Shell Kinesis in Juvenile Desert Tortoises, Gopherus agassizii

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ABSTRACT. – Inarticulate active shell kinesis includes the ability of some turtles and tortoises to reduce the size of the opening between the posterior margin of the carapace and the tips of the xiphiplastron by flexion without a hinge. This particular action pattern is designated posterior shell aperture reduction, or PSAR. When comparing mean percent kinetic PSAR capability of *Gopherus agassizii* neonates to juveniles and adults there is a significant relationship between neonates (8.4%), juveniles (12.5%), and adults (2.4%). When *G. agassizii* neonates were pecked and prodded with a raven model, their mean PSAR capability increased from 8.4 to 14.6%. Kinetic PSAR is also significant in juveniles and adults of *Homopus areolatus* (with a mean reduction of 11.2% in juveniles), and marginally perceptible in comparably sized juveniles of *Trachemys scripta elegans* (2.0%). As neonate and juvenile tortoises appear to have insufficient size or ossification to effectively protect them from large avian and carnivore predators, this inarticulate shell kinesis may protect the tail, soft tissues around the cloaca, and hind legs from smaller predators. But this action pattern could also be coincidental with general contractions of soft-bodied juveniles. Comparisons of juvenile *G. agassizii* with similarly sized juvenile *T. s. elegans* casts doubt on this alternative explanation; no comparable shell kinesis was evidenced in the latter species.

KEY WORDS. – Reptilia; Testudines; Testudinidae, Gopherus agassizii; Homopus areolatus; Trachemys scripta elegans; tortoise; turtle; carapace; plastron; kinesis; hinges; behavior; predation

My observations in the field first prompted this study. In May 1995 a radiotelemetered juvenile desert tortoise (*Gopherus agassizii*), 4 years old, was released from the Ft. Irwin, San Bernardino County, California, USA, tortoise hatchery – nursery exclosure (see Morafka et al., 1997). It was observed to reduce the posterior shell aperture to nearly complete closure when attacked by a raven. The raven was unable to seize the shell, or grasp the hind limbs. Contraction of the posterior shell aperture had completely obscured the view of the posterior soft tissues.

Chelonian shell hinges have often been assumed to function as active defenses, contracted to protect body extremities against predation (Bramble, 1974; Bramble and Hutchison, 1981; Greene, 1988). Other manifestations of shell kinesis actively or passively involve discrete movement of both carapacial and plastral elements, often without the demarcation of discrete externally visible hinges. Some plastral kinesis may passively depress the xiphiplastron to accommodate deposition of larger eggs in adult female Texas tortoise, G. berlandieri (Rose and Judd, 1991) and some south Asian batagurids (Moll, 1985; Pritchard, 1993). Other examples of passive kinesis in the absence of hinge mechanisms are found in the flexibility of carapacial and plastral elements in which several very different patterns of skeletal modifications have evolved to accommodate wedging into confined crevices, as illustrated by the pancake tortoise, Malacochersus tornieri (Ireland and Gans, 1972), and the Malayan softshell turtle, Dogania subplana (Pritchard, 1993).

The voluntary shell closure being studied here is an active hingeless action designated as posterior shell aperture

reduction, or PSAR. This motion reduces the posterior exposure of the tail, cloaca, and hind legs by the adduction downward of the proximate portion of carapace. While not addressing the underlying anatomy of this defense mechanism, this paper will examine the ontogeny of the response. It will also evaluate the PSAR in simulated predation trials. Previous literature (Bramble, 1974; Bramble and Hutchison, 1981; Bramble et al, 1984) has often referred primarily to active movement of shell components only by means of actual hinges (but see Pritchard, 1993). I will refer to any shell movement, flexion or motion not dependent upon hinges, active or passive in its initiation, as inarticulate kinesis.

I tested the possibility that neonates reduce the posterior shell aperture and that the threat of a predator elicits a greater reduction response. Specifically, I experimentally stimulated neonate and juvenile chelonians, of three taxa: Gopherus agassizii, Homopus areolatus, and Trachemys scripta elegans, to assess their response for reduction of the posterior shell aperture. This study examines PSAR as an active reduction of the aperture in response to specific stimulation. These experiments quantify the frequency and the degree of aperture response in a range of age and size classes of G. agassizii. Further experiments test for aperture contractions in comparable age or size classes among another testudinid and an emydid turtle. Experiments were designed to test the following null hypotheses: 1) no aperture reduction in any group tested, 2) no difference between ages of G. agassizii, 3) no difference between G. agassizii and H. areolatus, and 4) no difference between G. agassizii and T. s. elegans.

