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An Experimental Assessment of Color, Calcium, and Insect Dietary Preferences of Captive Juvenile Desert Tortoises (*Gopherus agassizii*)

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ABSTRACT. – Captive-bred juvenile desert tortoises (*Gopherus agassizii*) were placed in a trial arena to study feeding preferences regarding color, calcium, and insects. When presented with choices of colored food, the observed preference was green > yellow > red > orange. When presented with a choice between colored food and eggshell the observed preference was eggshell > green > yellow. When presented with a choice between colored food and cuttlebone the observed preference was cuttlebone > green > yellow. When presented with a choice between colored food and insects the observed preference was crickets > mealworms > green. These results suggest that juvenile desert tortoises may prefer some food colors over others and may consume insects opportunistically. This information may prove valuable for future captive breeding programs and for selecting an inoculation medium for disease vaccination.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; diet; food preference; herbivore; insect food; calcium; protein

Most published literature on desert tortoises (*Gopherus agassizii*) is based upon studies of adults. However, studies on naive young tortoises may provide insights on innate dietary preferences. Unfortunately such studies are rare in part because of difficulties in locating juvenile tortoises in the field (Douglass, 1978; Berry and Turner, 1986; Morafka, 1994; Goodwin et al., 1995).

This study addressed three null hypotheses about feeding preferences of juvenile *Gopherus agassizii* (Okamoto, 1995). These included: 1) no feeding preferences are manifest among colored food pellets, 2) no feeding preferences are manifest among bone, eggshell, or green food pellets, and 3) no feeding preferences are manifest in the choice among different insect food items.

METHODS

Most of the juvenile tortoises (age 1–2 yrs; $n = 20$) used in the trials were drawn from individuals hatched from the eggs of captives originally collected from western Mojave Desert populations ($n = 16$). Four individuals were from a Sonoran lineage (Tucson–Phoenix, Arizona) assemblage. The tortoises ranged in size from 54.5 mm to 89.2 mm in midline straight carapace length.

When they were not being tested, the tortoises were housed in 2 screened outdoor enclosures (152.4 cm x 61.0 cm x 152.4 cm). The enclosure substrate consisted of rabbit food pellets (alfalfa meal) which prevent gut impaction during accidental ingestion. When the juveniles were not being tested, they were fed a daily diet of finely chopped, mixed vegetables which included carrots, cauliflower, and broccoli. Finely chopping these vegetables prevented the tortoises from favoring one color over another. This food was supplemented by vitamins every other day as suggested by herpetoculturists (De Vosjoli, 1990, 1991).

The tortoises were randomly assigned to 4 test sets which included 5 juveniles in each set. Each set was placed into the trial arena for 1 hr and actions were recorded with a Sony™ Hi-8 camcorder. A different set was tested each day and only 1 trial was performed each day. Food was withheld from each test set for 24 hrs prior to the testing period. The testing apparatus consisted of an indoor circular trial arena measuring 88.9 cm in diameter (17.8 cm deep). Both light and heat were provided by two 150 watt incandescent flood lamps which were placed 78.7 cm away from the substrate. Hot areas in the arena averaged 32.8°C and the cooler areas had an average of approximately 23.9°C. As in the outdoor enclosure, the indoor apparatus also utilized rabbit food pellets as the substrate (2.5 cm deep). During the first experiment, the tortoises were exposed to colored food items only (26 trials total). In the second set of experiments, eggshell (8 trials total) or cuttlebone (2 trials total) and colored food items were presented as diet choices to the tortoises. In the third experiment, coleopteran larvae (*Tenebrio molitor*), crickets (*Acheta domesticus*), and green colored food items were presented to the tortoises as food item choices (10 trials total).

A behavioral inventory has already been created for the desert tortoise (Ruby and Niblick, 1994). One of the behaviors noted here and not included in that inventory was a head movement which is designated here as a "bump." In this behavior, the tortoise extends its head toward a food object and literally bumps the object with its mouth closed. This was a different behavior than a true bite when the mouth was open. Bumping may assist in food identification as a sensing device. Tortoises may be testing strength of resistance of a food item and olfactory chemosensing. Based on pilot studies (3 trials), bumps led to a bite approximately 60% of the time (45 total bumps), and 1 bite usually led to a series of 5 or more repeated bites. During the preference tests only the first bump or bite was recorded, not all subsequent bites during a feeding action. Because the trials recorded behaviors which indicated preference and intention, both bumps and bites were scored equally. The study was broken up into 3 sections.

Part 1: Color Preference Test. — Tortoises were exposed to arrays of 4 different colored food pellets (green, red, yellow, and orange). Each pellet measured ca. 45 mm by 10 mm. These were prepared commercially by Pretty Bird International, Inc. Only color varied among test food items. Five pieces each of the 4 colors were provided in equal numbers and scattered randomly across the trial arena. There were 26 trials on consecutive days.

