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Daily and Seasonal Activity Patterns and Movements of Juvenile Box Turtles (*Terrapene carolina bauri*) on Egmont Key, Florida

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Abstract. – Time of activity and environmental conditions influencing activity were determined in juvenile Florida box turtles (*Terrapene carolina bauri*) (n = 212) on Egmont Key, Florida, USA. Several individuals (n = 58) were monitored with thread bobbins to evaluate distance moved to determine environmental conditions influencing movement and to identify key features of areas used by juvenile box turtles. Juvenile activity, like that of adults, was bimodal with most activity occurring during cooler morning and late afternoon hours. More juvenile activity occurred in the morning than in the afternoon in both summer and fall, and type of activity did not vary with time of day. Juveniles made longer movements earlier in the day, and during summer months. Temperature influenced activity in juvenile box turtles, and may be more significant than moisture to the younger age classes. Juveniles frequently were found in areas with lower soil and ambient temperatures and higher relative humidities than adjacent areas. Distance moved by monitored juveniles did not appear to be influenced by any environmental factor, including the presence of rain.

Key Words. – Reptilia; Testudines; Emydidae; *Terrapene carolina bauri*; turtle; juvenile; movement; activity patterns; ambient temperature; soil temperature; relative humidity; thread trailing device; Florida; USA

The juvenile years represent gaps in our understanding of turtle ecologies. Detection of low numbers of juveniles in turtle population studies is common, occurring in freshwater (Gibbons, 1968; Pappas and Brecke, 1992), terrestrial (Woodbury and Hardy, 1948; Stickel, 1950; Legler, 1960) and marine species. Low sighting rates may result from three primary factors: (1) absence of recruitment into the population (Pilgrim et al., 1997), (2) inappropriate survey methodologies, such as traps with openings large enough to permit escape of small individuals (Ream and Ream, 1966), and/or (3) ontogenetic shifts in habitat use or activity patterns leading to lower detection probabilities within habitats searched or survey periods chosen (Moll and Legler, 1971; Pappas and Brecke, 1992; Wilson et al., 1999). Due to the importance of recruitment for the maintenance of viable populations, accurate estimates of juvenile abundance are desirable. Uncertainty in survival estimates can yield invalid conclusions regarding population trends. Therefore, it is important to evaluate the reasons why low numbers of juveniles may be detected, and eliminate as much bias as possible from survey methodologies.

The Florida box turtle, *Terrapene carolina bauri*, is restricted to peninsular Florida. Although this species historically has been considered common, this perception is unwarranted as it was listed as Near Threatened on the 2000 IUCN Red List. A long-term monitoring program was begun in 1991 for the Florida box turtle on Egmont Key, Florida. This population is a particularly good choice for ecological observations of juveniles, as it is large (density estimated at 16.4 turtles/ha or greater) and a number of juveniles were detected during previous survey work at this site (Dodd et al., 1994; Langtimm et al., 1996).

The difficulty often reported in locating juvenile turtles may be due partially to differential habitat use by juveniles and adults. For example, juvenile box turtles on Egmont Key use microhabitats with denser vegetation than adults (Hamilton, 2000), making them less obvious to observers than larger conspecifics. Behavioral differences may also, in part, explain the disparity in sighting rates. If activity patterns vary among age classes in response to the same environmental conditions, as in other terrestrial turtle species (Diemer, 1992; Wilson et al., 1994; Keller et al., 1997; Wilson et al., 1999), surveys conducted under peak conditions for adult activity may not detect juveniles, regardless of their abundance. Such differences in habitat use or behavior among age classes may be caused by different responses to environmental conditions. The response of juvenile box turtles to environmental factors is unknown, as young turtles rarely are encountered in the field. Activity in adult box turtles is related to external factors such as relative humidity (RH), air temperature (Reagan, 1974; Dodd et al., 1994), and substrate type (Nieuwolt, 1996). Adult box turtles are most active during or following rain (Stickel, 1950; Strang, 1983). It is not known whether juvenile box turtles are as dependent on rainfall or humidity as adults, or if other factors such as air temperature and/or soil temperature are more significant.

Given the uncertainty concerning the influence of environmental factors on juvenile box turtle activity patterns, as well as a lack of information regarding patterns of activity and movements in this age class, I addressed the following objectives: (1) describe daily and seasonal activity patterns of juvenile Florida box turtles on Egmont Key; (2) determine whether ontogenetic or seasonal shifts occur in these patterns; (3) clarify the role played by time of day and other factors (such as weather) in regulating activity; (4) determine distances that juvenile box turtles in this population regularly travel; (5) assess the potential influence of turtle size or ambient environmental conditions on movement; and (6) describe the shape and patterns of juvenile box turtle paths and identify common path features.

METHODS

Study Site. — My study was conducted on Egmont Key National Wildlife Refuge, located in the mouth of Tampa Bay, Hillsborough County, Florida, USA (27°36'N; 82°45'W). Egmont Key is a small island (< 180 ha) (Franz et al., 1992) with a subtropical climate. Detailed descriptions of the study site are available elsewhere (Dodd et al., 1994; Hamilton, 2000). The island has been modified extensively by clearing and the introduction and establishment of exotic plant and animal species, primarily Brazilian pepper (*Schinus terebinthifolius*) and Australian pine (*Casuarina equisetifolia*).