Reduction of the posterior shell aperture might be explained as an active defense if it were effective against native predators within a natural habitat. Such predators in the native habitat of *G. agassizii* could include coyotes, foxes, badgers, snakes, birds (especially ravens), and small rodents, arachnids, scorpions, and ants (U.S. Fish and Wildlife Service, 1994). While such an adaptationist explanation is attractive, it must not be assumed without evidence of causation. Such assumptions led to the belief that the gopher tortoise, *G. polyphemus*, excavated its burrow width as a purposeful accommodation of body size. In fact, burrow width was demonstrated to be a simple function of *G. polyphemus* forelimb positions in the excavation process, for which no more adaptationist explanation was necessary or appropriate (Wilson et al., 1991).

While it is uncertain how long the carapace and/or plastron remains flexible, it is certain that juvenile chelonians are smaller, weaker, and morphologically more susceptible to predation. Neonates (Morafka, 1994; Morafka et al., 2000) and juvenile tortoises will withdraw into their shells, perhaps both enhancing crypsis and simultaneously sheltering vulnerable extremities. In the case of small and young tortoises vulnerability to small and mesopredators becomes a particular issue (Greene, 1988; Morafka et al., 2000). Does the inarticulate kinesis phenomenon have adaptive significance, is it an exaptation linked to some other physical function, or is it simply a muscular contraction in response to being touched?

METHODS

For this study I employed experimental methods to elicit what appears to be a fixed action pattern using two innate releasers (Starr, 1994): 1) a cotton swab and/or a finger probe, and 2) a stuffed raven. All chelonians were measured along the midline carapace length (CL) from the posterior notch of the carapace to the nuchal notch to the nearest 0.1 mm. The posterior shell aperture of each tortoise was measured to the nearest 0.1 mm from the pygal notch to the center of the anal notch (Fig. 1). Initially each tortoise was probed with a cotton-covered swab or finger probe near and about the rear legs and cloacal vent until a shell closing response was elicited. Each tortoise was then remeasured across the previously described coordinates to determine degree of reduction. The index of posterior shell aperture reduction (PSAR) for morphometric comparisons was obtained by the following equation:

% reduction PSAR =
$$1 - \frac{\text{minimum aperture}}{\text{maximum aperture}} \times 100$$

Thirty-two naive *G. agassizii* neonates (in the sense of Morafka, 2002) were challenged. They were all hatched from eggs of captive tortoises provided by Southern California Chapters of the California Turtle and Tortoise Clubs. They were derived from approximately six clutches of eggs and randomly assigned to experimental groups to reduce clutch-specific effects on physical condition or behavior.

Other test groups were composed of individuals of randomly mixed origins as well. The first set of 32 captive hatched tortoises was challenged with the beak of a museum-prepared raven in the following manner. Each tortoise was placed upright on a large flat surface and allowed to adjust to the surface until it was moving about normally and then the posterior shell aperture was measured. The tortoise was then tested in a simulated raven attack. The raven model was moved over the tortoise to produce a shadow on the tortoise, which generally caused the tortoise to freeze in its position. The raven was then placed in front of the tortoise and a pecking action was made with the beak against the anterior carapace. Neonates first responded pugnaciously with the "hatchling hop" (Berry, 1986) and then would withdraw inside their shells, contracting to near closure. If a tortoise withdrew into its shell, the tortoise would then be turned plastron side up and the pecking motion was repeated on the posterior plastron. The posterior shell aperture was then remeasured. Other neonates, juveniles, and adults of G. agassizii, juveniles and adults H. areolatus, and juveniles T. s. elegans were challenged with finger probing or a swab using the same sequence of probes and turnovers as if the finger was the raven beak.

