

THE THERMAL ECOLOGY OF GRAVIDITY IN  
EASTERN FOX SNAKES (*ELAPHE GLOYDI*)

A Thesis

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by

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## ABSTRACT

### THE THERMAL ECOLOGY OF GRAVIDITY IN EASTERN FOX SNAKES (*ELAPHE GLOYDI*)

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University of Guelph, 2000

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Professor R. J. Brooks

Gravid females of viviparous snake species maintain higher and less variable body temperatures ( $T_b$ ) than their nongravid conspecifics. Although the benefits of higher and less variable  $T_b$ 's, mainly accelerated embryogenesis resulting in earlier parturition/oviposition, should also apply to oviparous snake species, few studies have adequately addressed this question. To test whether gravid and nongravid females of oviparous snakes exhibit different thermoregulatory behaviour, I surgically implanted temperature-sensitive radiotransmitters into 14 female (six gravid, eight nongravid) eastern fox snakes (*Elaphe gloydi*) and placed them in an outdoor enclosure. Snake  $T_b$ 's and environmental temperatures from thermal models were measured at 1-h intervals over 8 days ( $N = 146$ ). Gravid females did not maintain higher and less variable  $T_b$ 's than nongravid females, nor did they exhibit obvious differences in overt thermoregulatory behaviour. The combination of a thermally "benign" environment, along with a short period of egg retention, relative to viviparous species, may render careful thermoregulation unnecessary in this population.

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## INTRODUCTION

Snakes living in temperate zones often inhabit thermally variable environments where their physiology, behaviour, and ecology are significantly influenced by the body temperatures they select (Avery 1982, Lillywhite 1987, Peterson *et al.* 1993, Dorcas *et al.* 1997). To interpret thermoregulatory behaviour in snakes adequately, it is necessary to have data on the causes (e.g., environmental constraints, physiological condition of the individual), and consequences (e.g., increased metabolism, accelerated embryogenesis) of body temperature variation (Peterson *et al.* 1993). The proximate consequences of body temperature variation are often physiological, such as increased locomotor ability (Stevenson *et al.* 1985, Scribner and Weatherhead 1995), strike speed (Goode and Duvall 1989), and digestive rate (Dorcas *et al.* 1997); and these effects significantly influence a species' ecology (Peterson *et al.* 1993). For example, locomotor ability and strike speed affect when and where an animal can successfully forage, its ability to avoid predation, and its movement patterns. Also, many reptile species grow more slowly, reproduce less frequently, and live longer at higher latitudes and altitudes, presumably due to, at least in part, lower annual temperatures and shorter active seasons which limit the time spent at preferred temperatures (Brooks *et al.* 1992, Peterson *et al.* 1993, Parent 1997, Prior and Weatherhead 1998). The ecological consequences of body temperature variation clearly affect survivorship and reproductive success. Therefore, it follows that body temperature selection in snakes would be constrained by natural selection, presumably resulting in adaptive/optimal thermoregulatory behaviour. In conjunction, natural selection should also mould the thermal dependencies of important biological functions so that they

function optimally at body temperatures commonly experienced by the animals in their natural environment. This coadaptation (Huey and Bennett 1987, Dorcas 1995) predicts that important processes like embryogenesis will optimally occur at a temperature (or within a temperature range) that is not only attainable in the wild, but that balances the costs and benefits associated with that particular body temperature. The benefits of maintaining body temperatures optimal for important physiological processes are obvious; however, there are also many associated costs such as increased predation (Shine 1980, Seigel *et al.* 1987, Brodie 1989) and increased energy consumption resulting in depletion of fat reserves (Charland 1995).

The majority of body temperature ( $T_b$ ) data collected from free-ranging snakes have been spot measurements, either via a cloacal temperature probe inserted upon capture, or remotely from implanted temperature-sensitive radiotransmitters (e.g., Plummer 1993, Porchuk 1996, Parent 1997, Blazquez 1995, see Peterson *et al.* 1993 for review). Spot  $T_b$  measurements are often biased because they are usually taken from active animals, despite the fact that many reptiles are inactive or sequestered in retreats most of the time (Peterson 1987, Huey *et al.* 1989). Also, because snakes are often radiotracked during favourable environmental conditions, and when convenient for the researcher (e.g., a particular snake may end up being tracked last each day simply because of the spatial arrangement of the study animals), biases resulting from the sampling protocol are likely. Also, because differences in  $T_b$  selection between individuals, between demographic groups, and between reproductive groups may be small, they will probably go undetected with intermittent measurements.

Therefore, continuous  $T_b$  data are most desirable because they can reveal temporal

patterns of  $T_b$  variation, correlations with weather conditions, the effects of physiological condition (e.g., reproductive status), and intra- and interindividual differences in  $T_b$  variation (Peterson *et al.* 1993). Additionally, individual daily patterns of  $T_b$  variation can be documented (Peterson *et al.* 1993). Continuous  $T_b$ 's have become increasingly easier to obtain in recent years, both because of the improvement in radiotransmitters (increased signal strength and reliability/lifespan) and in the devices used to record the data (Beaupre and Beaupre 1994, Cobb 1994, Lutterschmidt *et al.* 1996, Dorcas and Peterson 1998, Brown and Weatherhead 2000).

Continuous  $T_b$  measurements, by themselves, provide an incomplete picture of the thermoregulatory behaviour of snakes. By simultaneously recording environmental temperatures, one can determine whether snake behaviour, or environmental conditions are the primary factors influencing  $T_b$  variation within individuals (Peterson 1987, Huey *et al.* 1989, Charland and Gregory 1990, Peterson *et al.* 1993, Charland 1995). For example, if climatic conditions were constraining a snake's ability to maintain high body temperatures, then simply measuring the snake  $T_b$  would lead one to erroneously conclude that the snake actually preferred that temperature. Environmental or "operative" temperatures ( $T_e$ ; Bakken and Gates 1975, Bakken 1992) are best measured with physical models that have thermal properties similar to those of the study species; and thus approximate the steady-state  $T_b$  of the animal in the same location (Huey *et al.* 1989). The  $T_e$  is superior to simply measuring the ambient air or ground temperature because it incorporates information about the study species' size, shape, and reflectance which are important variables determining the effect of solar radiation on the animal's temperature (Bakken 1992). Determining the maximum and minimum  $T_e$ 's allows one to

bound the possible range of  $T_b$ 's from which a snake can select.

Reproductive condition has profound effects on the physiology, behaviour, and ecology of female snakes (Cobb 1994, Graves and Duvall 1993), and these effects are most pronounced in temperate viviparous species (reviewed in Peterson *et al.* 1993). Changes in thermoregulatory behaviour as a result of becoming reproductive (i.e., gravid) have been documented in several North American species. For example, viviparous Great Basin rattlesnakes (*Crotalus viridis lutosus*) maintained higher and less variable  $T_b$ 's while gravid (Cobb 1994), and gravid rubber boas (*Charina bottae*), another viviparous species, also maintained higher and less variable  $T_b$ 's than nongravid females (Dorcas and Peterson 1998). Similarly, gravid eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) appeared to select microhabitats based on their thermal properties (e.g., large granite table rocks in exposed clearings), whereas nongravid females and males apparently selected habitats based largely on prey availability (Parent 1997), and as a result the latter thermoregulated less precisely (i.e., greater variability in selected  $T_b$ 's; Willson 1996). These differences in mean  $T_b$ , and the precision with which these  $T_b$ 's are maintained, probably do not arise from differences in preferred body temperatures (PBT), but rather a change in the priority a gravid female places on thermoregulation (Reinert 1993). For example, nongravid females frequently forage in thermally inferior microhabitats, whereas gravid females often forgo foraging during gestation, instead remaining in thermally favourable retreats (Graves and Duvall 1993, Reinert 1993, Cobb 1994, Willson 1996). The effects of reproductive status on the thermoregulatory behaviour of viviparous species are therefore well documented.

The thermal ecology of oviparous snakes is less well documented, particularly

with regard to changes in thermoregulatory behaviour during the period of egg retention (Peterson *et al.* 1993). Although it is possible that the period of egg retention in oviparous snakes is too short (Tu and Hutchinson 1994) to accelerate or enhance embryogenesis to a point where the benefits (via increased maternal and offspring survivorship) of earlier oviposition dates outweigh the costs of increased thermoregulatory behaviour; few studies have investigated this question with the techniques outlined above, particularly continuous  $T_b$  measurements recorded from multiple individuals. However, several studies have analyzed spot  $T_b$  measurements. For example, Plummer (1993) reported that gravid rough green snakes (*Opheodrys aestivus*) had significantly higher  $T_b$ 's (measured by cloacal thermometer upon capture) than males during June when ovulation occurs and oviposition begins; whereas Porchuk (1996) recorded spot  $T_b$  measurements of blue racers (*Coluber constrictor foxii*) using temperature-sensitive radiotransmitters and found no differences between the sexes during the period of egg retention and oviposition. Semi-continuous  $T_b$  data (i.e., 3-h intervals from 08:00 – 20:00 over 6 days) recorded from Montpellier snakes (*Malpolon monspessulanus*) indicated that gravid individuals maintained higher and less variable  $T_b$ 's than nongravid individuals (Blazquez 1995).

Although the duration of egg/embryo retention in oviparous snakes is significantly shorter than in viviparous species, (i.e., approximately 50 % of embryonic development occurs *in utero* in oviparous taxa, whereas 100 % occurs *in utero* in viviparous species; Shine 1983), it is reasonable to predict that selection for enhanced or accelerated embryogenesis, via its effects on oviposition dates and predation rates, may incur detectable differences in thermoregulatory behaviour between gravid and nongravid

individuals of oviparous species. Therefore, to test the hypothesis that gravid and nongravid females of oviparous snakes exhibit different thermoregulatory behaviour, I investigated the influence of reproductive condition on the thermal ecology of the eastern fox snake (*Elaphe gloydi*; Figure 1), an oviparous colubrid, over two years. I predicted that gravid females would maintain higher and less variable  $T_b$ 's than nongravid females during the period of egg retention. To provide a broader understanding of the thermoregulatory behaviour of *E. gloydi* I also asked the following questions: (1) What are the  $T_b$ 's of female fox snakes and how do they vary? (2) What is the range of possible  $T_b$ 's available to fox snakes within specific microhabitats?

Eastern fox snakes are large enough to easily accommodate temperature-sensitive radiotransmitters, and despite a relatively restricted global distribution, they can be locally abundant and often hibernate communally, facilitating high capture rates in the spring when transmitter implantation is most desirable. Eastern fox snakes also occur sympatrically with other viviparous species used in thermoregulatory studies (i.e., *S. c. catenatus*; Willson 1996), making comparisons between the two reproductive modes possible.

Monitoring free-ranging snakes with radiotelemetry over long periods is difficult, especially with vagile species that spread out over large areas during the active season. Most radio receivers can pick up transmitter signals from no farther than 1 km and this is under optimal conditions (e.g., atmospheric, snake location and position, radio frequency activity). Recent studies that monitored the  $T_b$ 's of multiple snakes for long periods have been possible because of the study species' tendency to aggregate in specific areas or habitats, e.g., northern water snakes (*Nerodia sipedon sipedon*) in semi-enclosed





Figure 1. A female eastern fox snake (*Elaphe gloydi*) with her eggs. The female laid her eggs in captivity in the artificial nest site less than 12 h prior to the photo.

wetlands (Brown and Weatherhead 2000) or rattlesnakes in isolated rock outcrops functioning as rookeries (Cobb 1994, Willson 1996). Species that disperse from hibernacula and exhibit little aggregative behaviour towards specific microhabitats can make monitoring several individuals extremely difficult (Shewchuk pers. comm.) or impossible (pers. obs.). However, it is possible to monitor multiple snakes if one has access to several single (Beaupre and Beaupre 1994, Lutterschmidt *et al.* 1996), or multiple channel receivers (Blouin-Demers pers. comm.).

Other researchers have constructed semi-natural enclosures to limit the spatial arrangement of the study animals, thus facilitating continuous  $T_b$  measurement, as well as continuous  $T_e$  measurement within a defined area (Moore 1978; Hammerson 1979, 1987; Charland and Gregory 1990; Charland 1995; Shewchuk 1996; Lee and Mills 2000). An enclosure can also provide a compromise between the controlled design of a laboratory study, and the more natural setting of a field experiment (Fitch 1987, Lee and Mills 2000). Unfortunately, many enclosures have been relatively small and probably did not allow snakes to exhibit normal thermoregulatory, or habitat selection behaviour (but see Lee and Mills 2000). For example, Hammerson's (1979) enclosure was only 12.25 m<sup>2</sup> (3.5 x 3.5 m) while Charland and Gregory's (1990) enclosure was 36 m<sup>2</sup> (6 x 6 m). Shewchuk's (1996) enclosure was significantly larger at 149 m<sup>2</sup> (12.2 x 12.2 m), however, it is probable that even an enclosure this large did not provide a suitable thermal range to allow snakes to maintain preferred  $T_b$ 's (Shewchuk pers. comm.). Because eastern fox snakes on Pelee Island are highly dispersed, and also because of their propensity to select radio-wave inhibiting objects (e.g., sheet metal, concrete pipes) for shelter, I constructed a large semi-natural enclosure to monitor their thermoregulatory behaviour.

## METHODS

### Study Area

Pelee Island is situated in the western basin of Lake Erie and at 4,261 hectares is the largest land mass in the Lake Erie archipelago (41°47' N, -82°40' W; Figure 2). Because much of the island is below lake level, there once existed an extensive array of wetlands covering approximately 60 % of the island's area (Wilkinson 1866). The implementation of an "efficient" drainage system consisting of numerous dikes and canals in the late 1800's reduced the island's wetlands to approximately 3 % of the present land mass. Open cash-crop agricultural fields make up nearly 70 % of the present land mass, while the remaining 30 % is distributed among six major habitat patches (Porchuk 1996). This remaining "natural" habitat is extremely fragmented and many patches are separated by areas relatively inhospitable to snakes. Agricultural hedgerows and vegetated buffer zones around drainage canals connect many of these habitat patches, and the island's snake species readily use these "corridors" for foraging, reproduction, and dispersal (Porchuk 1996). Unfortunately, the island is also dissected by 68 km of roadways upon which significant snake mortality occurs.