Surveys. — I collected juvenile and adult turtles by conducting manual searches from June to November 1997 and during June 1998. Survey periods were between three to five days in duration, for a total of 64 survey days. I considered turtles < 121 mm in carapace length (CL) to be juveniles. This determination was based on previous examination of the reproductive ecology of this population (Dodd, 1997a,b). *Terrapene c. bauri* is sexually dimorphic; males have a concave plastron, whereas females have no obvious secondary sexual characteristics. The smallest female with shelled eggs reported from this population was 124 mm CL (Dodd, 1997a,b); therefore, the consideration of turtles > 120 mm CL as adults should prevent the classification of sexually mature adults as juveniles.

Surveys were conducted while walking east-west paths across the island, thoroughly searching open areas, through the leaf litter, and under vegetation. Paths walked were roughly linear in nature, but search effort was not restricted to a transect or specified area. Methodology that enabled comparisons with data collected previously at this site (Dodd et al., 1994) was used, and resembled area searching, a technique used to census birds (Ralph et al., 1993). Search effort focused on different areas of the island during each survey period, although a core study area was searched at least once during each visit. All areas of the island were surveyed, although the majority of time was spent in areas where large numbers of juveniles were found. Surveys were conducted during all daylight hours (sunrise to dark) during the duration of the study, although effort was focused during times when box turtles were most active as determined during previous research at the site (Dodd et al., 1994). Therefore, daily search effort was focused primarily between sunrise and 1300 hrs (approximately 430 total search hrs) and between 1600 and 2130 hrs (approximately 430 total search hrs), while approximately 95 hrs were spent between 1300 and 1600 hrs. I recorded morphometric data and gave each individual a unique marginal notch to permit future identification (Cagle, 1939). Each turtle was released at its capture location. At each capture site, I recorded the following microenvironmental variables: air (T_a) and substrate (T_s) temperature (recorded to nearest °C with a hand-held thermocouple digital thermometer (Atkins Technical Inc.) directly over the location of the turtle and on the substrate directly beneath each individual), and relative humidity (RH, recorded with a digital humidity pen at the location of the turtle). Time of day and weather conditions, such as the presence of rain, were noted each time a turtle was located. Although the occurrence of rain on Egmont Key was noted, the amount of precipitation was not measured at the site during this study. Weather data were obtained from a Southwest Florida Water Management District weather station in Bradenton, the nearest mainland weather station, located 32 km from the study site. Data used from this station included daily maximum, minimum, and average daily temperatures, and average and lowest RH.

Daily and Seasonal Activity Patterns. — I examined juvenile capture histories to determine daily activity patterns; captures of active turtles were divided into hourly intervals to discern daily peaks in activity. Daily activity patterns of three juvenile age classes (small juveniles ≤ 80 mm CL; medium juveniles 81–100 mm CL; subadults 101–120 mm CL; Fig. 1) were examined separately to determine whether shifts in time of activity peak occur within the juvenile stage. Captures were examined for seasonal trends in activity. Additionally, patterns of juvenile activity were compared to adult patterns described previously for this population (Dodd et al., 1994).

I used log-linear models to quantify the influence of season, month, time of day, and juvenile size class on activity, and to evaluate the relative effects of these variables. I selected the most parsimonious model explaining the variation using a model fitting procedure. Chi-squared likelihood ratio tests were used to determine which factors included in the best fitting model had the most significant effect on activity.

Influence of Environmental Factors on Activity. — To assess the influence of environmental factors on activity, it was necessary to distinguish between captures of active and inactive individuals. Turtle behaviors at the time of sighting were categorized into the following activities: feeding (eating or with food visible in mouth when located), closed (turtle found resting above substrate with shell completely closed), walking (actively moving), resting (turtle found resting above the substrate with shell open and head either withdrawn inside shell or stretched out), inactive (mostly or completely covered by substrate such as soil, leaf litter, needle litter, or palm fronds), or other (e.g., swimming). Turtles classified as inactive were excluded from evaluation of optimal conditions for juvenile activity. Individuals resting or closed were considered active because they were not under cover, avoiding the current environmental conditions, but

Figure 1. Size (age) classes of juvenile Florida box turtles (*Terrapene carolina bauri*) on Egmont Key, Florida. Shown left to right: subadult (CL = 101–120 mm), medium juvenile (CL = 81–100 mm), and small juvenile (CL ≤ 80 mm).

were possibly resting in areas selected for behavioral thermoregulation, or may have been active prior to my presence.

To identify environmental variables that best characterized conditions associated with activity in juvenile box turtles, I used Principal Components Analysis (PCA). I included both environmental conditions recorded at the weather station in Bradenton (average daily and maximum and minimum temperatures, and average and low RH), as well as environmental variables recorded directly at the turtle location (T_a, T_s, and RH) in this exploratory multivariate analysis. To determine whether type of activity varied under different environmental conditions, I used Mann-Whitney U tests to assess the effect of ambient temperature on choice of activity, and a Bonferroni correction factor to keep the experiment-wise error rate at 0.05. To determine whether activity varied with respect to substrate temperatures, or RH, I used Kruskal-Wallis tests.

Movement Patterns, Descriptions of Turtle Paths, and Use of Refugia. — I used thread bobbins to monitor movements of juveniles for periods of up to five days (Wilson, 1994). A small spool of thread, weighing just under 2 g and containing approximately 250 m of thread, was attached to the rear of the carapace with duct tape. The smallest turtle monitored weighed 29 g, and the thread bobbin device was just over 6% of its body weight. There was no indication that attachment of this device inhibited movement. I used the thread trail data to describe mean daily distance moved, environmental conditions favoring or inhibiting movement, and the relationship between juvenile size and distance moved. I also trailed a few adults simultaneously to allow comparison of movements of juveniles and adults under identical environmental conditions.

