Portland State University

PDXScholar

Biology Faculty Publications and Presentations | Biology

6-1-2022

Terrestrial Movements, Activity Patterns and Habitat Use by Kinosternon Scorpioides (testudines: Kinosternidae) in Palo Verde National Park, Costa Rica

Jose M. Mora
Universidad Técnica Nacional

Franklin E. Castaneda
Portland State University

Follow this and additional works at: https://pdxscholar.library.pdx.edu/bio_fac

Part of the Biology Commons

Let us know how access to this document benefits you.

Citation Details

Mora, J. M., & Castañeda, F. E. (2022). Terrestrial movements, activity patterns and habitat use by Kinosternon scorpioides (Testudines: Kinosternidae) in Palo Verde National Park, Costa Rica. Phyllomedusa: Journal of Herpetology, 21(1), 3-15.

This Article is brought to you for free and open access. It has been accepted for inclusion in Biology Faculty Publications and Presentations by an authorized administrator of PDXScholar. Please contact us if we can make this document more accessible: pdxscholar@pdx.edu.

Phyllomedusa 21(1):3–15, 2022
© 2022 Universidade de São Paulo - ESALQ
ISSN 1519-1397 (print) / ISSN 2316-9079 (online)
doi: http://dx.doi.org/10.11606/issn.2316-9079.v21i1p3-15

Terrestrial movements, activity patterns and habitat use by *Kinosternon scorpioides* (Testudines: Kinosternidae) in Palo Verde National Park, Costa Rica

José M. Mora[1,2] and Franklin E. Castañeda[3]

[1] Universidad Técnica Nacional, Sede Central, Carrera de Gestión Ecoturística. Alajuela, Costa Rica. E-mail: jomora@pdx.edu.

[2] Portland State University, Department of Biology and Museum of Vertebrate Biology. Portland, Oregon 97207, USA.

[3] Fundación Panthera. Tegucigalpa, Honduras. E-mail: fcastaneda@panthera.org.

Abstract

Terrestrial movements, activity patterns and habitat use by *Kinosternon scorpioides* (Testudines: Kinosternidae) in Palo Verde National Park, Costa Rica. The Scorpion Mud turtle, *Kinosternon scorpioides,* is a widely distributed, semiaquatic species known to engage in regular terrestrial movement and terrestrial estivation. We studied terrestrial behavior in this species in Palo Verde National Park, northwestern Costa Rica. We determined terrestrial activity patterns by searching for active individuals during transects along 3.4 km of trails. We determined the distance that turtles traveled between the wetlands and estivation sites by fitting 10 terrestrially active individuals with a thread-bobbin tracking device attached to the rear of the carapace. We identified sex and marked and measured every turtle found active. We accumulated 92 observations of *K. scorpioides* active on land and we identified two behaviors: traveling and nesting. These turtles showed a bimodal activity pattern ($\chi^2 = 18.1$, $p < 0.02$, $df = 8$) with maximum activity during early morning hours (06:00 to 08:00 h) and twilight and early evening hours (16:00 to 20:00 h). We found 41 turtles estivating in deciduous dry forest at an average distance (± SE) of 156.4 ± 13.7 m (range 20.9–304.9 m) from the wetland border (water´s edge). Adults estivated at greater distances from the wetland than did juvenile turtles, and males estivated at greater distances than females. Turtles found estivating were in three different habitats: leaf litter (85%), rock cavities (10%), and tree buttresses (5%). *Kinosternon scorpioides* was observed to estivate for at least 84 days in PVNP during the dry season. We recorded several behavioral traits that may account for its ability to withstand desiccation during the estivation period. Our work underscores the need to include terrestrial habitats when considering the conservation needs of semiaquatic turtles.

Received 13 December 2021
Accepted 18 May 2022
Distributed June 2022

Keywords: Dry forest, Estivating sites, Freshwater turtles, Global climate change, Scorpion Mud Turtle.

Resumen

Movimientos terrestres, patrones de actividad y uso de hábitat por *Kinosternon scorpioides* (Testudines: Kinosternidae) en el Parque Nacional Palo Verde, Costa Rica. La tortuga candado, *Kinosternon scorpioides*, es una especie semiacuática ampliamente distribuida conocida por presentar movimientos terrestres regulares y estivación terrestre. Estudiamos el comportamiento terrestre de esta especie en el Parque Nacional Palo Verde, noroeste de Costa Rica. Determinamos sus patrones de actividad terrestre mediante la búsqueda de individuos activos en transectos a lo largo de 3,4 km de senderos. Determinamos la distancia que las tortugas viajaron entre el humedal y los sitios de estivación al seguir a 10 individuos activos en tierra a los que les pegamos un carrete de hilo en la parte posterior del caparazón. Identificamos el sexo y marcamos y medimos todas las tortugas que encontramos activas. Acumulamos 92 observaciones de *K. scorpioides* activas en tierra e identificamos dos comportamientos: viajar y anidar. Estas tortugas mostraron un patrón de actividad bimodal (χ^2 = 18,1, p < 0,02, gl = 8) con máxima actividad durante las primeras horas de la mañana (06:00–08:00 h) y el crepúsculo y las primeras horas de la noche (16:00–20:00 h). Encontramos 41 tortugas estivando en el bosque seco caducifolio a una distancia promedio (± SE) de 156.4 ± 13.7 m (20.9–304.9 m) del borde del humedal (borde del agua). Los adultos estivaron a mayor distancia del humedal que las tortugas juveniles y los machos estivaron a mayor distancia que las hembras. Las tortugas que encontramos estivando las encontramos en tres hábitats diferentes: hojarasca (85%), cavidades rocosas (10%) y raíces triangulares de árboles (5%). *Kinosternon scorpioides* estivó durante al menos 84 días en el Parque Nacional Palo Verde durante la estación seca. Registramos varios rasgos de comportamiento que pueden explicar su capacidad para resistir la desecación durante el período de estivación. Nuestro trabajo subraya la necesidad de incluir hábitats terrestres al considerar las necesidades de conservación de las tortugas semiacuáticas.

Palabras clave: Bosque seco, Cambio climático global, Sitios de estivación, Tortuga candado, Tortugas de agua dulce.