Part 2: Color vs. Bone/Eggshell. — Tortoises were exposed to 2 colored pellets (green and yellow) along with eggshell or cuttlebone. The latter 2 items were offered to represent potential calcium sources similar to eggshell and weathered bone fragments that might be encountered in the field. Five pieces each of the 2 colors were scattered across the trial arena along with 5 pieces of either eggshell (8 trials) or cuttlebone (2 trials). All of the bone/eggshell trials were completed on consecutive days beginning with the eggshell tests.

Part 3: Color vs. Insect. — Tortoises were exposed to colored pellets (green) along with orthopteran adult crickets (*Acheta domesticus*) and large coleopteran larvae (*Zophobas morio*, known as "super mealworms" in the pet trade). Five pieces of the green pellets were scattered throughout the trial arena along with 5 samples of both crickets and mealworms. Crickets and mealworms were chosen because they resemble insects such as larval lepidopterans and coleopterans or adult orthopterans which may be encountered by tortoises in the field. To prevent the insects from escaping the testing area and the tortoises, they were either frozen or disabled by crushing their heads with a forceps. Even though the insects had their heads crushed, they continued body movements (twitching or slow crawling). There were 5 trials of stunned (live) insects, and 5 trials of frozen (dead) insects. The dead/live insect choices were alternated randomly during the trial periods. All of the insect trials occurred on consecutive days.

RESULTS AND DISCUSSION

Part 1: Color Preference Test. — The first study suggested that the tortoises are able to distinguish between colors. Results indicated that a significant difference existed between color choices ($\chi^2 = 153.1862$, 3 df, $p < 0.001$). A total of 623 bumps and bites were recorded on the colored food choices. Out of these, 284 (45.6%) were directed toward the green pellets, 145 (23.3%) were toward yellow pellets, 111 (17.8%) were on the red pellets, and 83 (13.3%) were on the orange pellets (Fig. 1).

Numerous species of both reptiles and amphibians are able to differentiate between colors (Quaranta, 1952; Kasperczyk, 1971; Nuboer, 1986; Hews and Dickhaut, 1989). Chelonians (notably tortoises) possess color vision (Alderton, 1988) and can distinguish between hues (Walls, 1942). In reptiles recognition of colors may be used for food searching (Lostakova et al., 1979).

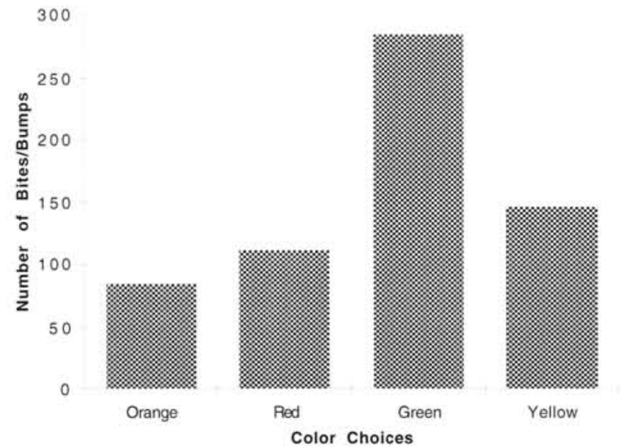

Figure 1. Color selection by juvenile tortoises among 4 differently colored food pellets.

Other studies on tortoises have reported similar outcomes to color preference tests. In one study of *G. berlandieri*, the tortoises preferred foods colored red or green over blue (Grant, 1960; Auffenberg and Weaver, 1969). In another, *Testudo graeca, T. hermanni, Geochelone pardalis*, and *G. (Aldabrachelys) gigantea* exhibited feeding behavior when exposed to red or green/yellow colors (Lostakova et al., 1979).

It seems that in at least some tortoises, certain sensory organs are used selectively to find food. *Testudo graeca, T. hermanni, Geochelone pardalis*, and *G. gigantea* search for food using sensory organs in the following order: color, perception, olfaction, and taste (Lostakova et al., 1979). *Gopherus berlandieri* uses sensory organs in the order of color perception, olfaction, and taste (Grant, 1960).

