

---

## A DIETARY STUDY OF THE ROUGH-FOOTED MUD TURTLE (*KINOSTERNON HIRTIPES*) IN TEXAS, USA

STEVEN G. PLATT<sup>1,2</sup>, ANDREW R. BEREZIN<sup>1,3</sup>, DENNIS J. MILLER<sup>4</sup>,  
AND THOMAS R. RAINWATER<sup>5,6</sup>

<sup>1</sup>Department of Biology, Box C-64, Sul Ross State University, Alpine, Texas 79832, USA

<sup>2</sup>Present address: Wildlife Conservation Society, Myanmar Program, Office Block C-1, Aye Yeik Mon 1<sup>st</sup> Street, Hlaing Township, Yangon, Myanmar

<sup>3</sup>Present address: Wharton County Junior College, 14004 University Boulevard, Sugar Land, Texas 77479, USA

<sup>4</sup>Box 792, Alpine, Texas 79831, USA

<sup>5</sup>Tom Yawkey Wildlife Center & Belle W. Baruch Institute of Coastal Ecology and Forest Science, Clemson University, Georgetown, South Carolina 29440, USA

<sup>6</sup>Corresponding author, e-mail address: trrainwater@gmail.com

**Abstract.**—We conducted a dietary study of the Rough-footed Mud Turtle (*Kinosternon hirtipes*) at Plata Wetland Complex (PWC) in Presidio County, Texas, USA, from 2007–2008. We collected feces from 88 turtles, including 42 males, 14 females, and 32 juveniles. Items recovered from fecal samples included filamentous algae, vegetation, seeds and fruits, aquatic, terrestrial, and flying arthropods, and aquatic gastropods. Based on percent occurrence (number of samples in which a particular dietary item occurs divided by the sample size), vegetation and insects were the principal foods consumed. Lesser amounts of filamentous algae, seeds and fruits, and aquatic gastropods were recovered from feces. *Kinosternon hirtipes* at PWC appear to be generalist omnivores. The remains of terrestrial arthropods in feces suggest some foraging activity occurs terrestrially or at the land-water interface. *Kinosternon hirtipes* undergoes an ontogenetic dietary shift from insects to vegetation as body size increases, which presumably facilitates rapid growth and minimizes the time an individual remains at a size vulnerable to predators. Although males are the larger sex at PWC, we found nothing to suggest that larger body size provided access to an expanded resource base. Instead we found high dietary overlap between sexes indicating that male and female *K. hirtipes* consume similar foods.

**Key Words.**—diet; fecal analysis; food habits; Kinosternidae; ontogenetic dietary change

---

### INTRODUCTION

Rough-footed Mud Turtles (*Kinosternon hirtipes*) occur from extreme west Texas, southwards into Chihuahua, Mexico, and south and east on the Mexican Plateau to the Chapala, Zapotlán, San Juanico, Pátzcuaro, and Valle de México basins (Iverson 1985a; Ernst and Lovich 2009). In the United States, *K. hirtipes* is known only from the Alamito Creek drainage in Presidio County, Texas (Ernst and Lovich 2009; Platt and Medlock 2015), where it is considered Threatened by conservation authorities (Texas Parks and Wildlife Department. 2013. Species of Conservation Concern. Available from: [www.tpwd.state.tx.us](http://www.tpwd.state.tx.us); [Accessed 15 April 2015]) owing to a limited geographic distribution within the state and habitat degradation resulting from past land management practices. *Kinosternon hirtipes* is one of the least-studied North American turtles and little is known concerning its natural history (Ernst and Lovich 2009; Lovich and Ennen 2013). Other than anecdotal observations of foraging (Iverson et al. 1991) and general statements describing food habits (Ernst and Lovich 2009), the diet of *K. hirtipes* remains unstudied.

Studies of diet are fundamental to understanding the ecology of an organism (Rosenberg and Cooper 1990) and among turtles, diet can influence habitat preferences (Plummer and Farrar 1981; Hart 1983; Compton et al. 2002; Howey and Dinkelacker 2009) and character divergence (Berry 1975; Tucker et al. 1995; Lindeman 2000). Ultimately these changes can affect energy allocation, which in turn determines survival, growth, and reproductive rates (Sloan et al. 1996; Dodd 1997; Ford and Moll 2004). Information on diet is also a necessary prerequisite for the study of complex ecological relationships, such as seed dispersal mutualisms (Moll and Jansen 1995; Liu et al. 2004; Jerolimski et al. 2009; Platt et al. 2009) and designing effective conservation strategies (Dayton 2003; Budischak et al. 2006; Lindeman 2006; Wilhelm and Plummer 2012). We here present the results of a dietary study based on fecal contents analysis of *K. hirtipes* from a wetland in Presidio County, Texas, USA. In this study we characterize the diet of *K. hirtipes*, investigate ontogenetic dietary trends, and quantify dietary specialization and overlap between the sexes.

## MATERIALS AND METHODS

**Study area.**—Our study was conducted at Plata Wetland Complex (PWC; elevation = 1,125 m), located on a private ranch in the Alamito Creek drainage approximately 56 km SE of Marfa in Presidio County, Texas, USA. Regional climate is characterized by mild winters and hot summers; air temperatures rarely fall below 0° C during the winter and often exceed 40° C during summer (Cottle 1932; Powell 1998). Annual rainfall (mean about 370 mm) is highly variable, with most precipitation occurring during a relatively brief monsoonal period from June to August (Leithead 1959; Powell 1998).

