

to finally strike the coil against the opposite side of the model (Fig. 2C). However, most "blows" were from a much closer range, involving arcs of 30°–90°. The snake either struck the model with the lateral edge of the coiled tail or the sweep of the posterior body turned the tail so that the ventral surface of the coil struck the model broadside. Fluid was often extruded from the cloaca during this strike. On two occasions, the tail was not formed into coils but was slashed, uncoiled, at the model. Such slashing strikes of the tail seemed to be the result of incomplete coil formation prior to the strike.

Greene (1988) listed 60 phenotypic categories of antipredator mechanisms in reptiles. Each of our types of defensive behavior of *O. formosanus* roughly corresponds to one of his categories: type 1 (defined here) = false strikes (of Greene); type 2 = strike; type 3 = tail-lash. Type 1 (head-butting) can be regarded as a kind of false strike because no tooth marks were found in the parafilm sheet. However, the "false strike" of *O. formosanus* differs from Greene's (1988) description in that the snake kept its mouth open, and did not close it on the model.

The type 2 defensive strike is quite peculiar and suggests the utilization of the edged posterior maxillary teeth for defense by *O. formosanus*. The snake attacks the predator with a rapid, laterally sweeping stroke of the head ("slashing"), rather than a quick back and forth movement of the head ("striking"). The combination of the enlarged, blade-like teeth (Fig. 3) and the "slashing" movement of the head makes a single, lengthwise cut on the predator. This mode of snake defense is unique and clearly distinguishable from defensive striking patterns of other snakes thus far reported (e.g., Klauber, 1972; Kardong, 1986; Greene, 1988). Thus, while the blade-like posterior maxillary teeth serve during feeding to open leathery reptilian eggs, they are also deployed occasionally during defensive behavior in *O. formosanus*.

Both elevating a curled tail (but not striking objects) and defecating are well-known antipredator behavior in snakes (Greene, 1973, 1988); however, the coiled-tail strike of *O. formosanus* is unknown in other snakes except the Australian elapid *Pseudechis guttatus* (McPhee, 1979), and corresponds most closely to tail-lashing reported in crocodiles and some lizards (Greene, 1988). This behavior may be a derived behavioral pattern from a more primitive behavior wherein an elevated, coiled tail was accompanied by cloacal discharge.

It is unclear what factors (e.g., perceived stimuli or behavioral context) elicit these different defensive responses, although strong stimuli seemed required to elicit the tail-strike. Observations on other *Oligodon* species possessing the blade-like posterior maxillary teeth are needed to determine the universality of these attacking behaviors, especially slashing, among members of this genus. Furthermore, defensive behavior of other snakes such as *Cemophora*, *Prosymna*, and *Stegonotus*, also characterized by blade-like teeth and reptilian egg eating habits (Minton and Anderson, 1963; Palmer and Tregembo, 1970; McDowell, 1972; Broadley, 1979), are worthy of study to examine the possibility of behavioral convergence linked with this feeding adaptation.