Most literature indicates that free ranging *G. agassizii* prefer to consume green forbs, grasses, and shrubs (Woodbury and Hardy, 1948; Burge and Bradley, 1976; Hansen et al., 1976; Burge, 1977; Nagy and Medica, 1977; Barrow, 1979; Coombs, 1979; Turner et al., 1984). One study indicated that *G. agassizii* prefers stems and leaves of plants over flowers (Jennings, 1993). Perhaps this is why the tortoises in this study chose green over the other colors. Yellow may have been a second choice because it is a recognizable color to tortoises. During the spring season, free ranging tortoises have been observed to consume yellow flowers of the desert dandelion *Malacothrix glabrata*. Color preferences may vary more between individuals than species (see individual vs. species differences for *Geochelone carbonaria* and *G. denticulata* in Moskovits and Bjorndal, 1990). Furthermore, food color preferences may shift in response to changes in available food composition and the abundance of individual items (Grant, 1960; Auffenberg and Weaver, 1969). Such changes commonly occur over seasons, different years, and different soils.

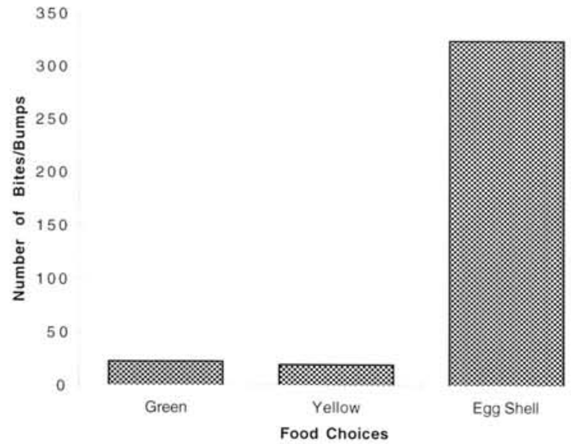

Figure 2. Food color vs. eggshell selection by juvenile tortoises.

Part 2: Color vs. Bone/Eggshell. — The results of these trials suggested that juvenile desert tortoises will choose eggshell and cuttlebone over green and yellow colors. Differences existed between the frequencies of color or eggshell choices ($\chi^2 = 494.6649$, 2 df, $p < 0.001$). During the eggshell trials, a total of 370 bumps and bites were recorded. Out of these 325 (87.8%) were on the eggshell, 24 (6.5%) were on the green-colored food, and 21 (5.7%) were on the yellow-colored food (Fig. 2).

During the cuttlebone trials, a total of 327 bumps and bites were recorded on the food choices. Although a test of heterogeneity could not be analyzed due to small sample size, the tortoises were more attracted to the cuttlebone than either of the colors. During this trial, 299 (91.5%) bites were on the cuttlebone, 23 (7.0%) were on the green-colored food, and 5 (1.5%) were on the yellow-colored food (Fig. 3). Only 2 trials were completed because the tortoises consumed most of the cuttlebone during this time.

Because a white food item of the same size as the green and yellow food item was not tested, it is unknown whether the tortoises actually preferred the color white or were attracted to the eggshell or cuttlebone. However, both eggshell and cuttlebone are calcium sources, and both bone and eggshell are white items that are available to tortoises. In many vertebrates, calcium requirements are higher for rapidly growing juveniles as well as gravid females. Tortoises especially have a substantial metabolic demand for calcium due to the mass of bone in their hard shells (Esque and Peters, 1994).

Tortoises commonly investigate and bite objects that are white in color, including stones (*pers. obs.* in the field at Fort Irwin, California), soils high in calcium content (Hansen et al., 1976; Marlow and Tollestrup, 1982; Esque and Peters, 1994), and bones (Carr, 1952; Auffenberg and Weaver, 1969; Sokol, 1971; Esque and Peters, 1994; Spangenberg, 1995), and eggshells (Nichols, 1953; Sokol, 1971). These items may be readily consumed when encountered in the field as available sources of calcium and other needed elements.

Part 3: Color vs. Insect. — A significant difference existed between color or live insect choices ($n = 261$, $\chi^2 = 38.3678$, 2 df, $p < 0.001$), suggesting that these juvenile desert tortoises preferred insect material over colored food. During this trial, 114 (43.7%) bites were recorded on the live crickets, 107 (41.0%) were on the live coleopteran larvae, and 40 (15.3%) were on the green-colored food (Fig. 4).

Differences were also observed between color or dead insect choices ($n = 193$, $\chi^2 = 47.5440$, 2 df, $p < 0.001$), with 97 bites (50.2%) on the frozen crickets, 75 (38.9%) on the frozen coleopteran larvae, and 21 (10.9%) on the green food (Fig. 4). The tortoises were found to readily bite and sometimes completely consume both crickets as well as coleopteran larvae.

