

Thermal and fitness-related consequences of nest location in Painted Turtles (*Chrysemys picta*)

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Summary

1. Laboratory experiments have documented substantial temperature effects on the physiological ecology of reptilian eggs, embryos and offspring. However, functional links between important habitat characteristics, nest microenvironments and fitness-related traits of neonates in natural nests have rarely been studied.

2. A field study of 11 Painted Turtle (*Chrysemys picta*) nests was conducted to quantify the relationships between a habitat characteristic (i.e. vegetational cover around nests at oviposition) and (1) developmental temperature and its effect on offspring sex ratio and (2) hibernation temperature and its effect on offspring survivorship.

3. Vegetational cover was negatively correlated with nest temperatures in July, the period when offspring sex is determined. However, neither vegetational cover nor mean nest temperature predicted nest sex ratios, although correlations among these variables were consistent with causal relationships derived from laboratory studies.

4. Summer vegetational cover was also negatively correlated with measures of winter nest temperatures. Of the three nests exhibiting overwinter mortality, two were surrounded by thick vegetation and all experienced temperatures below -8°C . The remaining nests reached temperatures as low as -6°C without mortality, indicating that hatchlings in these nests exhibited remarkable supercooling ability.

5. The results suggest that habitat characteristics and nest microenvironments are functionally linked and have fitness consequences for both embryos and offspring, implying that nest-site choice by female turtles could have considerable utility.

Key-words: Hibernation temperature, incubation temperature, sex ratio, survivorship, vegetational cover

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Introduction

Most studies of reptilian eggs have employed constant environmental conditions of incubation in the laboratory (reviewed in Deeming & Ferguson 1991; Janzen & Paukstis 1991; Packard 1991). These numerous studies have provided a wealth of detailed information on the physiological ecology of oviparous reptiles, including biologically important phenomena such as substantial water exchange by flexible-shelled eggs with the incubation substrate (reviewed in Ackerman 1991; Packard 1991), temperature-dependent sex determination (TSD) in many species (reviewed in Deeming & Ferguson 1991; Janzen & Paukstis 1991), and exceptional cold tolerance of offspring of several taxa (reviewed in Packard & Packard 1995). Validation of these laboratory-based results through field studies is clearly important, but relatively few such studies exist (e.g. Ratterman & Ackerman 1989;

Cagle *et al.* 1993; Packard 1997; Shine, Elphick & Harlow 1997).

Studies that assess the causes of microclimate variation within and among natural nests of reptiles are also important. For example, vegetational cover on nests is correlated with offspring sex ratio in Painted Turtles (*Chrysemys picta*, Schneider) (Janzen 1994a) and in other turtle species (e.g. Vogt & Bull 1984; Roosenburg 1996). This result implies a causal relationship between vegetational cover and sex ratio, yet the specific temperature effects are largely unknown. Establishing a functional link between such factors as vegetational cover and nest temperature would be useful because developmental temperature has numerous important effects on the resulting hatchling turtles in addition to sex determination (e.g. Deeming & Ferguson 1991; Janzen 1993, 1995; Rhen & Lang 1995). In turn, habitat characteristics may serve as significant cues for nest location by females during nesting activity.

Nest placement may be crucial not only during the incubation period, but also during the winter in

turtles such as *C. picta* whose offspring hibernate terrestrially (e.g. Paukstis, Shuman & Janzen 1989). Despite a well-developed capacity for cold tolerance, there is still a lower thermal limit below which these turtles will not survive (Storey *et al.* 1988; Paukstis *et al.* 1989; Packard & Packard 1993; Costanzo *et al.* 1995; Packard & Janzen 1996; Packard 1997; Packard *et al.* 1997). Just as during the summer, characteristics of the local habitat around a nest in winter, such as snow depth (Breitenbach, Congdon & van Loben Sels 1984; Paukstis *et al.* 1989), may determine the environmental conditions experienced by the hatchlings.