Raven-threatened *G. agassizii* neonate CL was 40.5– 52.6 mm. Finger-probed neonates aged 3 days to 1 month had CL 44.9–51.7 mm. Juveniles were 63.4–104.9 mm CL, age 3–8 yrs. Adults ranged from 280 to 350 mm CL. Ages of all neonate and juvenile *G. agassizii* tortoises were known because they were either hatched in incubators at our laboratory at California State University at Dominguez Hills, or were numbered tortoises hatched and maintained at our predator resistant study site located on the Ft. Irwin National Training Center in San Bernardino Co., California (see Morafka et al, 1997, for site and facility description).



Figure 1. Area of posterior shell aperture showing the relaxed position (left) and a contracted aperture (right) in *G. agassizii*, demonstrating the measurement of the aperture opening (b) in the two positions, with the difference (in percent) defined as the posterior shell aperture reduction (PSAR).

Neonate *Trachemys scripta elegans* were purchased from Thibodaux Live Supplies of Louisiana where they were supposedly hatched in their natural environment. Neonatal *T. s. elegans* were 34.8–37.2 mm CL, age 2 wks – 1 mo; juveniles had CL 92.7–99.0 mm, and were estimated to be 4– 7 yrs. I compared *G. agassizii* finger-probed neonates to *G. agassizii* juveniles and *T. s. elegans* neonates and juveniles using sets in comparing CL groups to see if there was a difference between families.

Homopus areolatus were provided by the West Cape Province Wildlife Commission, South Africa. They were maintained in planted and fenced outdoor pens in Los Angeles prior to measurement. Juveniles were 51.8–72.2 mm CL, and adults had CL 93.0–113.2 mm.

RESULTS

Those *G. agassizii* neonates that were challenged by a raven model demonstrated the greatest percent PSAR (mean 14.6%). The remaining groups are listed by their diminishing responses: *G. agassizii* juveniles (12.5%), *H. areolatus* juveniles (11.2%), *G. agassizii* non-raven threatened neonates (8.4%), *T. s. elegans* neonates (5.4%), *H. areolatus* adults (5.2%), *G. agassizii* adults (2.4%), and *T. s. elegans* juveniles (2.0%). In all tests where PSAR was observed, it was measurable even when the head and hind limbs had already been retracted, and was not simply incidental to those defensive movements.

The diagram in Fig. 2 compares finger probes vs. raven model in stimulating PSAR. Given the raven threat, neonate tortoises (n = 32) reduced the posterior shell aperture more (mean 14.6%) than those *G. agassizii* (n = 14, mean 8.4%) merely probed with a finger or touched with a swab. ANOVA arcsine was F = 9.781 and p = 0.0031 for this comparison.

I repeated the study for juveniles of *T. s. elegans* to test the response in relation to general shell softness by comparing juveniles of all three taxa. Figure 3 shows that juvenile *T. s. elegans* (n = 7, mean 2.0%) demonstrated less reduction than neonate *T. s. elegans* (n = 22, mean 5.4%). Juvenile *G. agassizii* (n = 45, mean 12.5%) had greater reduction than neonate *G. agassizii* (n = 14, mean 8.4%). ANOVA arcsine for the interspecies comparison was F = 91.384 with p <0.0001. The arcsine for the size comparison was F = 13.595with p = 0.0004. This may mean that the PSAR is not necessarily a function of the age of the tortoises but perhaps a function of size and/or taxon.

I expanded my study to another small testudinid, *H. areolatus*, to compare a small bodied species, never exceeding 150 mm CL, to *G. agassizii*, a species that attains over 250 mm CL. Figure 4 demonstrates that for species comparisons F = 196.057 and p < 0.0001, and that for size comparisons F = 18.564 and p < 0.0001. Note in Fig. 4 that there is a small difference between juvenile *G. agassizii* and juvenile *H. areolatus* (n = 4, mean 11.2), a minor difference between adult *G. agassizii* (n = 6, mean 2.4) and adult *H. areolatus* (n = 8, mean 5.2). However, there is a significant level of



Figure 2. Histogram of percent of posterior shell aperture reduction (PSAR) of *G. agassizii* neonates showing response to finger probes and to raven model. Standard error for finger probe is ± 1.46,



Figure 3. Histogram showing 2 pairwise contrasts of PSAR covering 4 separate experimental tests on *G. agassizii* neonates and juveniles, and *T. s. elegans* neonates and juveniles. Standard errors are as follows: ± 1.46 for neonate and ± 0.92 for juvenile *G. agassizii*; ± 0.62 for neonate and ± 0.92 for juvenile T. s. elegans.