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LITERATURE CITED

- BROADLEY, D. G. 1979. Predation on reptile eggs by African snakes of the genus *Prosymna*. *Herpetologica* 35:338–341.
- GREENE, H. W. 1973. Defensive tail display by snakes and amphisbaenians. *J. Herpetol.* 7:143–161.
- . 1988. Antipredator mechanisms in reptiles. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*, Vol. 16, Ecology B, Defense and Life History, pp. 1–152. Alan R. Liss, New York.
- KARDONG, K. V. 1975. Prey capture in the cottonmouth snake (*Agkistrodon piscivorus*). *J. Herpetol.* 9:169–175.
- . 1986. The predatory strike of the rattlesnake: when things go amiss. *Copeia* 1986:816–820.
- KLAUBER, L. M. 1972. *Rattlesnakes. Their Habits, Life Histories, and Influence on Mankind*, 2nd ed. Univ. California Press, Berkeley. 1533 pp.
- KUNTZ, R. E. 1963. Snakes of Taiwan. *Q. J. Taiwan Mus.* 16:1–80.
- MCDOWELL, S. B. 1972. The species of *Stegonotus* (Serpentes, Colubridae) in Papua New Guinea. *Zool. Meded.* 47:6–26.
- MCPHEE, D. R. 1979. *The Observer's Book of Snakes and Lizards of Australia*. Methuen, Sydney. 157 pp.
- MINTON, S. A., JR. 1966. A contribution to the herpetology of West Pakistan. *Bull. Amer. Mus. Nat. Hist.* 134:27–184.
- , AND J. A. ANDERSON. 1963. Feeding habits of the kukri snake, *Oligodon taeniolatus*. *Herpetologica* 19:147.
- PALMER, W. M., AND G. TREGEMBO. 1970. Notes on the natural history of the scarlet snake *Cemophora coccinea copei* Jan in North Carolina. *Herpetologica* 26:300–302.
- POPE, C. H. 1935. *The Reptiles of China*. Natural History of Central Asia, 10. *Amer. Mus. Nat. Hist.*, New York. 604 pp.
- SMITH, M. A. 1961. *The Fauna of British India, Ceylon and Burma, Including the Whole of the Indo-Chinese Sub-region*. Reptilia and Amphibia, Vol. 3. Serpentes. [Reprint]. India Press, Dehra Dun. 583 pp.
- TORIBA, M. 1987. Feeding behavior of two species of the genus *Oligodon* from China. *The Snake* 19: 5–9.
- WALL, F. 1923. A review of the Indian species of the genus *Oligodon* suppressing the genus *Simotes* (Ophidia). *Rec. Indian Mus.* 25:305–334.

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Observations on Basking Behavior of Hatchling Turtles in the Wild

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Thermoregulatory behavior is well-documented in turtles (reviewed in Hutchison, 1979; Mrosovsky, 1980; Avery, 1982; Meek and Avery, 1988). Adults of aquatic species of turtles have been observed basking above water (i.e., aerial basking *sensu* Moll and Legler, 1971) on material such as floating vegetation, logs, and rocks, on sandy areas (e.g., beaches, sand bars), or in shallow water where the temperature presumably is elevated. Turtles may engage in this behavior for several reasons, including: (1) promotion of digestion, assimilation, and/or passage of food or wastes; (2) elevation of metabolic rate in order to pursue subsequent activities; (3) removal of ectoparasites; (4) promotion of synthesis of vitamin D; and (5) acceleration of the rate of development of eggs maturing in adult females (reviewed in Auth, 1975; Avery, 1982).

Hatchlings and juvenile turtles are known to display thermoregulatory behavior in captivity. Hatchling and juvenile *Chelydra serpentina* have a distinct selected temperature when provided with either a terrestrial or aquatic thermal gradient (Williamson et al., 1989). Similar behavior has been observed in captive hatchlings of *Trachemys scripta* (Moll and Legler, 1971). Although hatchlings basked frequently, they showed a marked increase in basking behavior shortly after feeding. Likewise, juvenile *Chrysemys picta*, *Graptemys geographica*, *G. ouachitensis*, *G. pseudogeographica*, and even *Chelydra* spend much time exposed on floating wood or other material in the laboratory, commencing shortly after hatching (Janzen, pers. obs.). This basking behavior may allow increased performance (e.g., competition for food) or improve growth rates (e.g., Williamson et al., 1989).