The purposes of this field study were to quantify the relationships (1) between vegetational cover, summer nest temperature and offspring sex ratio and (2) between vegetational cover, winter nest temperature and offspring survivorship. Thus our intent was to document links between a habitat characteristic and the nest microenvironment and to elucidate the causal effect of these factors on traits related to offspring fitness. We examined natural nests of Painted Turtles (*Chrysemys picta*) because this species exhibits TSD and offspring overwinter in the nest. The population studied offered two other important benefits. A prior field study of TSD suggested that vegetational cover on nests, through its presumed influence on incubation temperature, was causally linked to offspring sex ratio (Janzen 1994a). However, incubation temperatures within the nests were not actually monitored, as they were in the present study. Also, a laboratory study of this population predicted that hibernating neonates would be unable to tolerate nest temperatures below -8°C (Packard & Janzen 1996). The present field study tests both hypotheses, thus evaluating the larger implications of maternal placement of nests (Resetarits 1996; Roosenburg 1996).

Materials and methods

The Painted Turtle nests used in this project were observed as part of a larger study of nesting ecology at South Potter's Marsh on the Thomson Causeway, Thomson, IL. All 132 nests were located during June 1995. Most nests used in this study were placed by females in loamy soil except for one nest that was constructed in gravel. Females were observed nesting and, after completion of nesting, all nests were mapped for future location. Vegetational cover readings around nests (% 'shaded') were taken using a spherical densiometer (Janzen 1994a). Briefly, facing in a cardinal direction (e.g. south) and holding the densiometer level on top of a nest, the number of quarters of the 24 squares ($n = 96$ quarters) on the mirrored surface of the densiometer reflecting vegetation were counted. This value was multiplied by 1.04 to generate a percentage of vegetational cover (often referred to as 'shade' hereafter for short). Nests were excavated immediately after oviposition to determine clutch size.

Eleven of the 49 nests surviving to the end of June were split into three groups: high ($n = 3$), intermediate ($n = 5$) and low ($n = 3$), based on the amount of south and west vegetational cover (Table 1). These nests were chosen to maximize our ability to detect the effects of vegetational cover on nest temperatures and offspring traits. South and west vegetational cover estimates were used as selection criteria for these nests because they produced the most significant effects on sex determination in a previous field study of this population (Janzen 1994a).

Nest temperatures were measured from 18 July to 26 August 1995. This time frame includes much of the temperature-sensitive period of sex determination in *C. picta* (Schwarzkopf & Brooks 1985; Janzen 1994b). July temperatures are specifically emphasized because they are likely to be most relevant to sex determination (Janzen 1994b). Temperatures for all but one nest were recorded with HOBO[®] XT temperature loggers (Onset Computer Corporation, Pocasset, MA). Loggers were wrapped in parafilm and enclosed in small plastic containers with CaSO_4 as desiccant. Each container had a ≈ 1 cm diameter hole in the side wall through which an external temperature probe extended from the logger into the nest. Once the probe had been strung through the hole, silicone gel was used to seal the hole to keep out moisture. Each logger was placed 1 m from the nest at nest depth and the external probe was extended underground into the side of the corresponding turtle nest. Loggers were programmed to record temperatures every 48 min.

Three HOBO[®]-TEMP temperature loggers with internal temperature sensors were also used in this study. Two of these were placed in separate zipper-seal bags with desiccant to record ambient air temperature. One was affixed to the bottom of a bench (≈ 40 cm above the ground) within the nesting area to avoid attracting human attention. The second temperature logger was placed in a north-facing hollow at the base of a tree behind a wire mesh screen. Ambient temperature data were also obtained from the National Weather Service recording station at Lock & Dam 13, located 5.5 km south of the field site. The third HOBO[®]-TEMP logger was used to measure temperatures in nest 87 from the intermediate 'shade' class (see Table 1).