Resumo

Movimentos terrestres, padrões de atividade e usio de hábitat em *Kinosternon scorpioides* (Testudines: Kinosternidae) no Parque Nacional de Palo Verde, Costa Rica. O cágado peito-de-mola, *Kinosternon scorpioides*, é uma espécie semiaquática amplamente distribuída, conhecida por se envolver em movimentos terrestres regulares e estivação terrestre. Estudamos o comportamento terrestre dessa espécie no Parque Nacional de Palo Verde, noroeste da Costa Rica. Determinamos padrões de atividade terrestre por meio da procura de indivíduos ativos durante os transectos ao longo de 3,4 km de trilhas. Determinamos a distância que as tartarugas percorriam entre as zonas úmidas e os locais de estivação dotando 10 indivíduos terrestres ativos com bobinas de rastreamento na porção posterior da carapaça. Identificamos o sexo e marcamos e medimos cada tartaruga encontrada em atividade. Acumulamos 92 observações de *K. scorpioides* ativas em terra e identificamos dois comportamentos: deslocamento e nidificação. Essas tartarugas mostraram um padrão de atividade bimodal (χ^2 = 18,1, p < 0,02, df = 8), com atividade máxima durante as primeiras horas da manhã (06:00–08:00 h) e o crepúsculo e as primeiras horas da noite (16:00–20:00 h). Encontramos 41 tartarugas estivando em floresta seca decídua a uma distância média (± SE) de 156,4 ± 13,7 m (intervalo de 20,9–304,9 m) da fronteira da zona úmida (borda da água). Os adultos estivaram a maiores distâncias da zona úmida do que os juvenis, e os machos estivaram a maiores distâncias do que as fêmeas. As tartarugas encontradas estivando encontravam-se em três diferentes habitats: serapilheira (85%), cavidades de rochas (10%) e raízes tabulares (5%). Observou-se que *K. scorpioides* estivou durante pelo menos 84 dias no Parque Nacional de Palo Verde durante a estação seca. Foram registradas várias características comportamentais que podem explicar sua capacidade de resistir ao dessecamento durante o período de estivação. Nosso trabalho ressalta a necessidade de incluir hábitats terrestres ao considerar as necessidades de conservação das tartarugas semiaquáticas.

Palavras-chave: Bosque seco, Cágados, Mudança climática global, Peito-de-mola, Sítios de estivação.

Introduction

Turtles are among the most threatened groups of vertebrates worldwide due to anthropogenic factors such as direct consumption for food, development, agriculture, and land and water pollution (Cox *et al*. 2022, Tan *et al*. 2022). Over half of all turtle species are included in at least one threat category (Rhodin *et al*. 2018, Stanford *et al*. 2020, TTWG 2021, Cox *et al*. 2022). In addition, rapid global change in climate patterns has the potential to further erode turtle populations (Lovich *et al*. 2018, Butler 2019). Increasing environmental temperatures are impacting spatial distribution, reproduction, physiological performance, behavior, and other life-history traits of ectothermic animals including turtles (Lovich *et al*. 2018, Berriozabal-Islas *et al*. 2020, Stanford *et al*. 2020). Climate change is likely to have severe consequences on semiaquatic species that rely on the health of multiple adjacent habitats in order to survive.

Studies of activity and movements of freshwater turtles can potentially reveal how variation in environmental parameters (i.e., weather, temperature) impact resource acquisition, and therefore an organism's life history (Rowe 2003, Rowe *et al*. 2009). Terrestrial activity of freshwater turtles has been widely documented and is known to be an important aspect of their ecology (Buhlmann and Gibbons 2001, Steen *et al.* 2012). Terrestrial behavior includes movements associated with nesting, hatchling emergence and transit from nests, dispersal of all life stages, movements to or from hibernating or estivating sites, and terrestrial migration in search of mates (Steen *et al.* 2012, Enders *et al*. 2021). Study of terrestrial movement patterns is a key aspect of chelonian conservation and survival (Burke and Gibbons 1995), but many species are still relatively understudied (Enders *et al*. 2021). The abundance and distribution of a particular species is often determined by the availability of habitat. This must include all necessary resources in different habitats (food, water, refuge, and nest sites) to ensure the species existence (Litvaitis *et al.* 1994). Aquatic or semiaquatic turtles that experience seasonal fluctuations of their aquatic habitat may be forced to use terrestrial habitats. Many organisms under these circumstances will either make terrestrial migrations to find other bodies of water or estivate until aquatic habitats are replenished (Ligon and Peterson 2002). Either way, the terrestrial habitat and its availability becomes an important component for the ecology and conservation of these organisms.

Mud turtles of the genus *Kinosternon* are small mostly semiaquatic turtles inhabiting a wide variety of natural (streams, rivers, lakes, lagoons, seasonal or perennial ponds and wetlands, and estuaries) and artificial aquatic environments (drainage ditches, irrigation canals, reservoirs, and water tanks) throughout their distribution (Iverson *et al*. 2013, Butler *et al*. 2016). They move overland for variable distances, approaching at least one km, in response to the seasonality of aquatic environments or in search of mates and/or nest sites (Cordero *et al*. 2012, Pérez-Pérez *et al*. 2017). *Kinosternon integrum* Le Conte, 1854 has been observed to estivate at distances > 560 m from the nearest lakeshore in Michoacán, Mexico (Aparicio *et al*. 2018). *Kinosternon subrubrum* Bonnaterre, 1789 in the mid-Atlantic region of the United States traveled distances of 903 and 887 m (Cordero *et al*. 2012). Even highly aquatic species such as *Kinosternon leucostomum* (Duméril, Bibron, and Duméril, 1851) can travel up to 600 m for nesting and estivating (Morales-Verdeja and Vogt 1997, Cordero and Swarth 2010). Multiple species in the genus rely on terrestrial activity. However, anthropogenic factors such as habitat fragmentation and urbanization cause loss of terrestrial connectivity that is required for populations of these species to survive or disperse to additional suitable habitat (Buhlmann and Gibbons 2001, Aparicio *et al*. 2018, Serrano *et al*. 2020).