I measured and mapped the path of each turtle and noted features of the trails, including refugia such as logs, palm fronds, and gopher tortoise (*Gopherus polyphemus*) burrows. Use of such refugia by box turtles was recorded when observed. I measured the amount of cover provided by vegetation, vegetative species composition, and substrate type every 10 m along each individual's path. Observations of the surrounding environment were made, but no systematic data were collected.

I estimated tortuosity of individual trails by dividing the straight-line distance from the turtle's starting point to its resting location by the actual distance traveled along the path by the turtle during each observation period, similar to the method used by McNeil et al. (2000). A tortuosity value near 1 indicates a relatively straight-line path, while a value closer to 0 suggests a more meandering, winding path.

I recorded vegetation (both amount of cover as well as species composition), and microclimatic factors (substrate temperature, ambient temperature, and RH) at each refugium used by monitored juveniles. To determine whether amount of vegetation at refugia varied with turtle size (CL), I used a general linear model in which CL was the dependent variable and amount of cover at the low (recorded directly over the carapace of the turtle), mid-story (recorded at a height of 1–2.5 m), and canopy (> 3 m) were the fixed factors. Cover categories were classified as dense (> 50%) or sparse (≤ 50%). There were no significant correlations between these cover variables, so all three were included in the model. To assess the possibility that environmental factors may vary among refugia of different-sized turtles, I used multiple linear regression with the environmental factors as the independent variables and CL as the response variable. Since ambient temperature and substrate temperature were highly correlated ($R = 0.971$, $p < 0.001$), I only included substrate temperature and RH in the model. To determine whether turtles were using refugia with significantly different relative humidities than the ambient RH, I used a paired t-test. To avoid pseudoreplication, only the first refugium site from each thread-spooled turtle was used in these analyses.

Distance Moved. — Monitored turtles were located at least twice daily, and distance moved was determined at two regular intervals: late morning and late afternoon. Because several turtles were monitored simultaneously, it was impossible to record all movements at exactly the same time each day, but an effort was made to be as consistent as possible. A sample of monitored turtles was checked early in the morning, and there was no indication of nocturnal movement; therefore movements measured in the late morning were assumed to have occurred primarily during the morning hours. Turtles were followed for five days, or until the turtle was lost (due to broken thread, detachment of trailing device, or thread running out). Thread bobbins were checked each time turtles were located and changed as necessary to minimize device failure.

To determine if there was a significant relationship between distance moved and CL, I used a linear regression model. I also compared turtles that made relatively short (< 50 m) or long (> 100 m) movements (Diaz-Paniagua et al., 1995), using a Kruskal-Wallis test to assess the influence of juvenile size (CL) on distance traveled.

To examine whether average distance moved by juvenile turtles within a 24-hr interval varied by month, I used a 1-way ANOVA with distance moved as the dependent

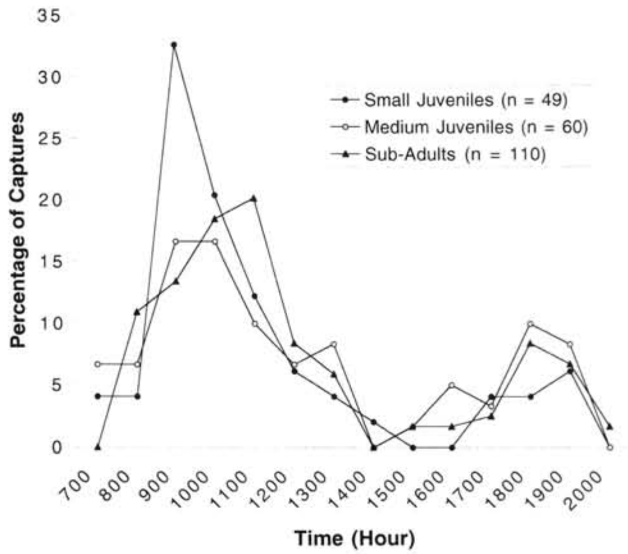

Figure 2. Temporal activity of juvenile box turtles (*Terrapene carolina bauri*) on Egmont Key, Florida, from June through November 1997 and June 1998, shown by age class; only captures of active turtles are included. This graph shows the percentage of captures for each age class that occurred during each hourly time interval. Age (size) classes are as defined in Fig. 1.