Loggers were removed from the ground on 27 August to download temperature data. The empty containers with external probes were left in the ground. All loggers were returned to the nests on 5 November and were programmed to record temperatures every 1.6 h for the next 120 days. Procedures for activating and installing the loggers were similar to those used in the summer. Before leaving the field site, nests were checked for the presence of hatchlings. All nests (except for nest 7 from which eggs were removed by a predator) contained live hatchlings. All loggers and containers were removed from the ground on 23 March 1996. All nests were also

Table 1. Summer vegetational cover values, temperatures, offspring sex ratios, and correlations with vegetational cover for 11 Painted Turtle nests from 1995. South and west vegetational cover values (S + W) were combined for each nest in all correlation analyses below

Vegetational cover class	Nest no. (no. eggs)	Julian date of nesting	% vegetational cover from south (S)	% vegetational cover from west (W)	Mean July temp. (°C)	Mean daily July max. temp. (°C)	Mean daily July min. temp. (°C)	Hours spent > 28.5 °C	Sex ratios (% males) (no. offspring)
Low	7 (13)	156	1	18	27.69	34.22	23.28	118.25	N/A
	8 (13)	155	1	7	27.02	32.05	23.45	97.50	65.4 (13)
	36 (11)	158	0	19	27.24	34.55	22.68	105.25	100 (11)
Intermediate	10 (10)	157	44	33	26.23	32.43	22.63	78.75	70 (10)
	25 (11)	156	42	48	28.15	34.82	23.83	125.25	0 (7)
	87 (14)	169	11	88	26.63	32.22	22.74	88.25	0 (11)
	104 (15)	172	50	62	27.73	32.93	23.99	116.50	25 (14)
High	115 (11)	174	49	64	27.50	33.10	23.90	113.75	83.3 (6)
	38 (10)	157	94	96	24.19	26.34	21.93	0	100 (9)
	90 (9)	170	87	53	24.50	28.55	22.01	14.25	100 (1)
S + W, <i>r</i> (<i>P</i>)	106 (11)	173	82	24.27	26.9	21.71	0	100 (11)	
				-0.70 (0.013)	-0.79 (0.003)	-0.50 (0.116)	-0.74 (0.009)		0.22 (0.546)

excavated and hatchlings, dead or alive, were brought back to the laboratory for sexing. Hatchlings were sexed by dissection and observation of the presence of testes or ovaries and associated structures (Janzen 1994a,b). To calculate sex ratio, males were assigned a 1, females a 0, and the two intersexes a 0.5. All loggers were calibrated in the laboratory against a Fisher Scientific Traceable™ digital thermometer (Fisher Scientific, Pittsburgh, PA) from -17.8 to 40.2 °C. With the exception of the malfunctioning logger from nest 25, all loggers were similar to each other and to the certified thermometer to within 0.5 °C at each temperature test.

Results

Ambient and nest temperatures varied considerably during embryonic development, with the former fluctuating more than the latter (Fig. 1). Nest temperatures tended to mirror changes in ambient temperatures overall, although nests surrounded by more vegetational cover were more buffered from environmental temperature shifts than were nests with less vegetational cover (Fig. 1).

Vegetational cover around nests at oviposition in June predicted mean July nest temperatures. Nests with more 'shade' had lower mean July temperatures than nests with intermediate or low amounts of vegetational cover (Table 1, Fig. 2). This same pattern was exhibited between nest vegetational cover and mean daily maximum and minimum temperatures in nests (Table 1). Overall then, nest vegetational cover was negatively correlated with July nest temperatures.

To identify nests that were likely to have female-biased sex ratios, the amount of time spent above 28.5 °C in July was calculated. Continuous incubation of Painted Turtle eggs from this population at this temperature in the laboratory produces approximately a 1:1 sex ratio of offspring (F. J. Janzen, unpublished data). Nests with the most vegetational cover spent the least amount of time above 28.5 °C in July; the other eight nests spent considerably more time above this sex-determining temperature threshold (Table 1). There was a significant negative correlation between vegetational cover from the south and west and the number of hours spent above 28.5 °C in July (Table 1, Fig. 3).

