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Thermoregulation When the Growing Season Is Short: Sex-Biased Basking Patterns in a Northern Population of Painted Turtles (*Chrysemys picta*)

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ABSTRACT.—**In reptiles, thermoregulation is important because it alters the rate of many physiological processes. Thermoregulation may be especially important to reproductive females that inhabit regions where the growing season is short, because the amount of thermal energy experienced during the season may limit the amount of energy devoted to egg production. We studied basking behavior of Painted Turtles (*Chrysemys picta*) in Algonquin Park, Ontario, during the period of follicular recrudescence, a time of year when females allocate energy to developing follicles. Based on the notion that females bask (in part) to increase the amount of energy they allocate to developing follicles, we tested whether basking duration was greater in females than in males. Between 14 and 21 August 2003, we found that females basked longer than males on three of seven days, but males never basked significantly longer than females. Within sex, male but not female body size was positively related to basking duration. Our study suggests that the energetic demands of egg production result in an increased basking duration for females in this northern population. Males may bask to reach a certain temperature then return to water because of potential mating opportunities. Future studies should combine body temperature measurements with behavioral observations to elucidate further the reasons for sex-biased basking.**

Like all reptiles, turtles are ectothermic, and their body temperature is largely dependent on that of their environment. Some turtles can maintain a fairly precise and constant body temperature if a heat source is available (Cossins and Bowler, 1987; Hammond et al., 1988) by engaging in thermoregulatory activities such as aerial basking (Boyer, 1965; Brattstrom, 1965; Auth, 1975; Crawford et al., 1983). By increasing their body temperatures, there is a corresponding increase in the rate of physiological processes (Crawford et al., 1983; Hammond et al., 1988), such as metabolic rate (Bennet, 1982), digestion speed, and digestion efficiency (Kepenis and McManus, 1974; Paramenter, 1981; Avery et al., 1993; Koper and Brooks, 2000).

The thermoregulatory behavior of reproductively active females is important in turtles and other reptiles. For example, increases in body temperature of female turtles can result in a greater rate of follicular development (Ganzhorn and Licht, 1983; Mendonca, 1987; Sarkar et al., 1996). In viviparous lizards, females that increase basking duration during periods when energy is being allocated to developing embryos may be capable of devoting more stored energy to reproduction (Wapstra, 2000). The rate at which energy is allocated to developing follicles may be especially important for females in populations occupying the northern limit of their species' range, because the amount of thermal energy that they experience during the short active season may set strict limits on the amount of harvested energy that can be allocated to egg production (Rollinson and Brooks, 2007).

In northern populations of Painted Turtles (*Chrysemys picta*), an estimated 14% of the annual energy budget of a female is devoted to the development of eggs, and about half of this energy is allocated to developing follicles during the recrudescent period, which comprises August to October of the year prior to oviposition (Congdon and Tinkle, 1982). The remaining half is completed in the spring, between emergence from hibernation (usually late April) and the end of May (nesting season; Congdon and Tinkle, 1982). Given that warm body temperatures may increase the rate at which energy is allocated to developing follicles (Mendonca, 1987; Sarkar et al., 1996; Rollinson and Brooks, 2007), females inhabiting northern populations may increase basking duration during the recrudescent period.

We examined thermoregulatory patterns of male and female *C. picta* during the recrudescent period. If the amount of thermal energy (but not food energy) experienced during the recrudescent period limits the amount of stored energy that can be allocated to developing follicles in this population (Rollinson and Brooks, 2007), then females should devote a greater portion of their time to thermoregulation during recrudescence. However, males do not experience the energetic demands of follicular development; thus, we predicted that females will bask for longer periods than males. Body size may also contribute to some differences in basking duration since heating rates are reduced in larger turtles because of slower evaporative water loss (Foley and Spotila, 1978). Therefore, as body size increases, we predict that basking duration will increase for all individuals. Finally, because it is intuitive that an inverse relationship between basking duration and basking frequency may exist, we expected that males would bask at equal or greater frequency than females.

MATERIALS AND METHODS

Study Site.—We observed the basking behavior of sexually mature *C. picta* at Wolf Howl Pond, Algonquin Park, Ontario. The pond is a 1.70-ha Black Spruce (*Picea mariana*) bog that is predominantly ~1.3 m deep

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TABLE 1. Mean (± SE) daily basking duration (min) for females and males. Values in parentheses are the number of individuals of each sex observed basking on each day. Mean basking duration was compared with independent samples *t*-tests (one-tailed).