### Study Species

The eastern fox snake (*Elaphe gloydi*) is a relatively large (91-137 cm snout-to-vent length; SVL) oviparous snake belonging to the family Colubridae (Powell 1990). The species was formerly classified as a subspecies of *Elaphe vulpina* but several authorities presently consider it to be distinct from the western fox snake (Collins 1997, see Willson and Prior 1998 for discussion) and I follow the latter nomenclature

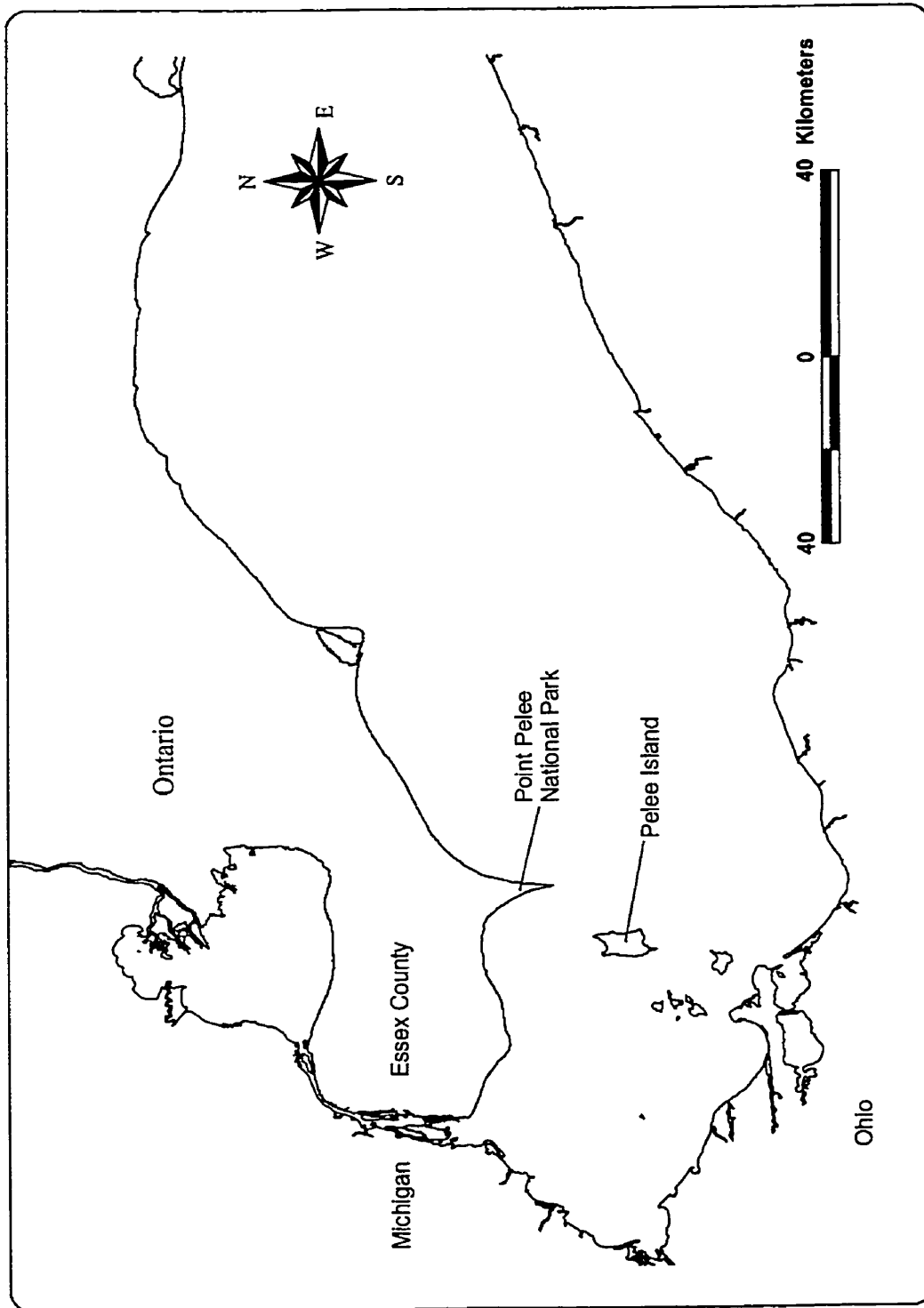


Figure 2. The island region of western Lake Erie and adjoining mainland areas of Ontario, Michigan, and Ohio.

here. *Elaphe gloydi* has a restricted global distribution with approximately 65-70 % of the species' range existing within Ontario. Eastern fox snakes inhabit mainly unforested, terrestrial shoreline ecosystems adjacent to marshes, and the species is found closely associated with forest-scrub ecotone, old field succession, and beach dune habitat (Rivard 1976, Willson and Prior 1998). On Pelee Island, *E. gloydi* is found in a variety of habitats including oak savanna, old fields, vegetated riparian habitats along man-made canals, and rocky and sandy shorelines. It is likely that fox snakes have been declining in numbers and distribution since the large scale conversion of marshland to open farm fields began in the late 1800's. In particular, loss of the extensive network of marshlands around the periphery of Lake Erie (Snell 1987) is thought to be one of the primary factors responsible for the decline of *E. gloydi* throughout the greater proportion of its range (Rivard 1979). However, on Pelee Island, the fox snake population appears to be relatively stable even though several other snake species (e.g., *Heterodon platirhinos*, *Crotalus horridus*, and *S. c. catenatus*) have been extirpated in the last 100 years (King *et al.* 1997).

Fox snakes are constrictors and employ both active searching and ambush (sit and wait) foraging tactics. Rodents make up a large percentage of their diet throughout the active season, but bird eggs and hatchlings are also commonly consumed during the late spring and early summer (Porchuk and Willson, unpubl. data). On Pelee Island, fox snakes probably reach sexual maturity in their fourth year and mating occurs throughout late May and into early June. Oviposition begins in late June and extends into mid July. Zehr (1969) reported an egg retention period of one month for a western fox snake (*E. vulpina*) that copulated in the laboratory. On Pelee Island, eggs are laid in composting

vegetation, sawdust piles, and decaying logs. Nest incubation periods range from 50 to 65 days (Harding 1997) and hatchlings emerge late August to early October depending on laying date, and the thermal and hydric characteristics of the nest site. Of the North American *Elaphe*, the fox snakes have probably received the least attention from scientists and hobbyists (Ernst and Barbour 1989) and relative to many other large snake species in North America, their biology is not well described.

### **Implantation of Transmitters**

From 27 April 1998 to 13 May 2000, 26 female eastern fox snakes were radiotracked on Pelee Island for periods ranging between 2 and 23 months (Table 1). Snakes were captured by hand and perimeter traps placed around known hibernacula. Snout-to-vent length (SVL) and vent-to-tail length (VTL) were recorded by gently stretching the snakes along a tape measure. Mass was recorded to the nearest 5 g with spring scale pesolas. The mean SVL of radiotracked females (N = 25) was  $107.6 \pm 10.62$  cm (SD), (range = 93 – 130 cm) and their mean mass was  $574.1 \pm 168.01$  g (SD), (range = 395 – 961 g). Sex was determined by either inserting a blunt sexing probe into the cloaca to detect the presence of hemipenes, or by VTL relative to SVL (males having proportionately longer tails). Reproductive condition of females was determined by gentle palpation of the abdomen to detect developing embryos, appearance relative to other females in the population (i.e., gravid females have a comparatively rounded abdomen), and a SVL to mass ratio. Additionally, reproductive condition was confirmed by pre- and post-oviposition female mass (i.e., females that were gravid experienced a significant mass loss after oviposition). Snakes were permanently marked with passive

integrated transponders (PIT tags; Avid Canada) which were inserted subcutaneously in the posterior 1/3 of the body.

I surgically implanted radiotransmitters into fox snakes following the general procedures of Reinert and Cundall (1982) with modifications from Reinert (1992), Blouin-Demers *et al.* (In Press B), and personal experience with massasauga rattlesnakes (Parent 1997). Snakes were anesthetized with isoflurane delivered via a precision vapourizer and Bain circuit. Most individuals were intubated with an endotracheal tube, whereas others were placed in a modified head mask to facilitate gas inhalation. Snakes were heated prior to surgical procedures to increase respiration rate as this significantly reduced induction times. Snakes took between 13 and 30 min to reach a surgical plane of anesthesia, although individual propensities for longer induction times were observed (i.e., longer induction times were observed during both transmitter implantation and removal for some individuals). Transmitters were submersed in cold sterilization fluid (Germiphene or Coldcide) for at least one hour prior to implantation. Transmitter mass was always less than 3% of snake body mass to minimize the effects of transmitter implantation. Species-specific insertion points for the transmitter (i.e., between the gall bladder and left ovary) were determined from dissections of individuals found as roadkills and yielded a ratio that could be used to estimate the optimal insertion point relative to SVL (as suggested by Reinert 1992). Transmitters were inserted through a 2-cm ventro-lateral incision made between the 1<sup>st</sup> and 2<sup>nd</sup> lateral scale rows and then through a small peritoneal incision. To prevent migration within the coelom, transmitters were sutured to the body wall. The whip antenna was placed under the skin of the snake using a short section of 17-gauge metallic tubing which was inserted anteriorly from the incision site. The antenna wire was fed through the tube until it was fully extended under the dermis.

Table 1. Eastern fox snakes radiotracked on Pelee Island, 1998 - 2000. SVL is snout-to-vent length and VTL is vent-to-tail length.

#	Snake ID <sup>a</sup>	Date of Implant	SVL (cm)	VTL (cm)	Mass (g)	Condition 1998	Condition 1999	Fate <sup>b</sup>
1	445	27-Apr-98	100	16.0	420	nongravid	unknown	transmitter removed
2	793	27-Apr-98	120	17.0	680	gravid	nongravid	transmitter removed
3	438	08-May-98	123	18.5	681	gravid	-	depredated May 99
4	671G	08-May-98	127	19.0	623	gravid	gravid	died Aug 99 <sup>c</sup>
5	731	11-May-98	101	16.0	396	gravid	nongravid	transmitter removed
6	353	11-May-98	106	16.0	461	nongravid	unknown	unknown
7	832G	14-May-98	114	8.5	580	nongravid	gravid	unknown
8	472G	15-May-98	96	15.0	395	nongravid	gravid	transmitter removed
9	558	16-May-98	110	15.0	520	gravid	nongravid	unknown
10	473	29-May-98	ND	ND	532	gravid	-	depredated Oct 99
11	392	29-May-98	94	15.0	410	gravid	unknown	transmitter removed
13	761	01-Jun-98	111	14.0	685	gravid	-	depredated Jul 98
12	698G	01-Jun-98	108	16.0	669	nongravid	gravid	depredated Aug 99
14	551	03-Jun-98	99	16.5	800	gravid	nongravid	transmitter removed
15	810	03-Jul-98	123	19.0	900	gravid	nongravid	unknown
16	772G	14-May-99	106	16.6	478	-	gravid	transmitter removed
17	193G	31-May-99	104	15.0	585	-	gravid	transmitter removed
18	231G	05-Jun-99	109	17.0	710	-	gravid	transmitter removed
19	48	06-Jun-99	101	16.5	400	-	nongravid	unknown
20	31	10-Jun-99	100	16.0	403	-	nongravid	depredated July 99
21	212G	10-Jun-99	130	18.0	961	-	gravid	transmitter removed
22	70G	13-Jun-99	93	15.5	407	-	gravid	unknown
24	164	21-Jun-99	98	16.0	448	-	nongravid	unknown
23	112G	21-Jun-99	99	14.5	429	-	gravid	unknown
25	384G	22-Jun-99	100	14.5	523	-	gravid	depredated Aug 99
26	753G	24-Jun-99	117	18.0	830	-	gravid	transmitter removed

<sup>a</sup>G denotes females that were gravid in 1999 and these ID's follow throughout text

<sup>b</sup>unknown indicates premature transmitter failure, and therefore the fate of these snakes is uncertain

<sup>c</sup>the only female to reproduce in consecutive years presumably died from reproductive complications associated with a single bound egg (dystocia; DeNardo 1996) following "partial" oviposition in the wild



The tube was then removed through a small 1-mm incision made approximately 20 cm anterior to the major incision. The small incision was closed with Vet Bond tissue adhesive, whereas the major incision (both peritoneum and scales) was sutured with 4-0 monofilament synthetic absorbable sutures (Biosyn). Anesthesia was usually discontinued during the suturing of the scales and snakes generally recovered (tongue flicking, movement) within 10 min. Post-operative snakes were administered an intramuscular injection of the antibiotic enrofloxacin (Baytril, Miles) as a preventative measure (Klingenberg 1996). An occlusive polyurethane film (Op-Site Spray Bandage; Smith and Nephew Inc.) was sprayed onto the incision sites in 1998 and 1999, and has been found to promote healing of cutaneous wounds in garter snakes (*Thamnophis*; Smith *et al.* 1988). The procedure generally took an hour to complete and snakes were released at their site of capture 24 - 48 h post-operative.