Vegetational cover was not a linear predictor of hatchling sex ratios: within the low and intermediate 'shade' classes, there was a mixture of all-male, all-female and mixed-sex nests (Table 1). In contrast, the three nests with the most vegetational cover all produced 100% males. Although not statistically significant, as expected the correlation between vegetational cover and nest sex ratio (% male) was positive (Table 1) and the correlation between the number of hours spent above 28.5 °C in July and nest sex ratio was negative ($r = -0.62$, $P = 0.0577$).

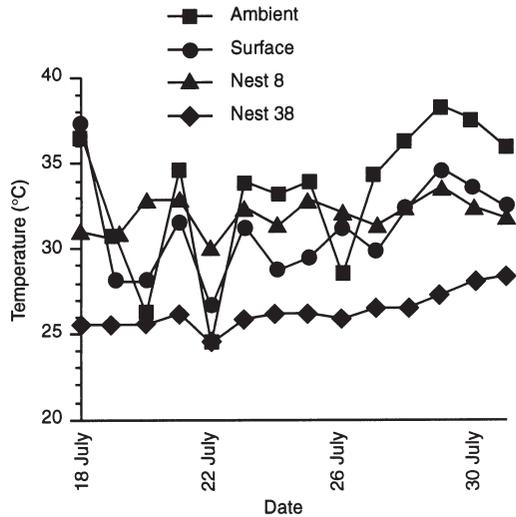


Fig. 1. Temporal changes in mean daily environmental and nest temperatures during a focal 2-week period of embryonic development of Painted Turtles in July 1995. Temperatures in nests, especially in less 'shaded' ones (e.g. nest 8; see Table 1), tended to reflect fluctuations in environmental temperatures.

Of the 11 nests examined, winter temperatures were available for 10 due to the failure of the temperature logger in nest 25 (see Table 2). Nests with the most summer vegetational cover tended to experience cooler winter temperatures (Table 2, Fig. 4) as well as the greatest variances in winter temperatures (Table 2, Fig. 5).

Hatchling mortality occurred in three nests (Table 2). Two of these nests (nests 38 and 106) had substantial vegetational cover and also experienced very cold temperatures. The third nest with hatchling mortality (nest 87) was surrounded by an intermediate amount of vegetational cover. This nest exhibited lower winter temperatures than other nests in its 'shade' category (Table 2), possibly because of its unusual location (i.e. in gravel as opposed to loam).

In the laboratory, temperatures below -8°C are lethal to *C. picta* hatchlings from this population (Packard & Janzen 1996). Concordant with the laboratory results, the only nests with any hatchling mortality were also the only nests to experience temperatures below -8°C (Table 2); this mortality effect was independent of the time spent below -8°C . Two other nests also spent considerable time below -6°C but above -8°C , yet did not exhibit any hatchling mortality (Table 2).

Discussion

Our data are largely congruent with laboratory investigations of relationships between incubation temperatures and offspring sex ratios (reviewed in Janzen & Paukstis 1991; Etchberger *et al.* 1992), field studies concerning vegetational cover around nests and offspring sex ratios (Janzen 1994a), and laboratory

experiments (e.g. Packard & Janzen 1996) and field studies (Packard 1997; Packard *et al.* 1997) regarding the lower thermal limits of hibernating hatchling Painted Turtles. Our results also provide insight into the surprising relationship between summer vegetational cover and winter nest temperature, and shed light on the debate over supercooling vs freeze tolerance as mechanisms of winter survival of hatchling Painted Turtles.