Figure 4. A comparison of PSAR in experimental trials of juvenile and adult *G. agassizii* and *H. areolatus*. Standard errors are as follows: ± 0.92 for juvenile and ± 0.89 for adult *G. agassizii*; ± 3.56 for juvenile and ± 0.99 for adult *H. areolatus*.



Figure 5. Comparison of PSAR of samples of juveniles of *G. agassizii*, *H. areolatus*, and *T. s. elegans* in response to finger probing. Standard errors are ± 0.92 for *G agassizii*, ± 3.56 for *H. areolatus*, and ± 0.92 for *T. s. elegans*.



Figure 6. The ontogenetic cohort testing of *G. agassizii* of neonates, juveniles, and adults for differences in PSAR. Standard errors are ± 1.46 for neonates, ± 0.92 for juveniles, and ± 0.89 for adults.

difference between the juvenile and adult cohorts. Comparing juveniles and adults of both species by ANOVA arcsine demonstrated that juveniles were more capable of reduction than adults in both species. Therefore, although this phenomenon is not entirely restricted to juveniles, its strongest manifestation is in the juvenile cohort.

I repeated the study using ANOVA arcsine for juveniles of *T. s. elegans*. The results, displayed in Fig. 5, comparing samples of juveniles of different species show that the terrestrial testudinid species were more capable of PSAR than the one aquatic emydid (F = 49.251, p < 0.0001). *Gopherus agassizii* juveniles had a 12.5% mean, *H. areolatus* had slightly less with an 11.2% mean, and *T. s. elegans* tests produced a 2.0% mean, statistically an effectively negative response to aperture reduction.

I also compared different age-size classes among *G. agassizii*, examining the role of ontogenetic changes as inferred by CL. Comparing the neonates to juveniles to adults by ANOVA arcsine, as shown in Fig. 6, juveniles manifest significantly greater percent PSAR (F = 7.115, p = 0.0017).

DISCUSSION

Active shell kinesis of parts of the carapace and plastron are common in small-sized species of chelonians (but see Pritchard, 1993). If such kineses are generally associated with small size, they may be a fundamental characteristic of young tortoises (Richmond, 1964). Thus, an adaptive explanation of PSAR could prove unnecessary if it is just an expression of the flexibility of small, poorly ossified shells. However, active inarticulate kinesis does not appear to be a simple function of size, as it is not found in all young turtles and tortoises, as illustrated by the results of tests of T. s. elegans in this study. Further, adult G. agassizii have little kinetic ability to reduce the posterior shell aperture, even when adult females may manifest the passive depression of the xiphiplastron previously cited for G. berlandieri. However, the reverse is manifest in the ontogeny in the passive carapacial kineses. For the pancake tortoise, (Malacochersus tornieri) (Obst, 1988) and the Malayan softshell turtle, Dogania subplana, flexibility is most evident in adults (Pritchard, 1993).

Data from field studies confirm the special vulnerability of young tortoises to predation. Wilson (1994) noted that of eleven subadult G. polyphemus found dead on her study plot, three showed evidence of predation by raptors, and the other eight seemed to have been eaten by mammals as their shells were torn apart in a manner indicative of mammalian predation. This was 34% out of a total of 32 radiotagged juvenile tortoises during one year of study. Morafka et al. (1997) indicated that 18 of 24 (75%) G. agassizii juveniles in an unroofed enclosure were lost to avian predators, and that 8 of 12 (67%) free-ranging radiotransmittered juveniles were similarly preyed upon. Additionally, Morafka (1997) reported that 3- and 4-yr old desert tortoises were released from their enclosure and only 66.7% survived. In contrast, total annual mortality for adult G. agassizii has been shown to be as low as about 2% (Berry and Turner, 1986).

There is considerable variation in the length of time that the plastron and carapace of desert tortoises remain soft. Ossification of the shell may be insufficient to provide resistance to predators for up to 7 yrs (Morafka, 1991). Luckenbach (1982), Appleton (1986), Adest et al. (1989b), and Morafka (1994) indicated that the plastra in both *G. flavomarginatus* and *G. agassizii* remained relatively soft for 5–10 yrs.