The PWC consists of four livestock tanks (ponds): Railroad (612 m<sup>2</sup>), Crotalus (900 m<sup>2</sup>), Turner One (2,520 m<sup>2</sup>), and Turner Two (3,780 m<sup>2</sup>). Railroad Tank is adjacent (about 10 m) to the Southwest Oriental Railroad and fed by an artesian spring. Railroad and Crotalus tanks are linked by a shallow drainage ditch, with excess water flowing 244 m from Railroad to Crotalus Tank. Turner Tank One is located approximately 190 m from Railroad Tank with water supplied by rainfall and a wind-driven pump. Turner Tank Two is located approximately 245 m from Turner Tank One (nearest waterbody) and reliant on rainfall for water. Because Railroad and Crotalus Tanks are spring fed, water levels remain relatively stable throughout the year with a maximum depth of about 1.5 m. Water depth in Turner Tanks One and Two varies depending on seasonal rainfall (less so at Turner One); maximum depth in each is about 1.2 m. Railroad Tank is surrounded by a stand of mature Cottonwoods (*Populus deltoides*) and contains an abundance of woody debris, but little submerged or emergent vegetation. In contrast, Turner Tanks One and Two lack surrounding tree cover and support dense stands of cattail (*Typha* sp.) and bulrush (*Scirpus* sp.), respectively. Thick mats of filamentous algae and muskgrass (*Chara* sp.) are present in Crotalus Tank and Turner Tank Two. Because interpond movements of turtles occasionally occur (14.5% of recaptured turtles had moved among ponds; Platt et al., unpubl. data), we treated the four tanks at PWC as a single sampling unit. The terrestrial habitat surrounding PWC was historically arid grassland, but is now dominated by Mesquite (*Prosopis glandulosa*) and Creosote Bush (*Larrea tridentata*) scrub as a result of past over-grazing and subsequent topsoil loss (Wilde and Platt 2011).

**Data collection.**—We trapped turtles at PWC from May through September 2007–2008 as part of a larger population study of *K. hirtipes* conducted in the Alamito Creek drainage (2007–2010). We used a combination of wire mesh funnel traps (1.0 m long × 50 cm diameter; mesh = 12.5 mm) and hoop nets (2.5 m long × 1.0 m diameter; mesh = 25 mm) to capture turtles for dietary

analysis. We deployed one wire mesh funnel trap in every tank; these were set from mid-morning to early evening (about 1000–2030) and checked at intervals of 1–2 h. We used hoop nets (one net/tank) only in Crotalus and Turner One tanks owing to shallow water and the presence of submerged woody debris in the other two tanks. To avoid drowning turtles, hoop nets were only partially submerged (at least 10 cm of net remaining above water). We usually set hoop nets in mid-morning (about 1030) on one day and checked them the following morning. We baited wire mesh traps and hoop nets with sardines (packed in oil or water) or fresh carcasses of locally captured fresh sunfish (*Lepomis* sp.). Turtles were processed (see below) and released within 2 h of being removed from traps.

We permanently marked each captured turtle by notching a unique series of marginal scutes (Cagle 1939). We measured straight-line carapace length (CL) and plastron length (PL) with dial (± 0.1 mm) or tree calipers (± 1.0 mm) depending on size of the turtle. Because *K. hirtipes* has a hinged plastron, we recorded separate measurements for the anterior and posterior lobes and summed these to obtain PL. Body mass (BM) was determined with spring scales (± 1.0 g). We determined sex of turtles using external secondary sexual characteristics; males exhibit a concave plastron and long thickened tail, characteristics that are absent in females (Iverson 1985b). In our study population, secondary sexual characteristics were evident in turtles with a CL ≥ 100 mm; we were unable to reliably determine the sex of turtles below this size threshold.

We collected feces from captured turtles and analyzed the contents to determine diet. Turtles usually defecated while being processed and feces were preserved in 70% ethanol. We later washed fecal material over a sieve (2.0 mm mesh), recovered food items, examined these under a dissecting microscope (40–100×), and identified each to the lowest possible taxonomic level. We calculated the percent occurrence of each food item recovered. We follow Rosenberg and Cooper (1990) and defined percent occurrence as the number of samples in which a particular item occurred divided by the sample size. Although often considered synonymous with frequency of occurrence, percent occurrence is the appropriate metric when individual food items cannot be quantified (Rosenberg and Cooper 1990).

Because some food items are rapidly digested (e.g., soft bodied prey and fruit) whereas others are more resistant (e.g., chitinous invertebrates and fibrous vegetation), differential digestibility of various foodstuffs can result in differential representation in the feces (Hart 1983; Putnam 1984). To reduce bias from this source, we analyzed ontogenetic trends within dietary categories under the assumption that digestion and gut passage kinetics are similar within any single

**TABLE 1.** Dietary items, and dietary diversity and evenness among *Kinosternon hirtipes* (n = 88) collected from Plata Wetland Complex in Presidio County, Texas, USA (2007–2008). Our sample included 32 juveniles, 42 adult males, and 14 adult females. Number of turtles from which a particular dietary item was recovered is followed by percent occurrence (%) in parentheses. Percentages do not sum to 100 because multiple items were usually recovered from the feces of a single turtle. The category Other arthropods includes a single scorpion and a single millipede.