While in captivity, recovering snakes were given access to a thermal gradient to facilitate healing at preferred  $T_b$ 's. All surgical procedures were conducted under aseptic conditions and were approved by the Animal Care Committee of the University of Guelph (Protocol # 98R037). Except for the first two implantations which were performed at the Leamington Animal Hospital, all surgeries were conducted at the "Wilds of Pelee Island's" Medical facility ("The Medical Shed"). Transmitters were removed from all snakes that could be relocated upon the study's conclusion (Table 1). There was no mortality directly attributable to either the surgical procedure, or carrying of the transmitter; however, two transmitters were removed prematurely because of poor healing of the incision sites. These individuals were kept in captivity for approximately 10 days post-operative, where they were given access to a thermal gradient, fed numerous

juvenile house mice, and given antibiotic therapy (i.e., enrofloxacin). Both individuals appeared to recover fully and were released at their site of capture. Poor healing at the incision site is uncommon, although it seems to happen with similar frequency in both blue racers (B. Porchuk pers. comm.) and eastern massasaugas (pers. obs.). Therefore, it seems to be interindividual in nature.

### **Snake Body Temperatures ( $T_b$ )**

Two radiotransmitter models (Holohil Systems Ltd) were used for this study. The SI-2T model (8.95-9.6 g) was implanted into 21 female fox snakes in both 1998 and 1999, and the BD-2GT (1.9 g) was implanted into five smaller females in 1999. Both models operated in the 172-MHZ bandwidth and were fitted with thermistors that varied the pulse rate of the transmitter with temperature. Depending on the model and the body temperatures selected by individual snakes, the transmitters were rated to function from approximately three months to a maximum of 18 months, although one transmitter still functioned after 23 months.

Prior to implantation, each transmitter was placed in a swirling water bath and calibrated (0.5 – 40°C) against a standardized thermometer with a resolution of 0.5°C. Resulting calibration data were fit to third order polynomials using a curve fitting program (mean standard error = 0.64°C; max standard error = 0.79°C; Sigma Plot 4.0, Jandel Scientific). Residuals indicated that the maximum standard error was significantly less within the range of  $T_b$ 's relevant to this study (i.e., 15 – 35°C). The regression equations derived for each transmitter were then used to convert recorded pulse intervals to temperatures (Figure 3). Transmitters implanted into the coelom would then be representative of the internal core body temperature of the snake.

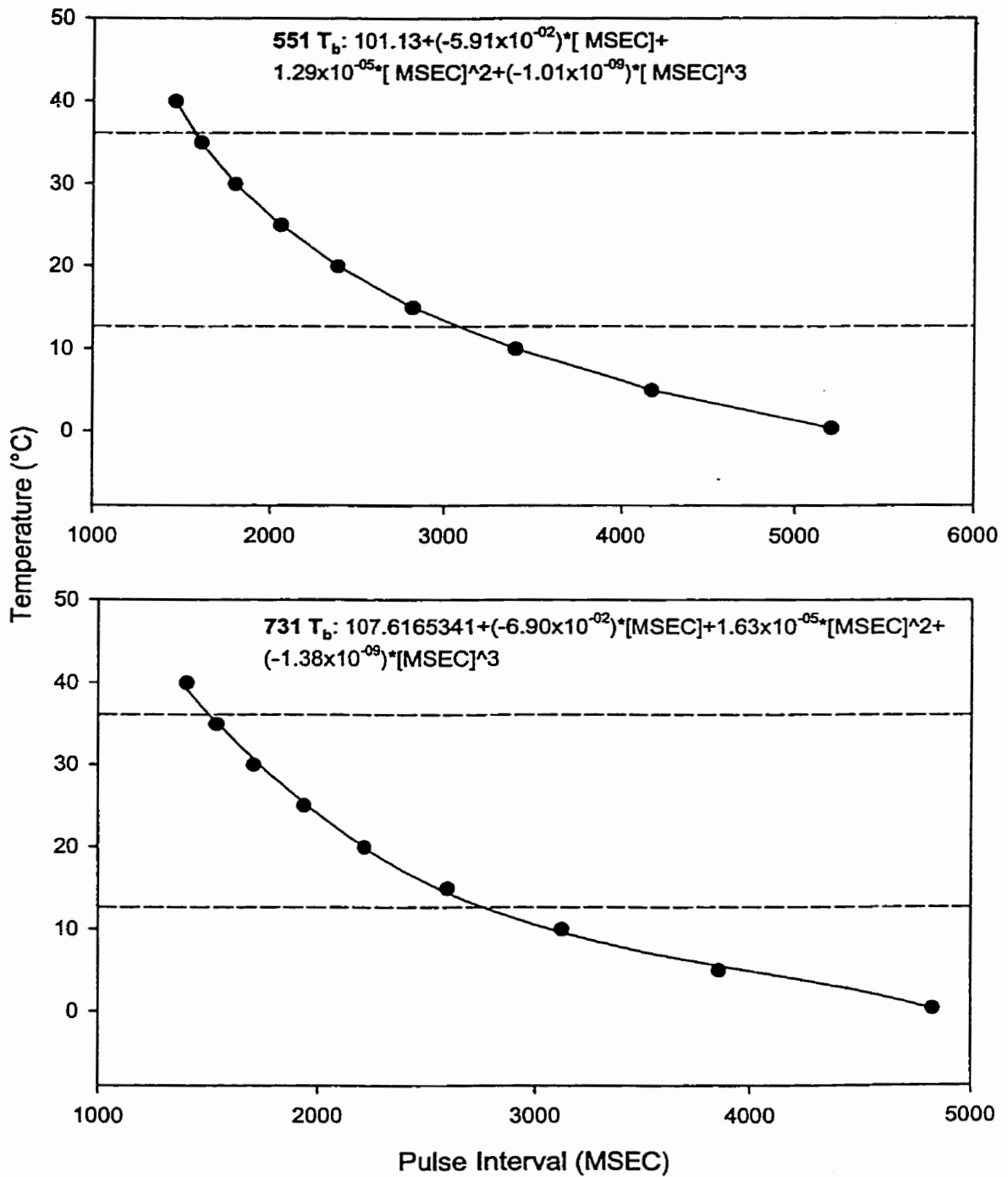


Figure 3. Typical calibration curves generated by immersing temperature-sensitive radiotransmitters in a circulating water bath and recording the pulse interval every 5°C. Cubic regression equations were then used to convert pulse interval into  $T_b$ . Broken horizontal lines delineate  $T_b$  range relevant to this study.

In 1998, transmitter pulse interval (i.e., snake  $T_b$ ) was measured using a stopwatch. For example, the time for 11 pulses was recorded and divided by 10 deriving a pulse interval (Reinert 1992). This was done twice for each measurement and then averaged. No pulse interval was included in any analysis if the difference between the first and the second measurement exceeded 50 msec. In 1999, a more accurate method was used to determine pulse interval (see Monitoring System below). All  $T_b$  data presented were collected from snakes greater than seven days post-operative as transmitter implantation has been shown to cause aberrant behaviour in snakes for several days after surgical procedures are completed (Charland 1991).

### **Spot $T_b$ Measurements**

In 1998, periodic spot  $T_b$  measurements were recorded from 15 radiotagged female fox snakes. Snakes were located approximately once every three days, although this interval varied with respect to subseason (e.g., egg laying vs fall ingress to hibernacula). Upon location, snake  $T_b$  (pulse interval), ambient air temperature ( $T_a$ ; 1 m above ground in shade) and ground temperature ( $T_g$ ; in a microenvironment similar to the one utilized by the snake) were recorded. In addition, three free-ranging females (two gravid, one nongravid) were monitored for 24 h on 1 July 1998 and  $T_b$ 's were recorded at 2-h intervals.

### **Operative Temperatures ( $T_e$ )**

To measure operative temperatures ( $T_e$ ), and hence assess the thermal environment available to snakes, models were constructed following designs described

by Peterson *et al.* (1993). Copper pipe approximating the thickness of a female fox snake (2.5-cm diameter) was cut into 30-cm lengths to produce five models. Thermistors were suspended in the centre of the models using wire supports. Models were filled with water to 3/4 volume and the ends sealed with copper test caps and silicone. Models were then spray painted with grey and brown primers to approximate the dorsal reflectance of a fox snake which was measured with a spectrophotometer in the field. Two-meter thermistor leads were connected to HOBO data loggers (Onset Computer Corp.) to record model  $T_c$ . To test the accuracy of the models for predicting snake  $T_b$ 's for a particular microclimate, the models were placed in an exposed location adjacent to a roadkilled fox snake in good condition (male, 120 cm SVL, approx. 650 g) which had a thermistor inserted rectally to mid-body. The dead snake and the five models had been cooled to the same ambient temperature and measurements were taken at 3-min intervals over 8 h (N = 159) starting at noon.

### **Semi-natural Enclosure**

Into the second field season, it became increasingly apparent that I would be unable to consistently pick up signals from widely scattered free-ranging fox snakes, and I therefore decided to construct a semi-natural enclosure where females could select from a range of thermally heterogeneous microhabitats, and yet remain in a single location optimal for radiotelemetric (behaviour and  $T_b$ ) monitoring. Radio interference from hydro wires and boat radios, receiver and antenna problems, and the proclivity of fox snakes to seek out metallic structures (e.g., discarded sheet metal, abandoned cars, tractors, pipes, etc.) for shelter, made continuous monitoring of snake  $T_b$ 's impossible.

Life history information gathered from this particular fox snake population through radiotelemetry and mark-recapture was used to determine not only the enclosure's size and location, but also its feasibility (i.e., whether it would significantly impede the female's spatial movements and hence bias the  $T_b$  data). For example, one of the criticisms of Charland and Gregory's (1990) study was that gravid and nongravid western rattlesnakes (*Crotalus viridis oregonus*) did not differ in the mean  $T_b$ 's selected within an enclosure, not because their thermoregulatory priorities (Reinert 1993) were the same, but because the small size of the enclosure prevented the significant divergence in habitat utilization that is characteristic of free-ranging *C. viridis* during gestation (Graves and Duvall 1993, Cobb 1994). Unlike *C. viridis*, casual observation while radiotracking female fox snakes suggested that gravid and nongravid females did not differ substantially in the spatial habitats they utilized. Therefore, I assumed that being sequestered in an enclosure of sufficient size and adequate temperature range, would not obscure potential differences in thermoregulatory priorities.

To facilitate the continuous monitoring of fox snake  $T_b$ 's, and to provide an "arena" within which individual snakes could be observed, a large circular enclosure was erected in a regenerating old field which had not been cultivated for five years (Figures 4, 5). The walls of the enclosure were made of 1-m high flexible sheet metal supported by wooden stakes driven into the ground at 90° and 45°. Soil was piled along the wall exterior to provide additional support, as well as to prevent fossorial escape routes. The final diameter was 36 m (1017 m<sup>2</sup>). Vegetation structure and plant species within the enclosure were similar to those found in habitats utilized by free-ranging fox snakes on Pelee Island. To reproduce the thermal environment available to free-ranging snakes, a

variety of microhabitats were placed within the enclosure to reflect the spatial habitat use of female fox snakes radiotracked during the 1998 active season. A 2.4 x 1.3 m (0.45 m depth) pit was excavated and flat slabs of limestone piled into the pit until the pile (henceforth referred to as the "rock pile") was approximately 0.25 m above the ground. Overhanging rock faces were provided on both the eastern and western exposures of the rock pile to provide dawn and dusk basking locations. A brush pile was also placed in the enclosure. Clumps of dead grass or "thatch" (commonly utilized by free-ranging individuals in all years) were spread throughout the enclosure, and there were already large patches of herbaceous shrubs (e.g., white sweet clover, *Melilotus alba*, approximately 2-m high) to provide adequate shading during the intense daytime heat. At completion, there were numerous potential basking areas exposed to full sunlight, and many were adjacent to retreat sites.

The enclosure was significantly larger than similar structures constructed to investigate snake thermal ecology (but see Lee and Mills 2000). Therefore, I was confident that a suitable thermal gradient existed within the enclosure to allow female fox snakes to select  $T_b$ 's within their preferred body temperature (PBT) range. To confirm that female fox snakes were not being constrained by the enclosure's thermal environment (i.e., an adequate thermal gradient was provided), snake models were placed in strategic locations throughout.