One possible concern with the results of this study involves the number of nests examined. Although the sample size is comparable to that of many such field studies (e.g. Breitenbach *et al.* 1984; Cagle *et al.* 1993; DePari 1996; Packard 1997; Packard *et al.* 1997), the possibility remains that the results, especially those illustrated in Figs 2 and 3, could have been influenced unduly by a few nests. Preliminary analyses of data from subsequent years, however, confirm the results of the present study. To illustrate, as in 1995, nests with more vegetational cover exhibited

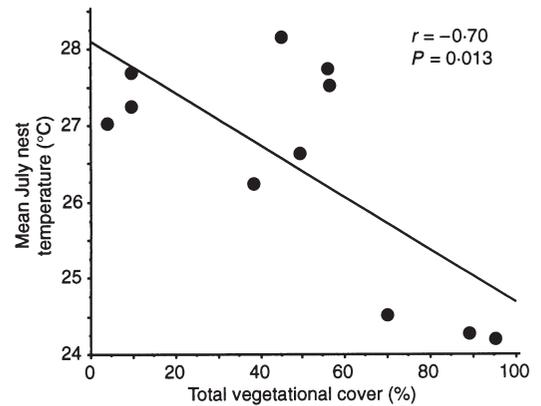


Fig. 2. Mean July temperatures in Painted Turtle nests in relation to total vegetational cover around the nests at oviposition (i.e. the mean of the percentage vegetational cover on the south and west sides of the nests).

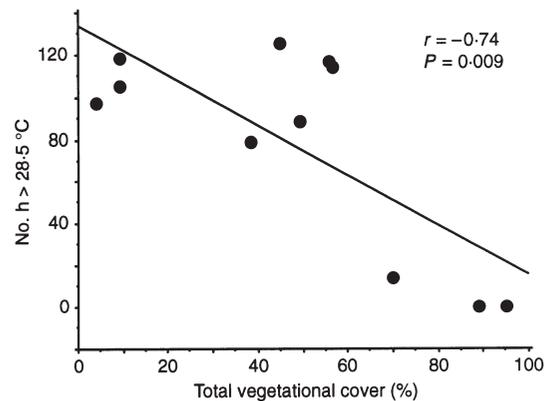


Fig. 3. Number of hours in July that Painted Turtle nests spent above the threshold temperature of sex determination (see Results) as a function of total vegetational cover around the nests at oviposition (i.e. the mean of the percentage vegetational cover on the south and west sides of the nests).

Table 2. Winter temperatures, offspring survivorship, and correlations with vegetational cover for 10 Painted Turtle nests from November 1995–March 1996. Nest 25 has been excluded because its temperature logger failed. South and west vegetational cover values (S + W) were combined for each nest in all correlation analyses below

Vegetational cover class	Nest no.	Mean winter temp. (°C)	Mean daily winter max. temp. (°C)	Mean daily winter min. temp. (°C)	Variance of winter temp. (°C)	Min. winter temp. (°C)	No. hours spent < -6 °C	No. hours spent < -8 °C	Winter survivorship (no. survivors)
Low	7	1.45	2.16	0.74	4.64	-3.63	0	0	N/A
	8	2.10	2.87	1.38	5.15	-4.07	0	0	100 (13)
Intermediate	36	1.18	2.05	0.42	3.98	-3.63	0	0	100 (11)
	10	2.76	3.44	2.10	3.71	-2.35	0	0	100 (10)
	87	-1.22	-0.50	-1.93	3.60	-9.22	12	7	18 (2)
	104	-0.07	-0.15	-1.36	5.07	-6.79	28	0	100 (14)
High	115	0.28	0.51	0.05	4.50	-3.21	0	0	100 (6)
	38	-1.35	-0.14	-2.43	9.54	-12.32	211.5	120	33 (3)
	90	-0.41	0.24	-1.05	5.63	-7.27	46	0	100 (1)
	106	-1.21	0.03	-2.30	8.58	-11.25	153	96	0 (0)
S + W, <i>r</i> (<i>P</i>)		-0.80 (0.005)	-0.75 (0.011)	-0.79 (0.006)	0.72 (0.018)	-0.80 (0.005)	0.80 (0.005)	0.72 (0.018)	-0.60 (0.066)

