northern Mediterranean Sea, Turkey. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithson. Inst. Press, pp. 425-434.

GRAMENTZ, D. 1990. Beobachtungen an der Afrikanischen Weichschildkröte *Trionyx triunguis* (Forskål, 1775) in der Türkei. Herpetofauna (Weinstadt) 12(67):22-26.

GRAY, J.E. 1855. Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata (Tortoises). London: British Museum, 79 pp.

GRUVEL, A. 1931. Les etats de Syrie. Richesses marines et fluviales. Exploitattion actuelle-Avenir. Paris, 453 pp.

HAAS, G. 1951. On the present state of our knowledge of the herpetofauna of Palestine. Bull. Res. Counc. Israel 1:67-95.

HATHAWAY, R. 1972. Unanswered questions about sea turtles in Turkey. Balik ve Balikcilik (Ankara) 20:1-8.

ILANI, G. 1983. Soft-shelled turtles. Israel Land Nat. 8(3):126-127.

ILANI, G., AND SHALMON, B. 1984. Soft-shelled turtles in the crocodile river. Israel Land Nat. 10(1):36.

IVERSON, J.B. 1986. A Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately Printed, 283 pp.

KASPAREK, M., AND KINZELBACH, R. 1992. Distribution and bionomics of the Nile soft-shelled turtle, *Trionyx triunguis*, in the eastern Mediterranean. Zeitschr. Angewandte Zool. 78:137-159.

KINZELBACH, R. 1986. Recent records of the Nile soft-shelled turtle, *Trionyx triunguis*, and of the Euphrates soft-shelled turtle, *T. euphraticus*, in the Middle East. Zool. Middle East, Heidelberg 1:83-87.

LANZA, B., AND SASSI, A. 1966. Le testuggini terrestri e d'acqua dolce della Somalia (Reptilia, Testudines). Monit. Zool. Ital. 74 (Suppl.):257-272.

LORTET, L. 1887. Observations sur les tortues terrestres et paludines du bassin de la Méditerranée. Archives Mus. Hist. Nat. Lyon 4:1-26.

ORUC, A., DEMIRAYAK, F., AND SAT, G. 1996. Fishery in the eastern Mediterranean and its impact on sea turtles. Istanbul: Report for WWF International and DHKD. Coastal Management Section Report No. 96/1, 17 pp.

PENRITH, M.J. 1971. *Trionyx triunguis* (Forskal), a reptile new to the south-west African fauna. Madoqua 1(3):77-79.

SELLA, I. 1982. Sea turtles in the eastern Mediterranean and northern Red Sea. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithson. Inst. Press, pp. 417-423.

SERRUYA, C. 1978. Lake Kinneret. The Hague, 501 pp.

SIEBENROCK, F. 1913. Schildkröten aus Syrien und Mesopotamien. Wissenschaftliche Ergebnisse der Expedition nach Mesopotamien, 1910. Ann. Naturhist. Mus. Wien 27:171-225.

STRAUCH, A. 1890. Bemerkungen uber die Schildkrötensammlung im Zoologischen Museum der kaiserlichen Akademie der Wissenschaften zu St.-Petersburg. Mem. Ac. St. Petersb. (7)38(2):1-127.

VAN DEN BERK, V.M., LANGEVELD, M.J., AND SARIGUL, G. 1988. Observations of Cheloniidae and Trionychidae along the Cukurova coast, southern Turkey, Spring 1986 and 1987. In: Van Der Have, T.M., Van Den Berk, V.M., Cronau, J.P., and Langeveld, M.J. (Eds.). South Turkey Project – WIWO Report No. 22, pp. 167-171.

WERNER, Y.L. 1988. Herpetofaunal survey of Israel (1950-1985), with comments on Sinai and Jordan and on zoogeographical heterogeneity. In: Yom-Tov, Y., and Tchernov, E. (Eds.). The zoogeography of Israel. Dordrecht, Boston and Lancaster, pp. 355-388..

YOM-TOV, Y., AND MENDELSSOHN, H. 1988. Changes in the distribution and abundance of vertebrates in Israel during the 20th century. In: Yom-Tov, Y., and Tchernov, E. (Eds.). The zoogeography of Israel. Dordrecht, Boston and Lancaster, pp. 515-547.