Basking by hatchling and juvenile turtles is important to document because of the potential physiological significance and fitness consequences of this behavior. Physiological models of chelonian thermoregulation typically focus on adult animals. Nearly all studies of basking and thermoregulatory behavior in turtles have involved large juveniles or adults. Young turtles, however, experience the thermal environment differently, owing to their small size which allows for more rapid thermal equilibration (Spotila and Gates, 1975). Furthermore, most studies on the interrelationships among egg size, incubation conditions, and embryonic growth do not investigate the ecological consequences of differential post-hatching growth and survivorship (reviewed in Packard and Packard, 1988), although these traits are thought to be strongly influenced by basking behavior. Additionally, the first years of life essentially comprise the period during which turtles are most susceptible to predation. Most individuals live many years once they

have passed through the "window of vulnerability" of body size (reviewed in Wilbur and Morin, 1988). Nonetheless, we are aware of only four reports documenting basking behavior of hatchling turtles in the wild (Moll and Legler, 1971; Waters, 1974; Auth, 1975; Shealy, 1976).

In this paper we describe three separate instances of basking behavior by hatchling and small juvenile emydid (*Trachemys scripta* and *Chrysemys picta*) and kinosternid (*Sternotherus odoratus*) turtles under natural conditions. We also report the circumstances and climatic conditions under which these animals were found, because these factors may affect behavioral thermoregulation (reviewed in Meek and Avery, 1988; see discussion below).

We made our initial observations of aerial basking of hatchling turtles in roadside sloughs near Horseshoe Lake, Alexander Co., Illinois (37°9'N, 89°21'W), from approximately 1300–1500 h on 26 April 1990. The semi-permanent bodies of water contained considerable quantities of algae and various other aquatic plants and insects, but also contained submerged and emergent non-aquatic vegetation. Ambient temperature was 26.7 C and temperature on the surface of one of the logs in the slough used by hatchlings for basking was 28.3 C. Water temperature at a depth of 1 cm was 25.6 C and at a depth of 10 cm was 24.1 C. We observed nine separate instances of hatchling *T. scripta* basking on floating wood or emergent logs in this habitat. We encountered hatchlings on exposed material from one to several meters from the shoreline. All individuals had been out of water long enough for their carapaces to dry. One individual that we were able to capture had the following measurements (straight-line): carapace length (CL) = 32 mm, carapace width at mid-body = 33 mm, plastron length = 30 mm, and plastron width = 19 mm. All turtles that we observed were approximately the same size.

Our second set of observations of basking behavior of juvenile turtles took place near Gorham, Jackson Co., Illinois (37°43'N, 89°29'W), on 27 April 1990. The site consisted of numerous ponds surrounded by tall grass. The surfaces of the ponds generally were free of vegetation or exposed material. We encountered several potential predators (*Rana catesbeiana*, *Thamnophis sirtalis*, and *Nerodia* spp.) at the edges of the ponds. Additionally, we observed adult *Chrysemys picta* and *Sternotherus odoratus* basking aerially on exposed mud at the edges of the ponds and several individuals of *S. odoratus* that apparently were basking in the shallow water near shore. Air temperature was approximately 25 C. We initially captured a hatchling *Trachemys scripta* at the muddy edge of one pond and a yearling *S. odoratus* basking on a clump of dry mud near the edge of a different pond. As with the other turtles we observed basking, the carapaces of both individuals were completely dry.

The final observations took place in cypress groves along the edge of Horseshoe Lake, Alexander Co., Illinois (37°9'N, 89°21'W), from 1130–1530 h on 13 May 1991. The area was characterized by numerous cypress, floating logs, and patches of sedge grass. During this observation period, we sighted potential predators (*Rana catesbeiana*, *Nerodia* spp., and *Ardea herodias*), as well as adult *Trachemys scripta* and *Chrysemys picta* basking on logs. Ambient temperature was about 28 C and there was intermittent drizzle. We observed seven hatchling and yearling *T. scripta* (x

CL = 34.3 mm, range = 31–38 mm, n = 6), and two *C. picta* (\bar{x} CL = 32.5 mm, range = 31–34 mm, n = 2) basking on cypress knees, fallen trees, and sedges. All individuals had dry carapaces, indicating prolonged intervals out of water.