The Scorpion Mud turtle *Kinosternon scorpioides* (Linnaeus, 1766) is the most widely distributed species in the genus. It is distributed from Mexico (Oaxaca in the west and Tamaulipas in the east), to southern Bolivia and northern Peru, Brazil and Argentina (Iverson 2010, Berry and Iverson 2011). It uses a variety of aquatic habitats throughout its range (Pritchard and Trebbau 1984, Ernst and Barbour 1989, Savage 2002). It is common on the Pacific slope of Costa Rica where it inhabits nearly any body of shallow water but prefers habitats with abundant aquatic vegetation (Acuña-Mesén 1998). It is found in marshes, permanent and temporary ponds, streams, rivers, and swamps (Acuña-Mesén 1998, Bedoya-Cañón *et al*. 2018). In Belize, *K. scorpioides* is known to move from drying ephemeral habitats through terrestrial environments into permanent streams as the dry season progresses (Moll and Moll 2004). It is also known to make substantial overland movements in Costa Rica (175–500 m from water), and to leave drying water bodies to estivate in adjacent terrestrial habitats (Teska 1976, Acuña-Mesén 1998, Savage 2002, Moll and Moll 2004). However, no research has been devoted specifically to the detailed study of terrestrial movements and terrestrial habits of this species. Because most climate models predict increases in temperature and seasonality in the tropics and other biomes, it is important to collect baseline data about the mechanisms by which organisms respond to present day seasonal droughts in order to predict their potential responses to climate change (Butterfield *et al*. 2018). The main objective of this research was to determine the temporal and spatial terrestrial movement patterns of *K. scorpiodes* in a protected dry forest in northwestern Costa Rica, and to examine the relationship of this activity to daily temperature and humidity changes.

Materials and Methods

We conducted our research in Palo Verde National Park (PVNP), an area of 19,800 ha in the northwestern lowlands of Guanacaste Province, Costa Rica (10°21' N, 85°21' W; Figure 1). At this site annual average temperature is 27°C, and annual precipitation is 2,296 mm (Castañeda and Mora 2010, Mora and Castañeda 2021). The dry season lasts from December to April and the rainy season from May to November (Mora 1989). A large variety of habitats are represented in PVNP: including primary and secondary deciduous dry forest, riparian forest, savannas, and wetlands (Hartshorn 1983, Mora 1989). A single wetland, Palo Verde Marsh or Palo Verde Lagoon covers 1,207 ha and accounts for 6.1% of the park's area (Trama *et al*. 2009). It is formed by a mosaic of aquatic and woody vegetation (Trama *et al*. 2009). During the rainy season, the lagoon's water level can rise to 1.5 m, but it gradually declines until it dries out completely at the end of the dry season in April or May (Trama *et al*. 2009).

We conducted our research from October 2003 at the onset of the rainy season to November 2004 at the end of the following rainy season. During these months we also monitored Guayacán waterhole, ca. 3 km west of the Hacienda Park Ranger Station. This natural waterhole varies in diameter from 4 m during the rainy season to 1 m during the driest months. As of 2001, it had apparently not gone completely dry for more than 25 years (Stoner 2001). It is the only source of water in the forest at our study area.

During the dry season, as the lagoon water level diminishes, mud turtles are commonly seen moving on land (Acuña-Mesén 1990). To determine daily terrestrial activity patterns, during the dry season of 2004 (February to May) we searched for active turtles by walking three transects. Transect A was a dirt road between the MINAE station and "Puerto Chamorro" on the Tempisque River (2000 m); transect B was a dirt road between the OTS station and the MINAE station (900 m); and transect C was a trail leading east from the MINAE station (500 m). All transects were oriented parallel to the ecotone between the wetland and the dry forest (Figure 1). Surveys were conducted between 06:00 and 24:00 h, and observations were divided into nine

Figure 1. Study site at Palo Verde National Park in northwestern Costa Rica. 1 = Puerto Chamorro, 2 = MINAE station, 3 = OTS station, A = trail of 2000 m, B = trail of 900 m, C = trail of 500 m.

periods of 2 hours each (i.e., from 06:00 to 08:00 h; from 08:01 to 10:00 h … from 22:01 to 24:00 h). We walked transects during 4–5 periods each day chosen randomly but making sure all nine time periods were covered three times each week. We searched for active mud turtles for 57 days (16 in February, 15 in March, 14 in April, and 12 in May). During these days, we actively searched for a total of 233 person-hours. To determine variation in terrestrial movements throughout the day we kept records of the sampling effort and the number of active turtles found for each 2 hours period. The frequency of active turtles was given by the number of individuals found moving per unit search time during each of the nine periods. We individually identified sex and marked and measured each turtle captured. We also recorded the direction each turtle was traveling. Measurements included curved carapace length (CCL, type D of Iverson and Lewis 2018) and curved carapace width (CCW) in mm to the nearest 1 mm taken with a flexible measuring tape, and body mass to the nearest 0.1 g (using either a 300 g or a 1,000 g capacity Pesola spring balances). Turtle activity was correlated with ambient temperature and humidity using data from the OTS facility weather station. The station automatically records readings every 30 min, which allowed us to construct a profile of temperature and humidity from 06:00 to 24:00 h during the study months.

To determine the distance that turtles travel from the wetland to the estivation sites, we fitted 10 individuals found active on land with a thread-bobbin tracking device, which we attached to the rear of the carapace (Wilson 1998). Turtles equipped with thread bobbins were released within a few hours, at their capture location. We attached the free end of the thread to the vegetation, which allowed the thread to unwind as the turtle walked away. Twenty-four hours later we followed the thread until we found the turtle. We also searched for estivating turtles in the leaf litter using a hand rake, and between tree buttresses and rock crevices. Searches for estivating turtles were carried out to a maximum of 350 m from the wetland. We marked each site where an estivating turtle was found and determined the geographic location (using a Garmin Geko 201 GPS). GPS points were plotted on an Ikonos satellite image of PVNP and the straight-line distance from the wetland (defined as the water's edge) to each GPS point (estivating site in the dry forest) was measured in m using ArcGIS 3.2 (Esri Inc. 2002). All turtles equipped with thread bobbins moved mostly in straight lines (south to north) from the wetland to the estivating sites in the forest. Thus, a straight-line movement was assumed for all turtles found estivating.

We recorded data for each turtle found estivating including microhabitat or refuge selected. We measured the temperature of 13 estivation sites, and humidity in five sites. We took readings inside and outside estivating refuges during the hottest time of the day (11:00 to 14:00 h). To measure air temperature and humidity we used a digital hygro-thermometer (model 445582 Extech Instruments), and for soil temperature we used a digital thermometer (model HI-145-30 Hanna Instruments).