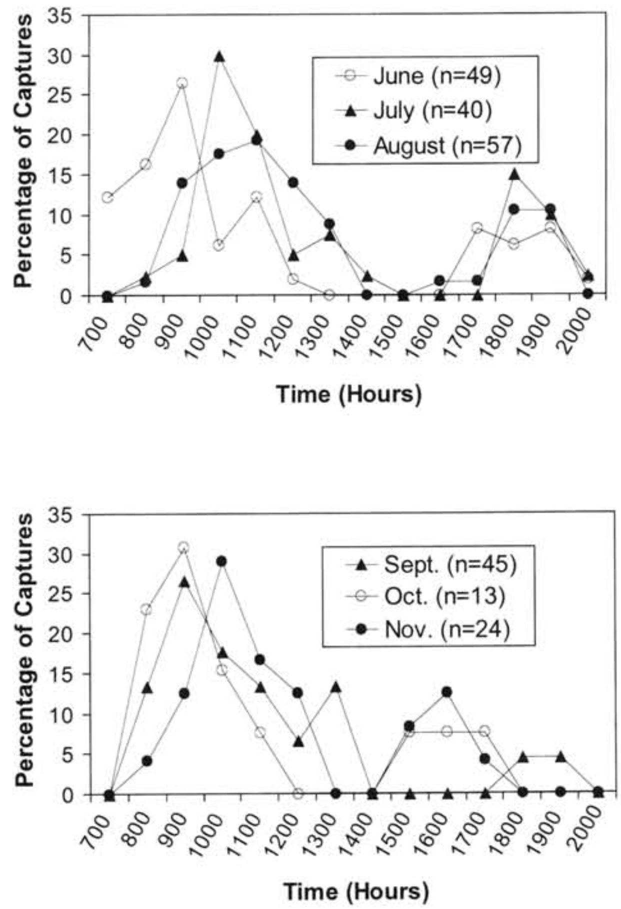

Figure 3. Temporal activity of juvenile box turtles on Egmont Key, Florida, by month; only captures of active turtles are included. Activity patterns are based on the percentage of each month's captures found active in each hourly time period to compensate for unequal sample sizes between months. Number of individuals included: June ($n = 34$), July ($n = 31$), August ($n = 41$), September ($n = 41$), October ($n = 8$), November ($n = 16$).

variable and month as the fixed factor. Additionally, I tested the *a priori* hypothesis that average daily distance moved would vary between summer (June–September) and fall (October–November), using an F-test. To determine whether distance moved varied with time of day, I used a Kruskal-Wallis test.

I examined environmental data collected from the Bradenton weather station to determine whether distances moved by juveniles were influenced by ambient environmental conditions. Average daily distance moved was used as a measure of activity, enabling comparisons of environmental conditions present on days with varying levels of activity.

RESULTS

I located 212 juvenile box turtles in this study, of which 25% ($n = 53$) were considered to be inactive when first located, buried under soil or leaf litter, or hiding under palm fronds. The remaining 159 juvenile turtles were categorized as resting (82%), closed (9%), walking (8%), or feeding (1%). Other activities, such as swimming, were not included in analyses because standing water was available only after heavy rain, and thus the number of days on which this activity could have been observed was limited.

Daily and Seasonal Activity Patterns. — All three size classes of juveniles exhibited bimodal daily activity patterns, with time and length of initial activity peak varying with juvenile size class (Fig. 2). Subadult activity was greatest between 0800 and 1300 hrs, whereas morning activity of both small and medium-sized juveniles peaked during a narrower time interval. A secondary peak in late afternoon between 1800 and 1900 hrs was seen in all size classes. Juvenile box turtle activity during June–August was strongly bimodal, with pronounced peaks in activity occurring during the cooler morning and late afternoon hours (Fig. 3). In September–November, juvenile turtle activity did not have such a pronounced bimodal pattern (Fig. 3).

The most parsimonious model providing an explanation of variation in number of captures included time of day, type of activity, season, juvenile size, and joint effects of activity and turtle size and activity and season (Table 1). Only time of day had a significant effect on the number of turtles located. The majority of juvenile captures (40%) occurred during the morning hours, whereas 31 and 29% occurred during afternoon and evening hours, respectively.

Table 1. Relative effects of most parsimonious log-linear model parameters on juvenile capture probabilities.

Parameter	df	χ^2	p
Activity	6	10.78	0.096
Season	1	1.11	0.291
Time	**2**	**11.55**	**0.003**
Juvenile Age Class	2	2.29	0.319
Activity * Juvenile Age Class	9	2.77	0.973
Activity * Season	2	3.03	0.220

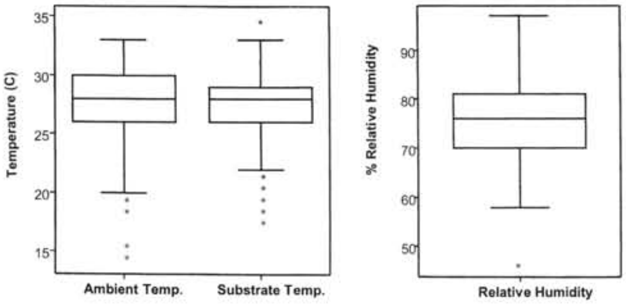

Figure 4. Environmental conditions at which active juvenile box turtles were located. The box includes 50% of the cases (interquartile range) and includes the median value, represented by the line; the whiskers include the upper and lower 1.5 interquartile ranges; asterisks represent values outside of the 1.5 interquartile range (Sokal and Rohlf, 1995).

Influence of Environmental Factors on Activity. — Turtles were active at a broad range of ambient and substrate temperatures (Fig. 4). The mean air temperature at which active juvenile box turtles were located was 26.9°C ± 0.24 (1 SEM), and a substrate temperature of 27.3°C ± 0.27. The range of relative humidities at which turtle were found to be active also was broad, although generally within the higher relative humidities (Fig. 4). Mean RH was 76% ± 0.57.

When all environmental factors (both microclimatic conditions recorded at the turtle location, as well as weather variables recorded at the station in Bradenton) were examined using PCA, 58%, 24%, and 14% of the total variance was localized to the first, second, and third eigenvectors of the correlation matrix, respectively (Table 2). These principal components were associated with 96% of the total variance. All temperature measurements loaded equally and fairly heavily on the first principal component (Table 2) suggesting the importance of this factor for juvenile box turtle activity at this site. Average daily RH and daily low RH recorded in Bradenton loaded heavily on the second principal component (Table 2), suggesting that moisture

Table 2. Eigenvalues of the first three principal components axes, and correlations between environmental variables and the principal component axes. Principal component 1 is associated with 58% of the variation, principal component 2 is associated with 24%, and principal component 3 is associated with 14%. Bold type indicates values that load heavily on each component.