While observations of wild tortoises consuming insect or other animal matter are rare, references do exist in the literature (Table 1). For example, insect parts have been found in fecal samples from many reptiles that are considered to be strict herbivores. Moskovits and Bjorndal (1990) did not observe insectivory in foraging tortoises, however, insects were recovered in scat analysis. Insects appear in scats fairly regularly in Sonoran Desert Arizona *G. agassizii* populations (T. Van Devender, *pers. comm.*). It is possible that insects appear in tortoise scat due to an incidental bite where the insect may have been consumed while it hid under a leaf or inside a flower. This would occur without any feeding preferences of the tortoises. However, Carr (1952)

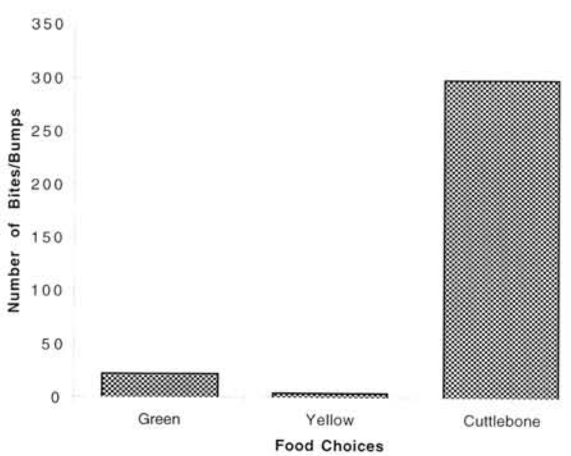

Figure 3. Food color vs. cuttlebone selection by juvenile tortoises.

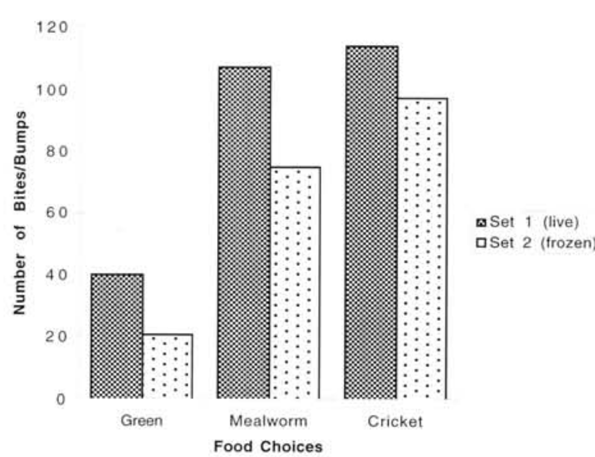

Figure 4. Food color vs. insect selection by juvenile tortoises.

Table 1. Records of tortoise feeding observations on non-vegetative material or scat containing non-vegetative material. * Indicates captive feeding observation.

Species	Food Material	Source
*Chersina angulata**	Meat	Pritchard, 1979
*Chersina angulata**	Raw Beef, Dog Food	Ernst and Barbour, 1989
Geochelone carbonaria	Carrion	Ernst and Barbour, 1989
Geochelone carbonaria	Invertebrate/Vertebrate (unspecified)	Moskovits et al., 1990
Geochelone carbonaria	Carrion	Walker, 1989a
*Geochelone chilensis**	Meat	Walker, 1989b
Geochelone denticulata	Carrion	Ernst and Barbour, 1989
Geochelone denticulata	Invertebrate/Vertebrate (unspecified)	Moskovits et al., 1990
Geochelone elegans	Carrion	Ernst and Barbour, 1989
Geochelone elegans	Snails	Moll, 1989a
Geochelone gigantea	Dead Crabs, Dead Tortoises, Feces	Ernst and Barbour, 1989
*Geochelone gigantea**	Dead Tortoises, Pigets, Chickens	Pritchard, 1979
Geochelone pardalis	Dog Feces, Owl Pellets	Broadley, 1989a
Geochelone pardalis	Insects	Milton, 1992
*Geochelone yniphora**	Bird Eggs, Raw Meat, Dead Chicks	Durrell et al., 1989
Gopherus agassizii	Moth Larvae (*Hyles lineata*)	Avery et al., 1997
Gopherus agassizii	Misc. Animal Matter	Coombs, 1979
*Gopherus agassizii**	Snails, Insects	Ernst and Barbour, 1989
Gopherus agassizii	Arthropods, Reptile Sheddings	Hansen et al., 1976
Gopherus agassizii	Arthropod Parts	Turner et al., 1984
*Gopherus agassizii**	Insects, Rabbit Meat	Woodbury and Hardy, 1948
Gopherus berlandieri	Insects, Snails, Feces	Ernst and Barbour, 1989
Gopherus flavomarginatus	Insects	Ernst and Barbour, 1989
*Gopherus polyphemus**	Insects, Hamburger, Dog Food	Ernst and Barbour, 1989
Gopherus polyphemus	Insects	Macdonald and Mushinsky, 1988
Indotestudo elongata	Slugs	Ernst and Barbour, 1989
Indotestudo elongata	Slugs	Moll, 1989b
*Indotestudo forstenii**	Beef	Moll, 1989c
Kinixys belliana	Millipedes, Snails, Carrion	Broadley, 1989b
Kinixys belliana	Insects, Millipedes, Snails	Ernst and Barbour, 1989
Kinixys erosa	Omnivorous (unspecified)	Broadley, 1989c
Kinixys erosa	Small Invertebrates, Carrion	Ernst and Barbour, 1989
Kinixys homeana	Omnivorous (unspecified)	Broadley, 1989d
Kinixys homeana	Omnivorous (unspecified)	Ernst and Barbour, 1989
*Kinixys natalensis**	Insects, Snails	Broadley, 1989e
Kinixys spekii	Millipedes, Snails, Carrion	Broadley, 1989b
Manouria emys	Animal Food (unspecified)	Moll, 1989d
Psammobates geometricus	Snails	Baard, 1989
*Psammobates oculifer**	Hyena Feces, Grasshoppers	Boycott and Branch, 1989
*Testudo graeca**	Dog Food, Ham Rind	Pritchard, 1979
Testudo hermanni	Earthworms, Snails, Insects	Ernst and Barbour, 1989