Turtles were assigned to 10 mm size-class categories, but for some analyses were assigned only to age class: juvenile or adult. To determine age class, we used the size of the smallest known mature female of *K. scorpioides* (Savage 2002): 122 mm straight-line carapace length (CSL). Since we used CCL in our study, we measured the CSL and the CCL of 103 mud turtles from PVNP (Castañeda and Mora 2010), and found the mean difference to be 22.9 mm. Thus, we considered all individuals < 140 mm CCL to be juveniles, and all measuring ≥ 141 mm to be adults.

We tested the relationship between activity and humidity, activity and temperature, and turtle size and distance moved from the wetland, using a Pearson correlation ($\alpha = 0.05$). We tested for differences in distances from the wetland among sex and age of turtles with the Mann-Whitney U test ($\alpha = 0.05$) in SYSTAT 9 for Windows (Systat 9 1999). Measurements and all other calculations are given as mean $\pm$ SE.

Results

During this study, we observed a total of 92 *Kinosternon scorpioides* active on land during both dry and rainy seasons, and two behaviors were identified: traveling and nesting. We did not observe feeding or social behavior on land. All turtles reacted to observers by closing their plastron when we approached. After five to 10 min of handling (for measurements and marking) most turtles emptied their urinary bladder and liberated a strong musk odor.

During the dry season of 2004, we found 76 mud turtles actively moving on land between

February and May; 18 were juveniles and 58 were adults of both sexes (Figure 2). Turtles were already leaving the wetland and entering the forest to estivate by early February. All turtles we observed from February to April were moving from the wetland towards the forest (south to north). During February we followed 12 females moving from the wetland to the forest where they nested. After nesting they returned to the wetland. We found actively nesting females between 07:00 and 10:00 h and between 15:00 and 23:00 h (Mora and Castañeda 2021). During April, we found three turtles moving on land (south to north) after a single isolated heavy rain event. During May we found only one turtle moving north (towards the forest), but from the last week of May onwards, all active turtles were moving back from the forest to the wetland (north to south). During the dry season we recorded the highest terrestrial activity in March and the lowest in April (Figure 3). During this dry season (2004) we found only two *K. scorpioides* in Guayacán waterhole before it was completely dry by the end of March.

During the rainy season of 2004 (October and November), we found 16 *K. scorpioides* active on land. Fourteen of these individuals were females (four were nesting). The two males found on land were less than 1 m from the water; females were farther from water (some more than 200 m).

Kinosternon scorpioides in PVNP showed a bimodal daily activity pattern (χ^2 = 18.1, p < 0.02, df = 8; Figure 4), with maximum activity during early morning hours (06:00 to 08:00 h) and twilight and early evening hours (16:00 to 20:00 h). Their daily activity pattern was positively correlated with relative humidity but not significantly (r^2 = 0.33, p = 0.11, N = 12) and barely negatively correlated with ambient temperature (r^2 = 0.37, p = 0.08, N = 12) during the day (from 06:00 to 24:00 h). During night hours (from 18:00 to 24:00) turtle activity diminished even though ambient temperature continued to drop and humidity continued to increase (Figure 5).

We found 41 estivating turtles in the deciduous dry forest north of the wetland (Figure 1) at an average distance of 156.4 ± 13.7 m (range 20.9 to 304.9 m) from the wetland border (water´s edge). Adults (N = 28) were found at a significantly greater distance from the water (183.2 ± 15.0 m) than juveniles (N = 3) (98.7 ± 21.3 m) (U = 274.5, p = 0.009). The average distance traveled by males (190.7 ± 25.6 m, N = 13) was not significantly different from that traveled by females (163.2 ± 18.4 m, N = 19) (U = 94.5, p = 0.26). Most juveniles were found within the first 150 m from the wetland, females were more evenly distributed from 0 to 300 m, and males tended to be found at the farthest distances (Figure 6). The largest number of turtles was found between 50 and 100 m from the wetland, and only one individual was found between 300 and 350 m. Estivating turtles ranged in size from 85 to 214 mm CCL (Figure 2), from 77 to 189 mm CCW, and from 59 to 870 g. There was a direct but very weak relationship between turtle size and distance from the wetland to estivating sites (CCL: r^2 = 0.20, p = 0.003; CCW: r^2 = 0.18, p = 0.005; weight: r^2 = 0.15, p = 0.009).

Turtles found estivating were in three different types of habitats: leaf litter, rock cavities and between tree buttresses. Thirty-five turtles (85%) estivated under leaf litter; these individuals constructed a shallow form in the soil (about 5 cm deep) that covered the plastron and the lower half of the carapace, while the rest of the shell was covered by leaves. Four turtles (10%) were found estivating inside natural limestone cavities, and two (5%) were found between tree buttresses. When measured during the hottest time of the day (11:00 to 14:00 h), the estivation sites maintained lower temperatures and higher humidity than the environment external to the refuge. Average temperature was 29.6 ± 0.5°C and 34.3 ± 0.6°C inside and outside refuges respectively. Average humidity was 59.9 ± 6.2% and 41.1 ± 3.8% inside and outside refuges, respectively.

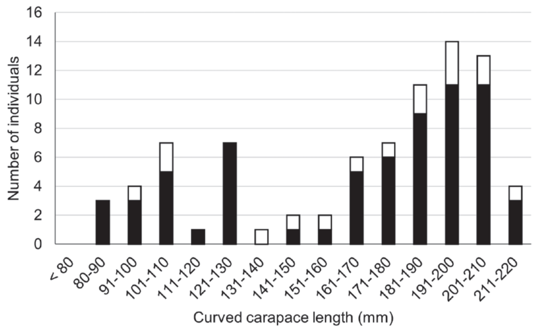

Figure 2. Population size structure of Scorpion Mud turtles (*Kinosternon scorpioides*) (*N* = 76) found on land during the dry season of 2004 (February to May), in Palo Verde National Park northwestern Costa Rica. Black bars = females, white bars = males

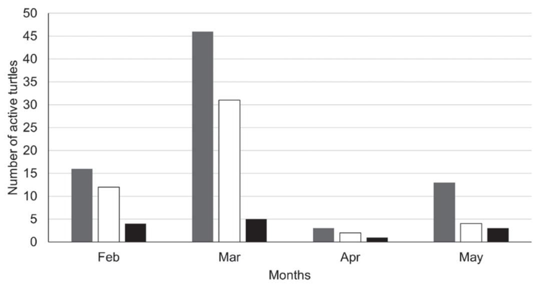

Figure 3. Number of Scorpion Mud turtles (*Kinosternon scorpioides*) active on land from February to May 2004 in Palo Verde National Park, northwestern Costa Rica. White bars = females, black bars = males, gray bars = total