Neonate and juvenile desert tortoise shells have been found at raven nesting sites with holes punctured in the carapace or plastron (Boarman, 1993; Morafka et al., 1997).

Ravens may also scavenge tortoise carcasses from other predators, or may obtain the remains of recent deaths due to disease or dehydration. High raven densities may be relatively new to the Mojave Desert (Boarman, 1993). Therefore, the long term roles of other tortoise predators might be overlooked, especially those of non-passerine avian predators, as well as canids, small cats, some mustelids such as badgers (Taxidea taxus), and many viverrids. In California deserts juvenile tortoise carcasses have been found in association with nests and perches of eagle, Aquila chryaetos, roadrunner, Geococcyx californicus, hawk, Buteo jamaicensis, and owl, Athene cunicularia (Boarman, 1993). Kinesis (PSAR) may be most effective for juveniles where the carapace had hardened somewhat but the plastron was still slightly soft. Smaller avian predators such as shrikes, jays (Greene, 1988), buteos, and accipitors would be unable to readily penetrate the carapace or gain access to the soft plastron unless they could overturn the tortoise. Although the benefits of PSAR are potentially greater in young tortoises because of their obvious vulnerability, the overall effectiveness of shell kinesis for predator protection remains to be established, possibly in arenas where captive prey-predator encounters may be stereotyped and quantified, perhaps following a methodology adopted from Okamoto (2002).

Reduction may be effective against smaller mammalian predators that gnaw, such as insectivores and rodents. Grasshopper mice (*Onychomys torridus*) might use tortoises as a rich source of protein. Tail and hind limbs might also be protected from attacks from large predatory arthropods, such as scorpions and beetles. Such mechanical protection as PSAR however, would not provide protection against very small arthropods, such as mosquitoes, ticks, flies, ants, or any other known insects. Likewise PSAR would afford no protection against very large predators, like canids, which could swallow young tortoises whole.

Several alternative functional consequences of juvenile shell kinesis in tortoises may be considered. Could it be for conservation of water; that is to prevent water loss in an arid environment? If that were the case the PSAR would be evident when the tortoise was at rest. Reduction is a definite motion of actively drawing the carapace down and, as a response to touch, an active depression. Might it be an ontogenetic precursor to female xiphiplastral hinging described by Rose and Judd (1991) to enlarge the posterior shell aperture for egg deposition? Or is this manifestation a non-functional byproduct of muscle contraction on a poorly calcified shell? Indeed, Ernst and Barbour (1989) recognized greater flexibility of young tortoise shells, which might predispose such individuals to more general body contractions when they were probed. The responsive nature of inarticulate kinesis in juvenile tortoises suggests that it is an active protective manifestation, rather than a coincidental biproduct of general body movements or contraction. This conclusion is supported by three observations: 1) an innate releaser, fixed action pattern elicited most strongly in response to the raven model, 2) the correlation of small shell

length with the incidence of kinesis is not universal to all young chelonians, virtually absent in the generalized and presumably representative juvenile *T.s. elegans*, and 3) PSAR is an active adduction of the posterior carapace, not simply a passive flexor in response to extreme pressure, or a motion coincidental with hind limb contraction.

This study has confirmed that neonate and juvenile *G. agassizii* can actively reduce the posterior shell aperture. However, future studies need to determine the anatomical mechanism involved in this reduction phenomenon, the role of crypsis in hatchling predator/prey relations, and as well to identify predators that would be deterred by PSAR. This phenomenon also needs to be examined in *G. agassizii* of CL between 100–200 mm, other *Gopherus* species, and a thorough survey of other testudinids.

ACKNOWLEDGMENTS

I thank D.J. Morafka for suggesting this investigation and for many useful discussions of the phenomenon, as well as moral support and guidance in the writing of this paper. I also thank D. Hadley for the tortoise illustrations; W. Alley for assistance with the statistical analysis and graphs; and D. Richards for her data on exotic species compiled in 1987. This study was funded by contracts awarded to D.J. Morafka by So. California Edison, World Wildlife Fund, and the Directorate of Public Works (DPW) of the U.S. Army National Training Center at Ft. Irwin, California. I am particularly appreciative of the continued support of M. Quillman, Natural and Cultural Resources Director, DPW, Ft. Irwin.