described an account of *G. polyphemus* catching and eating grasshoppers. Avery and Neibergs (1997) further reported free-ranging *G. agassizii* feeding on sphinx moth larvae (*Hyles lineata*).

If tortoises are including insects in their diets, are there benefits to this omnivory? There are several definite advantages to having an omnivorous diet (Table 2). For example, omnivory may allow tortoises to change preferences depending on the availability of food. Omnivorous diets may increase digestibility of foods in some turtles (Bjorndal, 1991). Young chelonians need higher protein in their diet (Avery et al., 1993), and this need may be satisfied by omnivorous diets which include insects.

If *G. agassizii* (and other tortoises) feed on insects and if insects are so abundant worldwide, why have so few observations of insect consumption been reported?

1. *Feeding on insects may occur in limited seasonal episodes during which few field observations are made.*

Lepidopterans, coleopterans, and hymenopterans are commonly encountered diurnal epigean insects in the Mojave Desert. All of these insects physically undergo complete metamorphosis during their life cycle and thus preferred stages may only be available or accessible to tortoises during certain periods of the year. Adult desert tortoises fed on sphinx moth larvae (*H. lineata*), only during a 2 week span before larvae metamorphosis occurred (Avery and Neibergs, 1997). Similarly, the western painted turtle (*Chrysemys picta*) fed mainly on insects in the summer and switched to vegetation in the fall (Pearse, 1923), while the desert iguana (*Dipsosaurus dorsalis*) manifested much the opposite chronology with progressive carnivory developing over the summer (Johnson, 1965). This switch, which is common in some reptiles, was attributed to the seasonal availability of insects (Harless and Morlock, 1979; Dearing and Schall, 1992). Continuous observations over long time periods may be required to capture unpredictable episodes in which insects become available, such as during rainstorms when larvae may be stimulated to epigean activity.

2. *Tortoises may only consume insects that are not energetically costly to catch.*

Tortoises may have a preference for certain insect species and morphs due to the shorter handling times or

Table 2. Advantages to an omnivorous diet for reptiles.

Reasons for Omnivory	Evidence	Source
Mixed diets are beneficial to animals in changing environments	• Herbivorous diets mixed with larvae may support greater numbers or diversity of microbes and improve digestibility.	Bjorndal, 1991
	• Plant cell wall digestibility may be higher in omnivores than herbivores.	Bjorndal and Bolten, 1993
	• Tortoises feed on a variety of plants.	Hansen et al., 1976
	• Tortoises switch food types depending on availability.	Jennings and Fontenot, 1992
	• Changing diets from herbivory to partial carnivory may enable herbivores to continue activity when other food sources are dominant.	Johnson, 1965
	• Specialized diets fluctuate in abundance and nutrient content over time.	Real, 1980
Protein levels may be higher in insect food over plant food and may increase growth levels	• Available plant material for tortoises have low 8% to 16% wet weight protein amounts.	Adest et al., 1989
	• In *Trachemys scripta* higher crude protein diets led to faster growth rates of juveniles.	Avery et al., 1993
	• Other species of insects contain from 35% to 50% digestible protein.	DeFoliart, 1975
	• In *Sauromalus obesus*, individuals that consumed larvae had faster growth rates than others that did not consume larvae.	Mayhew, 1963
	• Mealworms may have up to 21% wet weight to 55% dry weight crude protein amounts.	Martin et al., 1975
	• Crickets may have up to 15% wet weight to 60% dry weight crude protein amounts.	Woodring et al., 1977, 1979

because these prey have different energetic handling costs (Grimmond et al, 1994). Most insects are too fast for tortoises to capture and many such as coleopterans have a hard exoskeleton which may be difficult to consume. For this reason, tortoises may only pursue slow soft bodied prey insects or deceased insects.