Our observations clearly document aerial basking behavior of hatchling and juvenile turtles under natural conditions. We have been informed of additional unpublished observations of basking behavior of hatchlings of other species of turtles in Illinois (*Clemmys guttata*, *Emydoidea blandingii*, *Graptemys geographica*, and *G. pseudogeographica*; D. Moll and E. Moll, pers. comm.). Basking in the field has been described numerous times for adult *T. scripta* and *C. picta* (Boyer, 1965; Ernst, 1971; Moll and Legler, 1971; Auth, 1975; Bury et al., 1979; Spotila et al., 1984; Schwarzkopf and Brooks, 1985; Lovich, 1988). The duration and frequency of basking behavior in larger individuals of these species are known to be dependent on many factors including ambient temperature, water temperature, incipient radiation, windiness, precipitation, acclimation temperature, feeding status, sex, season, time of day, and body size (Boyer, 1965; Ernst, 1971; Moll and Legler, 1971; Gatten, 1974; Auth, 1975; Bury et al., 1979; Crawford et al., 1983; Jarling et al., 1984; Spotila et al., 1984; Schwarzkopf and Brooks, 1985; Hammond et al., 1988; Lovich, 1988). Ernst (1986) infrequently observed aerial basking in adult *S. odoratus* in the field. More commonly he encountered individuals basking just beneath the surface of the water while clinging to submerged vegetation. We confirm these observations. Only two of these studies reported basking behavior of small turtles in the field. Moll and Legler (1971) described aerial basking of a hatchling *T. scripta* (CL = 39 mm) on emergent grass stems in a pondlike area of a lagoon in Panama. Similarly, Auth (1975) observed a single small *T. scripta* (CL = 39 mm) basking on floating material in a small pond in Florida. Additionally, Waters (1974) stated that hatchling *Graptemys nigrinoda* basked on small branches and twigs near river banks and Shealy (1976) briefly mentioned that hatchling *G. pulchra* in Alabama basked, but provided no specific data.

Aerial basking may place small turtles under a considerable risk of predation. Hatchling and juvenile turtles are dietary items for many predators that frequently use or visit aquatic habitats. Known predators of hatchling turtles that occur in the areas visited during this study include raccoons (*Procyon lotor*; Legler, 1960), coyotes (*Canis latrans*; Minckley, 1966), gulls (*Larus* spp.; Bustard, 1979), common crows (*Corvus brachyrhynchos*; e.g., Cagle, 1950), hognose snakes (*Heterodon* spp.; e.g., Platt, 1969), water snakes (*Nerodia* spp.; Janzen and Paukstis, pers. obs.), cottonmouths (*Agkistrodon piscivorus*; e.g., Klimstra, 1959), and bullfrogs (*Rana catesbeiana*; e.g., Graham, 1984). Other suspected predators on basking hatchlings that are known to occur in the area include long-legged wading birds such as herons, egrets, and bitterns (Ardeidae). Basking behavior in adult turtles may provide many benefits, including improved metabolism, increased growth, and removal of parasites. Although these benefits of aerial basking may also accrue to juveniles, the behavior itself clearly may place the individuals under a greater risk of predation.

Our findings suggest that aerial basking by hatchling and juvenile turtles in the wild may be more

common than previously documented. This may be the result of difficulty in finding and observing hatchlings in the field or merely the result of a failure to report a common behavior. Regardless, basking behavior is important because life history models make assumptions about susceptibility to predation and growth of juvenile turtles, which, especially in the former case, are relatively unknown. The data presented herein do not directly address factors that affect basking behavior of hatchling turtles and, clearly, rigorous and detailed analyses of hatchling basking behavior are needed. Our observations provide the ecological basis for such studies.