	Basking duration		
Date (2003)	Female	Male	*P*
14 August	52.2 ± 12.5 (9)	52.5 ± 10.1 (6)	0.49
15 August	68.1 ± 9.66 (21)	29.4 ± 6.91 (8)	0.001
17 August	91.2 ± 15.0 (21)	89.4 ± 18.3 (9)	0.48
18 August	101.9 ± 9.11 (24)	72.8 ± 20.0 (9)	0.07
19 August	93.6 ± 9.67 (31)	50.0 ± 7.56 (7)	< 0.001
20 August	69.7 ± 8.02 (30)	40.0 ± 6.54 (7)	0.004
21 August	88.3 ± 9.46 (27)	91.3 ± 25.5 (4)	0.45

and is bisected by 4-m high abandoned railway embankment. Wolf Howl Pond contains many floating bog mats consisting of *Sphagnum* species, leatherleaf (*Chamaedaphne cayculata*), and sedges (*Rynchnospora alba* and *Eleocharis smallii*).

Data Collection.—Basking behavior of Painted Turtles was studied for eight consecutive days between 14 and 21 August 2003, from 0800–1200 h. The observation period was restricted to mornings because previous studies of this population demonstrated that the majority of basking occurred at this time (Schwarzkopf and Brooks, 1985; Lefevre and Brooks, 1995). We observed turtles from the embankment using binoculars, and our transect along the pond provided a good view of the majority of possible basking sites. Most turtles in this population are marked with alphanumeric tags that are wired through holes drilled in the marginal scutes of the carapace, and every spring, each individual's alpha-numeric code is painted across their carapace so that they can be identified from a distance: females are painted white; and males are painted orange.

A turtle was considered to be basking if at least three-quarters of the carapace was out of the water (Schwarzkopf and Brooks, 1985). When an individual was observed basking, we recorded the sex and identity of the individual, and basking duration was measured by observing the individual at 5-min intervals until it departed from the basking site.

Analyses.—Because it was easy to discriminate between males and females (i.e., white paint vs. orange paint), all basking observations (including unidentified individuals) were included in sex ratio calculations. We calculated the sex ratio from observations that occurred across all days of the study and compared this value to the expected sex ratio of 3.44 females for every male, which was previously recorded in this population by Samson (2003). Second, we compared basking duration of males and females for each day of the study using independent samples *t*-tests (one-tailed). All individuals for which basking duration exceeded 5 min (including those whose alphanumeric codes were not positively identified) were included in these analyses. However, some individuals were observed on more than one day. Therefore, daily comparisons of basking duration were not independent, and it is likely that we underestimated the population-level variance in basking duration, which can lead to Type I errors. We used a Bonferroni correction and divided alpha (0.05) by the number of days in the observation period; we used the modified alpha value (0.006) to assess statistical significance. Third, we used linear regression to test for an effect of body size on basking duration of males and females. For individuals that were observed basking more than once in the study, basking duration was averaged across all basking events so that our regression analyses included only one data point per individual.

RESULTS

Population Sex Ratio.—The sex ratio of all turtles observed basking across all days of our study was 3.2 females: 1 male (204 females, 63 males), and it did not differ from the expected ratio of 3.44 : 1 ($X^2_1 = 0.194$, $P = 0.66$).

Daily Comparisons of Basking Duration.—We did not compare basking duration between sexes on 16 August because there were only six basking observations on that day. Daily comparisons of basking duration included individuals with alphanumeric codes that were not positively identified. Females basked significantly longer than males on three of seven days of the study period, and males never basked significantly longer than females (Table 1).

Body Size and Basking Duration.—Across all days, a total of eight different males and 37 different females were individually identified using their alphanumeric codes during our basking surveys. Mean (± SE) basking duration of these males was 80.5 ± 14.0 min, and basking duration of these individuals was positively related to body size (Fig. 1, $N = 8$, $r^2 = 0.729$, $F_{1,6} = 16.1$, $P = 0.007$). Mean basking time of females was 97.9 ± 6.82 min and was inversely, but insignificantly, related to body size (Fig. 1, $N = 37$, $r^2 = 0.095$, $F_{1,35} = 3.9$, $P = 0.063$).