	Principal Components		
	1	2	3
Eigenvalue	4.621	1.919	1.104
Cumulative Proportion Explained	0.578	0.817	0.955
Variables[a]			
Average Daily Temperature	**-0.450**	-0.069	-0.162
High Temperature	**-0.430**	-0.131	-0.166
Low Temperature	**-0.448**	-0.027	-0.117
Average Relative Humidity	-0.153	**0.673**	0.138
Low Relative Humidity	-0.151	**0.674**	0.142
Ambient Temperature (Site)	**-0.422**	-0.129	0.214
Substrate Temperature (Site)	**-0.432**	-0.126	0.184
Relative Humidity (Site)	-0.018	0.193	**-0.902**

[a] (Site) indicates that these variables were recorded directly at the turtle location. Other variables were recorded at a weather station in Bradenton, Florida.

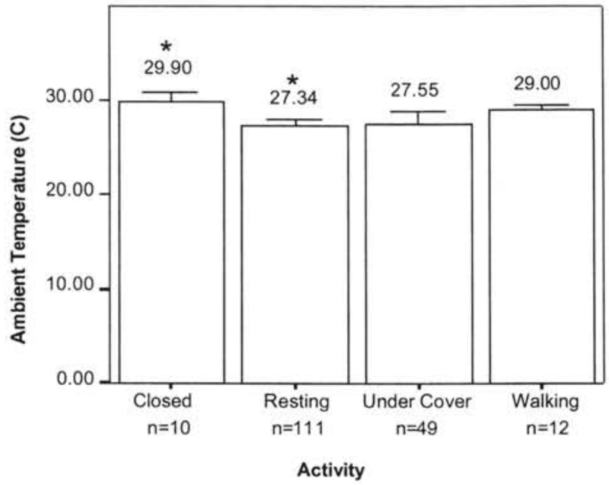

Figure 5. Activity of juvenile box turtles on Egmont Key, Florida, in relation to ambient temperature recorded at the location of the turtle. Differences in median air temperatures at different activities were detected using Mann Whitney U tests (U = 261.0, n_1 = 10, n_2 = 111, and p = 0.005). The median temperature, as well as the range of ambient temperatures at which each activity was recorded, are shown. * The median ambient temperatures of resting juveniles and closed juveniles are significantly different.

influenced activity, but probably was not as important as temperature.

Box turtles have hinged plastrons and are able to pull their bodies completely into their shells. Juvenile box turtles rest with their shells closed at higher ambient temperatures ($\bar{x}$ = 29.9°C) and rest with their shells open at lower ambient temperatures ($\bar{x}$ = 27.34°C; Fig. 5). The difference between T_a recorded for juvenile turtles resting with shells open and closed was small, but significant after adjusting for multiple comparisons (U = 261, p = 0.005). No significant differences were found between the T_a at which any other types of activities were undertaken (U < 2222, p > 0.06 for all comparisons; Fig. 5). The relationship between T_s and activity needs further investigation, as no statistically significant differences were detected, although a relationship between these two variables may have been masked by the highly unequal sample sizes (χ^2 = 8.46, df = 4, p = 0.076). Relative humidity recorded at capture did not influence juvenile activity (χ^2 = 7.671, df = 4, p = 0.10).

Movement. — A total of 58 turtles (27 subadults, 12 medium-sized juveniles, 10 small juveniles, 8 adults, and one juvenile of unknown CL) were monitored with thread bobbins for periods of one to five days. The majority of individuals (n = 54) were followed for periods of three days or fewer. Four individuals were followed for four days and one turtle was monitored for five days. Problems encountered with the thread bobbin technique included the thread breaking or running out due to unusually long movements, or loss of the bobbin due to extremely humid or wet conditions.

Juvenile turtles made longer movements than I expected. Distance moved by juvenile turtles during a 24-hr period ranged from 0 to 200.5 m ($\bar{x}$ = 60.3 ± 6.3 m). The largest movement recorded in a 24-hr period (200.5 m) was made by a subadult individual (CL = 109 mm). However,

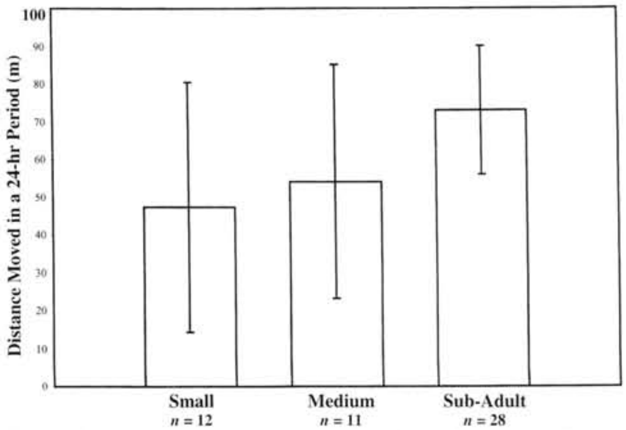

Figure 6. Average distance moved by juvenile box turtles on Egmont Key during a 24-hr period shown by size class. Average values for each size class are indicated by the bars; the error bars represent 95% confidence intervals.

daily movements of ≥ 100 m were recorded regularly. When the average distance moved over a 24-hr period was compared among size classes, the average values were not statistically different (Fig. 6). The large, overlapping 95% confidence intervals most likely result from the small and highly unequal sample sizes in this dataset, making it impossible to determine whether any significant biological relationship exists between distance moved and juvenile size.