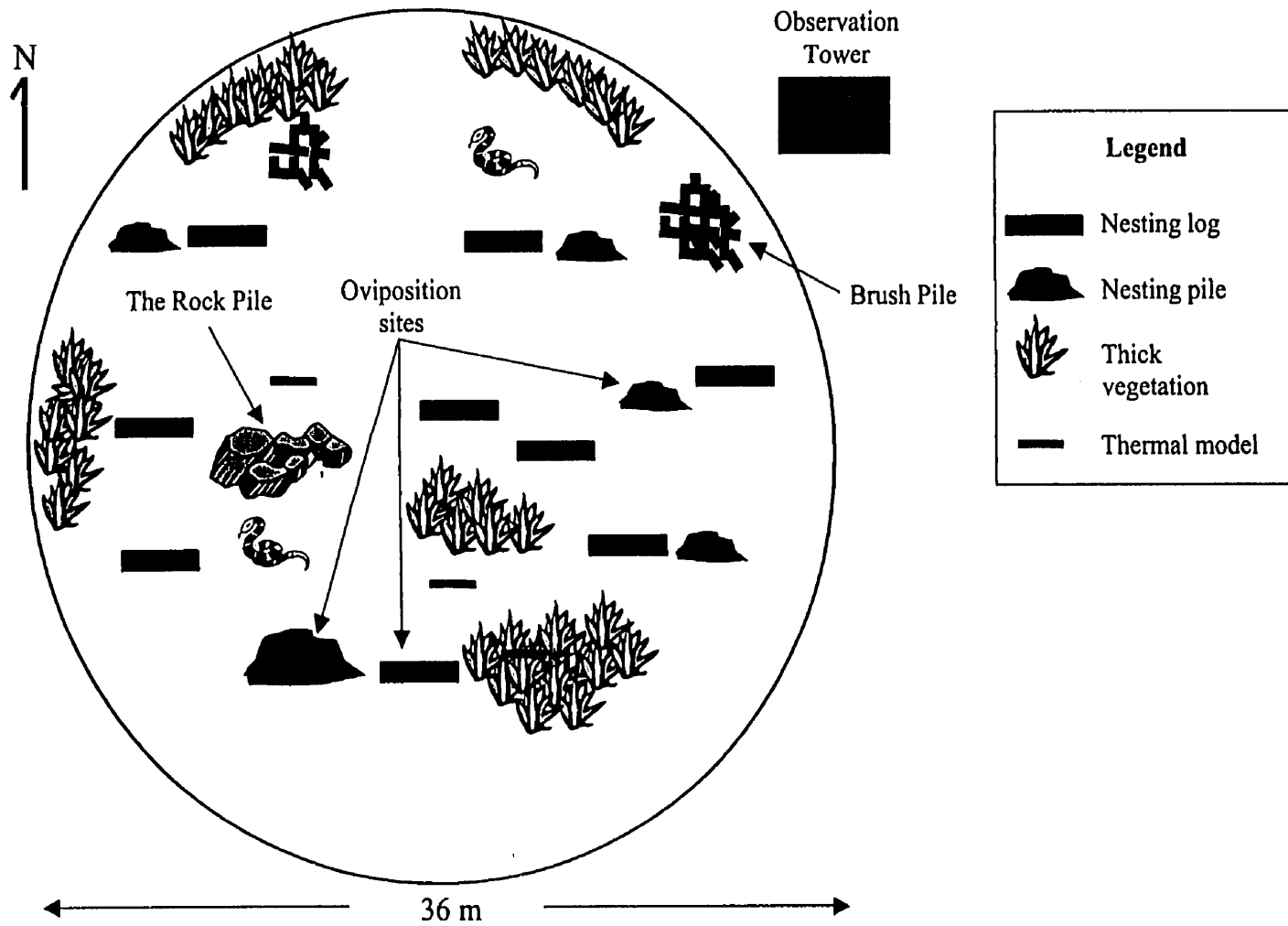


Figure 4. Schematic of the semi-natural enclosure constructed to monitor the thermoregulatory behaviour of female eastern fox snakes.





Figure 5. Photograph of the semi-natural enclosure constructed to monitor the thermoregulatory behaviour of female eastern fox snakes.

In addition to satisfying the spatial requirements of gravid and nongravid fox snakes, I also wanted to provide suitable nesting sites within the enclosure. Artificial nest sites had been constructed in 1997 to determine the feasibility of using them to augment natural nest sites away from roadways (Porchuk and Willson unpubl. data). Two types of nesting sites were constructed. The first were large fallen cottonwoods (*Populus deltoides*) with their interiors hollowed by chain saw and other implements. They were filled with decaying wood matter and had small entrances cut into their long axes. The second type of nest site constructed consisted of piles of dead grass, fine wood shavings, and other decaying vegetative matter. These artificially constructed microhabitats were modelled after interspecific communal nest sites (*E. gloydi* and *C. c. foxii*) discovered while radiotracking and searching for blue racers on Pelee island (Porchuk and Brooks 1995, Porchuk 1996). Nine nesting logs were placed within the enclosure and five nesting piles were placed adjacent to them, as well as adjacent to other shelter material (e.g., herbaceous ground cover, the rock pile, brush pile, etc.; Figure 4). Logs were positioned perpendicular to the north south axis. All nest sites placed in the enclosure were saturated with water to provide moisture throughout the oviposition (females likely use chemical/hydric cues during nest site selection) and post-oviposition subseasons.

On average, three adult white-footed mice (*Peromyscus leucopus*) were live trapped and released into the enclosure each morning to supplement natural food sources available (e.g., mice that were already within the enclosure, and small passerines that regularly perched within). Twelve eggs from free-ranging chickens were also placed in the enclosure and 50 % of the eggs were consumed within 48 h. To provide an unobstructed view of several key basking locations, particularly the rock pile, a 3-m high

observation tower was erected just outside the enclosure wall.

### **Monitoring System**

Because models accurately predicted (see results) the steady-state or equilibrium  $T_b$ 's of snakes in a particular microclimate (e.g., fully exposed, under a rock), the models were placed in strategic locations within the enclosure. Operative temperatures from the five models, as well as ambient air temperature ( $T_a$ ) in a shaded location within the enclosure were recorded continuously at 15-min intervals by data loggers. To estimate the maximum operative temperature ( $T_{e,max}$ ) within the enclosure, two models were placed in areas fully exposed to sunlight. To determine the lowest operative temperature ( $T_{e,min}$ ) within the enclosure, one model was placed in complete shade within a large patch of white sweet clover. A "free" radiotransmitter was also placed near the bottom of the rock pile while it was being constructed. To investigate the thermal properties of retreat sites commonly used by fox snakes, one model was placed under thatch, and another model was placed under an overhanging limestone slab within the rock pile.

Although an automated data acquisition system (e.g., Cobb 1994, Dorcas and Peterson 1998, Brown and Weatherhead 2000) was not available to record snake  $T_b$ 's, a relatively efficient method was employed to quickly and accurately log pulse intervals from multiple snakes simultaneously. To increase the reception range for those snakes not in the enclosure (see below), a 3-m antenna tower was attached to the observation platform (6 m in total), atop which was mounted a three-element Yagi antenna. The antenna could then be manually rotated. An in-line amplifier (10 db, Radio Shack) was also inserted to pick up weak signals (Dorcas 1995). Coaxial cable (86 m) then led from

the antenna tower back to the research facility and was connected to a single channel receiver (Wildlife Materials Inc. - TRX-2000S). The receiver's audio output was then connected via a 3-conductor stereo cable to the audio line-in port of a notebook computer. Frequencies were manually tuned, and the audible pulses stored as separate wav files on the computer. Pulse intervals were determined later using digital audio editing software (Cool Edit 96; Syntrillium Software Corp.). With this monitoring system, 3 - 4 pulses from each frequency (each snake) could be quickly recorded; hence time between first and last snake  $T_b$  sampled at each interval (hourly) was kept to 10 min. Because the recorded files were digital, problems associated with calibrating analogue tape recorders were avoided (see Beaupre and Beaupre 1994).

### **Thermal Profiles**

Six gravid and eight nongravid radiotagged female fox snakes were released into the enclosure between 18 and 27 June 1999. In addition to the females within the enclosure, five free-ranging gravid females within a 1-km radius of our antenna tower were also implanted with transmitters. By simultaneously monitoring the  $T_b$ 's of free-ranging and enclosure-bound snakes, I hoped to determine if females in the enclosure were exhibiting normal thermoregulatory behaviour. Two free-ranging gravid fox snakes were also being tracked as part of an investigation of spatial habitat use, however, they were well outside the range of our antenna tower and therefore only provided data pertinent to relative oviposition dates. Individual snakes were given 7 days to acclimate to their new surroundings before  $T_b$  measurements were taken. To compare  $T_b$ 's of gravid and nongravid female fox snakes within the enclosure,  $T_b$ 's were recorded at

hourly intervals from 29 June to 7 July. Individual  $T_b$  measurements were discontinued when visual appearance indicated the female had oviposited, and all measurements ceased when a majority of the gravid females had oviposited. Operative temperatures within the enclosure were recorded simultaneously at 15-min intervals.

## **Data analysis**

### *Spot $T_b$ Measurements*

To compare the  $T_b$ 's selected by gravid and nongravid females in 1998, I used  $T_b$ 's recorded from 1 June – 2 July which roughly corresponds to the period of egg retention in *E. gloydi* on Pelee Island. I divided the  $T_b$ 's into those recorded early in the egg retention period (1 – 16 June) and those recorded in the latter half (17 June – 2 July). Mean  $T_b$ 's were then calculated for each snake in each "sub-period". Because environmental temperature can significantly influence the  $T_b$ 's selected by individual snakes at different times, and in different microhabitats; I used mean  $T_a$  calculated for each snake, as a covariate in a two-way ANCOVA with reproductive condition and egg retention sub-period as factors, and compared the mean  $T_b$ 's of gravid and nongravid snakes.

### *Thermal Profiles*

A series of  $T_b$ 's recorded from a single individual are not independent observations, and because gaps in the data set (due to weak transmitter signals) precluded a repeated measures analysis, I calculated the mean, standard error, min, max, and range for each snake for the entire profile. Because the environmental conditions

corresponding to  $T_b$  observations may have varied among individuals, I used mean  $T_{e,max}$  as a covariate in a one-way ANCOVA, with reproductive condition as the factor, to compare the mean descriptives. By removing variation attributable to differences in environmental temperatures I could better compare  $T_b$  selection among individuals during the profile. To test for differences between gravid and nongravid snakes only at times when I was sure individuals were not being constrained by environmental temperatures, I repeated this analysis for  $T_b$ 's recorded when  $T_{e,max}$  was  $\geq 30^\circ\text{C}$ . I used  $30^\circ\text{C}$  as a cut off temperature because I predicted that *E. gloydi*'s PBT would be lower than this value based on similar work conducted with black rat snakes (*Elaphe obsoleta obsoleta*) in eastern Ontario (Blouin-Demers *et al.* In Press). This cut off temperature also effectively allowed me to compare only daytime  $T_b$ 's.

All analyses were performed with SPSS 10.0. Prior to analysis, data were checked for significant deviations from normality, and homogeneity of variances. Means  $\pm$  one standard error (SE) are reported unless otherwise indicated, and an alpha value of 0.05 was used for all analyses.

## RESULTS

### Spot $T_b$ Measurements

In 1998, spot  $T_b$  measurements for 15 female fox snakes were recorded from May to October for a total of 484 body temperatures. After removing unreliable records (e.g., calibration error for one transmitter) there were 427 active season (May – October)  $T_b$ 's from 14 females (Table 2). The grand mean  $T_b$  for all females was  $26.5 \pm 4.92$  (SD),  $N = 427$ . Ten of the 15 radiotagged females were gravid in 1998. Several snakes

radiotracked in 1998 were also monitored in 1999, and of six snakes that were gravid in 1998, and were still being tracked in 1999, only one was reproductive in both years (Table 1).

During June 1998, 118 spot  $T_b$ 's were recorded from 13 female fox snakes (Table 2). Gravid and nongravid females did not differ in mean  $T_b$  during June (mean gravid  $T_b = 27.7 \pm 0.73$ ,  $N = 8$ ; mean nongravid  $T_b = 27.2 \pm 1.29$ ,  $N = 4$ ;  $F_{1,19} = 0.483$ ,  $P = 0.496$ ). Mean  $T_b$ 's recorded during the first half of June also did not differ significantly from those recorded during the second half ( $F_{1,19} = 0.127$ ,  $P = 0.725$ ), and there was no interaction between reproductive condition and gestation sub-period ( $F_{1,19} = 0.005$ ,  $P = 0.945$ ).

The mean  $T_b$ 's for the two gravid females monitored for 24 h, 1 July 1998, were  $28.1 \pm 0.46$  (SD) and  $24.9 \pm 5.99$  (SD), whereas the mean  $T_b$  of the lone nongravid female was  $27.0 \pm 4.06$  (SD). Each female exhibited a slightly different pattern of  $T_b$  variation over the 24-h period (Figure 6), and selected  $T_b$ 's were similar to those of enclosure-bound females.

## **Enclosure Study**

### *Thermal Models*

Thermal models accurately tracked the internal temperature of the dead fox snake ( $T_d$ ), however, they did lag approximately 3 Celsius degrees behind during rapid heating and cooling phases (Figure 7). Maximum difference between  $T_d$  and any of the model  $T_c$ 's for any measurement interval was  $3.8^\circ\text{C}$ , however, this temperature difference quickly decreased when rates of temperature change decreased and model temperatures

Table 2. Summary statistics of spot  $T_b$  measurements taken from female eastern fox snakes implanted with temperature-sensitive radiotransmitters in 1998. Condition: G = gravid and NG = nongravid. Mean  $T_b$ 's  $\pm$  1 SE ( $^{\circ}$ C) are presented.