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LITERATURE CITED

- AUTH, D. L. 1975. Behavioral ecology of basking in the yellow-bellied turtle, *Chrysemys scripta scripta* (Schoepff). Bull. Florida State Mus. Biol. Sci. 20:1–45.
- AVERY, R. A. 1982. Field studies of body temperatures and thermoregulation. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 12C, pp. 93–166. Academic Press, New York.
- BOYER, D. R. 1965. Ecology of the basking habit in turtles. *Ecology* 46:99–118.
- BURY, R. B., J. H. WOLFHEIM, AND R. A. LUCKENBACH. 1979. Agonistic behavior in free-living painted turtles (*Chrysemys picta bellii*). *Biol. Behav.* 4:227–239.
- BUSTARD, H. R. 1979. Population dynamics of sea turtles. In M. Harless and H. Morlock (eds.), *Turtles: Perspectives and Research*, pp. 523–540. Wiley, New York.
- CAGLE, F. R. 1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). *Ecol. Monogr.* 20:31–54.
- CRAWFORD, K. M., J. R. SPOTILA, AND E. A. STANDORA. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. *Ecology* 64:989–999.
- ERNST, C. H. 1971. Population dynamics and activity cycles of *Chrysemys picta* in southeastern Pennsylvania. *J. Herpetol.* 5:151–160.
- . 1986. Ecology of the turtle, *Sternotherus odoratus*, in southeastern Pennsylvania. *J. Herpetol.* 20:341–352.
- GATTEN, R. E., JR. 1974. Effect of nutritional status on the preferred body temperature of the turtles *Pseudemys scripta* and *Terrapene ornata*. *Copeia* 1974: 912–917.
- GRAHAM, T. E. 1984. *Pseudemys rubriventris*. *Predation*. *Herpetol. Rev.* 15:19–20.
- HAMMOND, K. A., J. R. SPOTILA, AND E. A. STANDORA. 1988. Basking behavior of the turtle *Pseudemys scripta*: effects of digestive state, acclimation temperature, sex, and season. *Physiol. Zool.* 61:69–77.
- HUTCHISON, V. H. 1979. Thermoregulation. In M. Harless and H. Morlock (eds.), *Turtles: Perspectives and Research*, pp. 207–228. Wiley, New York.
- JARLING, C., M. SCARPERI, AND A. BLEICHERT. 1984. Thermoregulatory behavior of the turtle, *Pseudemys scripta elegans*, in the thermal gradient. *Comp. Biochem. Physiol.* 77A:675–678.
- KLIMSTRA, W. D. 1959. Food habits of the cottonmouth in southern Illinois. *Nat. Hist. Misc.* 168: 1–8.
- LOVICH, J. 1988. Aggressive basking behavior in eastern painted turtles (*Chrysemys picta picta*). *Herpetologica* 44:197–202.
- MEEK, R., AND R. A. AVERY. 1988. Thermoregulation in chelonians. *Herpetol. J.* 1:253–259.
- MINCKLEY, W. L. 1966. Coyote predation on aquatic turtles. *J. Mammal.* 47:137.
- MOLL, E. O., AND J. M. LEGLER. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. *Bull. Los Angeles County Mus. Nat. Hist. Sci.* 11:1–102.
- MROSOVSKY, N. 1980. Thermal biology of sea turtles. *Amer. Zool.* 20:531–547.
- PACKARD, G. C., AND M. J. PACKARD. 1988. The physiological ecology of reptilian eggs and embryos. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*, Vol. 16B, pp. 523–605. Alan R. Liss, New York.
- PLATT, D. R. 1969. Natural history of the hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. *Univ. Kansas Publ. Mus. Nat. Hist.* 18:253–420.
- SCHWARZKOPF, L., AND R. J. BROOKS. 1985. Application of operative environmental temperatures to analysis of basking behavior in *Chrysemys picta*. *Herpetologica* 41:206–212.
- SHEALY, R. M. 1976. The natural history of the Alabama map turtle, *Graptemys pulchra* Baur, in Alabama. *Bull. Florida State Mus. Biol. Sci.* 21:47–111.
- SPOTILA, J. R., R. E. FOLEY, J. P. SCHUBAUER, R. D. SEM-LITSCHE, K. M. CRAWFORD, E. A. STANDORA, AND J. W. GIBBONS. 1984. Opportunistic behavioral thermoregulation of turtles, *Pseudemys scripta*, in response to microclimatology of a nuclear reactor cooling reservoir. *Herpetologica* 40:299–308.
- , AND D. M. GATES. 1975. Body size, insulation and optimum body temperatures of homeotherms. In D. M. Gates and R. B. Schmerl (eds.), *Perspectives of Biophysical Ecology*, pp. 291–301. Springer-Verlag, New York.
- WATERS, J. C. 1974. The biological significance of the basking habit in the black-knobbed sawback, *Graptemys nigrinoda* Cagle. Unpubl. M.S. Thesis, Auburn University, Auburn, Alabama. 81 pp.
- WILBUR, H. M., AND P. J. MORIN. 1988. Life history evolution in turtles. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*, Vol. 16B, pp. 387–439. Alan R. Liss, New York.
- WILLIAMSON, L. U., J. R. SPOTILA, AND E. A. STANDORA. 1989. Growth, selected temperature and CTM of young snapping turtles, *Chelydra serpentina*. *J. Therm. Biol.* 14:33–39.