Descriptions of Turtle Paths. — Most turtles moved primarily through areas with dense vegetation, especially at the understory level. Many turtle trails doubled back on themselves and wound extensively through thick areas of Brazilian pepper. Individuals did not seem to avoid each other, and particularly favorable areas were frequently used simultaneously by more than one tracked turtle (Fig. 7). Two turtles (CL = 95 and 120 mm) were observed using the same Brazilian pepper bush and both moved extensively underneath it, occasionally crossing each other's paths. The trails of some individuals were predominantly underneath this plant species, with movements between bushes being direct, whereas movements under the bushes were circuitous, often causing the trail to be so convoluted that the direct path of an individual was impossible to discern. This pattern of movement was exhibited by several juvenile individuals.

Two tracked turtles moved through areas providing very dense cover and high humidity, as well as slightly more open areas, avoiding very dry, open areas with very little cover, with most of their trails under and through Brazilian pepper (Fig. 7), which provides protection from ambient environmental conditions. Use of wet areas was seen frequently. Individuals crossed depressions with wet soils and damp leaf litter and also water filled depressions (Fig. 7). Such use of cool, damp soils may be important for thermoregulation in juveniles at this site (see discussion).

Turtles frequently made meandering movements, crisscrossing their paths in areas with dense canopy and understory cover, but made extremely direct movements when they traversed more open areas with less ground cover. Of the juvenile and adult turtles ($n = 59$) for which adequate maps of movement were made, 53% did not cross their own paths, 25%

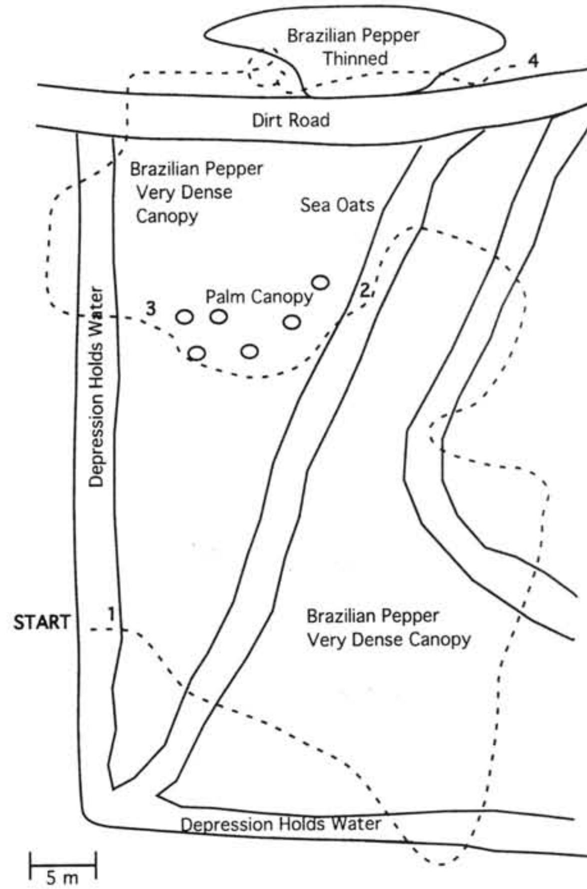

Figure 7. Trail of a medium-sized juvenile turtle, during September 1997. This individual moved through areas providing a dense level of vegetative cover and frequently crossed the ditches in the area; these ditches frequently have cooler, moister soils as well as extensive ground cover (leaf litter or palm fronds). Locations at which the turtle was found are depicted with numbers. The turtle was released at 1000 hrs on 6 September 1997. 1) 1900 hrs on day 1 – turtle was buried beneath leaf litter in moist soil under Brazilian Pepper; 2) 1100 hrs on day 2 – turtle resting under Brazilian Pepper (individual stayed there approximately 20 hrs); 3) 0900 hrs on day 3 – turtle under palm fronds. Total distance moved was 167.5 m.

crossed their own trail once or twice, 18% crossed it three or four times, and 8% crossed it at least five times.

Thick cover at the substrate level is another conspicuous feature of turtle paths. Juveniles generally appeared to move through areas with a thick layer of leaf litter or needle litter or to move between thick clumps of grass. Individuals buried beneath leaf litter or inside patches of grass were often completely covered and would have been impossible to locate without following the thread trail. Additionally, individuals often buried inside a hole or depression several inches below the surface, underneath both soil and leaf litter.

Trail Tortuosity and Shape. — Overall trail tortuosity ranged from 0.1 to 1 for monitored juvenile box turtles. The average trail tortuosity for juveniles ($n = 50$) was 0.59. For the adults ($n = 9$) monitored, the average tortuosity index was 0.64.

When trail shapes were compared, trails made by most individuals were categorized as linear, representing a more direct move in one primary direction (45%), circular, encompassing primarily one area and returning to approxi-

Table 3. General Linear Model table for the effects of low-level vegetation, mid-story cover, and canopy cover at refugia locations (fixed factors) on the size (CL) of the turtles using the refugia on Egmont Key, Florida.

Source	Sum-of-squares	df	F	p
Model	8020.0	6	2.642	.048
Low Cover	121.5	1	.224	.640
Mid-story	3569.9	1	6.574	.016
Canopy Cover	793.5	1	1.461	.236
Low Cover * Mid-story	2617.8	1	4.821	.036
Low Cover * Canopy Cover	177.9	1	.328	.571
Canopy Cover * Mid-story	132.5	1	.244	.625
Error	15747.2	29		
Total	23767.2	35		

mately the point of origin (33%), or horseshoe-shaped (22%). Trails classified as horseshoe-shaped were primarily linear in one direction, with a change in direction of travel and the return of an individual to approximately the same area as the point of origin, but not the same location.