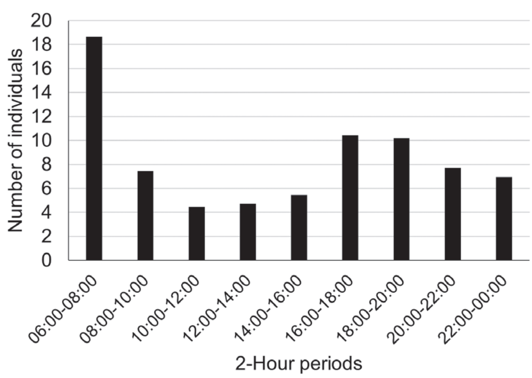

Figure 4. Number of individuals of Scorpion Mud turtles (*Kinosternon scorpioides*) active during each 2-hour sampling period in Palo Verde National Park, northwestern Costa Rica.

Discussion

In PVNP, during the dry season, *Kinosternon scorpioides* engages in terrestrial activity apparently for only two purposes, either to estivate or to nest. Feeding and social behavior were never observed in this species while on land. Nesting seems to be the main purpose of the terrestrial activity observed during the rainy season. Turtles that abandoned the wetland during February would have to spend 80 days or more estivating in the forest. Moreover, since the dry season in PVNP begins in December, it is possible that some individuals migrated as early as January. The seasonal drying of wetlands is well-known to force aquatic turtles to move to other wetlands, e.g., *Clemmys guttata* (Schneider, 1792) (Rowe *et al*. 2013), and *Sternotherus odoratus* (Latreille, 1802) (Seburn and Burns 2021). Because no other water source is available for *K. scorpioides* in PVNP, the turtles that migrated to the forest do not have access to water (the waterhole dried out by March) and must estivate until they return to the wetland in May or during an occasional rain in April. The distance from estivation sites to the wetland were only weakly related to individual size (Figure 6), as was found for *Kinosternon leucostomum* in Mexico (Morales-Verdeja and Vogt 1997).

Many individuals of *K. scorpioides* have been found buried under mud and dry aquatic plants in the wetland during April and May (Castañeda and Mora 2010) suggesting that not all turtles leave the wetland and enter the forest to estivate (Acuña-Mesén 1990). Although, the dry season in PVNP starts in December, in a normal year the wetland holds water until March and some small, scattered puddles remain even until the first half of April. Thus, turtles that remain in the wetland would be able to significantly shorten the inactivity and deprivation period, probably to only about 30 days or even less. Why some individuals of *K. scorpioides* start to migrate to the forest of PVNP during February (not counting nesting

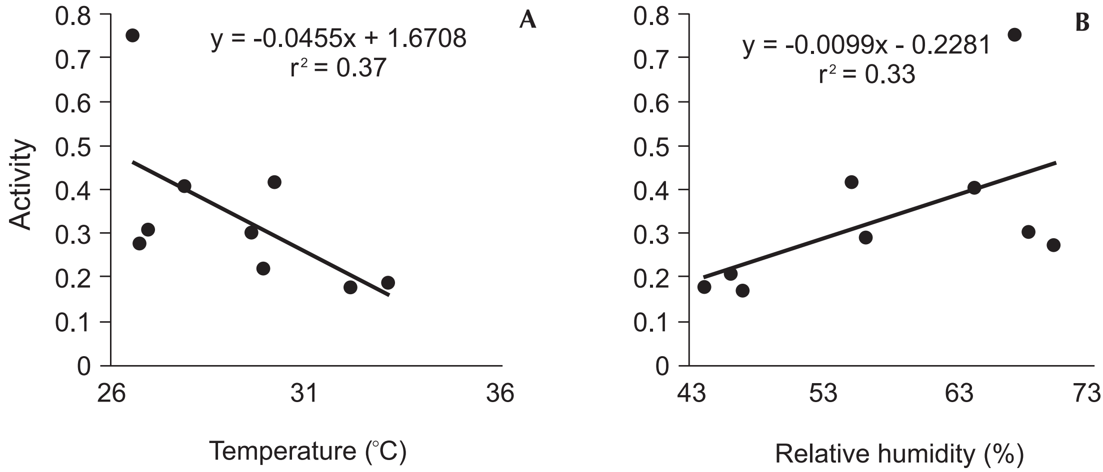

Figure 5. Scorpion Mud turtles (*Kinosternon scorpioides*) daily activity pattern (number of individuals found moving per 2-hr unit) correlated to ambient temperature (**A**), and to ambient relative humidity (**B**) in Palo Verde National Park, northwestern Costa Rica.

females) when there is still plenty of water in the lagoon, and what factors determine which individuals stay in the wetland and which migrate to the forest, remain unknown.

Because of the physiological constraints of ectothermy, environmental parameters such as temperature and humidity have an important effect on the activity patterns of turtles. Terrestrial movements by *Kinosternon integrum* in Mexico clearly relate to seasonality and especially rainfall (Pérez-Pérez *et al*. 2017). Individuals of *Kinosternon baurii* (Garman, 1891) in Florida spend a significant amount of time on land when aquatic areas dry out (Stemle *et al*. 2019). Apparently, heavy rainfall initiates mass migration in this species and extreme temperature inhibits terrestrial movement (Wygoda 1979). As was observed in this study, seasonal terrestrial movement may involve nesting as well as estivation. Seasonal drying of a lake and the nesting season induced terrestrial activity in *K. leucostomum* in Veracruz, Mexico (Morales-Verdeja and Vogt 1997). In Nebraska, female *K. flavescens* moved to nest sites, excavated a body cavity, and dug an additional nest cavity, and then often remained buried with the eggs for up to 38 days (Iverson 1990). *Kinosternon subrubrum* also remain buried after nesting up to 29 days until the next rainstorm (Burke *et al*. 1994). Several of these mud turtles used estivation sites within forests to afford

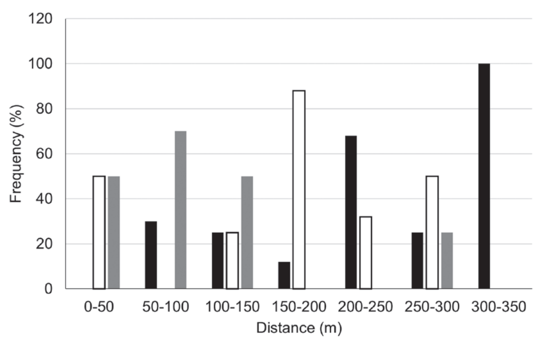

Figure 6. Frequency expressed as 100% at each distance category of estivating individuals of Scorpion Mud turtles (*Kinosternon scorpioides*) by sex, and age, in Palo Verde National Park, northwestern Costa Rica. White bars = females, black bars = males, gray bars = juveniles

protection from high temperature, dehydration and predation (Wygoda 1979, Morales-Verdeja and Vogt 1997).