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Socially Facilitated Behavior in Tadpoles of *Rana catesbeiana* and *Rana heckscheri* (Anura: Ranidae)

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Social facilitation results in a change in an individual's behavior resulting from the presence of other individuals (Clayton, 1978). It has been shown that the mere presence of passive spectators or conspecifics (audience effects) can improve the performance of motor tasks and non-learned responses in humans and other mammals (Zajonc, 1965; Bekoff, 1977). Similar responses have been shown to improve when behavior occurs in the presence of others who are simultaneously involved in the performance of the same task (coactive effects). Individual birds and mammals will consume significantly more food in the presence of others compared to amounts consumed in isolation (Zentall and Levine, 1972; Staddon, 1983). Coactive social facilitation has also been demonstrated in nest-building ants (Chen, 1937). Ants working in groups of two and three excavated significantly greater amounts of soil (proportionately) than those working alone. Motor responses such as running speed in rats and dogs and nest building in birds are also enhanced through social facilitation (see review by Clayton, 1978). Despite these previous studies, with the exception of research concerning kin selection, sibling recognition, and schooling behavior in larval amphibians (Wassersug, 1973; Blaustein and O'Hara, 1983; Waldman, 1985, 1986), investigations of socially facilitated behavior in fish, amphibians, and reptiles remain largely unexplored (Punzo, 1991). This is surprising in view of the adaptive significance that has been attributed to the schooling behavior of certain fishes (Breder, 1968) and larval amphibians (Bragg, 1968; Wassersug, 1973; Beiswenger, 1975; Caldwell, 1989). The purpose of the present study was to investigate the coactive effects of social facilitation on swimming speed (motor response) in tadpoles of the bullfrog, *Rana catesbeiana*, and the river frog, *Rana heckscheri*. The tadpoles of *R. heckscheri* are known to aggregate in large schools (Altig and Christensen, 1981), whereas those of *R. catesbeiana* do not form aggregations (Wassersug, 1973).

All tadpoles used in this study were reared from a single egg mass of each species collected from the Hillsborough River, Hillsborough County, Tampa, Florida (28°05'N, 82°21'W), during April, 1989. The eggs were placed in glass finger bowls containing aerated, filtered river water (FRW, pH 6.8 ± 0.1) and maintained at 25 ± 1.0 °C under a 14L:10D photoperiod regime. Upon hatching, tadpoles were housed in an aerated 2200 L glass aquarium and fed on a diet of rabbit pellets described by Altig and Christensen (1981). Forty-eight h prior to testing, groups of 12–15 tadpoles were transferred to 38 L aquaria containing aerated FRW. All experiments were conducted over a five day period using tadpoles that had just reached stage 25 of development (Gosner, 1960).