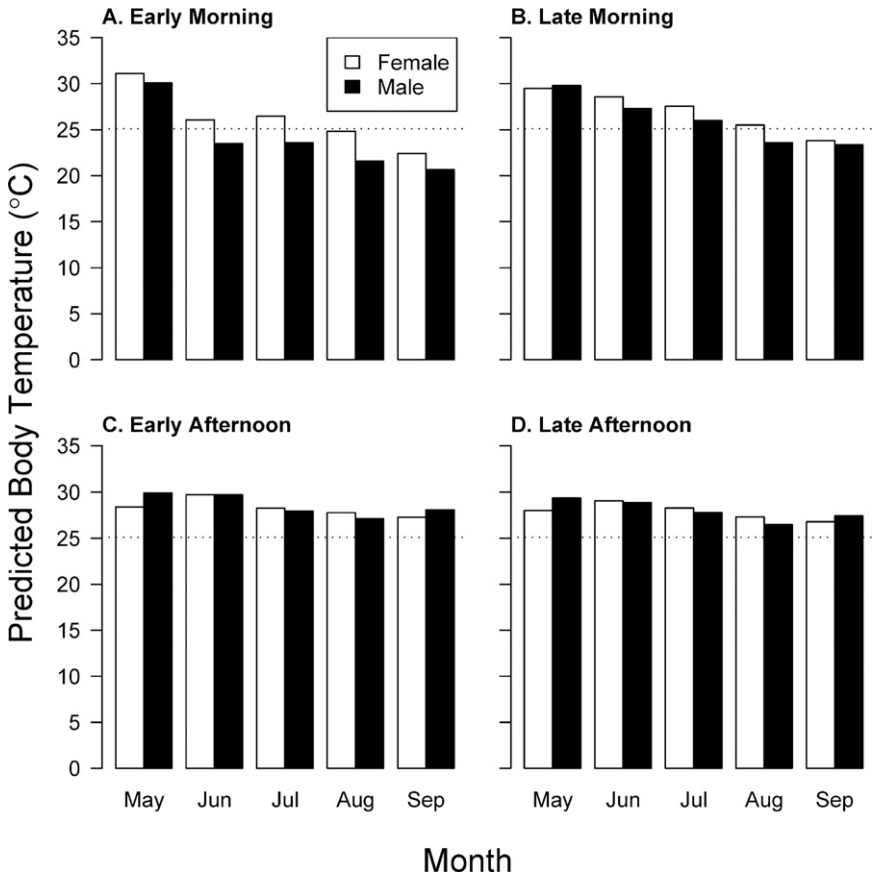

Fig. 5. Active season monthly predicted body temperatures for male and female Giant Gartersnakes at different times of day based upon the best-fit model (T_b = sex*month+month*TOD+sex*TOD+cTe). The horizontal dotted line indicates the mean environmental temperature. (A) Early morning, (B) late morning, (C) early afternoon and (C) late afternoon.

Acknowledgements

We are grateful for the help provided to us by T. Graham and the late G. Hansen in starting our work on the Giant Gartersnake. We are especially grateful to L. Phillips, K. Gilardi, and R. Wack for their veterinary expertise. Funding was provided by the U.S. Fish and Wildlife Service and the U.S. Bureau of Reclamation representatives on the Central Valley Project Improvement Act b1 Committee. We also thank personnel from the Sacramento National Wildlife Refuge Complex for their cooperation. L. Martin provided data management, P. Coates provided an introduction to and stimulating discussion of linear mixed models, and many biologists collected the data for this project. J. Yee provided helpful review of statistical methodology, and P. Gore provided administrative support. Snakes were handled in accordance with the University of California–Davis Animal Care and Use Protocol 9699 and as stipulated in U.S. Fish and Wildlife Service Recovery Permit TE-020548-5. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

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