During the dry season in PVNP, the average daily temperature exhibited a range of 6.5°C, changing from a low of 26.7°C in early morning and late afternoon hours to 33.2°C during midday hours. However, environmental temperatures in the study area were relatively uniform across all days with readings (Mora and Castañeda 2021). Additionally, average daily humidity varied from 60 to 71% in late afternoon and early morning hours to 44% during midday hours. Thus, the bimodal activity pattern exhibited by *K. scorpioides* in PVNP (Figure 4) is a convenient mechanism to reduce the risk of dehydration and avoid extreme temperatures while migrating terrestrially during the dry season. In the forest, turtles remained buried mainly in leaf litter, or hid in rock cavities or among tree buttresses, which further protects estivating turtles from desiccation and predation.

Several behavioral traits of *Kinosternon scorpioides* may account for its ability to withstand desiccation during the estivation period in PVNP (prompted by an extended dry season and the reduction or disappearance of their aquatic habitat): (1) the use of estivating refuges with a lower temperature and higher humidity than the environment; (2) a bimodal daily activity pattern that ensures the turtle´s terrestrial movements occur during hours with optimum conditions of ambient temperature and humidity; (3) juveniles (which are more prone to dehydration than adults) travel shorter distances than adults from the wetland to estivation sites; and (4) the storage of water in the urinary bladder might be a possibility given our observation of fluid voiding during handling.

There are many seasonal wetlands in northwestern Costa Rica that probably support local populations of *K. scorpioides*. The results of this study provide basic information to promote the conservation of these populations that are not in protected areas. Agriculture, development and logging are the top threats to reptiles (Cox *et al.* 2022). These factors negatively impact uplands adjacent to wetlands that are used by turtles as critical components of their overall habitat (Buhlmann and Gibbons 2001). The negative effects of these threats could lead to local extinctions, the prelude to a species global extinction.

Clearly, terrestrial habitats are vitally important for aquatic and semiaquatic turtles (Buhlmann and Gibbons 2001, McKnight and Ligon 2019). The core area needed to protect nesting, estivation and hibernation, and other terrestrial activities, varies by species (Steen *et al.* 2012), but detailed data are essential to conservation. For example, to protect 100% of the *K. scorpioides* nests at PVNP, the core protected area would have to extend 175 m from the wetland, but protection of the first 25 m from the wetland would protect 86.4% of nests (Mora and Castañeda 2021). This observation about the use of terrestrial environments by *K. scorpioides* in PVNP illustrates how studies like the one reported here are necessary to ensure the future of species that are very often associated only with wetland habitats in the public view. We have been able to show that adjacent terrestrial habitats are indispensable for this mud turtle species.

Acknowledgments

We are grateful to PVNP personnel for the facilities provided for this work, and R. Acuña-Mesén for his friendship and his work to protect turtles. Both authors thank Peter Meylan, and two anonymous reviewers for their suggestions to improve this paper. We also thank Gerardo Chaves for the preparation of figure 1, Tomás Carlo and Lucía López for statistical advice and figure preparation, and José Andrés Mora for retyping the text of the paper. JMM acknowledges Emilce Rivera, department head, Carrera de Gestión Ecoturística, Sede Central, Universidad Técnica Nacional (UTN), for their support and time provided to complete this work.

References

Acuña-Mesén, R. A. 1990. El impacto del fuego y la sequía sobre la estructura de la población de *Kinosternon scorpioides* (Testudines: Kinosternidae) en Palo Verde, Guanacaste, Costa Rica. *Brenesia 33:* 85–97.

Acuña-Mesén, R. A. 1998. *Las Tortugas Continentales de Costa Rica.* 2nd ed. San José. Universidad de Costa Rica. 92 pp.

Aparicio, Á., I. E. Mercado, A. M. Ugalde, E. Gaona-Murillo, T. Butterfield, and R. Macip-Ríos. 2018. Ecological observations of the Mexican mud turtle (*Kinosternon integrum*) in the Pátzcuaro Basin, Michoacán, Mexico. *Chelonian Conservation and Biology 17:* 284–290.

Bedoya-Cañón, M. A., J. A. Muñoz-Avila, and F. Vargas-Salinas. 2018. Morphology and natural history of the mud turtle *Kinosternon scorpioides scorpioides* in populations of northern Colombia. *Herpetological Review 49:* 210–214.

Berriozabal-Islas, C., A. Ramírez-Bautista, F. Torres-Ángeles, J. F. M. Rodrigues, R. Macip-Ríos, and P. Octavio-Aguilar. 2020. Climate change effects on turtles of the genus *Kinosternon* (Testudines: Kinosternidae): an assessment of habitat suitability and climate niche conservatism. *Hydrobiologia 847:* 4091–4110.

Berry, J. F., and J. B. Iverson. 2011. *Kinosternon scorpioides* (Linnaeus 1766) - Scorpion Mud Turtle. Pp 063.1–063.15 *in* A. G. J. Rhodin, P. C. H. Pritchard, P. P van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier (eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. Chelonian Research Monographs No. 5.

Buhlmann, K. A. and J. W. Gibbons. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. *Chelonian Conservation and Biology 4:* 115–127.

Burke, V. J. and J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. *Conservation Biology 9:* 1365–1369.

Burke, V. J., J. W. Gibbons, and J. L. Greene. 1994. Prolonged nesting forays by common mud turtles (*Kinosternon subrubrum*). *American Midland Naturalist 131:* 190–195.

Butler, C. J. 2019. A review of the effects of climate change on chelonians. *Diversity 11:* 1–22.