3. *Young tortoises may feed on insect material more frequently than do adults.*

Different species may have age-specific differences in food choices. In the yellow-bellied turtle (*Pseudemys scripta*) it has been noted that young turtles are chiefly carnivorous but become omnivorous or herbivorous as age and size increase (Marchand, 1942; Clark and Gibbons, 1969). Similar dietary shifts have been observed in *Chrysemys picta*, *Graptemys pseudogeographica*, and *Sternotherus carinatus*. Protein demand by young tortoises may exceed 10% by dry weight in order to sustain growth (Avery et al., 1993). Yet young tortoises are rarely encountered in the field and their use of insectivory to increase protein content may therefore be rarely observed. A partially carnivorous diet may both better satisfy the need for protein and at the same time, may reduce interspecific competition for food (Bury, 1986). Foraging for herbaceous food consumes more total time than active predation, therefore we would expect to see more of the former rather than the latter in field observations (Morafka, 1994).

These findings may be relevant to the future conservation of *G. agassizii*. If hatcheries/nurseries are established for releasing field-raised juveniles, it will be important to know which foods are preferred over others as well as which types maximize growth and good health. However, protein levels in food should be monitored to encourage stable growth and to avoid shell abnormalities (which can occur with excessive rapid growth). Furthermore, with the increasing incidence of upper respiratory tract disease (URTD) in desert tortoises (Jacobson, 1994), antibiotic pellets might be delivered in a preferred color for voluntary ingestion by infected tortoises. Often, infected tortoises may have a loss of appetite, which may be encouraged by using bright colors to mimic desirable flowers or plant parts.

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LITERATURE CITED

Adest, G.A., Aguirre L., G., Morafka, D.J., and Jarchow, J.V. 1989. Bolson tortoise (*Gopherus flavomarginatus*) conservation: I. Life history. Vida Silvestre Neotrop. 2(1):7-13.

ALDERTON, D. 1988. Turtles and Tortoises of the World. New York: Facts On File Publ., 191 pp.

AUFFENBERG, W. AND WEAVER, W.G., JR. 1969. *Gopherus berlandieri* in southeastern Texas. Bull. Florida St. Mus. 13:141-203.

AVERY, H.W. AND NEIBERGS, A.G. 1997. Effects of cattle grazing on the desert tortoise, *Gopherus agassizii*: nutritional and behavioral interactions. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference. N.Y. Turtle and Tortoise Society, pp. 13-20.

AVERY, H.W., SPOTILA, J.R., CONGDON, J.D., FISHER, R.U.JR., AND STANDORA, E.A. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of the slider turtle, *Trachemys scripta*. Physiol. Zool. 66:902-925.

BAARD, E.H.W. 1989. *Psammobates geometricus*, geometric tortoise (English), suurpootjie (Afrikaans). In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 85-87.

BARROW, J. 1979. Aspects of ecology of the desert tortoise, *Gopherus agassizi*, in Joshua Tree National Monument, Pinto Basin, Riverside County, California. Desert Tortoise Council, Proceedings of 1979 Symposium, pp. 105-131.

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.

BJORNDAL, K.A. 1991. Diet mixing: nonadditive interactions of diet items in an omnivorous freshwater turtle. Ecology 72(4):1234-1241.

BJORNDAL, K.A. AND BOLTEN, A.B. 1993. Digestive efficiencies in herbivorous and omnivorous freshwater turtles on plant diets - do herbivores have a nutritional advantage? Physiol. Zool. 66(3):384-395.

BOYCOTT, R.C. AND BRANCH, W. 1989. *Psammobates oculifer*, serrated tortoise; Kalahari tent tortoise; Kalahari geometric tortoise (English), skulprandskilpad; Kalahari-skilpad (Afrikaans). In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 88-90.

BROADLEY, D.G. 1989a. *Geochelone pardalis*, leopard tortoise (English), bergskilpad (Afrikaans). In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 43-46.

BROADLEY, D.G. 1989b. *Kinixys belliana*, Bell's hinged tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 49-55.

BROADLEY, D.G. 1989c. *Kinixys erosa*, serrated hinged tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 56-57.

BROADLEY, D.G. 1989d. *Kinixys homeana*, Home's hinged tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 58-59.

BROADLEY, D.G. 1989e. *Kinixys natalensis*, Natal hinged tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 60-61.

BURGE, B.L. 1977. Daily and seasonal behaviour, and areas utilized by the desert tortoise *Gopherus agassizii* in southern Nevada. Proceedings of the 1977 Symposium of the Desert Tortoise Council, pp. 59-94.