Dietary item	Juveniles	Males	Females	All turtles
Filamentous algae	5 (15.6)	7 (16.6)	7 (50.0)	19 (21.5)
Vegetation (leaves and stems)	10 (31.2)	25 (59.5)	8 (57.1)	43 (48.8)
Seeds/fruit	4 (12.5)	8 (19.0)	1 (7.1)	13 (14.7)
Aquatic gastropods	4 (12.5)	1 (2.3)	2 (14.2)	7 (7.9)
Insects	20 (62.5)	18 (42.8)	5 (35.7)	43 (48.8)
Other arthropods	1 (3.1)	1 (2.3)	0	2 (2.2)
Diversity (H')	1.45	1.37	1.40	1.46
Evenness (J')	0.81	0.76	0.78	0.82

food category (Magnusson et al. 1987; Thorbjarnarson 1993). We determined ontogenetic trends using overlapping group analysis (Wallace and Leslie 2008; Platt et al. 2013). This technique involves placing turtles into overlapping size classes of 15 individuals ranked according to CL. The first group consisted of 15 turtles with the smallest CL, the next group incorporated the next five larger turtles and excluded the five smallest turtles, and so on (Wallace and Leslie 2008). This overlapping technique provides a continuous transition of progressively larger turtles and allows recognition of dietary trends that might otherwise be obscured by standard comparisons of only two or three size classes (Wallace and Leslie 2008). We transformed percent occurrence data using a square-root arcsine transformation (Zar 1996) before searching for correlations in dietary composition across size classes.

We used the Shannon-Wiener diversity index (H') to estimate dietary niche breadth and determine the degree of dietary specialization of each sex (Schoener 1968). The Shannon-Wiener index is calculated as:

$$H' = - \sum pj \log pj$$

where  $pj$  is the proportion of individuals using resource  $j$  (prey category). Because H' may range from 0 to  $\infty$ , we standardized the index on a scale of 0 to 1 using the evenness measure J' calculated as

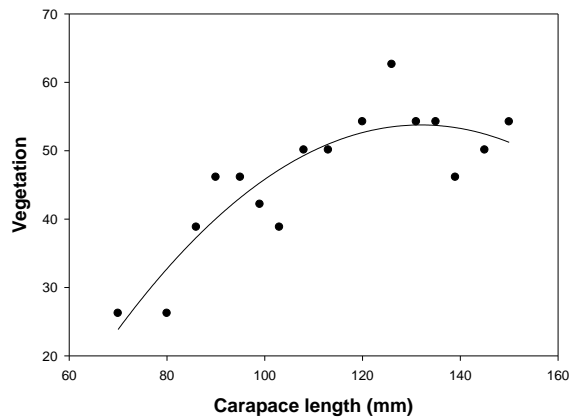
$$J' = H' (\log n)^{-1}$$

where  $n$  is the number of prey categories (Krebs 1989). The lower the value of J', the more specialized the feeding habits of a particular sex; i.e., the lowest J' value indicates the least diversity of prey consumed, and hence a greater degree of specialization (Schoener 1968; Krebs 1989).

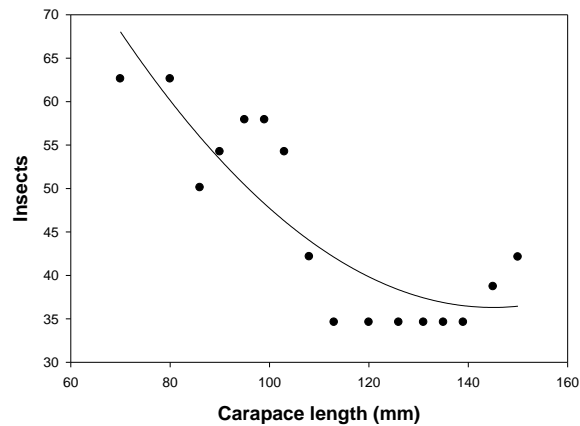
We determined dietary niche overlap between the sexes using percent overlap (P), which measures the area of overlap of the resource utilization curves of males (m) and females (f) (Krebs 1989). The value of P is estimated by  $\sum (\text{minimum } p_{im}, p_{if}) \times 100$ , where  $p_{im}$  and  $p_{if}$  are the proportion of prey item ( $i$ ) used by males and females, respectively, and ranges from 0 (no overlap) to 1 (complete overlap; Krebs 1989). Following Tucker et al. (1995), we considered dietary overlap to be minimal if  $P < 0.4$  and of biological significance if  $P > 0.6$ .