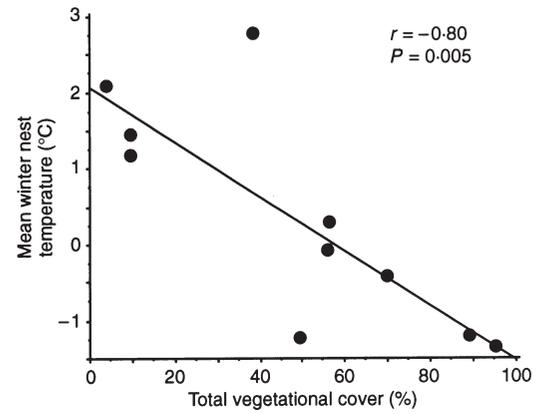


Fig. 4. Mean winter temperatures in Painted Turtle nests as a function of total vegetational cover around the nests at oviposition (i.e. the mean of the percentage vegetational cover on the south and west sides of the nests). Temperatures were monitored from 5 November 1995 to 4 March 1996.

lower mean July temperatures in 1996 and 1997 ($r = -0.62$, $P = 0.0002$, $n = 30$ and $r = -0.67$, $P = 0.0001$, $n = 29$, respectively; cf. Fig. 2). Patterns for the other analyses similar to those detected in the 1995 data were also observed in the 1996 and 1997 data where available (results not shown). Consequently, the results of this study appear to be robust with respect to sample size.

EMBRYONIC DEVELOPMENT

Laboratory studies of sex determination in Painted Turtles demonstrate a threshold temperature of ≈ 28.5 °C during the temperature-sensitive period, above which females are produced and below which males are produced (Janzen & Paukstis 1991). Our field data are roughly consistent with these laboratory findings. All nests from the high vegetational cover class produced males and had the coolest mean July

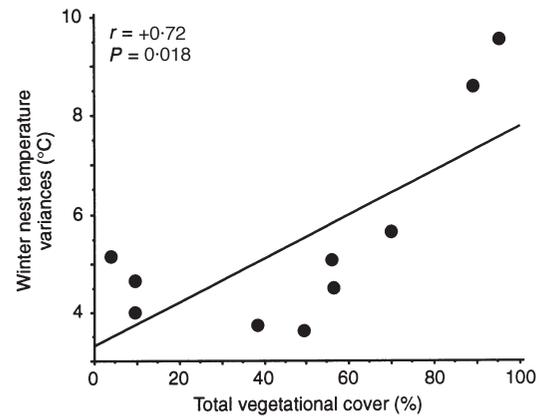


Fig. 5. Variances in winter temperatures in Painted Turtle nests as a function of total vegetational cover around the nests at oviposition (i.e. the mean of the percentage vegetational cover on the south and west sides of the nests). Temperatures were monitored from 5 November 1995 to 4 March 1996.

temperatures, experiencing typical thermal conditions well below 28.5 °C (Table 1). Nests from the intermediate and low vegetation classes ranged from all-male to all-female and experienced a range of mean July temperatures below 28.5 °C. No apparent relationship existed between mean July nest temperatures in these two classes and sex ratios of hatchlings from those nests. These results are similar to those observed in a prior field study of heat-unit accumulation in nests and offspring sex ratios in Painted Turtles (Schwarzkopf & Brooks 1987). Still, additional field studies of the functional relationship between fluctuating nest temperatures and offspring sex ratio are warranted (*sensu* Schwarzkopf & Brooks 1985; Georges, Limpus & Stoutjesdijk 1994).