LITERATURE CITED

- ADEST, G.A., AGUIRRE L., G., MORAFKA, D.J., AND JARCHOW, J.V. 1989a. Bolson tortoise (*Gopherus flavomarginatus*) conservation: I. Life history. Vida Silvestre Neotrop. 2(1):7-13.
- ADEST, G.A., AGUIRRE L., G., MORAFKA, D.J., AND JARCHOW, J.V. 1989b. Bolson tortoise (*Gopherus flavomarginatus*) conservation: II. Husbandry and reintroduction. Vida Silvestre Neotrop. 2(1):14-20.
- APPLETON, A. 1986. Further observations of Bolson tortoises (Gopherus flavomarginatus) at the Appleton-Whittell Research Ranch. Desert Tortoise Council, Proceedings of the 1983 Symposium, pp. 108-114.
- BERRY, K.H. 1976. A comparison of size classes and sex ratios in four populations of the desert tortoise. Desert Tortoise Council, Proceedings of the 1976 Symposium, pp. 38-50.
- BERRY, K.H. 1981. State report California. Desert Tortoise Council Proceedings 1981 Symposium, pp. 49-52.
- BERRY, K.H. 1986. Desert tortoise (*Gopherus agassizii*) relocation: implications of social behavior and movements. Herpetologica 42(1):113-125.
- BERRY, K.H. AND NICHOLSON, L.L. 1984. Attributes of populations at twenty-seven sites in California. In: Berry, K.H. (Ed.). The status of the desert tortoise (*Gopherus agassizii*) in the United States. Report to U.S. Fish and Wildlife Service from the Desert Tortoise Council on Order No. 11310-0083-81, pp. 154-241.
- BERRY, K.H. AND TURNER, F.B. 1986. Spring activities and habits of juvenile desert tortoises. *Gopherus agassizii*, in California. Copeia 1986(4):1010-1012.
- BOARMAN, W.I. 1993. When a native predator becomes a pest: a case

study. In: Majumdar, S.K., et al. (Eds.). Conservation and Resource Management. Pennsylvania Academy of Science.

- BOYCOTT, R.C. AND BOURQUIN, O. 1988. The South African Tortoise Book. A Guide to South African Tortoises, Terrapins and Turtles. Johannesburg: Southern Book Publ., 148 pp.
- BRAMBLE, D.M. 1974. Emydid shell kinesis: biomechanics and evolution. Copeia 1974(3):707-727.
- BRAMBLE, D.M. AND HUTCHISON, J.H. 1981. A reevaluation of plastral kinesis in African turtles of the genus *Pelusios*. Herpetologica 37(4):205-212.
- BRAMBLE, D.M., HUTCHISON, J.H., AND LEGLER, J.M. 1984. Kinosternid shell kinesis: structure, function and evolution. Copeia 1984:456-475.
- ERNST, C.H. AND BARBOUR, R.W. 1989. Turtles of the World. Washington, DC: Smithsonian Institution Press, 313 pp.
- GANS, C. 1974. Biomechanics: An Approach to Vertebrate Biology. Philadelphia, PA: J.B. Lippincott.
- GERMANO, D.J. 1988. Age and growth histories of desert tortoises using scute annuli. Copeia 1988(4):914-920.
- GERMANO, D.J. 1989. Growth and life histories of North American tortoises (genus: *Gopherus*) with special emphasis on the desert tortoise (*G. agassizii*). Ph.D. Thesis, University of New Mexico, Albuquerque.
- GRANT, C. 1936. The southwestern desert tortoise, *Gopherus agassizii*. Zoologica 21:225-229.
- GREENE, H.W. 1988. Antipredation mechanisms in reptiles. In: Gans, C. and Huey, R.B. (Eds.). Biology of the Reptilia. Vol. 16. New York: Alan R. Liss, pp. 1-152.
- IRELAND, L.C. AND GANS, C. 1972. The adaptive significance of the flexible shell of the tortoise *Malacochersus tornieri*. Anim. Behav. 20:778-781.
- LUCKENBACH, R.A. 1982. Ecology and management of the desert tortoise (*Gopherus agassizii*) in California. In: Bury, R.B. (Ed.). North American Tortoises: Conservation and Ecology. U.S. Dept. Int. Fish Wildl. Serv. Wildl. Res. Rep. No. 12, pp. 1-37.
- MOLL, E.O. 1985. Comment: sexually dimorphic plastral kinesis the forgotten papers. Herp. Rev. 16(1):16.
- MORAFKA, D.J. 1994. Neonates: missing links in the life histories of North American tortoises. In: Bury, R.B. and Germano, D.J. (Eds.). Biology of North American Tortoises. Fish and Wildlife Research 13:161-173.
- MORAFKA, D.J. AND GRIFFITH, M.J. 1991. Second 1991 Progress Report of Desert Tortoise Biology. Southern California Edison Company, System Planning and Research, Environmental Affairs. Rosemead, California.
- MORAFKA, D.J. AND JOYNER, M. 1990. Neonatal Desert Tortoise (*Gopherus agassizii*) Biology, Second Interim Report. Southern California Edison Company, System Planning and Research, Environmental Affairs.
- MORAFKA, D.J., BERRY, K.H., AND SPANGENBERG, E.K. 1997. Predatorproof field enclosures for enhancing hatching success and survivorship of juvenile tortoises: a critical evaluation. In: Van Abbema,