## RESULTS

We obtained feces from 88 (42 males, 14 females, and 32 juveniles) *K. hirtipes* with CL ranging from 42–163 mm (mean CL  $\pm$  1 SE = 28  $\pm$  3 mm). Items recovered from fecal samples included filamentous algae (Chlorophyta), vegetation, seeds and fruits, insects, other arthropods, and aquatic gastropods (Table 1). Vegetation and insect remains were the dietary items most frequently recovered from turtle feces. Most vegetation in the feces appeared to be an aquatic grass (*Paspalum distichum*) common at PWC; seeds and fruits included Mesquite and *P. distichum*. Arthropod remains generally consisted of crushed bits of chitin unassignable to a particular taxonomic group; however, representatives of six insect orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Odonata), Scorpiones, and Diplopoda (*Orthoporus* sp.) were among the identifiable remains. Identifiable arthropod prey included aquatic (Tabinidae larva, Coleoptera), aerial (adult Cicadidae and Odonata), and terrestrial (Lepidopteran larva, Coleoptera, Formicidae, *Orthoporus* sp., Scorpiones) forms. Identifiable remains of aquatic, aerial, and terrestrial arthropods were found in 1.1, 2.2, and 12.5% of fecal samples, respectively. Most arthropod remains that could not be positively



**FIGURE 1.** The relationship between carapace length and percent occurrence of vegetation in the diet of *Kinosternon hirtipes* (n = 88) captured in Presidio County, Texas, USA (2007–2008).



**FIGURE 2.** The relationship between carapace length and percent occurrence of insects in the diet of *Kinosternon hirtipes* (n = 88) captured in Presidio County, Texas, USA (2007–2008).

identified to a particular taxonomic group probably consisted of various aquatic Coleopterans (Dytiscidae and Hydrophilidae), which are abundant at PWC.

Our over-lapping dietary analysis found a significant non-linear relationship between the percent occurrence of vegetation (VG) and CL ( $VG = -81.95 + 2.05CL - 0.0078CL^2$ ;  $r^2 = 0.74$ ;  $P < 0.05$ ; Fig. 1) indicating the percent occurrence of vegetation in the diet increased with increasing CL. In contrast, the percent occurrence of insects (IN) in the diet decreased with increasing CL ( $IN = 154.88 - 1.63CL + 0.005CL^2$ ;  $r^2 = 0.72$ ;  $P < 0.05$ ; Fig. 2). Relationships between CL and other dietary categories (algae, seeds/fruits, gastropods) and dietary diversity and evenness were not significant. Evenness (J') values indicated the diets of juveniles, males, and females were relatively unspecialized (Table 1). Dietary overlap (P) between male and female *K. hirtipes* was biologically significant (73.8%).

### DISCUSSION

Various techniques, each with particular limitations have been used to study the diet of kinosternids, including fecal analysis (Folkerts 1968; Ford and Moll 2004; Wilhelm and Plummer 2012), stomach flushing (Ford and Moll 2004), and dissection (Hulse 1974; Berry 1975). Sacrificing turtles to obtain stomach contents was unacceptable given the threatened conservation status of *K. hirtipes* in Texas, and an earlier attempt we made to flush stomach contents from Yellow Mud Turtles (*Kinosternon flavescens*) yielded few ingesta. Furthermore, accidental mortality has resulted from stomach flushing (De Lima et al. 1997), making us reluctant to use this technique on *K. hirtipes*. Although we recognize that some soft-bodied prey probably escaped detection in our study (Marion et al. 1991;

Lindeman 2006; Wilhelm and Plummer 2012), fecal analysis is safe, non-invasive, and allows turtles to be processed and rapidly released (Graham 1979; Tucker et al. 1995; De Lima et al. 1997).

Our investigation appears to be the first quantitative dietary study of *K. hirtipes*. Previous reports include a general description of diet (Ernst and Lovich 2009) and observations of turtles foraging on mollusks and Trichopteran larvae (Iverson et al. 1991), but otherwise dietary information for *K. hirtipes* is lacking from the literature. Our fecal analysis suggests that like most other kinosternids (e.g., Mahmoud 1968; Folkerts 1968; Hulse 1974; Ford and Moll 2004; Wilhelm and Plummer 2012), *K. hirtipes* is a generalist omnivore that consumes a variety of plant and animal foods with insects and leafy vegetation as the dietary mainstays. In this respect, the population of *K. hirtipes* at PWC seems to differ from those in Mexico, which Iverson (pers. comm. cited in Ernst and Lovich 2009) suggested are almost wholly carnivorous, feeding on snails, aquatic insects, crustaceans, fish, and amphibians. The diverse diet among *K. hirtipes* in our study may also be due in part to the range of habitats available in the four ponds comprising PWC. Furthermore, the diversity of prey items we recovered from fecal samples suggests *K. hirtipes* is an active forager like other kinosternids rather than a sit-and-wait predator.

Most foraging by *K. hirtipes* probably takes place in the water, although the relatively high prevalence of terrestrial arthropods among our fecal samples suggests some feeding also occurs on land or at the land-water interface. Terrestrial foraging has been reported in other kinosternids, but seems most common among those species that spend a great deal of time on land (Moll 1979; Ashton and Ashton 2004; Ernst and Lovich 2009). *Kinosternon hirtipes* by contrast, is considered a highly

aquatic species that rarely leaves the water owing to a physiological sensitivity to dehydration (Seidel and Reynolds 1980; Ligon and Peterson 2002), and therefore terrestrial foraging behavior is somewhat unexpected. However, our observations of occasional overland movements (up to 250 m) among ponds at PWC (Steven Platt et al., unpubl. data) indicate that *K. hirtipes* is certainly capable of brief terrestrial forays in search of prey. Some terrestrial prey might also be captured by turtles after falling into the water, although this pathway is unlikely to account for all terrestrial prey recovered in fecal samples.