ID	Condition 1998	Entire Season			1 Jun - 2 Jul		
		$T_b$	Range	N	$T_b^a$	Range	N
392	G	28.7 $\pm$ 1.21	18.3 - 34.2	15	29.8 $\pm$ 0.87	26.1 - 32.5	7
473	G	27.8 $\pm$ 0.57	19.0 - 34.0	34	28.6 $\pm$ 0.87	26.0 - 34.0	9
761	G	27.6 $\pm$ 1.13	12.7 - 33.8	21	26.7 $\pm$ 1.95	12.7 - 32.4	10
793	G	27.5 $\pm$ 0.83	12.1 - 34.2	35	27.8 $\pm$ 1.77	18.5 - 34.2	9
731	G	27.2 $\pm$ 0.77	15.6 - 33.5	39	29.4 $\pm$ 1.21	18.6 - 33.2	12
551 <sup>b</sup>	G	26.8 $\pm$ 0.91	13.0 - 34.1	28	28.8 $\pm$ 1.37	25.4 - 32.9	5
558	G	26.3 $\pm$ 0.78	14.5 - 35.2	41	27.3 $\pm$ 1.50	14.5 - 33.1	12
438	G	26.1 $\pm$ 0.90	12.3 - 33.2	36	27.9 $\pm$ 1.43	20.3 - 33.0	10
810	G	25.6 $\pm$ 1.12	14.9 - 32.7	16	NA	-	-
671G	G	24.9 $\pm$ 0.88	14.4 - 33.5	35	23.9 $\pm$ 2.47	14.4 - 31.6	7
832G	NG	26.3 $\pm$ 0.74	13.6 - 33.6	34	26.6 $\pm$ 1.58	20.7 - 33.0	8
445	NG	26.1 $\pm$ 1.04	13.0 - 34.0	32	27.8 $\pm$ 1.25	18.0 - 33.7	12
353	NG	26.0 $\pm$ 1.23	13.7 - 33.1	22	30.9 $\pm$ 0.91	27.6 - 32.7	5
472G	NG	25.7 $\pm$ 0.74	12.4 - 33.6	39	25.5 $\pm$ 1.50	17.1 - 32.5	12

<sup>a</sup>mean  $T_b$ 's of gravid (N = 8) and nongravid (N = 4) females were not significantly different (two-factor ANCOVA;  $F_{1,19} = 0.483$ ,  $P = 0.496$ )

<sup>b</sup>not used in analysis because of later implantation date (see Table 1)



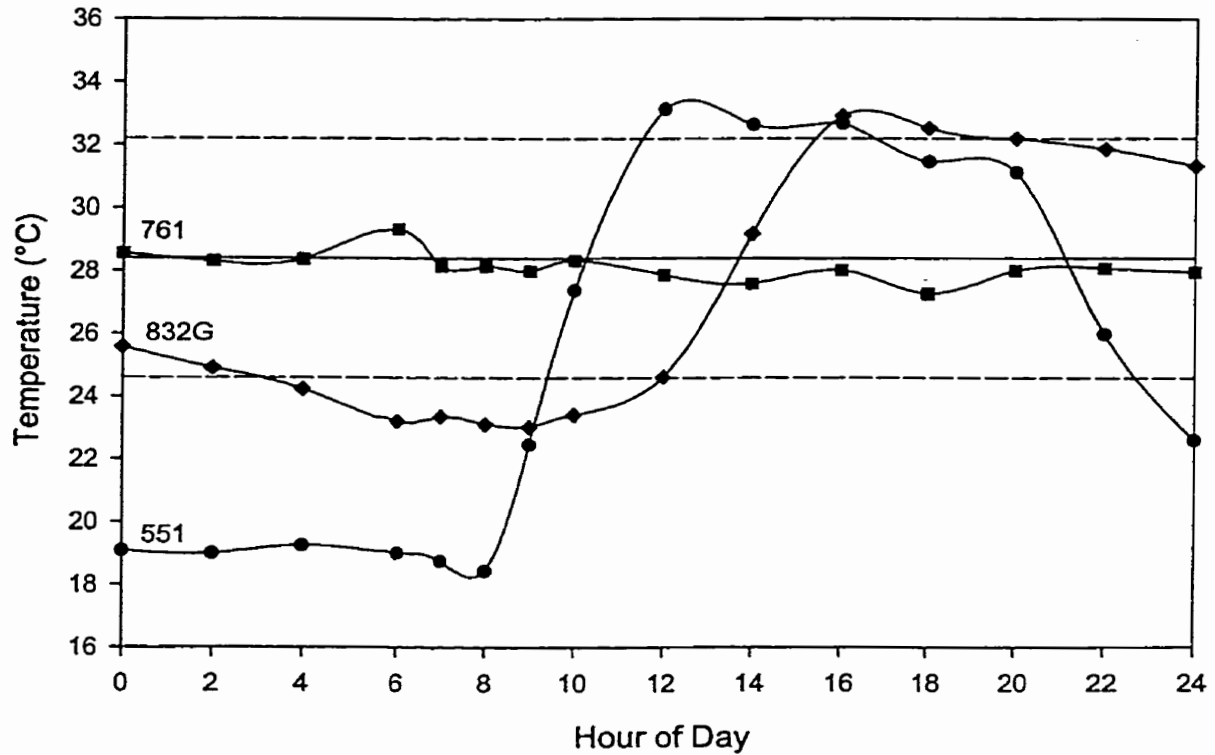


Figure 6. Twenty-four hour thermal profile of three free-ranging fox snakes monitored 1 July 1998. Pulse intervals were recorded every 2 h except between 06:00 and 10:00 when they were taken hourly for finer resolution. 761 and 551 were gravid whereas 832G was nongravid (G denotes reproductive status in 1999, see Table 1). Solid horizontal line is the grand mean  $T_b$  of all females in the enclosure and dashed lines indicate  $\pm 1$  SD ( $N = 1,729$   $T_b$  measurements).

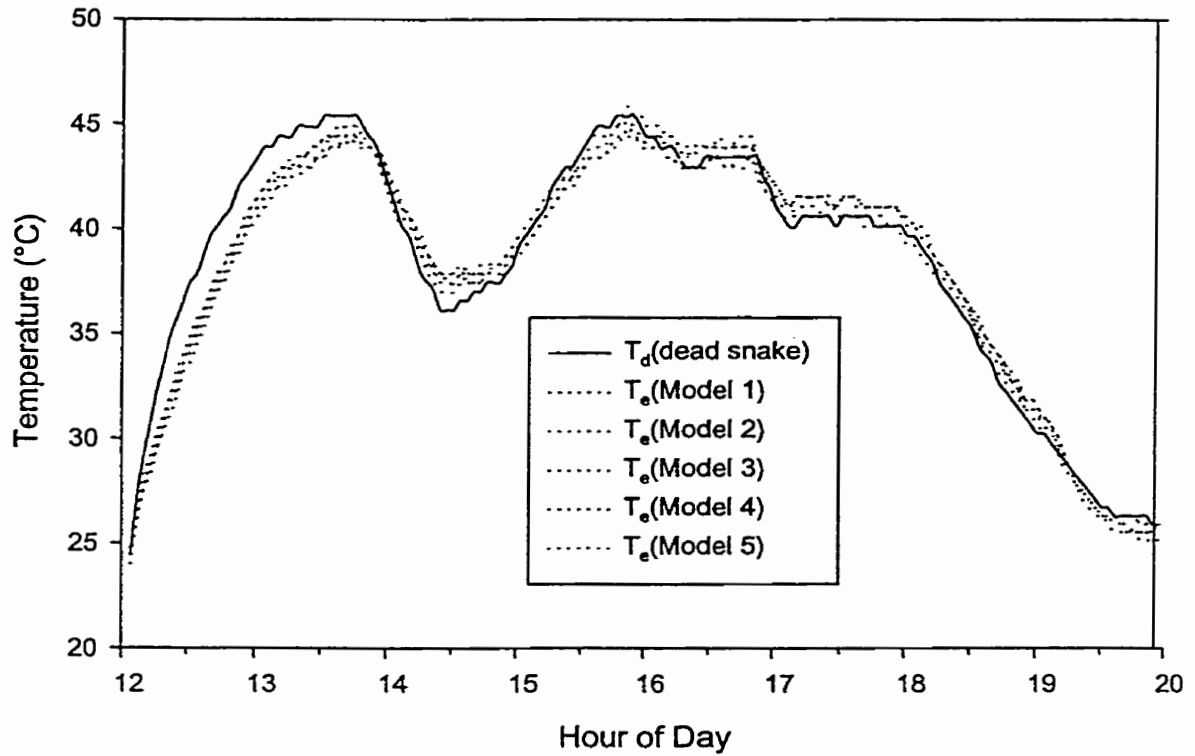


Figure 7. Comparison of model temperatures ( $T_e$ ; operative temperature) and the internal temperature ( $T_d$ ) of a dead fox snake. Models and snake were placed side by side in an exposed location for 8 h. A single hatch pattern was used for the models to allow for comparison to  $T_d$ .

approached equilibrium. The maximum mean difference between  $T_d$  and any model was 1.0°C. I therefore considered the models to be reasonable estimators of fox snake  $T_b$  when placed in similar microhabitats.

### *Operative Temperatures*

Maximum  $T_e$ 's measured within the enclosure showed that snakes had ample opportunity to thermoregulate at  $T_b$ 's experienced by free-ranging animals ( $T_{e,max}$ : range = 14.5°C - 55.4°C, mean =  $31.1 \pm 0.96^\circ\text{C}$ , N = 146). Maximum  $T_e$  reached at least 32°C on each day of the sampling period and was greater than 36.1°C (the maximum  $T_b$  selected by *E. gloydi* in this study; voluntary thermal maximum) on 6 of the 7 days (Figure 8). Minimum  $T_e$ 's indicated that sufficiently cool retreat sites were available at all times within the enclosure ( $T_{e,min}$  range = 15.6°C – 26.4°C; Figure 8). The models placed in the rock pile ( $T_{e,rock}$ ) and under the thatch ( $T_{e,thatch}$ ) yielded temperature profiles intermediate to  $T_{e,max}$  and  $T_{e,min}$  (Figure 9). The thatch model actually maintained temperatures close to "optimal" (see discussion) for much of the profile (i.e., 3 – 6 July) and never heated to temperatures above *E. gloydi*'s voluntary thermal maximum; indicating that snakes could remain in this microhabitat most of the time.

### *1999 Thermal Profiles*

Snake  $T_b$ 's and corresponding  $T_e$ 's were recorded from 14 snakes and five models respectively, over a 8-day period (29 Jun - 7 Jul; N = 146 h). One additional radiotagged snake that had escaped from its restraints (broke through a seam in a snake bag) and taken up residence in the walls of our research facility was also monitored, but not used

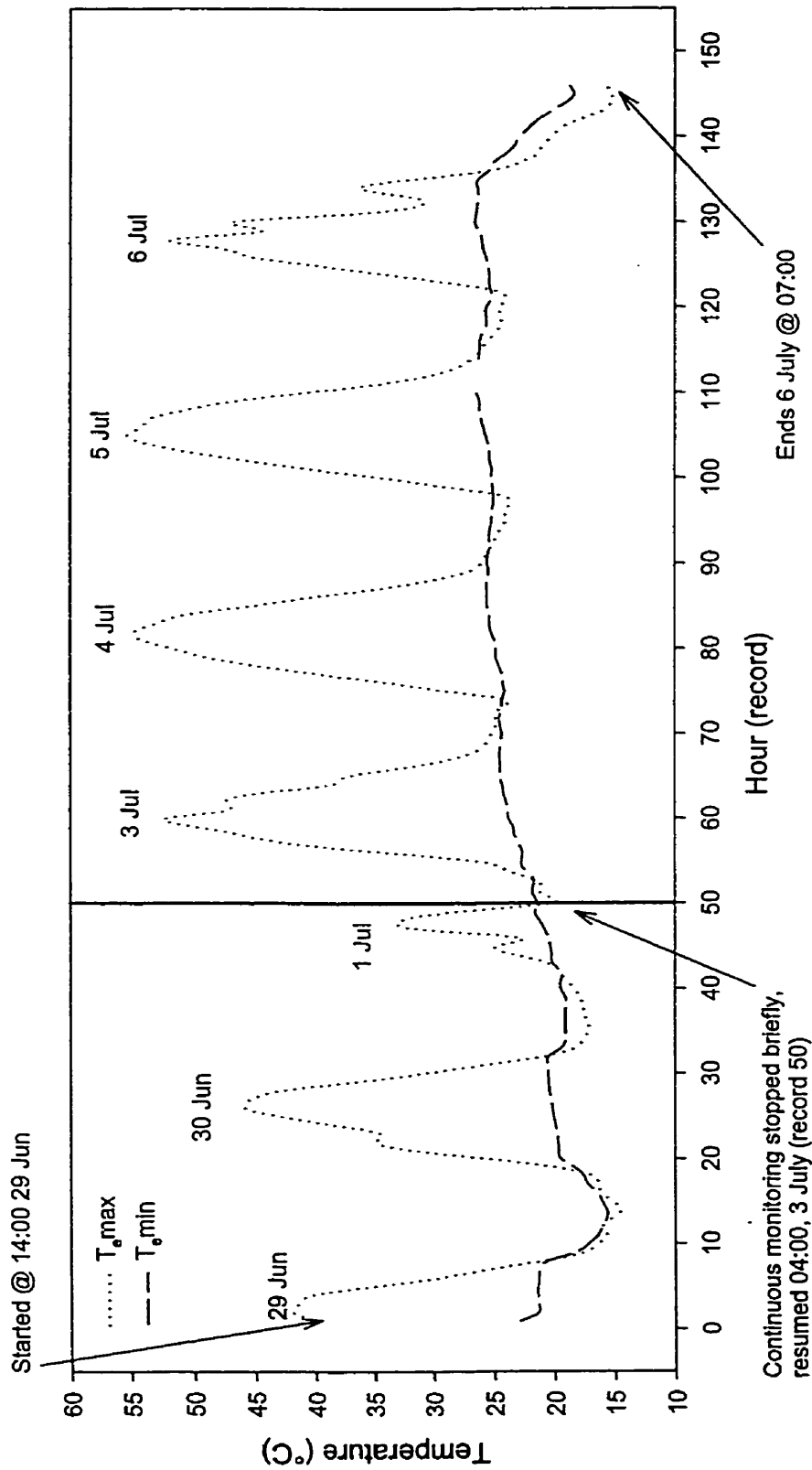


Figure 8. Thermal environment available to snakes in the enclosure over the monitoring period, 29 Jun - 6 Jul 1999 as indicated by minimum ( $T_{e,min}$ ) and maximum ( $T_{e,max}$ ) operative temperatures.  $T_{e,max}$  models were placed in direct sunlight, whereas  $T_{e,min}$  models were placed in shaded locations.  $T_e$ 's were recorded at 1-h intervals and  $T_{e,max}$  peaks correspond to daytime environmental temperatures.