Received: 3 June 1998
Reviewed: 26 July 1999
Revised and Accepted: 22 October 1999

Chelonian Conservation and Biology, 1999, 3(3):512–515

Cutaneous Surface Area in Freshwater Turtles

PAUL A. STONE[1] AND JOHN B. IVERSON[2]

[1]*Department of Biology, University of Central Oklahoma, Edmond, Oklahoma 73034 USA [Fax: 405-974-3824; E-mail: pstone@ucok.edu]*; [2]*Department of Biology, Earlham College, Richmond, Indiana 47374 USA*

Cutaneous surface area has a profound influence on the biology of organisms. Body size and shape determine the amount of cutaneous surface area in most organisms. However, turtles have a relatively inert bony shell (Dunson, 1986) that also affects cutaneous surface area variation (Stone et al., 1992). Because different turtle species often have different shell morphologies, turtles are unusual among vertebrates in that two species of similar size and shape can have significant differences in the amount of cutaneous surface area.

In freshwater turtles, two important physiological processes are linked to cutaneous surface area: aquatic respiration and desiccation. Turtles with high cutaneous surface area have increased potential for exchange of respiratory gases with water (Stone et al., 1992), but probably have increased susceptibility to desiccation (e.g., Costanzo et al., in press). These physiological processes may greatly influence an organism's behavior and ecology. For example, capacity for aquatic respiration may influence submergence times, vulnerability to surface predation, foraging efficiency, habitat requirements, and choice of hibernacula, whereas susceptibility to desiccation may influence dispersal, nesting ecology, ability to survive drought or extreme temperatures, and choice of hibernacula.

Given that cutaneous surface area may explain variation in so many important physiological and ecological aspects of the biology of freshwater turtles, it is surprising that only scattered measurements of cutaneous surface area have been made. This paper presents new data on cutaneous surface area in freshwater turtles, compares two methods for collecting such data, reviews previous data, and attempts to synthesize these data in a relevant ecological and physiological framework.

Methods. — We measured surface area using two methods. First, we skinned 56 common musk turtles, *Sternotherus odoratus*, that had been collected for other research (Iverson, 1984, and unpublished; Seidel et al., 1986). These turtles came from three sources: Kosciosko Co., Indiana (13 males and 22 females); Mayes Co., Oklahoma (1 male and 2 females); and Garland Co., Arkansas (13 males, 5 females). In addition to these turtles, we also skinned two eastern mud turtles (*Kinosternon s. subrubrum*) from the Arkansas site. Turtles were sacrificed immediately before skinning, and all of the skin of each turtle was removed. The skin was laid flat on toweling, covered with glass, and its outline traced on Mylar (a thin, transparent plastic used for art overlays). Skin area was then measured using an APPLE graphics tablet calibrated to 0.1 cm^2. The skin outline was traced on the tablet at least once clockwise and once counterclockwise. If the areas calculated were not within 2%, at least a third tracing was made. Reported areas are therefore means of at least two values. Tracing errors were usually < 1%.

Second, we used electrical tape to cover the entire skin surface of intact preserved specimens of the common snapping turtle, *Chelydra serpentina* (n = 11), spiny softshell turtle, *Apalone spinifera* (n = 5), and red-eared slider, *Trachemys scripta* (n = 6). Only animals that were preserved with the head, neck, and limbs fully extended were used. The tape was removed from the turtles, and cutaneous surface area was measured from the tape outline. This was done either by tracing the outline onto graph paper and counting the number of squares occupied by the tape, or by running the tape outline through a LI-COR 3000 leaf area meter. These methods are similar to those of Bagatto et al. (1997). We then compared data obtained from this method to those in Dunson (1986), who skinned freshly captured *C. serpentina* (n = 11) and *Apalone* spp. (*A. mutica*, n = 3, *A. spinifera*, n = 2).

The skin-covered shell of the smooth softshell turtle, *A. mutica*, is much more permeable to water than the bony shell of *C. serpentina*, *S. odoratus*, or *K. subrubrum* (Dunson, 1986). In fact, the shell of *A. mutica* is more permeable to water than the cutaneous surfaces of the three species above (Dunson, 1986). We therefore considered the shell of *A. spinifera* as a "cutaneous" surface, and the surface areas we report for this species are total surface areas (skin and shell). This is an important distinction because it more than doubles our estimates for cutaneous surface area for softshell turtles. If only the actual skin is considered as cutaneous surface area, softshell turtles have about the same cutaneous surface area as *C. serpentina* (Dunson, 1986).

For most turtles, mass was obtained directly from individuals prior to skinning. However, for all taped turtles and 17 of the skinned turtles, mass was estimated from carapace length using species-specific regression equations (Iverson, 1984, and unpublished).