To our knowledge, the scorpion we recovered from an adult *K. hirtipes* is the first report of this prey being consumed by any kinosternid. The presence of millipede remains in *K. hirtipes* feces is also of interest because these invertebrates secrete a variety of toxic compounds (e.g., hydrogen cyanide and benzoquinone), which cause many predators to cease an attack and perform vigorous cleansing actions (Eisner and Meinwald 1966). In addition to *K. hirtipes*, millipedes are consumed by Loggerhead Musk Turtles (*Sternotherus minor*; Ernst and Lovich 2009) and comprise a significant portion of the diet of Desert Box Turtles (*Terrapene ornata luteola*) in terrestrial habitats surrounding PWC (Platt et al. 2012). Collectively, these findings indicate that some chelonians are undeterred by the chemical defenses of millipedes.

Gastropods are important prey for many kinosternids (Folkerts 1968; Berry 1975; Bardwell 2006; Wilhelm and Plummer 2012), but appear less so for *K. hirtipes* at PWC. Gastropods may be especially important as a source of calcium for eggshell formation and bone growth in reproductive females and juveniles, respectively (Beasom and Pattee 1978; Esque and Peters 1994). Folkerts (1968) observed *S. minor* feeding on snails in algal mats and suggested filamentous algae recovered from feces was incidentally consumed while turtles were consuming snails. This is probably not the case for *K. hirtipes* in our study given the disparity between the percent occurrence of filamentous algae and gastropods in the diet.

Algae and aquatic plants (e.g., *P. distichum*) are generally less digestible (Bjorndal 1991) and contain considerably less dietary protein compared to invertebrates (Boyd 1968; Bowen et al. 1995; Ford and Moll 2004). However, dietary generalists such as *K. hirtipes* typically compliment protein from animal prey with energy from more abundant plant foods (Ahlgren 1990). In some turtles, the growth of symbiotic flora in the small intestine that facilitates digestion of plant foods through fermentation is enhanced by the addition of nitrogen from protein sources (Bjorndal and Bolten 1990; Bjorndal 1991; Moskovits and Bjorndal 1990). Although intestinal fermentation remains unstudied in kinosternids, Ford and Moll (2004) suggested such an

associative effect (one dietary item affecting digestion of another item; Bjorndal 1991) might play a role in the digestion of algae by Stinkpots (*Sternotherus odoratus*).

The occurrence of seeds in the feces of *K. hirtipes* is unsurprising, as similar items have been found in dietary studies of other kinosternids (Vogt and Guzman 1988; Marion et al. 1991; Ford and Moll 2004; Graham and Sorrell 2008; Wilhelm and Plummer 2012). Mesquite seeds are probably ingested when *K. hirtipes* feeds on the sugar-rich legumes (pods) containing the seeds (Barlow 2000), and smaller seeds (e.g., grasses) are most likely ingested together with leafy foliage (i.e., foliage as fruit hypothesis; Janzen 1984). What role *K. hirtipes* and other kinosternids play in seed dispersal has yet to be determined, although the presence of propagules in the feces suggests these turtles are potential dispersal agents. In general, seed dispersal by chelonians is a neglected area of research (Traveset 1998), although a limited number of studies have demonstrated that passage of seeds through the digestive tract of turtles can affect germination rates (Liu et al. 2004; Elbers and Moll 2011).

Our analysis indicates that an ontogenetic change occurs in the diet of *K. hirtipes*, with the percent occurrence of insects declining and plant consumption increasing as turtles grow larger. Similar ontogenetic dietary changes are reported in other kinosternids, although in some cases (e.g., *Sternotherus carinatus* and *S. minor*) these reflect shifts from an insectivorous to a molluscivorous rather than a more herbivorous diet as individuals mature (Tinkle 1958; Mahmoud 1968; Berry 1975; Ernst and Lovich 2009). Such ontogenetic dietary shifts undoubtedly confer energetic and survival advantages to the individual (Hart 1983). Among *K. hirtipes*, the insect-rich diet of smaller turtles supplies an abundance of highly digestible protein, which is required to sustain the rapid growth of juveniles (Avery et al. 1993). Because predation on smaller turtles is generally high, a protein-rich diet insures rapid growth and presumably minimizes the time an individual remains at a size vulnerable to predators (Graham 1971; Wilbur 1975; Avery et al. 1993). In other turtles, as individuals approach sexual maturity, a shift away from carnivory to a more herbivorous diet is correlated with the reduced growth rates of adults (Hart 1983).

Body size in *K. hirtipes* is sexually dimorphic, with males generally being the larger sex (Iverson 1985b). When the sexes differ in body size, they often exploit different food resources, possibly as a means of reducing potential intraspecific competition (Wilson 1975; Slatkin 1984). Although male *K. hirtipes* were the larger sex at PWC (Steven Platt et al., unpubl. data.), we found no indication that larger body size provided males with access to an expanded dietary resource base. The high dietary overlap we found between the sexes indicates that male and female *K. hirtipes* consume similar foods.