DISCUSSION

The results of the present study show that the thermoregulatory behavior of females differs from that of males during a portion of the recrudescent period. The positive correlation observed between male body size and basking duration suggests that males are warming themselves to an optimal temperature (Dawson, 1975; Crawford et al., 1983; Kingsbury, 1993) before returning to the water. The lack of correlation between basking duration and female body size (Fig. 1), coupled with a tendency for

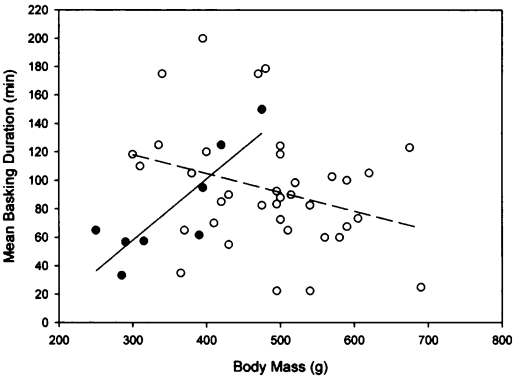

FIG. 1. The relationship between body mass (g) and basking duration (min) for males (r^2 = 0.729, closed circles, solid line) and females (r^2 = 0.095, open circles, dotted line).

females to bask longer than males (Table 1), suggests that females may be basking to maintain body temperatures within a certain range.

A recent study on this population (Rollinson and Brooks, 2007) showed that clutch frequency (the number of clutches a female produces in a season) was related to the temperatures experienced during the recrudescent period, but clutch frequency was not related to the temperatures experienced while follicles were not developing (i.e., July temperatures). Because elevated temperatures may increase the amount of stored energy that can be allocated to developing follicles in the fall (Mendonca, 1987; Sarkar et al., 1996), this phenomenon suggests that reproductive output is limited not by resource acquisition, but by the amount of thermal energy experienced during the recrudescent period. The data from the present study appear to support these findings: females engaged in relatively long basking bouts; and body size was not related to basking duration. This pattern of thermoregulation may reflect the need for females to allocate stored energy to developing follicles during the period of follicular development.

Hammond et al. (1988) postulated that, if female turtles are able to increase fat mobilization by increasing the time spent thermoregulating, and if indeed this energy is available for reproduction, then females should spend more time thermoregulating in the spring (just prior to nesting) than at other times of the year. In support of this notion, a previous study found that basking duration of females in the present population was greater than that of males in the week prior to and during the nesting season (Krawchuk and Brooks, 1998). It is indeed possible that the observed bias is related to the energetic costs of reproduction incurred to females, where increased body temperatures improve performance in digging nests or where increased basking duration accelerates the final stages of follicular development (Krawchuk and Brooks, 1998). Interestingly, there is no difference in basking frequency and duration between sexes when follicles are not developing (July) in the present population (Lefevre and Brooks, 1995; Krawchuk and Brooks, 1998), and the latter result would likewise be expected if sex-biased basking is largely related to the reproductive status of females.

Alternatively, males appear to court females throughout the active season in this northern population, especially in the spring and fall (NR, pers. obs., also see Gist et al., 1990). Thus, in addition to feeding, which is performed by both sexes, there may be an added incentive for males to return to the water. In the present study, the tendency for females to bask for longer periods than males, coupled with the fact that the overall sex ratio of basking turtles was not male-biased, suggests that males were indeed spending more time in the water than females. Accordingly, the observed bias in basking duration may be related to the behavior of males and not to the energetic cost of reproduction incurred to females. Likewise, the basking bias that has been observed in late May and early June in this population (Krawchuck and Brooks, 1998) could be explained in similar terms. Both males and females bask a great deal in early May (NR, pers. obs.), and there is no difference among sexes in basking duration during this time (Krawchuck and Brooks 1998). This may be because water temperatures are generally cold in the spring and because basking just after emergence from hibernation may help eliminate lactic acid that is accumulated in the turtles' bodies over the winter (Jackson and Heisler, 1982). However, as the water warms toward the end of May, and after lactic acid is eliminated from the turtles' bodies, there may be a greater propensity for males to return to the water to court females. As such, the observed basking bias just prior to and during the nesting season (Krawchuck and Brooks, 1998) may also be unrelated to reproductive energetics of females. That no difference in basking duration occurs in July (i.e., when follicles are not developing) is also consistent with this notion (Lefevre and Brooks, 1995; Krawchuck and Brooks, 1998). More courtship behavior is observed when water temperatures are cool (e.g., in the spring and fall, NR, pers. obs., Gist et al., 1990); thus, similar basking frequencies in July may be related to reduced courtship behavior by males.

Notwithstanding, studies of basking frequency and duration performed during periods of follicular development and follicular quiescence support the notion that the energetic demands of reproduction incurred to females in this population result in a greater basking duration for females (Lefevre and Brooks, 1995; Krawchuk and Brooks, 1998); but clearly, further research is needed to draw more definitive conclusions. It would be valuable to perform an integrative study in which the body temperatures of males and females are monitored over the active season and where behavioral observations are recorded (courtship frequency, basking duration). Such a study would ultimately help elucidate underlying reasons for the observed sex-biased basking patterns.

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