We used analysis of covariance (ANCOVA), with mass as the covariate, to evaluate possible sources of variation in cutaneous surface area. First, we examined sexual and geographic variation in cutaneous surface area in the sample of *S. odoratus*. For this analysis, we included only adult turtles from Indiana and Arkansas, the two largest samples. Second, we made intraspecific comparisons of the two methods (skinning vs. taping) in *A. spinifera* and *C. serpentina* (the skinning data come from Dunson, 1986). Third, we made interspecific comparisons of cutaneous surface area in five species (*A. spinifera*, *C. serpentina*, *S. odoratus*, *K. subrubrum*, and *T. scripta*), using the combined data from this study, Dunson (1986), and Stone et al. (1992). After performing the general ANCOVA we performed Fisher PLSD multiple comparisons to investigate pairwise differences among species. The data for each analysis appeared to satisfy the assumptions implicit in ANCOVA (normality, homogeneity of variances, parallel slopes). All data were transformed using natural logarithms prior to statistical analysis. Statistical analyses were performed using Systat.

Results and Discussion. — The regression lines (cutaneous surface area vs. mass) obtained by the taping method and the skinning method (Dunson, 1986) were statistically indistinguishable for softshell turtles ($F = 0.26$, $p = 0.63$, Fig. 1) and for snapping turtles ($F = 0.003$, $p = 0.96$, Fig. 1). The taping method is a less destructive alternative to skinning that yields accurate estimates of cutaneous surface area, providing the animal is preserved with the head, neck, and limbs fully extended. Using the taping method will allow the collection of data on cutaneous surface area in turtles without sacrificing animals or damaging museum specimens.

There were sexual and geographic differences in cutaneous surface area in *S. odoratus* (Fig. 2). For Indiana specimens, males had higher cutaneous surface areas than females ($F = 52.35$, $p < 0.001$, Fig. 2). In addition, males from Indiana had higher cutaneous surface areas than males from Arkansas ($F = 4.20$, $p = 0.039$, Fig. 2). The sexual differences are at least partly the result of the enlarged tail and deep notch in the rear of the plastron of male *S. odoratus*, both of which contribute to increased cutaneous surface

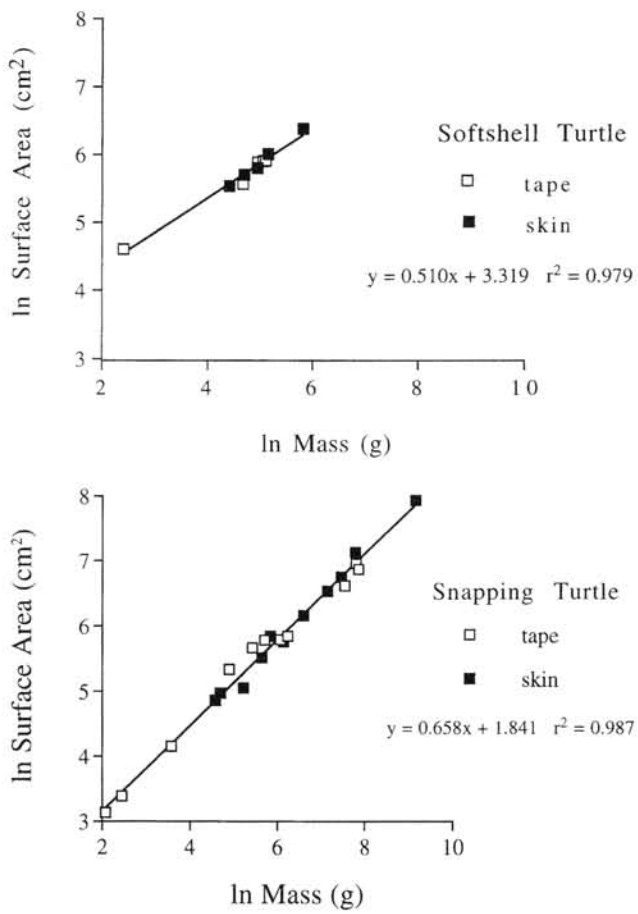

Figure 1. Cutaneous surface area vs. body mass in (**top**) softshell turtles, *Apalone* spp. (n = 10) and (**bottom**) snapping turtles, *Chelydra serpentina* (n = 22). Taped turtles are from this study, skinned turtles are from Dunson (1986).