Refugia. — Different-sized turtles were found to use refugia that differed with respect to amount of vegetation. The amount of vegetation present at a refugium location accounted for 34% of the variation in CL in the turtle capture data ($F = 2.642$, $df = 6$, $p = 0.048$). The amount of mid-story vegetation (dense or sparse) was important in influencing refugia use by juvenile turtles and explained 15% of the variation in captured individuals with respect to CL (Table 3). The interaction between amount of cover present directly over the turtle and at mid-story height was also an important factor and explained 11% of the variation in CL in the capture data (Table 3).

No significant differences were detected between T_s or RH at refugia used by juvenile and adult box turtles ($F = 0.048$, $df = 2$, $p = .953$). Juvenile box turtles chose forms (refugia) with RHs that were significantly different from the ambient RH recorded directly outside the form ($t = 0.434$, $df = 12$, $p = 0.005$). Juvenile box turtles on Egmont Key chose refugia with an RH 4.5% higher on average than the ambient RH.

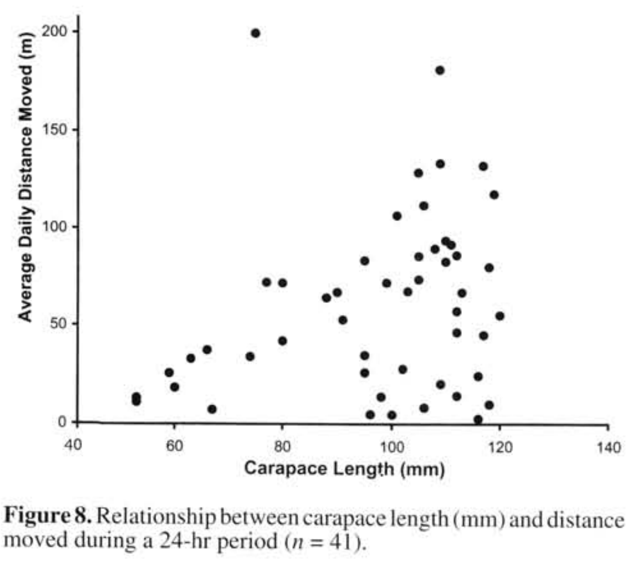

Figure 8. Relationship between carapace length (mm) and distance moved during a 24-hr period ($n = 41$).

Table 4. ANOVA table for the effect of month (fixed factor) on the average distance moved in a 24-hr period by juvenile Florida box turtles on Egmont Key, Florida.

Source	Sum-of-squares	df	Mean square	F-ratio	p
Month	24434.6	5	4886.9	2.809	.027
Summer vs. Fall	20792.3	1	9.837	2113.7	<.0001
Error	78299.1	45	1740.0		
Total	102733.8	50			

Factors Influencing Movement. — A significant positive relationship between CL and distance moved was indicated by the linear regression model (Fig. 8); however, CL alone explained only 15% of the variation in distance moved. A significant difference in mean CL between turtles moving long distances (CL = 109.3 mm) and those making shorter movements (CL = 96.8 mm) was detected ($\chi^2 = 6.10$, $df = 1$, $p = 0.014$).

Average distance moved in a 24-hr interval was found to vary by month (Table 4). Month explained 24% of the variation in distance moved. Juveniles turtles moved 106% further in the summer months (June–September) than during fall months (October–November) ($F = 2113.7$, $df = 1$, $p < 0.0001$; Fig. 9). Distances moved by juveniles also varied with time of day ($F = 7.622$, $df = 1$, $p = 0.007$); juveniles moved 92% further on average during morning ($\bar{x} = 33.3$ m, $n = 75$) than afternoon ($\bar{x} = 17.3$ m, $n = 60$).

Environmental Factors Influencing Movement. — Turtles moved under a broad range of environmental conditions. The daily distances moved by all monitored juveniles were averaged to obtain an activity index for each day. When the environmental conditions of high (long distance movements) and low (short or no movements) activity days were compared, no differences were detected. Mean ambient temperatures for high activity days ranged from 18.9 to 29.4°C. No relationship was detected between environmen-

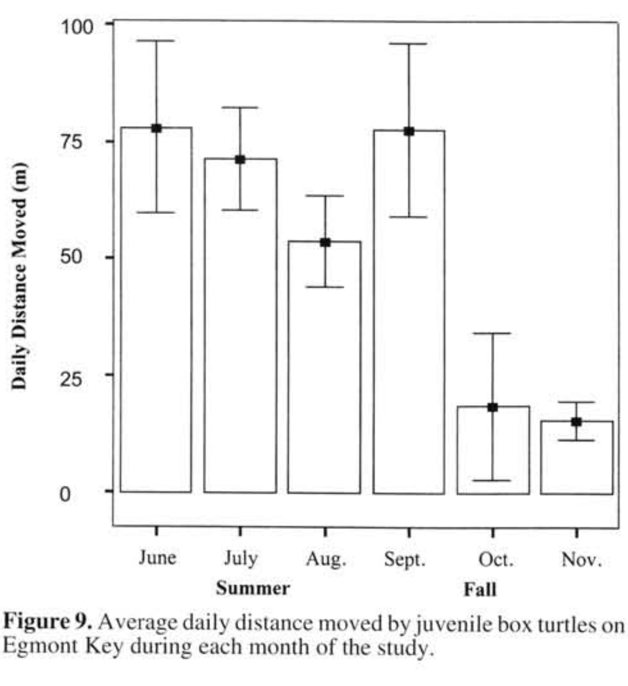

Figure 9. Average daily distance moved by juvenile box turtles on Egmont Key during each month of the study.

tal conditions recorded at the Bradenton weather station and juvenile movement. Additionally, rainfall did not appear to influence juvenile movement. Juveniles did not move significantly further on rainy days ($\chi^2 = 1.29$, df = 1, $p = 0.25$) or following rain events ($\chi^2 = 2.01$, df = 1, $p = 0.16$) than they did during periods with no rain.