J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference. N.Y. Turtle and Tortoise Society, pp. 147-165.

- MORAFKA, D.J., SPANGENBERG, E.K., AND LANCE, V.A. 2000. Neonatology of reptiles. Herpetol. Monogr. 14:353-370.
- OBST, F.J. 1986. Turtles, Tortoises and Terrapins. Leipzig: Edition Leipzig, 231 pp.
- Okamoto, C.L. 2002. An experimental assessment of color, calcium, and insect dietary preferences of captive juvenile desert tortoises (*Gopherus agassizii*). Chelonian Conservation and Biology 4(2):359-365.
- PRITCHARD, P.C.H. 1979. Encyclopedia of Turtles. Neptune, NJ: TFH Publ., 895 pp.
- PRITCHARD, P.C.H. 1993. Carapacial pankinesis in the Malayan softshell turtle, *Dogania subplana*. Chelonian Conservation and Biology 1(1):31-36.
- RICHMOND, N.D. 1964. The mechanical functions of the testudinate plastron. Amer. Midl. Nat. 72(1):50-56.
- ROMER, A.S. 1956. Osteology of the Reptiles. Chicago: Univ. Chicago Press, 772 pp.
- ROSE, F.L. AND JUDD, F.W. 1991. Egg size versus carapacexiphiplastron aperture size in *Gopherus berlandieri*. J. Herpetol. 25(2):248-250.
- STARR, C. 1994. Biology: Concepts and Applications, 2nd Edition. Belmont, CA: Wadsworth Publishing.
- STUBBS, D. 1989. Testudo horsfieldi, Horsfield's tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 37-38.
- U.S. FISH AND WILDLIFE SERVICE. 1994. Desert tortoise (Mojave population) Recovery Plan. Portland, OR: U.S. Fish and Wildlife Service, 73 pp.
- WEINSTEIN, M. AND BERRY, K.H. 1987. Morphometric analysis of desert tortoise populations. Report No. CA950-CT7-003. US Department of Interior, Bureau of Land Management, Riverside, California.
- WEINSTEIN, M., BERRY, K.H., AND TURNER, F.B. 1987. An analysis of habitat relationships of the desert tortoise in California. Report to Southern California Edison Co.
- WILSON, D.S. 1991. Estimates of survival for juvenile gopher tortoises, *Gopherus polyphemus*. J. Herpetol. 25(3):376-379.
- WILSON, D.S., MUSHINSKY, H.R., AND MCCOY, E.D. 1991. Relationship between gopher tortoise body size and burrow width. Herp. Review 22(4):122-124.
- WILSON, D.S., MUSHINSKY, H.R., AND MCCOY, E.D. 1994. Home range, activity, and use of burrows of juvenile gopher tortoises in central Florida. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American Tortoises. Fish and Wildlife Research 13:147-160.

Received: 30 January 2001

Reviewed: 24 June 2002

Revised and Accepted: 24 September 2002