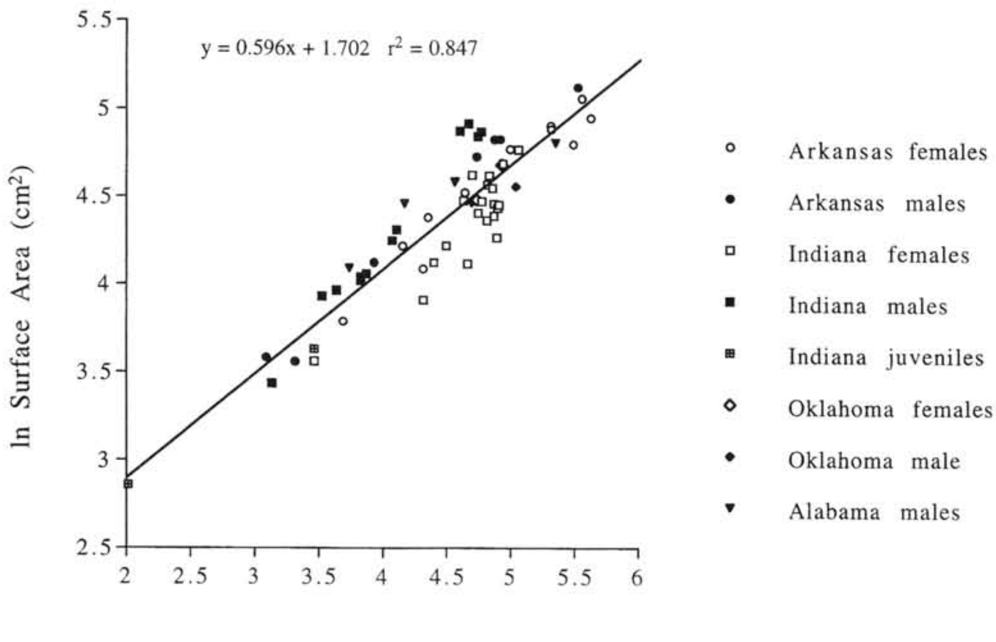

Figure 2. Cutaneous surface area vs. body mass in *Sternotherus odoratus* (n = 61 turtles, including 5 from Stone et al., 1992).

area. The geographic differences are consistent with latitudinal variation in the duration of hibernation: *S. odoratus* in northern latitudes hibernate underwater for several months, whereas more southern populations tend to have much shorter periods of hibernation (Ultsch, 1988). The increased cutaneous surface area of northern *S. odoratus* may promote increased aquatic gas exchange during these long bouts of hibernation.

To our knowledge, there have been three studies involving six species in which values for cutaneous surface area in turtles have been reported (Dunson, 1986; Stone et al., 1992; Bagatto et al., 1997). The largest sample size for any species in these studies was 11 animals (Dunson, 1986, *C. serpentina*). Given the sexual and geographic differences we report here for *S. odoratus*, a quantitative analysis of interspecific variation in cutaneous surface area in turtles may be premature.

However, such an analysis reveals significant differences in cutaneous surface area among North American freshwater turtles ($F = 120.9$, $p = 0.0001$, Table 1, Fig. 3). Multiple comparisons show that cutaneous surface area varies as follows: *A. spinifera* > *C. serpentina* > *S. odoratus* > *T. scripta* = *K. subrubrum* (Table 1, Fig. 3). These results agree with a similar analysis from a smaller data set in Stone et al. (1992). However, this pattern is somewhat complicated by variation in adult body size. When body size is considered, the small kinosternids have mass-specific surface areas more similar to the trionychids and exceeding those of the larger chelydrids and the emydids (Table 1).

Data on rates of desiccation and aquatic respiration are even more scarce than data on cutaneous surface area. Interspecific comparisons among the data that do exist are complicated by differences in the temperature at which measurements were taken, small sample sizes, and samples that do not represent the full range of body sizes that a given species attains. However, there are indications that rates of desiccation and aquatic respiration are correlated with cutaneous surface area, and with each other (Stone et al., 1992, Table 1). Turtles with high values for cutaneous surface area appear to be more susceptible to desiccation and more capable of aquatic respiration than turtles with less cutaneous surface area (Table 1).

Table 1. Surface area, mass, water loss, and aquatic oxygen uptake in representative North American freshwater turtles. Values are means and (source), except for the cutaneous surface areas, which are the calculated surface areas from the regression equations presented in Figs. 1, 2, and 3. Cutaneous surface areas are only provided if a particular species reaches the body mass specified by a given column.