However, high dietary overlap does not necessarily mean that competition between the sexes is occurring (Pianka 1988). First, there is nothing to indicate that food resources are limiting at PWC, especially among adult *K. hirtipes* that feed heavily on the abundant aquatic vegetation. Indeed, a high degree of overlap is more likely to reflect a superabundance of dietary resources rather than competition between the sexes (Tucker et al. 1995). Second, while males and females consume the same foods, foraging activity may be spatially and temporally segregated as a means of avoiding competition (Ford and Moll 2004). Unfortunately, this question cannot be addressed given our current understanding of *K. hirtipes* ecology

*Acknowledgments.*—This research was conducted under a scientific research permit (SPR-0307-844) issued to SGP by the Texas Department of Parks and Wildlife and with the approval of the Sul Ross State University (SRSU) Institutional Animal Care and Use Committee. Support for this project was provided by Research Enhancement Grants from SRSU to SGP. We thank Lewis Medlock and the many SRSU students enrolled in Herpetology and Field Zoology classes for their field assistance. Kendall Craig and Patti Manning identified invertebrates and seeds, respectively, recovered from turtle feces. The assistance of Madeline Thompson and Deb Levinson at Wildlife Conservation Society (New York) was most appreciated. The Hardrock Mining Company is thanked for allowing us to conduct research on their properties. Comments and suggestions by John Iverson and Lewis Medlock were most appreciated.

### LITERATURE CITED

- Ahlgren, M.O. 1990. Nutritional significance of facultative detritivory to the juvenile White Sucker (*Catostomus commersoni*). *Canadian Journal of Fisheries and Aquatic Sciences* 47:49–54.
- Ashton, P.S., and R.E. Ashton. 2004. *The Gopher Tortoise: A Life History*. Pineapple Press, Sarasota, Florida, USA.
- Avery, H.W., J.R. Spotila, J.D. Congdon, R.V. Fischer, Jr., E.A. Standora, and S.B. Avery. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of juvenile Slider Turtles, *Trachemys scripta*. *Physiological Zoology* 66:902–925.
- Bardwell, J.H. 2006. Dietary habits and prey selection among Yellow Mud Turtles (*Kinosternon flavescens flavescens*). M.S. Thesis, Sul Ross State University, Alpine, Texas, USA. 61 pp.
- Barlow, C. 2000. *The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms*. Basic Books, New York, New York, USA.
- Beasom, S.L., and O.H. Pattee. 1978. Utilization of snails by Rio Grande Turkey hens. *Journal of Wildlife Management* 42:916–919.
- Berry, J.F. 1975. The population effects of ecological sympatry on Musk Turtles in northern Florida. *Copeia* 1975:692–701.
- Bjorndal, K.A. 1991. Diet mixing: non-additive interactions of diet items in an omnivorous freshwater turtle. *Ecology* 72:1234–1241.
- Bjorndal, K.A., and A.B. Bolten. 1990. Digestive processing in a herbivorous freshwater turtle: consequences of small intestine fermentation. *Physiological Zoology* 63:1232–1247.
- Bowen, S.H., E.V. Lutz, and M.O. Ahlgren. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology* 76:899–907.
- Boyd, C.E. 1968. Fresh-water plants: a potential source of protein. *Economic Botany* 22:359–368.
- Budischak, S.A., J.M. Hester, S.J. Price, and M.E. Dorcas. 2006. Natural history of *Terrapene carolina* (box turtles) in an urbanized landscape. *Southeastern Naturalist* 5:191–204.
- Cagle, F.R. 1939. A system for marking turtles for future identification. *Copeia* 1939:170–173.
- Compton, B.W., J.M. Rhymer, and M. McCullough. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83:833–843.
- Cottle, H.J. 1932. Vegetation on north and south slopes of mountains in southwest Texas. *Ecology* 13:121–134.
- Dayton, P.K. 2003. The importance of the natural sciences to conservation. *American Naturalist* 162:1–13.
- De Lima, A.C., W.E. Magnusson, and V.L. de Costa. 1997. Diet of the turtle *Phrynops rufipes* in Central Amazonia. *Copeia* 1997:216–219.
- Dodd, C.K., Jr. 1997. Clutch size and frequency in Florida Box Turtles (*Terrapene carolina bauri*): implications for conservation. *Chelonian Conservation and Biology* 2:370–377.
- Eisner, T., and J. Meinwald. 1966. Defensive secretions of arthropods. *Science* 153:1341–1350.
- Elbers, J.P., and D. Moll. 2011. Ingestion by a freshwater turtle alters germination of bottomland hardwood seeds. *Wetlands* 31:757–761.
- Ernst, C.H., and J.E. Lovich. 2009. *Turtles of the United States and Canada*. 2<sup>nd</sup> Edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Esque, T.C., and E.L. Peters. 1994. Ingestion of bones, stones, and soil by Desert Tortoises. Pp. 105–111 *In* *Biology of North American Tortoises*. Bury, R.B., and D.J. Germano (Eds.). Fish and Wildlife Research Report 13. US Department of Interior, National Biological Survey, Washington, D.C., USA.