BURGE, B.L. AND BRADLEY, W.G. 1977. Population density, structure and feeding habits of the desert tortoise, *Gopherus agassizi*, in a low desert study area in southern Nevada. Desert Tortoise Council, Proceedings of 1976 Symposium, pp. 51-74.

BURY, R.B. 1986. Feeding ecology of the turtle, *Clemmys marmorata*. J. Herp. 20(4):515-521.

CARR, A.F. 1952. Handbook of Turtles. The Turtles of the United States, Canada, and Baja California. Ithaca, NY: Cornell Univ. Press, 542 pp.

CLARK, D.B. AND GIBBONS, J.W. 1969. Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. Copeia 1969:704-706.

COOMBS, E.M. 1979. Food habits and livestock competition with the desert tortoise on the Beaver Dam slope, Utah. Desert Tortoise Council, Proceedings of 1979 Symposium, pp. 132-147.

DEARING, M.D. AND SCHALL, J.J. 1992. Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorous murinus*. Ecology 73:845-858.

DEFOLIART, G.R. 1975. Insects as a source of protein. Bull. Entomol. Soc. Am. 16:161-163.

DE VOSJOLI, P. 1990. The Right Way to Feed Insect-eating Lizards. Lakeside, CA: Advanced Vivarium Systems, 32 pp.

DE VOSJOLI, P. 1991. The General Care and Maintenance of Box Turtles. Lakeside, CA: Advanced Vivarium Systems, 36 pp.

DOUGLASS, J.F. 1978. Refugia of juvenile gopher tortoises, *Gopherus polyphemus* (Reptilia, Testudines, Testudinidae). J. Herpetol. 12(3):413-415.

DURRELL, L., GROOMBRIDGE, B., TONGE, S., AND BLOXAM, Q. 1989. *Geochelone yniphora*, ploughshare tortoise, plowshare tortoise, angulated tortoise, angonoka. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 99-102.

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

ERNST, C.H., LOVICH, J.E., AND BARBOUR, R.W. 1994. Turtles of the United States and Canada. Washington: Smithsonian Institution Press, 578 pp.

ESQUE, T.C. AND PETERS, E.L. 1994. Ingestion of bones, stones, and soil by desert tortoises. In: Bury, R.B. and Germano, D.J. (Eds.). Biology of North American Tortoises. Fish and Wildlife Research 13:105-111.

GRANT, C. 1960. Differentiation of the southwestern tortoises (genus *Gopherus*) with notes on their habits. Trans. San Diego Soc. Nat. Hist. 12:441-448.

GRIMMOND, N.M., PREEST, M.R., AND POUGH, F.H. 1994. Energetic cost of feeding on different kinds of prey for the lizard *Chalcides ocellatus*. Funct. Ecol. 8:17-21.

HANSEN, R.M., JOHNSON, M.K., AND VAN DEVENDER, T.R. 1976. Foods of the desert tortoise, *Gopherus agassizii*, in Arizona and Utah. Herpetologica 32(3):247-251.

HARLESS, M. AND MORLOCK, H. (Eds.). 1979. Turtles: Perspectives and Research. New York: Wiley and Sons, 695 pp.

HEWS, D.K. AND DICKHAUT, J.C. 1989. Differential response to colors by the lizard *Uta palmeri* (Reptilia: Iguanidae). Ethology 82:134-140.

JACOBSON, E.R. 1994. Cause of mortality and diseases in tortoises: a review. J. Zoo Wild. Med. 25(1):2-17.

JENNINGS, W.B. 1993. Foraging ecology of the desert tortoise (*Gopherus agassizii*) in the western Mojave Desert. M.S. Thesis, University of Texas at Arlington.

JENNINGS, W.B. AND FONTENOT, C.L., JR. 1992. Observations on the feeding behavior of desert tortoises (*Gopherus agassizii*) at the Desert Tortoise Research Natural Area, Kern County, California. Desert Tortoise Council, Proceedings of the 1992 Symposium, pp. 69-81.

JOHNSON, S.R. 1965. An ecological study of the chuckwalla, *Sauromalus obesus* Baird, in the western Mojave Desert. Amer. Midl. Nat. 73:1-29.

KASPERCZYK, M. 1971. Comparative studies on colour sense in *Amphibia* (*Rana temporaria* L,. *a lamandra salamandra* L. and *Triturus cristatus* Laur.) Folia Biol. 19:241-288.

LOSTAKOVA, H., KNOZ, J., AND HANAK, F. 1979. Notes on food habits in Testudinid turtles (Chelonia: *Testudo*). Scr. Fac. Sci. Nat. Univ. Purkynianae Brun. Biol. 9:79-84.