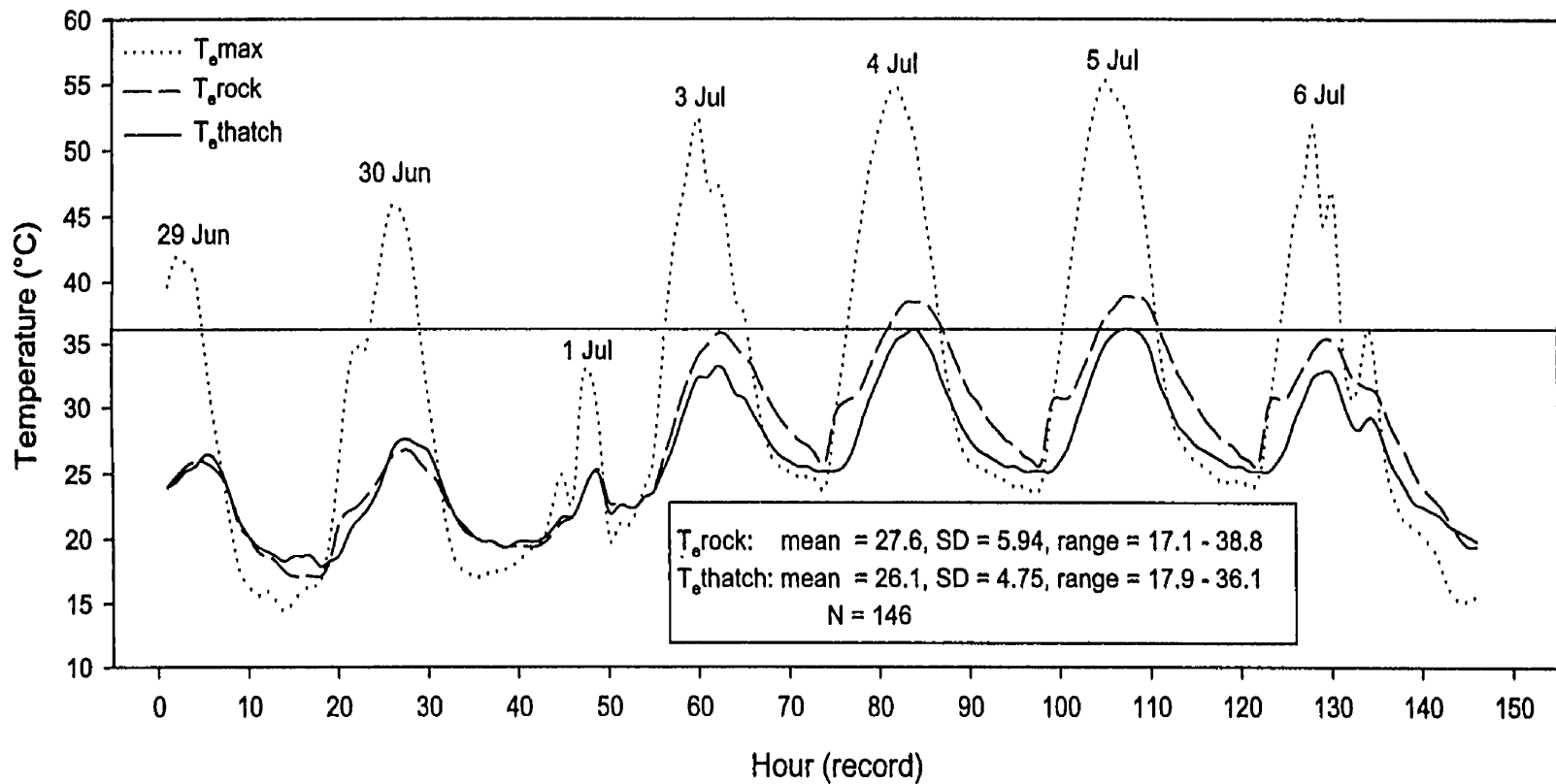


Figure 9. Temperature profiles of models placed in microhabitats regularly used as shelter by eastern fox snakes. The thermal model  $T_{e,rock}$  was placed in the rock pile, whereas  $T_{e,thatch}$  was covered with dead grass (thatch).  $T_e$ 's were recorded at 1-h intervals. The solid horizontal line indicates the highest  $T_b$  selected by female fox snakes in this study (*Elaphe gloydi*'s voluntary thermal maximum).

in analyses. Unfortunately, I was unable to consistently pick up signals from any of the five free-ranging snakes, even with the antenna tower enhancements, and despite the fact that several of these individuals were within 1 km of our tower. Therefore, I was not able to compare enclosure-bound and free-ranging snakes. In total, 2,098  $T_b$  measurements were collected during the thermal profile, and from these a subset of 1,729  $T_b$  measurements were used in analyses. In addition, 3,867  $T_e$  measurements were recorded concurrently.

Visual inspection of  $T_b$  plots suggested that gravid females selected  $T_b$ 's similar to those of nongravid females (Figure 10). One-way ANCOVA indicated no significant differences between gravid ( $N = 6$ ) and nongravid females ( $N = 8$ ) for any of the descriptive statistics calculated (Table 3). One-way ANCOVA also indicated no significant differences between any of the descriptives calculated for gravid and nongravid females when the analysis was restricted to  $T_b$ 's recorded when  $T_{e,max}$  was  $\geq 30^\circ\text{C}$  (Table 3, Figure 10). Therefore, females of different reproductive condition did not select significantly different  $T_b$ 's, nor did they differ in the precision of those  $T_b$ 's (variance); and this result was true over the entire period of monitoring, and only during the day when  $T_e$ 's were high (i.e.,  $T_{e,max} \geq 30^\circ\text{C}$ ).

Temperature plots revealed interesting patterns of  $T_b$  variation and individuals differed significantly in their selection of  $T_b$ 's. For example, the  $T_b$  of gravid female 231G regularly tracked  $T_{e,max}$  throughout the profile, whereas the  $T_b$  of nongravid female 164 remained relatively constant and showed little variation (Figure 11). This result is opposite to what I predicted based on studies of viviparous snakes; however, this pattern (i.e., nongravid females maintaining higher and less variable  $T_b$ 's) did not

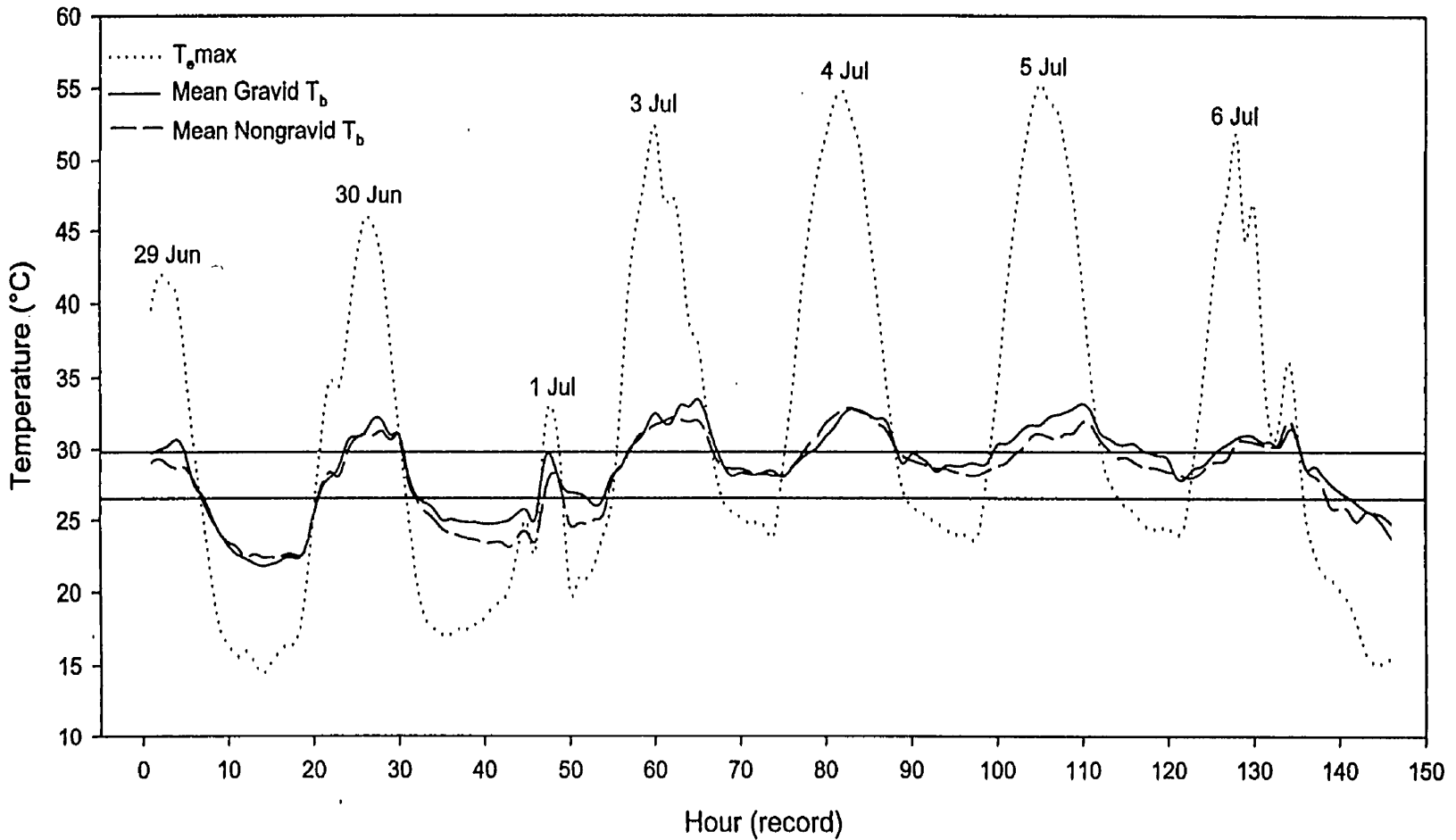


Figure 10. Mean gravid and nongravid  $T_b$ 's of fox snakes within the enclosure over the entire period of continuous monitoring, 29 June – 6 July.  $T_b$ 's were recorded at 1-h intervals and hourly means calculated for each reproductive group.  $T_e$ 's were also recorded at 1-h intervals. The  $T_b$ 's above the solid horizontal line were used in the analysis restricted to times when  $T_e \text{ max}$  was  $\geq 30^\circ\text{C}$ .

Table 3. Summary statistics, and results from one-way ANCOVA comparing  $T_b$ 's of gravid and nongravid fox snakes within the enclosure, 29 June - 7 July 1999. Results from the entire period of continuous monitoring, and only when  $T_e$ 's indicated that snakes were not being constrained by the environment ( $T_{e,max} \geq 30^\circ\text{C}$ ) are shown. Means  $\pm 1$  SE ( $^\circ\text{C}$ ) are presented.

Mean Value	All Temperatures (N = 146 hrs)			$T_{e,max} \geq 30^\circ\text{C}$ (N = 66 hrs)		
	Descriptives	F ratio	P	Descriptives	F ratio	P
Gravid $T_b$	28.7 $\pm$ 0.26	$F_{1,11} = 0.975, P = 0.345$		30.9 $\pm$ 0.48	$F_{1,11} = 0.531, P = 0.481$	
Nongravid $T_b$	28.0 $\pm$ 0.55			30.4 $\pm$ 0.30		
Gravid SE	0.31 $\pm$ 0.05	$F_{1,11} = 0.022, P = 0.885$		0.25 $\pm$ 0.03	$F_{1,11} = 0.046, P = 0.834$	
Nongravid SE	0.32 $\pm$ 0.05			0.27 $\pm$ 0.05		
Gravid Min	20.8 $\pm$ 1.53	$F_{1,11} = 0.074, P = 0.79$		26.8 $\pm$ 0.46	$F_{1,11} = 1.893, P = 0.196$	
Nongravid Min	20.2 $\pm$ 1.31			25.5 $\pm$ 0.65		
Gravid Max	34.3 $\pm$ 0.31	$F_{1,11} = 0.001, P = 0.977$		34.3 $\pm$ 0.31	$F_{1,11} = 0.005, P = 0.947$	
Nongravid Max	34.3 $\pm$ 0.46			34.3 $\pm$ 0.46		
Gravid Range	13.5 $\pm$ 1.64	$F_{1,11} = 0.051, P = 0.826$		7.5 $\pm$ 0.23	$F_{1,11} = 1.033, P = 0.331$	
Nongravid Range	14.1 $\pm$ 1.72			8.8 $\pm$ 0.93		