Previous research demonstrated a negative correlation between vegetational cover and summer nest temperatures, using sex ratios of the resulting hatchlings as measures of nest temperatures (Janzen 1994a). What had not been documented was the actual nest temperatures experienced by the incubating eggs. We found that nests with little or moderate vegetational cover were relatively similar in nest temperature, whereas the 'high-shade' nests were substantially cooler. Our findings therefore confirm the functional link between vegetational cover and nest temperatures implied by Janzen (1994a) (see also Roosenburg 1996).

These results also suggest a non-linear decrease in July nest temperature with increasing amount of vegetational cover. This effect may be caused by a vegetation threshold which, when reached, blocks the sun sufficiently to buffer nest temperatures. Accordingly, July 1995 was very warm (12th warmest in the last 55 years) so partial 'shading' may have been an inadequate shield from the heat (Janzen 1994a,b), causing temperatures in such nests to exceed 28.5 °C frequently enough to produce female-biased sex ratios similar to those in relatively 'unshaded' nests. Similarly, years that are extremely cool should show a reverse relationship, with temperatures in partially 'shaded' nests resembling those in nests with considerable vegetational cover (e.g. Janzen 1994a). Under this hypothesis, vegetational cover in years with moderate ambient temperatures would exert a more influential role on nest temperatures and hatchling traits.

Significant correlations between sex ratio and either vegetational cover or mean nest temperature were not detected. Relationships between these variables may have been obscured because many nests were laid early in June (Table 1) and we began measuring nest temperatures only in mid-July. Still, vegetational cover was negatively correlated with time spent above 28.5 °C and this temperature measure was negatively correlated with nest sex ratio (see Results). Nest temperatures thus were a function of vegetational cover around the nests, consistent with predictions of a previous field study of this popula-

tion (Janzen 1994a). In turn, nest sex ratios were related to an important measure of nest temperature in accordance with laboratory investigations of TSD (reviewed in Janzen & Paukstis 1991) and a prior field study of Painted Turtle nests (Schwarzkopf & Brooks 1987).

HATCHLING HIBERNATION

As it was with summer nest temperature, vegetational cover at oviposition was inversely related to winter nest temperature. Although most of the leafy, sun-blocking foliage except for conifers is absent during winter at the field site, plants (mainly large trees at this field site) can still exert temperature effects by blocking wind and acting as snow fences, keeping the ground free of insulatory snow cover (D. W. Weisrock & F. J. Janzen, personal observation). Nests without this protective snow cover should be more prone to large temperature fluctuations and hence to lower temperatures (Breitenbach *et al.* 1984; Paukstis *et al.* 1989; Packard 1997). Congruent with this hypothesis, variances of winter nest temperatures were positively correlated with summer vegetational cover (Fig. 5), indicating a more thermally extreme environment for nests with more summer vegetational cover. In other words, 'high-shade' nests may be less buffered from winter temperatures because of decreased snow cover. We are currently testing this hypothesis with a field experiment using Painted Turtle nests.

The direct effect of temperature was evident in the pattern of overwinter survivorship of the hatchlings. Only nests that fell below the laboratory-determined lower limit of supercooling for this population of -8 °C (Packard & Janzen 1996) exhibited any mortality. The amount of time these three nests spent below -8 °C was unrelated to the extent of mortality (e.g. nest 87 only spent 7 h below -8 °C). Two additional nests experienced temperatures below -6 °C for large amounts of time (Table 2), yet neither nest exhibited any overwinter mortality, demonstrating that this population of *C. picta* can tolerate extremely cold temperatures near -8 °C in natural nests without lethal effects. Our results are remarkably congruent with those of a prior laboratory study of this population (Packard & Janzen 1996).

Numerous studies have addressed the mechanisms utilized by hatchling turtles to survive subzero temperatures (see recent reviews in Costanzo *et al.* 1995 and Packard & Packard 1995). Debate has centred on the use of freeze tolerance (actual freezing of tissues) vs supercooling (resistance to tissue freezing) as an overwintering strategy (Packard & Packard 1995). Our results are most consistent with the supercooling hypothesis. Temperatures below -6 °C were reached by some nests without resulting in hatchling mortality (Table 2). This temperature is lower than the freezing threshold below which frozen hatchlings do not successfully recover (Storey *et al.* 1988;

Costanzo *et al.* 1995). Supercooling, however, is effective at such low temperatures (Packard & Packard 1993; Packard & Janzen 1996).