- Folkerts, G.W. 1968. Food habits of the Stripe-necked Musk Turtle, *Sternotherus minor peltifer* Smith and Glass. *Journal of Herpetology* 2:171–173.
- Ford, D.K., and D. Moll. 2004. Sexual and seasonal variation in foraging patterns in the Stinkpot, *Sternotherus odoratus*, in southwestern Missouri. *Journal of Herpetology* 38:296–301.
- Graham, P., and G.G. Sorrell. 2008. *Kinosternon subrubrum* (Eastern Mud Turtle). *Diet. Herpetological Review* 39:218.
- Graham, T.E. 1971. Growth rate of the Red-bellied Turtle, *Chrysemys rubiventris*, at Plymouth, Massachusetts. *Copeia* 1971:353–356.
- Graham, T.E. 1979. Life history techniques. Pp. 73–95 *In* *Turtles: Perspectives and Research*. Harless, M., and H. Morlock (Eds.). J. Wiley and Sons, New York, New York, USA.
- Hart, D.R. 1983. Dietary and habitat shift with size of Red-eared Turtles (*Pseudemys scripta*) in a southern Louisiana population. *Herpetologica* 39:285–290.
- Howey, C.A.F., and S.A. Dinkelacker. 2009. Habitat selection of the Alligator Snapping Turtle (*Macrochelys temminckii*) in Arkansas. *Journal of Herpetology* 43:589–596.
- Hulse, A.C. 1974. Food habits and feeding behavior of *Kinosternon sonoriense* (Chelonia: Kinosternidae). *Journal of Herpetology* 8:195–199.
- Iverson, J.B. 1985a. *Kinosternon hirtipes*. *Catalogue of American Reptiles and Amphibians* 361:1–4.
- Iverson, J.B. 1985b. Geographic variation in sexual dimorphism in the Mud Turtle *Kinosternon hirtipes*. *Copeia* 1985:388–395.
- Iverson, J.B., E.L. Barthelme, G.R. Smith, and C.E. DeRivera. 1991. Growth and reproduction in the Mud Turtle *Kinosternon hirtipes* in Chihuahua, México. *Journal of Herpetology* 25:64–72.
- Janzen, D.H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* 123:338–353.
- Jerozolinski, A., M.B.N. Ribeiro, and M. Martins. 2009. Are tortoises important seed dispersers in Amazonian forests? *Oecologia* 161:517–528.
- Krebs, C.J. 1989. *Ecological Methodology*. Harper Collins, New York, New York, USA.
- Leithhead, H. 1959. Runoff in relation to range conditions in the Big Bend-Davis Mountains section of Texas. *Journal of Range Management* 12:83–87.
- Ligon, D.B., and C.C. Peterson. 2002. Physiological and behavioral variation in estivation among mud turtles (*Kinosternon* spp.). *Physiological and Biochemical Zoology* 75:283–293.
- Lindeman, P.V. 2000. Resource use of five sympatric turtle species: effects of competition, phylogeny, and morphology. *Canadian Journal of Zoology* 75:992–1008.
- Lindeman, P.V. 2006. Diet of the Texas Map Turtle (*Graptemys versa*): relationships to sexually dimorphic trophic morphology and changes over five decades as influenced by an invasive mollusk. *Chelonian Conservation and Biology* 5:25–31.
- Liu, H., S.G. Platt, and C.K. Borg. 2004. Seed dispersal by the Florida Box Turtle (*Terrapene carolina bauri*) in Pine Rockland Forests of the lower Florida Keys, United States. *Oecologia* 138:539–546.
- Lovich, J.E., and J.R. Ennen. 2013. A quantitative analysis of the state of the knowledge of turtles of the United States and Canada. *Amphibia-Reptilia* 34:11–23.
- Magnusson, W.E., E.V. Da Silva, and A.P. Lima. 1987. Diets of Amazonian crocodylians. *Journal of Herpetology* 21:85–95.
- Mahmoud, I.Y. 1968. Feeding behavior in kinosternid turtles. *Herpetologica* 24:300–305.
- Marion, K.R., W.A. Cox, and C.H. Ernst. 1991. Prey of the Flattened Musk Turtle, *Sternotherus depressus*. *Journal of Herpetology* 25:385–382.
- Moll, D. 1979. Subterranean feeding by the Illinois Mud Turtle, *Kinosternon flavescens spooneri* (Reptilia, Testudines, Kinosternidae). *Journal of Herpetology* 13:371–373.
- Moll, D., and K.P. Jansen. 1995. Evidence for a role in seed dispersal by two tropical herbivorous turtles. *Biotropica* 27:121–127.
- Moskovits, D.K., and K.A. Bjorndal. 1990. Diet and food preferences of tortoises *Geochelone carbonaria* and *G. denticulata* in northwestern Brazil. *Herpetologica* 46:207–218.
- Pianka, E.R. 1988. *Evolutionary Ecology*. Harper and Row, New York, New York, USA.
- Platt, S.G., C. Hall, H. Liu, and C.K. Borg. 2009. Wet-season food habits and intersexual dietary overlap of Florida Box Turtles (*Terrapene carolina bauri*) on National Key Deer Wildlife Refuge, Florida. *Southeastern Naturalist* 8:335–346.
- Platt, S.G., and L. Medlock. 2015. *Kinosternon hirtipes* (Rough-footed Mud Turtle). Aerial basking, winter activity, habitat, and new locality. *Herpetological Review* 46:424–425.
- Platt, S.G., C.M. Ritzi, K. Craig, D.J. Miller, and T.R. Rainwater. 2012. *Terrapene ornata luteola* (Desert Box Turtle). Diet. *Herpetological Review* 43:641.
- Platt, S.G., J.B. Thorbjarnarson, T.R. Rainwater, and D.R. Martin. 2013. Diet of the American Crocodile (*Crocodylus acutus*) in marine environments of coastal Belize. *Journal of Herpetology* 47:1–10.
- Plummer, M.V., and D.B. Farrar. 1981. Sexual dietary differences in a population of *Trionyx muticus*. *Journal of Herpetology* 15:175–179.
- Powell, M.A. 1998. *Trees and Shrubs of the Trans-Pecos and Adjacent Areas*. University of Texas Press, Austin, Texas, USA.