	Cutaneous Surface Area (cm²)/g			Evap H_2O Loss	Aquatic O_2 Uptake
Species	(100 g turtle)	(1000 g turtle)	(10,000 g turtle)	(g/Kg x hr)	(ml/Kg x hr)
A. spinifera	2.89 (1,2)	0.94 (1,2)	–	10.28 (3)	11.05 (4)
S. odoratus	0.85 (1,4)	–	–	1.62 (5)	9.03 (4)
K. subrubrum	0.71 (1,4)	–	–	1.89 (6)	4.89 (4)
C. serpentina	1.30 (1,2)	0.59 (1,2)	0.27 (1,2)	1.34 (5)	1.95 (7)
T. scripta	0.78 (1)	0.27 (1)	–	0.80 (8)	1.19 (9)

1. This study
2. Dunson, 1986
3. Robertson and Smith, 1982 (25°C)
4. Stone et al., 1992 (23-25°C)
5. Ernst, 1968 (10-29°C)
6. Bogert and Cowles, 1947 (one turtle at 27°C)
7. Gatten, 1980 (20°C)
8. Bentley and Schmidt-Nielsen, 1970 (23°C)
9. Belkin, 1968 (22°C)

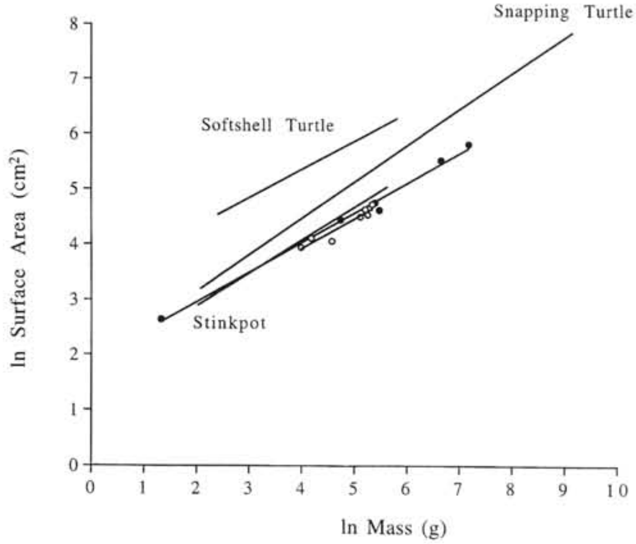

Figure 3. Cutaneous surface area vs. body mass in 5 species of North American turtles. The lines for softshell turtles, snapping turtles, and stinkpots are from Figs. 1 and 2; o = *Kinosternon subrubrum* ($n = 7$, including 5 from Stone et al., 1992), $y = 0.540x + 1.773$, $r^2 = 0.91$; ● = *Trachemys scripta* ($n = 6$), $y = 0.537x + 1.889$, $r^2 = 0.99$.

How the ecology of freshwater turtles is related to these physiological and morphological patterns is unclear. However, there are data that suggest that species prone to terrestrial activity have less cutaneous surface area than strictly aquatic species. In a comparative study involving three species of Australian side-necked turtles, tendency for terrestrial activity was negatively correlated with evaporative water loss (Chessman, 1984) and possibly cutaneous surface area (qualitative estimates based on Ernst and Barbour, 1989). The species in our study show a similar pattern, with the highly aquatic softshell turtles having high cutaneous surface area, and the more terrestrial mud turtles and red-eared sliders having low cutaneous surface area (Table 1).

Rates of aquatic respiration and desiccation are also affected by other physiological, behavioral, and morphological variables. For example, differences in skin permeability or perfusion rates could affect rates of water loss and cutaneous respiration (Burggren and Moalli, 1984; Feder and Burggren, 1985; Dunson, 1986). Such differences could explain why Bagatto et al. (1997) found similar rates of aquatic respiration in two species (*Staurotypus triporcatus* and *Kinosternon leucostomum*) that showed significant differences in cutaneous surface area. In addition, behavioral mechanisms such as closing the plastral hinge have marked affects on cutaneous water loss in *Kinosternon sonoriense* (Wygoda and Chmura, 1990). Finally, several studies have shown that significant rates of aquatic respiration can occur across non-cutaneous structures, such as the buccopharynx or the cloaca (e.g., Dunson, 1960; King and Heatwole, 1994).