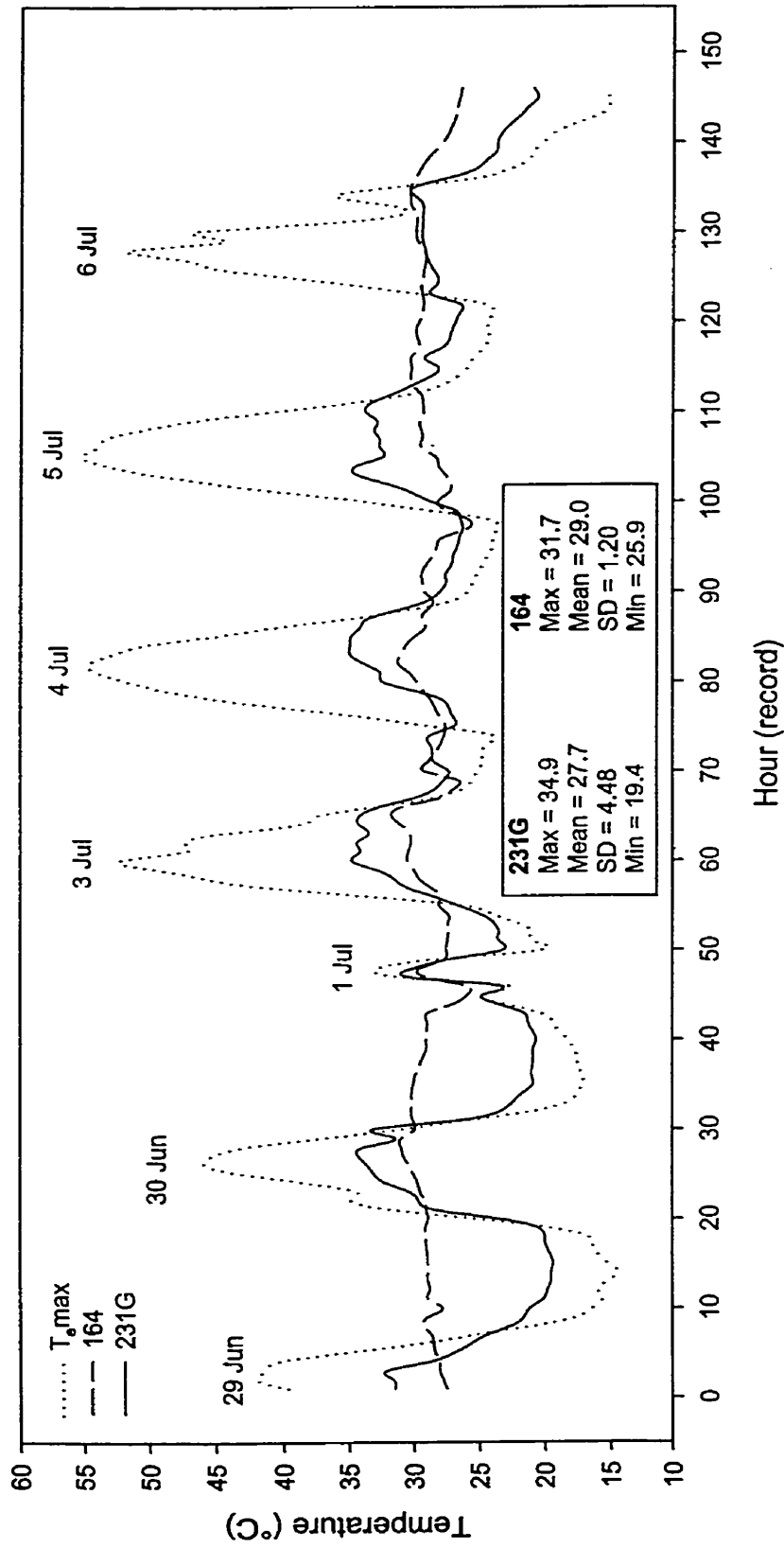


Figure 11. Body temperature variation of one gravid fox snake (231G) and one nongravid fox snake (164) within the enclosure over the entire period of continuous monitoring, 29 June – 6 July.  $T_b$ 's and  $T_c$ 's were recorded at 1-h intervals.

hold, and substantial interindividual variation within reproductive groups likely obscured any differences in thermoregulation between groups (Figure 12).

### *Oviposition*

All gravid snakes oviposited within the enclosure and their post-oviposition state was determined from visual appearance and a sudden decrease in mass. Oviposition dates within the enclosure ranged from 3 to 12 July. Three separate nest sites were located within the enclosure (Figure 4) and these were monitored as part of a study investigating nest site incubation temperatures. One nesting site in a log contained 16 eggs and was likely the clutch of one female, while the other two nests were in nesting piles (wood chips and vegetation) and contained 19 and 84 eggs respectively. Egg incubation was successful in two of the three nest sites and hatchlings began to emerge 23 August (Table 4). The eggs laid in the log were parasitized by the carrion beetle (*Nicrophorus pustulatus*) approximately midway through development. The larvae of this beetle have been observed in other fox snake nests in previous years, and have also been observed parasitizing the eggs of *E. o. obsoleta* in eastern Ontario (Blouin-Demers and Weatherhead In Press). Anecdotal evidence suggests that the eggs were still viable until *N. pustulatus* arrived (i.e., it was not the odour of decaying eggs that attracted this beetle; see Blouin-Demers and Weatherhead In Press). Temperature data from each nest site also revealed thermal conditions that were well within the range necessary for successful incubation (Table 4). The enclosure thus provided adequate nest sites, both in terms of cues used by females during the process of nest site selection, and in function (i.e., successful incubation).

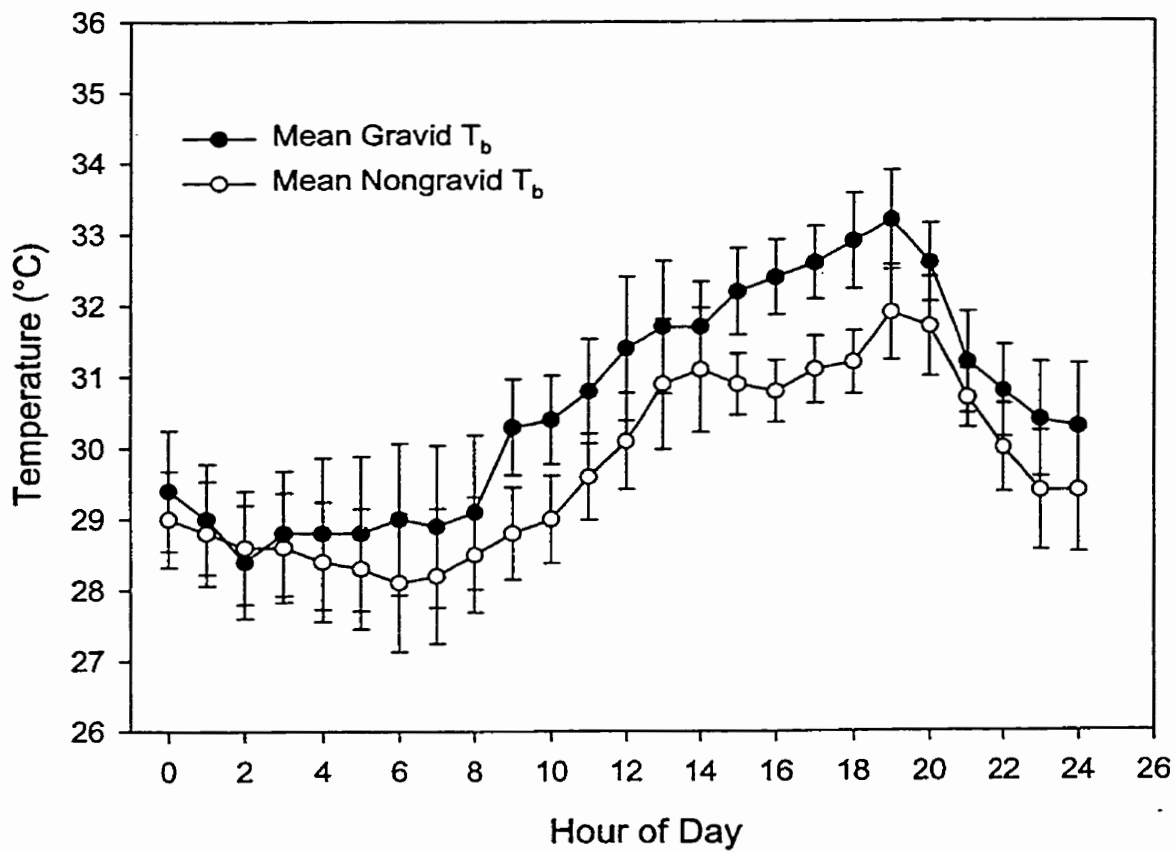


Figure 12. Mean gravid (N = 5) and nongravid (N = 7) fox snake  $T_b$ 's at hourly intervals, 5 July 2000. Values are hourly means and error bars represent  $\pm 1$  SE.

Table 4. Microhabitats used as oviposition sites by gravid fox snakes within the enclosure. In late August, funnel traps and perimeter fence were placed around nest piles to capture emerging hatchlings. Incubation temperatures were obtained from thermistors inserted into the nesting piles without disturbing the piles, or eggs. Nest temperatures (°C) were recorded at 2-h intervals (N = 1,923), 25 July – 3 September 1999.

Nesting Material	# of eggs	# of hatchlings trapped <sup>a</sup>	# of females ovipositing	mean nest temperature	SD	min nest temperature	max nest temperature
log	16	0	1				
vegetation pile	19	5	1	23.6	± 2.71	17.5	31.5
large vegetation pile	84	43	4	24.7	± 3.12	17.1	32.8

<sup>a</sup>Funnel traps had to be removed 3 September and therefore the disparity between # of eggs and # of hatchlings trapped is partly due to hatchlings continuing to emerge throughout September (pers. obs.)

## DISCUSSION

### Spot $T_b$ Measurements

Based on my observations while radiotracking female fox snakes on Pelee Island, there did not appear to be any differences in overt thermoregulatory behaviour between females of different reproductive condition, and it is therefore not surprising that spot  $T_b$  measurements did not reveal a difference in mean  $T_b$ 's. However, given the possibility of a subtle difference in thermoregulatory behaviour between gravid and nongravid individuals, I suspect that such a difference would go undetected with spot  $T_b$  measurements. Additionally, the intermittent nature of spot  $T_b$  measurements makes them poor estimators of the amount of time that an individual spends at higher, or less variable  $T_b$ 's, and because oviposition dates (via the rate of embryogenesis) are directly influenced by the amount of time an embryo spends at a given temperature, continuous  $T_b$  measurements from both gravid and nongravid individuals will yield the most interesting insights into differences in thermoregulatory behaviour.

### Thermoregulation Within a Semi-Natural Enclosure

A necessary assumption of my study was that neither the novelty of a new environment presented to the snakes, nor the lack of thermally suitable microenvironments within the enclosure, would prevent snakes from selecting  $T_b$ 's within their PBT range. If the enclosure did significantly influence the thermoregulatory behaviour of gravid and nongravid females in different ways (i.e., causing gravid females to thermoregulate less carefully while not affecting nongravid females) then my results

must be viewed with caution. To address this issue, I first discuss data that support the validity of the enclosure results.

Although I was not able to monitor the  $T_b$ 's of the five free-ranging females in 1999, the range of  $T_b$ 's selected by the three free-ranging females in 1998 was similar to the range of  $T_b$ 's selected by females in the enclosure (Figure 10). Additionally, the two gravid females exhibited substantial differences from one another in mean  $T_b$  and thermoregulatory precision, and these differences were like those observed among gravid females within the enclosure. The nongravid female exhibited  $T_b$ 's intermediate between the two. These data lend support to the validity of the enclosure results, where differences between gravid and nongravid females were not found, and interindividual variation within reproductive groups was high.

Both operative temperatures (i.e., the range of temperatures from which snakes could select) and relative oviposition dates, indicated that gravid females within the enclosure were able to maintain  $T_b$ 's suitable for embryogenesis. Operative temperatures showed that enclosure-bound females could select  $T_b$ 's within the range recorded for free-ranging snakes in 1998 (Figure 5; Table 2). Unlike other enclosure studies that reported female snakes failing to give birth at normal times (Charland and Gregory 1990) or to oviposit in appropriate nesting sites (Shewchuk pers. comm.), all of the gravid females in my study oviposited in the artificial nest sites that had been created, and laying dates were within the range demonstrated by free-ranging individuals. In addition, egg incubation was successfully completed in five of six clutches in the enclosure.

Individuals of many snake species, including female fox snakes on Pelee Island, show considerable fidelity to microhabitats year after year. Site-specific fidelities

commonly mentioned in the literature include affinity for particular hibernacula (Macartney *et al.* 1989, Prior and Weatherhead 1996, Blouin-Demers *et al.* 2000), rookery or brooding sites (Graves and Duvall 1993, Parent 1997, Willson 1996), and oviposition sites (Plummer 1990, Burger and Zappalorti 1992). In species with biennial, or greater, reproductive cycles, these sites can even alternate between years (e.g., specific rookery rocks are used by the same *S. c. catenatus* in 2-3 yr intervals, pers. obs.).

Although not as conspicuous as the rookery rocks of viviparous species, there may be specific microhabitats (e.g., large decaying logs, brush piles, front porches) utilized by oviparous snakes during reproductive years, and individuals may show strong fidelity to these sites. If these sites have a high "thermal value" and have been successfully used in the past (i.e., they provided optimal rates of embryogenesis and protection from predation), then the removal of these sites, either through habitat change or translocation to an enclosure, may significantly affect observed thermoregulatory behaviour. For example, female 793 utilized a large upright tractor tire as a retreat site for several weeks while she was gravid. During this period, I never saw her exposed even though she was radiotracked at several different times of the day. It appeared that she was exploiting the thermal gradient within the tire by moving to the top each morning, and then shuttling around inside the tire like the hands of a clock. Presumably she was able to maintain  $T_b$ 's within her PBT range most of the time because she spent a significant amount of time at this site. Continuous  $T_b$  monitoring during this period would have been invaluable, unfortunately only spot measurements were recorded. Although thermally optimal retreat sites were available within the enclosure, and females were allowed a week to acclimate to the new environment, these familiar "hot spots" (e.g., a preferred tire or log) would

have been absent. Therefore, it is possible that gravid females accepted lower  $T_b$ 's because searching for new sites (i.e., leaving cover and moving) is risky (Bonnet *et al.* 1999).

### **Thermoregulatory Behaviour of Female *Elaphe gloydi***

In general, my enclosure data failed to support the hypothesis that gravid and nongravid oviparous females exhibit different thermoregulatory behaviour. Gravid fox snakes did not maintain higher  $T_b$ 's, nor did they thermoregulate more precisely by maintaining their  $T_b$  within a narrower range. I also did not observe differences in overt thermoregulatory behaviour between females of different reproductive condition. These results contrast with those of other studies that have documented significant thermoregulatory differences attributable to reproductive state in both viviparous (Charland and Gregory 1990, Graves and Duvall 1993, Tu and Hutchison 1994, Cobb 1994, Charland 1995, Dorcas and Peterson 1998, Brown and Weatherhead 2000) and oviparous (Plummer 1993, Blazquez 1995) snakes. However, some studies examining oviparous snakes have failed to find an effect of reproductive condition on thermoregulatory behaviour (e.g., Porchuk 1996) or have found evidence of gravid females thermoregulating less precisely and at lower  $T_b$ 's than nongravid females (Shewchuk 1996). Porchuk's (1996) study, examining the thermal ecology of *C. c. foxii*, was also conducted on Pelee Island. Therefore, it is possible that Pelee Island acts as a thermally favourable environment during the period of egg retention in these snakes, making it unnecessary for either fox snakes or blue racers to thermoregulate more carefully in years when they are gravid versus years when they are nongravid. Oviparous



snakes retain embryos *in utero* for only a fraction of the time that viviparous species do. The shorter period of egg retention may reduce the importance of careful thermoregulation to a point where risky thermoregulatory behaviour (i.e., increased basking, increased shuttling to good basking areas) no longer confers a selective advantage.