Butler, C. J., B. D. Stanila, J. B. Iverson, P. A. Stone, and M. Bryson. 2016. Projected changes in climatic suitability for *Kinosternon* turtles by 2050 and 2070. *Ecology and Evolution 6:* 7690–7705.

Butterfield, T. G., A. Scoville, A. García, and D. D. Beck. 2018. Habitat use and activity patterns of a terrestrial turtle (*Rhinoclemmys rubida perixantha*) in a seasonally dry tropical forest. *Herpetologica 74:* 226–235.

Castañeda, F. E., and J. M. Mora. 2010. Impact of fire on a wetland population of the Scorpion Mud Turtle (*Kinosternon scorpioides*) in northwestern Costa Rica. Pp. 706–715 *in* L. D. Wilson, J. H. Townsend, and J. D. Johnson (eds.), *Conservation of Mesoamerican Amphibians and Reptiles*. Eagle Mountain. Eagle Mountain Publishing, LC.

Cordero, G. A. and C. W. Swarth. 2010. Notes on the movement and aquatic behaviour of some kinosternid turtles. *Acta Zoológica Mexicana 26:* 233–35.

Cordero, G. A., R. Reeves, and C. W. Swarth. 2012. Long distance aquatic movement and home range size of an eastern mud turtle, *Kinosternon subrubrum,* population in the mid-Atlantic region of the United States. *Chelonian Conservation and Biology 11:* 121–124.

Cox, N., B. E. Young, P. Bowles, M. Fernandez, J. Marin, G. Rapacciuolo, M. Böhm, T. M. Brooks, S. Blair Hedges, C. Hilton-Taylor, M. Hoffmann, R. K. B. Jenkins, M. F. Tognelli, G. J. Alexander, A. Allison, N. B. Ananjeva, M. Auliya, L. J. Avila, D. G. Chapple, D. F. Cisneros-Heredia, H. G. Cogger, G. R. Colli, A. de Silva, C. C. Eisemberg, J. Els, A. Fong G., T. D. Grant, R. A. Hitchmough, D. T. Iskandar, N. Kidera, M. Martins, S. Meiri, N. J. Mitchell, S. Molur, C. de C. Nogueira, J. C. Ortiz, J. Penner, A. G. J. Rhodin, G. A. Rivas, M-O. Rödel, U. Roll, K. L. Sanders, G. Santos-Barrera, G. M. Shea, S. Spawls, B. L. Stuart, K. A. Tolley, J-F. Trape, M. A. Vidal, P. Wagner, B. P. Wallace, and Y. Xie. 2022. A global reptile assessment highlights shared conservation needs of tetrapods. *Nature* 2022. https://doi.org/10.1038/s41586-022-04664-7

Enders, S. J., A. S. Weber, B. P. Butterfield, A. Walde, A. Ross, B. Hauge, T. Hootman, W. Osborne, and E. C. Munscher. 2021. Movements of *Sternotherus minor* (Testudines: Kinosternidae) in a central Florida spring-run. *Herpetology Notes 14:* 1043–1049.

Ernst, C. H., and R. W. Barbour. 1989. *Turtles of the World*. Washington, D.C. Smithsonian Institution Press. 313 pp.

Esri Inc. 2002. ArcGIS (Version 3.2). Esri Inc. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Hartshorn, G. 1983. Introduction. Pp. 119–186 *in* D. H. Janzen (ed.), *Costa Rican Natural History.* Chicago. University of Chicago Press.

Iverson, J. B. 1990. Nesting and parental care in the mud turtle, *Kinosternon flavescens*. *Canadian Journal of Zoology 68:* 230–233.

Iverson, J. B. 2010. Reproduction in the Red-cheeked Mud Turtle (*Kinosternon scorpioides cruentatum*) in southeastern Mexico and Belize, with comparisons across the species range. *Chelonian Conservation and Biology 9:* 250–261.

Iverson, J. B., and E. L. Lewis. 2018. How to measure a turtle. *Herpetological Review 49:* 453–460.

Iverson, J. B., L. Minh, and C. Ingram. 2013. Molecular phylogenetics of the mud and musk turtle family Kinosternidae. *Molecular Phylogenetics and Evolution 69:* 929–939.

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.

Litvaitis. J., K. Titus, and E. Anderson. 1994. Measuring vertebrate use of terrestrial habitats and foods. Pp. 254–274 *in* T. Bookhout (ed.), *Research and Management Techniques for Wildlife and Habitats.* Baltimore, Maryland. The Wildlife Society.

Lovich, J. E., J. R. Ennen, M. Agha, and J. W. Gibbons. 2018. Where have all the turtles gone, and why does it matter? *BioScience 68:* 771–781.

McKnight, D. T. and D. B. Ligon. 2019. Estivation site selection of western chicken turtles (*Deirochelys reticularia miaria*). *Southwestern Naturalist 64:* 187–194.

Moll, D., and E. O. Moll. 2004. *The Ecology, Exploitation and Conservation of River Turtles*. New York. Oxford University Press. 393 pp.

Mora, J. M. 1989. Eco-behavioral aspects of two communally nesting iguanas and the structure of their shared nesting burrows. *Herpetologica 45:* 293–298.

Mora, J. M. and E. F. Castañeda. 2021. Nest site selection and nesting behavior of the mud turtle *Kinosternon scorpiodes* (Testudines: Kinosternidae) in Palo Verde National Park, Costa Rica: implications for management. *Neotropical Biology and Conservation 16:* 273–287.

Morales-Verdeja, S. A. and R. C. Vogt. 1997. Terrestrial movements in relation to aestivation and the annual reproductive cycle of *Kinosternon leucostomum*. *Copeia 1997:* 123–130.

Pérez-Pérez, A., A. E. López-Moreno, O. Suárez-Rodríguez, J. L. Rheubert, and O. Hernández-Gallegos. 2017. How far do adult turtles move? Home range and dispersal of *Kinosternon integrum*. *Ecology and Evolution 7:* 8220–8231.

Pritchard, P. C. H. and P. Trebbau. 1984. *The Turtles of Venezuela*. Ithaca. Society for the Study of Amphibians and Reptiles. 414 pp.