## Herpetological Conservation and Biology

- Putnam, R.J. 1984. Facts from faeces. *Mammal Review* 14:79–97.
- Rosenberg, K.V., and R.J. Cooper. 1990. Approaches to avian diet analysis. *Studies in Avian Biology* 13:80–90.
- Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- Seidel, M.E., and S.L. Reynolds. 1980. Aspects of evaporative water loss in the mud turtles *Kinosternon hirtipes* and *Kinosternon flavescens*. *Comparative Biochemistry and Physiology* 67A:593–598.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622–630.
- Sloan, K.N., K.A. Buhmann, and J.E. Lovich. 1996. Stomach contents of commercially harvested adult Alligator Snapping Turtles, *Macrolemys temminckii*. *Chelonian Conservation and Biology* 2:96–99.
- Thorbjarnarson, J.B. 1993. Diet of the Spectacled Caiman (*Caiman crocodilus*) in the Venezuelan Llanos. *Herpetologica* 49:108–117.
- Tinkle, D.W. 1958. The systematics and ecology of the *Sternothaerus carinatus* complex (Testudinata, Chelydridae). *Tulane Studies in Zoology* 6:1–56.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives on Plant Ecology and Evolutionary Systematics* 1:151–190.
- Tucker, A.D., N.N. Fitzsimmons, and J.W. Gibbons. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica* 51:167–181.
- Vogt, R.C., and S.G. Guzman. 1988. Food partitioning in a Neotropical freshwater turtle community. *Copeia* 1988:31–47.
- Wallace, K.M., and A.J. Leslie. 2008. Diet of the Nile Crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42:361–368.
- Wilbur, H.M. 1975. A growth model for the turtle, *Chrysemys picta*. *Copeia* 1975:337–343.
- Wilde, M., and S. Platt. 2011. A life-giving trail: documenting the environmental history of Alamito Creek. *Journal of Big Bend Studies* 23:85–106.



**Steven G. Platt** was formerly an Associate Professor in the Biology Department at Sul Ross State University (2006–2011), and now serves as a Conservation Herpetologist for the Wildlife Conservation Society in Southeast Asia. He received his B.S. in Forestry and Wildlife Management from Louisiana State University (1985), M.S. in Biology from Southeastern Louisiana University (1990), and Ph.D. in Zoology from Clemson University (1996). His current focus is the study and conservation of turtles and crocodilians in Southeast Asia, with an emphasis on Myanmar, Thailand, and Laos. (Photographed by Lewis Medlock).



**Andrew R. Berezin** is a Biology Instructor at Wharton County Junior College in Sugar Land, Texas, USA, where he currently teaches Biology and Nutrition courses. He received his B.Sc. with honors (2007) and M.Sc. (2009) in Biology from Sul Ross State University in Alpine, Texas, USA. He has conducted field research related to the dietary habits of the American Black Bear (*Ursus americanus*) as well as implemented a successful salt cedar (*Tamarisk* sp.) biocontrol program along the Rio Grande in Presidio and Brewster counties, Texas. (Photographed by Alisa Berezin).



**Dennis J. Miller** received a B.S. Biology and M.S. Biology from Sul Ross State University in Alpine, Texas, USA. His life-long field of interest is herpetology. He served as Executive Director of the Chihuahuan Desert Research Institute (CDRI) near Fort Davis, Texas from 1979–2002, during which time he participated in a broad range of research activities. He has authored a number of research reports and publications and was co-editor of the Third Symposium on Resources of the Chihuahuan Desert Region. He was a member of the distinguished CDRI Board of Scientists, and served as President of the Texas Herpetological Society in 1994. Since 2003, he has been a teacher, a newspaper reporter, and is currently Training Professional of the Big Bend Region Small Business Development Center in Alpine. (Photographed by Beth Miller).



**Thomas R. Rainwater** is Wildlife Research Coordinator at the Tom Yawkey Wildlife Center and the Baruch Institute of Coastal Ecology and Forest Science with Clemson University in Georgetown, South Carolina, USA. He received his B.S. in Biology from Furman University (1989), M.S. in Environmental Toxicology from Clemson University (1994), and Ph.D. in Environmental Toxicology from Texas Tech University (2003). He has worked on various field projects in the United States, Central America, and Asia focusing on the biology, ecotoxicology, and conservation of wildlife, particularly reptiles and birds. Much of his recent research has focused on the impacts of environmental pollution, habitat alteration, and over-exploitation on endangered crocodilians and turtles. (Photographed by Tom Pop).