MACDONALD, L.A. AND MUSHINSKY, H.R. 1988. Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. Herpetologica 44(3):345-353.

MARCHAND, L.J. 1942. A contribution to a knowledge of the natural history of certain freshwater turtles. M.S. Thesis, Univ. of Florida.

MARLOW, R.W. AND TOLLESTRUP, K. 1982. Mining and exploitation of natural mineral deposits by the desert tortoise, *Gopherus agassizi*. Anim. Behav. 30:475-478.

MARTIN, R.D., RIVERS, J.P.W., AND COWGILL, U.M. 1975. Culturing mealworms as food for animals in captivity. Int. Zoo. Yearb. 16:63-70.

MAYHEW, W.W. 1963. Some food preferences of captive *Sauromalus obesus*. Herpetologica 19:10-16.

MILTON, S.J. 1992. Plants eaten and dispersed by adult leopard *Geochelone pardalis* (Reptilia: Chelonii) in the southern Karoo. S. Afr. J. Zool. 27:45-49.

MOLL, E.O. 1989a. *Geochelone elegans*, Indian star tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 113-114.

MOLL, E.O. 1989b. *Indotestudo elongata*, elongated tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm, pp. 116-117.

MOLL, E.O. 1989c. *Indotestudo forstenii*, Travancore tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm, p. 118.

MOLL, E.O. 1989d. *Manouria emys*, Asian brown tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 119-120.

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.

MOSKOVITS, D.K. AND BJORNDAL, K.A. 1990. Diet and food preferences of the tortoises *Geochelone carbonaria* and *G. denticulata* in northwestern Brazil. Herpetologica 46(2):207-218.

NAGY, K.A. AND MEDICA, P.A. 1977. Seasonal water and energy relations of free-living desert tortoises in Nevada: a preliminary report. Desert Tortoise Council, Proceedings of 1977 Symposium, pp. 152-157.

NICHOLS, U.G. 1953. Habits of the desert tortoise, *Gopherus agassizii*. Herpetologica 9:65-69.

NUBOER, J.F.W. 1986. A comparative view on colour vision. Neth. J. Zool. 36:344-380.

OKAMOTO, C.L. 1995. Color, calcium, and insect choice trials performed with captive juvenile desert tortoises (*Gopherus agassizii*). M.S. Thesis, California State University, Dominguez Hills.

PEARSE, A.S. 1923. The growth of the painted turtle. Biol. Bull. 45:145-148.

PRITCHARD, P.C.H. 1979. Encyclopedia of Turtles. Neptune, NJ: TFH Publ., 895 pp.

QUARANTA, J.V. 1952. Color vision of a giant tortoise, *Testudo*. Zoologica 37:295-312.

REAL, L.A. 1980. Fitness, uncertainty, and the role of diversification in evolution and behavior. Am. Nat. 115:623-638.

RUBY, D.E. AND NIBLICK, H.A. 1994. A behavioral inventory of the desert tortoise: development of an ethogram. Herpetological Monographs 8:88-102.

SOKOL, O.M. 1971. Lithophagy and geophagy in reptiles. J. Herp. 5:69-70.

SPANGENBERG, E.K. 1995. Plants eaten by juvenile desert tortoises (*Gopherus agassizii*) in late spring and early summer at Fort Irwin Study Site (FISS), San Bernardino County, California. National Biological Service, Desert Tortoise Nutrition Workshop. Zzyzx, California.

SYLBER, C.K. 1988. Feeding habits of the lizards *Sauromalus varius* and *S. hispidus* in the Gulf of California. J. Herpetol. 22:413-424.

TURNER, F.B., MEDICA, P.A., AND LYONS, C.L. 1984. Reproduction and survival of the desert tortoise (*Scaptochelys agassizii*) in Ivanpah Valley, California. Copeia 1984(4):811-820.

WALKER, P. 1989a. *Geochelone carbonaria*, red-footed tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 17-19.

WALKER, P. 1989b. *Geochelone chilensis* , Chaco tortoise. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occ. Pap. IUCN Spec. Surv. Comm., pp. 20-21.

WALLS, G.L. 1942. The Vertebrate Eye and its Adaptive Radiation. Hafner Publishing Company, New York, pp. 494-519.

WOODBURY, A.M. AND HARDY, R. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecol. Monogr. 18:145-200.

WOODRING, J.P., ROE, R.M., AND CLIFFORD, C.W. 1977. Relation of feeding, growth, and metabolism to age in the larval, female house cricket. J. Insect Physiol. 23:207-212.

WOODRING, J.P., CLIFFORD, C.W., AND BECKMAN, B.R. 1979. Food utilization and metabolic efficiency in larval and adult house crickets. J. Insect Physiol. 25:903-912.

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