Shine and Madsen (1996) also found little evidence of overt thermoregulatory behaviour in water pythons (*Liasis fuscus*) throughout much of the active season and attributed these observations to northern Australia's benign thermal environment, as well as to the accessibility of thermally suitable microhabitats (e.g., grass clumps, soil cracks, water). While I do not suggest that Pelee Island's climate (although hot by my standards) offers female fox snakes a thermal environment similar to northern Australia, I do suspect that thermal conditions during the period of egg retention (especially late June to early July) are quite favourable in terms of allowing fox snakes to maintain  $T_b$ 's within their PBT range. In addition, most of the fox snakes I radiotracked had access to thermally favourable microhabitats. In particular, the layer of dead grass (thatch) was a favourite retreat site during the summer. This layer of dead grass offers suitable thermal conditions as indicated by the model  $T_{c,thatch}$  (Figure 9), and also provides an easily accessed food resource. For example, I observed several radio-tagged female fox snakes consuming rodents under the grass, along "rodent runways" and within rodent nests. It is also extremely difficult to find and/or "extract" a fox snake from beneath the thatch, making predation by avian or mammalian predators unlikely. Both gravid and nongravid females frequently utilized this microhabitat and I suspect that gravid females may be "unwilling"

to leave the protection of the thatch to engage in risky thermoregulatory activities such as basking.

### **Evaluating Thermoregulation in Snakes**

Three components deemed necessary for effectively evaluating thermoregulation in snakes, mainly continuous  $T_b$  measurements from multiple individuals, a knowledge of the thermal environment available to snakes, and the physiological condition (i.e., gravid vs nongravid) of those individuals being monitored (Peterson *et al.* 1993) were satisfied in my study. These components enabled me to compare  $T_b$ 's selected by snakes within the enclosure with "possible"  $T_b$ 's (i.e., the range of  $T_e$ 's), and therefore allowed me to determine if individuals were fully exploiting the thermal environment available to them.

For example, I observed several fox snakes remaining in their respective retreat sites longer than would be predicted by examining  $T_e$  plots which indicated that surface temperatures would have allowed the snakes to maintain  $T_b$ 's closer to their PBT (assuming that *E. gloydi*'s PBT is  $>20^\circ\text{C}$ ). Brown and Weatherhead (2000) also observed northern water snakes accepting lower  $T_b$ 's, rather than emerge from the water as soon as  $T_e$ 's indicated it would be optimal to do so. It has been suggested that snakes, as ectotherms, may be at risk of predation by endothermic predators immediately upon emerging from cool retreat sites (e.g., emergence in the morning or from hibernacula in the spring). By delaying emergence they can avoid temperatures where locomotory abilities would be impaired. One female fox snake was observed poking her head out from her retreat site (the front step of a cottage) for approximately 20 min before emerging, and Hammerson (1979) regularly observed this behaviour in racers (*C.*

*constrictor*) maintained in an outdoor enclosure. Therefore, evidence would suggest that snakes are willing to accept lower  $T_b$ 's in cooler retreat sites rather than risk predation by endotherms on the surface.

One additional technique which I was not able to utilize, and that can provide significant insight into the thermoregulatory behaviour of snakes is to compare the  $T_b$ 's selected by individuals in a laboratory thermal gradient with  $T_b$ 's selected by snakes in the field. This technique, outlined by Hertz *et al.* (1993) and field tested with varanid lizards (*Varanus* spp.; Christian and Weavers 1996), northern water snakes (Brown and Weatherhead 2000), and black rat snakes (Blouin-Demers unpubl. data) relies on  $T_b$  data collected from snakes in a controlled laboratory thermal gradient to derive a PBT or body temperature range (T-set). It is assumed that snakes in a laboratory environment are more likely to select  $T_b$ 's within a preferred range because certain thermoregulatory costs (e.g., predation) have been removed. To what degree snakes discern the decrease in predation risk in captivity is debateable, and in addition, snakes may be responding to some unknown level of stress (Christian and Weavers 1996). Acknowledging these potential problems, the  $T_b$  data yielded from the laboratory gradient are still extremely useful when evaluating field  $T_b$ 's. Several useful indices can be derived that calculate the degree to which free-ranging snakes exploit the thermal environment available, and comparisons of snakes of different reproductive conditions made (Brown and Weatherhead 2000, Blouin-Demers pers. comm.).

Power limitations at our field station (i.e., a 24-h laboratory thermal gradient would have required a significantly larger solar array and wind turbine!), as well as obvious time and travel constraints prevented me from deriving a laboratory-determined

PBT or T-set for *E. gloydi*. However, to illustrate the utility of Hertz *et al.*'s (1993) approach, I have plotted the mean gravid and nongravid  $T_b$ 's of female fox snakes in the enclosure, and superimposed the T-set determined for *E. o. obsoleta* (Blouin-Demers *et al.* In Press A), an oviparous congener of *E. gloydi* with similar life history characteristics (Blouin-Demers pers. comm.; Figure 13). *Elaphe o. obsoleta*'s T-set was determined by using the bounds of the central 50 % of the observed  $T_b$ 's (i.e., the mean 25 % and 75 % quartiles) selected by individuals (N = 26) in a laboratory thermal gradient (Blouin-Demers *et al.* In Press A). Using the T-set allows one to determine the amount of time snakes in the field maintain  $T_b$ 's within the preferred  $T_b$  range. For example, the amount of time that gravid and nongravid fox snakes within the enclosure spent within the preferred  $T_b$  range could be compared. In addition, the amount of time that fox snakes potentially could have maintained  $T_b$ 's within their preferred  $T_b$  range (as indicated by  $T_c$ 's) could be also be calculated.

### **Fitness Implications of Thermoregulating Carefully**

In this study, I predicted that gravid females would thermoregulate more "carefully" (i.e., maintain higher and less variable  $T_b$ 's) during the period of egg retention. This prediction followed from the hypothesis that gravid and nongravid fox snakes should exhibit different thermoregulatory behaviour as a result of the benefits conferred to those gravid females that accelerated embryogenesis, and oviposited earlier. The postulated benefits would be: decreased predation on females after they had oviposited, higher survival of females that oviposit early because of increased opportunities to feed before hibernation, and higher overwinter survival of hatchlings that emerge earlier

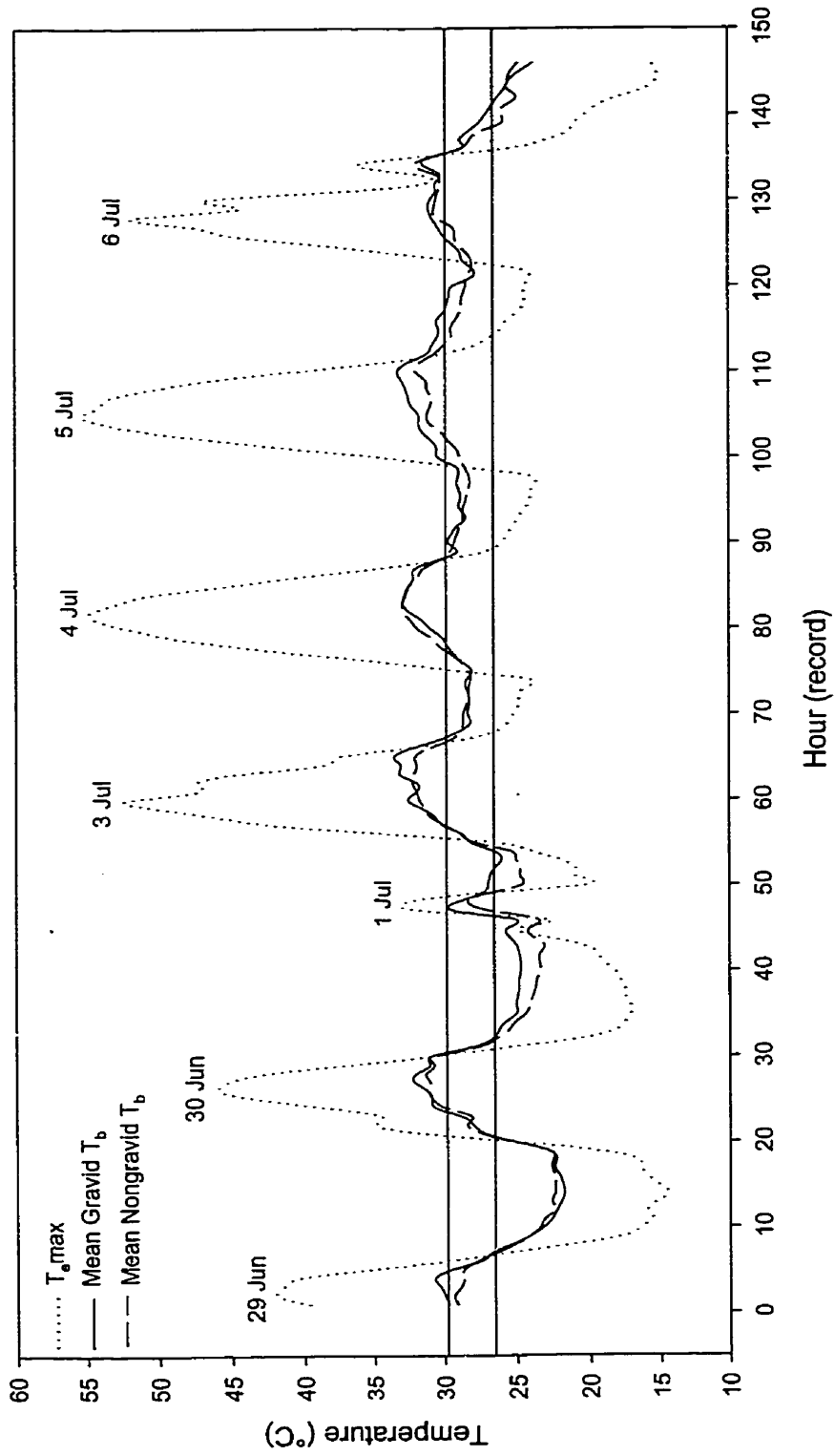


Figure 13. Mean gravid and nongravid fox snake  $T_b$ 's recorded within the enclosure over the entire period of continuous monitoring.  $T_b$ 's were recorded at 1-h intervals and hourly means calculated for each reproductive class. The solid horizontal lines delineate the  $T_b$  set (Preferred  $T_b$  Range) of *Elaphe o. obsoleta* (Blouin-Demers *et al.* In Press A).

because of increased feeding opportunities before hibernation, as well as more time to find suitable hibernacula. In addition to these potential selective advantages derived by females that thermoregulate carefully, studies have shown profound influences of incubation (considered here to be the entire duration of development) temperatures on offspring phenotypes (both behavioural and morphological) of turtles (Brooks *et al.* 1991), lizards (Shine and Harlow 1993, Shine 1995) and snakes (Burger 1990, 1998, Shine *et al.* 1997). The phenotypic differences expressed in offspring incubated under different biologically relevant thermal regimes have also recently been shown to influence survivorship, particularly vulnerability to predators (Downes and Shine 1999). Therefore, the thermal regimes experienced by embryos during incubation have significant implications for offspring fitness. Most studies investigating the effects of incubation temperatures on embryos of oviparous snakes have focused on the latter half of development (i.e., post-oviposition); and I am aware of only one study where the effects of maternal thermoregulation on offspring phenotypes during the period of egg retention was examined, and this study involved scincid lizards (Shine 1995). Therefore, a study that maintained gravid oviparous snakes at different  $T_b$ 's until oviposition, and then incubated eggs under identical conditions would provide an important test of the relevance of maternal thermoregulation to offspring phenotypes during the period of egg retention.

## CONCLUSIONS

From my observations of the thermal ecology of female fox snakes on Pelee Island, I do not believe that overt thermoregulatory behaviour (i.e., increased basking to reach higher  $T_b$ 's) nor careful  $T_b$  regulation, are necessary precursors for the successful production of offspring. I suggest that Pelee Island's benign thermal environment, along with the thermally favourable microclimates of distinct habitat types (e.g., thatch) may allow gravid females significant leeway in thermoregulatory behaviour. Because of extrinsic factors beyond my control, this study had to be moved to a semi-natural environment, however, it is possible that I would have observed the same results had I been able to monitor free-ranging individuals. A comparative study of the thermal ecology of fox snakes from the Georgian Bay region of their range (a more northerly and hence thermally harsher climate) may reveal differences in thermoregulatory behaviour not observed on Pelee Island.

When enclosures are large enough, they can provide conditions suitable for the study of snake thermoregulatory behaviour. Monitoring both free-ranging and enclosure-bound snakes simultaneously would not only provide a test of possible enclosure effects, but also reveal insights into the nest site selection process of oviparous snakes. Because snakes are extremely secretive, discovering where, and when, they nest is a difficult prospect even when radiotelemetry is used. An enclosure provides a more controlled environment in which to test questions concerning nest site selection, as well as the utility of creating artificial nest sites for species of conservation concern. Although the walls of

the enclosure were removed in the fall of 1999, the microhabitats within were left intact and during the spring and early summer of 2000, numerous snakes including *E. gloydi*, northern brown snakes (*Storeria dekayi*; viviparous), and eastern garter snakes (*Thamnophis s. sirtalis*; viviparous) were found using several of the nesting logs for shelter on multiple occasions. Up to five gravid garter snakes were found under a single log, presumably because thermal properties allowed them to maintain  $T_b$ 's optimal for gestation. At present, I do not know whether any of the sites were used for nesting in 2000 because nesting piles were left intact.



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