Rhodin, A. G. J., C. B. Stanford, P. P. V. Dijk, C. Eisemberg, L. Luiselli, R. A. Mittermeier, R. Hudson, B. D. Horne, E. V. Goode, G. Kuchling, A. Walde, E. H. W. Baard, K. H. Berry, A. Bertolero, T. E. G. Blanck, R. Bour, K. A. Buhlmann, L. J. Cayot, S. Collett, A. Currylow, I. Das, T. Diagne, J. R. Ennen, G. Forero-Medina, M. G. Frankel, U. Fritz, G. García, J. W. Gibbons, P. M. Gibbons, G. Shiping, J. Guntoro, M. D. Hofmeyr, J. B. Iverson, A. R. Kiester, M. Lau, D. P. Lawson, J. E. Lovich, E. O. Moll, V. P. Páez, R. Palomo-Ramos, K. Platt, S. G. Platt, P. C. H. Pritchard, H. R. Quinn, S. C. Rahman, S. T. Randrianjafizanaka, J. Schaffer, W. Selman, H. B. Shaffer, D. S. K. Sharma, S. Haitao, S. Singh, R. Spencer, K. Stannard, S. Sutcliffe, S. Thomson, and R. C. Vogt. 2018. Global conservation status of turtles and tortoises (Order Testudines). *Chelonian Conservation and Biology 17:* 135–161.

Rowe, J. W. 2003. Activity and movements of midland painted turtles (*Chrysemys picta marginata*) living in a small marsh system on Beaver Island, Michigan. *Journal of Herpetology 37:* 342–353.

Rowe, J. W., J. R Gradel, and C. F. Bunce. 2013. Effects of weather conditions and drought on activity of spotted turtles (*Clemmys guttata*) in a southwestern Michigan wetland. *American Midland Naturalist 169:* 97–110.

Rowe, J. W., G. C. Lehr, P. M. McCarthy, and P. M. Converse. 2009. Activity, movements and activity area size in Stinkpot Turtles (*Sternotherus odoratus*) in a southwestern Michigan Lake. *American Midland Naturalist 162:* 269–278.

Savage, J. 2002. *The Amphibians and Reptiles of Costa Rica*. Chicago. University of Chicago Press. 934 pp.

Seburn, D. C. and M. Burns. 2021. Overland movement by an eastern musk turtle (*Sternotherus odoratus*). *Herpetology Notes 14:* 775–776.

Serrano, F., R. Pita, M. Mota-Ferreira, P. Beja, and P. Segurado. 2020. Landscape connectivity affects individual survival in unstable patch networks: The case of a freshwater turtle inhabiting temporary ponds. *Freshwater Biology 65:* 540–551.

Stanford, C. B., J. B. Iverson, A. G. J. Rhodin, P. P. v. Dijk, R. A. Mittermeier, G. Kuchling, K. H. Berry, A. Bertolero, K. A. Bjorndal, T. E. G. Blanck, K. A. Buhlmann, R. L. Burke, J. D. Congdon, T. Diagne, T. Edwards, C. C. Eisemberg, J. R. Ennen, G. Forero-

Medina, M. Frankel, U. Fritz, N. Gallego-García, A. Georges, J. W. Gibbons, S. Gong, E. V. Goode, H. T. Shi, H. Hoang, M. D. Hofmeyr, B. D. Horne, R. Hudson, J. O. Juvik, R. A. Kiester, P. Koval, M. Le, P. V. Lindeman, J. E. Lovich, L. Luiselli, T. E. M. McCormack, G. A. Meyer, V. P. Páez, K. Platt, S. G. Platt, P. C. H. Pritchard, H. R. Quinn, W. M. Roosenburg, J. A. Seminoff, H. B. Shaffer, R. Spencer, J. U. V. Dyke, R. C. Vogt, and A. D. Walde. 2020. Turtles and tortoises are in trouble. *Current Biology 30:* R721–R735.

Steen, D. A., J. P. Gibbs, K. A. Buhlmann, J. L. Carr, B. W. Compton, J. D. Congdon, J. S. Doody, J. C. Godwin, K. L. Holcomb, D. R. Jackson, F. J. Janzen, G. Johnson, M. T. Jones, J. T. Lamer, T. A. Langen, M. V. Plummer, J. W. Rowe, R. A. Saumure, J. K. Tucker, and D. S. Wilson. 2012. Terrestrial habitat requirements of nesting freshwater turtles. *Biological Conservation 150:* 121–128.

Stemle, L. R., K. M. Martinet, and G. J. Langford. 2019. Spatial ecology of the Striped Mud Turtle, *Kinosternon baurii,* in a restored Florida wetland. *Herpetological Review 50:* 695–698.

Stoner, K. E. 2001. Differential habitat use and reproductive patterns of frugivorous bats in tropical dry forest of northwestern Costa Rica. *Canadian Journal of Zoology 79:* 1626–1633.

Systat 9. 1999. Systat®, release 9 for Windows. Chicago, Illinois, USA.

Tan, W. C., P. Ginal, A. G. J. Rhodin, J. B. Iverson, and D. Rödder. 2022. A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia. *Frontiers of Biogeography 14.1:* e50928.

Teska, W. R. 1976. Terrestrial movements of mud turtle *Kinosternon scorpioides* in Costa Rica. *Copeia 1976:* 579–580.

Trama, F. A., F. L. Rizo-Patrón, A. Kumar, E. González, D. Somma, and M. B. McCoy. 2009. Wetland cover types and plant community changes in response to cattail-control activities in the Palo Verde Marsh, Costa Rica. *Ecological Restoration 27:* 278–289.

TTWG (Turtle Taxonomy Working Group; Rhodin, A. G. J, J. B. Iverson, R. Bour, U. Fritz, A. Georges, H. B. Shaffer, and P. P. van Dijk). 2021. Turtles of the World: Annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status (9th edition). *In* Rhodin, A. G. J, J. B. Iverson, P. P. van Dijk, C. B. Stanford, E. V. Goode, E. V. Buhlmann, and R. A. Mittermeier (Eds.), Conservation Biology of Freshwater Turtles and Tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. *Chelonian Research Monographs 8:* 1–142.

Wilson, D. 1998. Nest-site selection: Microhabitat variation and its effect on the survival of turtle embryos. *Ecology 79:* 1884–1892.

Wygoda, M. L. 1979. Terrestrial activity of striped mud turtles, *Kinosternon baurii* (Reptilia, Testudines, Kinosternidae) in west-central Florida. *Journal of Herpetology 13:* 469–480.

Editor: Peter Meylan