Although we cannot rule out the operation of freeze tolerance at relatively higher subzero temperatures (i.e. 0 to -4 °C), its coexistence with the exceptional supercooling ability that has been documented seems unlikely (Packard & Janzen 1996). To use one mechanism or the other selectively depending on thermal conditions, the freezing process in modest subzero conditions would have to be reversed before supercooling could operate at lower temperatures. If any crystals existed as the temperature dropped, the turtle would probably die or at least suffer tissue damage. Because nest temperatures often hover at high subzero temperatures before declining (Fig. 6), depending on both mechanisms would thus be disadvantageous for hatchling *C. picta*. Although freeze tolerance may allow for survival in some situations, it should be advantageous for a hatchling to *depend* on a supercooling strategy, one that permits survival at both temperature ranges.

IMPLICATIONS FOR NEST-SITE CHOICE

Where shall a female lay her nest? Nesting conditions vary among different populations and nesting sites such that local adaptations in nesting behaviour could conceivably exist. But are all nests within a locale the same? A nest in a forest clearly experiences a different thermal environment from a nest in a sandbar. Our results document physiologically significant temperature differences among nests on a still finer scale: among different levels of vegeta-

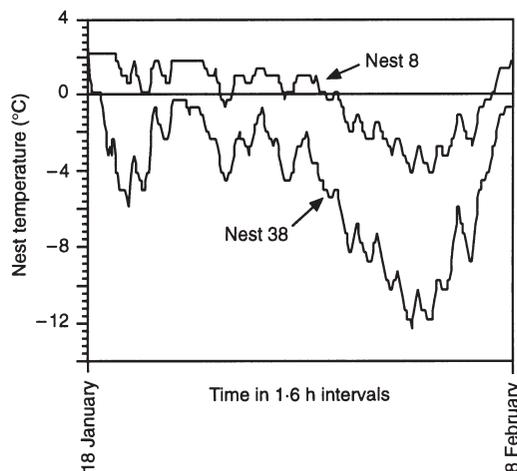


Fig. 6. Winter temperatures in Painted Turtle nests during an example 3-week period. Nest 8 had little vegetational cover and nest 38 was surrounded by considerable vegetation (Table 1). Hatchlings from the former nest exhibited 100% overwinter survivorship, whereas offspring from the latter nest, which fell below the laboratory-determined lower limit of supercooling of -8 °C for this population (Packard & Janzen 1996), experienced low overwinter survivorship (Table 2).

tional cover *within* a nesting locality (*sensu* Vogt & Bull 1984; Roosenburg 1996). This thermal variation was implied by Janzen (1994a). Our data confirm these differences in temperature and show that they are linked to key aspects of hatchling fitness (i.e. sex and winter survivorship). Thus, a thermally heterogeneous nesting area and the causal inter-relationships among these variables together provide the ecological foundation for a female's ability to choose where her eggs are best suited (Resetarits 1996).

A female turtle may indeed be able to benefit from these observable cues in determining the sex of her offspring (Janzen 1994a, 1995; Roosenburg 1996), given that the nest produces viable offspring (Schwarzkopf & Brooks 1987). Our findings provide the basis for additional benefits of nest-site choice in the form of differential overwinter survivorship, because winter mortality in nests was positively correlated with vegetational cover at oviposition. For these traits, a mother's fitness thus consists of an interaction between Fisherian sex ratio selection and viability selection of her offspring. Although our results do not guarantee the existence of nest-site choice, the profound fitness consequences of nest location do provide additional incentive to more closely examine this infrequently tested hypothesis.

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