It is clear that cutaneous surface area varies among species. This variation may influence differences in important physiological processes such as aquatic respiration and desiccation, as well as important ecological processes such as degree of terrestriality. More work is needed in all of these areas.

Acknowledgments. — We wish to thank R.G. Spencer and T. Mazzolini for taping turtles, V. Kuglar for help measuring turtle skins, W.A. Dunson for providing unpublished data, S. Hallgren and D. Ferris for providing access to the leaf area meter, J.M. Hranitz for statistical assistance, the Office of Faculty Research at UCO for financial assistance, and C. Guyer, P. King, A.G.J. Rhodin, and P.C.H. Pritchard for thoughtful reviews of the manuscript.

Literature Cited

BAGATTO, B., GUYER, C., HAUGE, B., AND HENRY, R.P. 1997. Bimodal respiration in two species of Central American turtles. Copeia 1997:834-839.

BELKIN, D.A. 1968. Aquatic respiration and underwater survival of two freshwater turtle species. Resp. Physiol. 4:1-14.

BENTLEY, P.J., AND SCHMIDT-NIELSEN, K. 1970. Comparison of water exchange in two aquatic turtles, *Trionyx spinifer* and *Pseudemys scripta*. Comp. Biochem. Physiol. 32:363-365.

BOGERT, C.M., AND COWLES, R.B. 1947. Moisture loss in relation to habitat selection in some Floridian reptiles. Amer. Mus. Novitates 1358:1-34.

BURGGREN, W.W., AND MOALLI, R. 1984. 'Active' regulation of cutaneous gas exchange by capillary recruitment in amphibians: experimental evidence and a revised model for skin respiration. Respir. Physiol. 55:379-392.

CHESSMAN, B.C. 1984. Evaporative water loss from three south-eastern Australian species of freshwater turtle. Aust. J. Zool. 32:649-655.

COSTANZO, J., LITZGUS, J., IVERSON, J., AND LEE, R. In press. Hydration state affects cold tolerance in turtles. J. Exp. Zool.

DUNSON, W.A. 1960. Aquatic respiration in *Trionyx spinifer asper*. Herpetologica 16:277-283.

DUNSON, W.A. 1986. Estuarine populations of the snapping turtle (*Chelydra*) as a model for the evolution of marine adaptations in reptiles. Copeia 1986:741-756.

ERNST, C.H. 1968. Evaporative water-loss relationships of turtles. J. Herpetol. 2:159-161.

ERNST, C.H., AND BARBOUR, R.W. 1989. Turtles of the World. Washington, DC: Smithsonian Inst. Press, 313 pp.

FEDER, M.E., AND BURGGREN, W.W. 1985. Cutaneous gas exchange in vertebrates: design, patterns, control and implications. Biol. Rev. 60:1-45.

GATTEN, R.E., JR. 1980. Aerial and aquatic oxygen uptake by freely-diving snapping turtles (*Chelydra serpentina*). Oecologia 46:266-271.

IVERSON, J.B. 1984. Proportional skeletal mass in turtles. Fla. Scient. 47:1-11.

KING, P., AND HEATWOLE, H. 1994. Partitioning of aquatic oxygen uptake among different respiratory surfaces in a freely diving pleurodiran turtle, *Elseya latisternum*. Copeia 1994:802-806.

ROBERTSON, S.L., AND SMITH, E.N. 1982. Evaporative water loss in the spiny soft-shelled turtle *Trionyx spiniferus*. Physiol Zool. 55:124-129.

SEIDEL, M.E., IVERSON, J.B., AND ADKINS, M.D. 1986. Biochemical comparisons and phylogenetic relationships in the family Kinosternidae (Testudines). Copeia 1986:285-294.

STONE, P.A., DOBIE, J.L., AND HENRY, R.P. 1992. Cutaneous surface area and bimodal respiration in soft-shelled (*Trionyx spiniferus*), stinkpot (*Sternotherus odoratus*), and mud turtles (*Kinosternon subrubrum*). Physiol. Zool. 65:311-330.

ULTSCH, G.R. 1988. Blood gases, hematocrit, plasma ion concentrations, and acid-base status of musk turtles (*Sternotherus odoratus*) during simulated hibernation. Physiol. Zool. 61:78-94.

WYGODA, M.L., AND CHMURA, C.M. 1990. Effects of shell closure on water loss in the Sonoran mud turtle, *Kinosternon sonoriense*. Southwest. Nat. 35:228-229.

Received: 19 June 1998
Reviewed: 26 July 1999
Revised and Accepted: 20 October 1999