DISCUSSION

Daily and Seasonal Activity Patterns. — All age classes of juveniles displayed bimodal activity patterns during the summer months, with activity restricted primarily to the cooler morning and late afternoon hours, a pattern also seen in adults (Dodd et al., 1994). An ontogenetic shift was detected in the time of morning activity peak, with juvenile peak activity occurring later than adult peak activity. This shift in time of peak activity may be due to differences in thermal preferences between juveniles and adults. Adult box turtles were active at air temperatures as low as 17ºC, whereas small and medium-sized juveniles (individuals ≤ 100 mm) were never found active below 21ºC, although searches were conducted at lower temperatures. Minimum substrate temperatures were 16ºC at adult capture locations, 18ºC at subadult capture locations, and 21ºC for smaller juveniles. Peaks in juvenile activity occurred within a narrower time interval than adult activity. As smaller turtles heat more quickly than larger individuals (Rose and Judd, 1982), above-ground exposure may be more restricted for smaller turtles more susceptible to overheating.

Juvenile use of areas with higher substrate and air temperatures than adults may reflect higher preferred body temperatures in the smaller age classes, as was found in desert tortoises (Naegle, 1976). In desert tortoises, small (< 125 mm CL) individuals were found to have significantly higher cloacal and preferred body temperatures than larger individuals, and individuals < 90 mm had higher critical thermal maximum temperatures than larger animals (Naegle, 1976). Several small box turtles were located between 1100 and 1200 hrs sitting in patches of sunlight on the forest floor and appeared to be basking. Fifty percent of all individuals CL ≤ 61 mm ($n = 16$), were collected between 1055 and 1320 hrs, during the hottest part of the day. In this study, subadults (101–120 mm) were found active under a broader range of conditions, however, suggesting that as body size increases, activity may be less restricted by environmental conditions.

Differences in the range of RH at which activity occurred were detected between adult and juvenile box turtles on Egmont Key. Adults were active when RH was as low as 24% (Dodd et al., 1994), but juveniles were never observed to be active when RH dropped below 58%. However, most adult activity occurred at relative humidities above 60%, similar to juveniles. Activity in juvenile box turtles may be restricted to a narrow range of environmental conditions, whereas adults are able to be active under less optimal conditions.

When activity patterns were compared among months (Fig. 3), two distinct seasonal patterns were evident. Summer (June–August) activity patterns were strongly bimodal; whereas fall (September–November) patterns showed the majority of activity occurring in the morning. Based on mean monthly temperatures and average relative humidities, September would be classified with June, July, and August as summer. As precipitation did not vary between seasons, this variable is unlikely to be the cause of the activity shift detected between summer and fall. A trend was noted in RH recorded at the nearby weather station, however, that could have influenced activity in juveniles. During June through August, daily minimum RH was much lower than during the period from September through November. Although average daily humidites were higher during summer than fall, the minimum RH values were occasionally more extreme during summer, and may be responsible for the seasonal differences in observed juvenile activity. Another factor influencing time and length of the afternoon activity interval is the hour of sunset, which varies between periods in which summer and fall patterns were observed.

Environmental Factors. — The relationship between environmental conditions and activity in box turtles is well established. Relative humidity and rainfall significantly affected activity of adult box turtles at this site (Dodd et al., 1994), and were found to be an important factor influencing habitat use and movement in populations of *T. carolina* (Stickel, 1950) and *T. c. triunguis* (Reagan, 1974). Although environmental conditions were recorded and rain was noted, the influence of the amount of precipitation on juvenile activity cannot be evaluated as no reliable data regarding amount of rainfall were collected during this study. On several occasions monitored juveniles made long movements during rainstorms. However, long-distance movements occurred during dry periods as well, and not all monitored individuals moved during rain events. Additionally, there were no significant overall statistical differences in distances moved by juvenile turtles on rainy days, the day following rain, or during a dry period. Juveniles used puddles created during heavy rain, although adults were observed soaking in water more frequently than were smaller animals. Turtles monitored with thread bobbins often crossed or walked along ditches, which frequently had moister soils than the surrounding micro-environments and usually held water following rain. Juvenile turtles frequently utilized areas with moist soils, and were found resting in areas with high levels of soil moisture (Hamilton, 2000). Whether the use of cool, moist soils serves a thermoregulatory purpose, a moisture-conserving function, or both, is unknown. Since *Terrapene ornata* were found to lose moisture primarily through their carapace and not their plastron (Rose, 1969), the use of moist soil substrates by juvenile Florida box turtles more likely serves a thermoregulatory role. However, juveniles buried beneath leaf litter with moist soils covering their carapace may have done so to conserve moisture.

The relationship between rainfall and activity in adult box turtles (Stickel, 1950; Reagan, 1974; Dodd et al., 1994) is more clear than what was observed for juveniles on Egmont Key during this study. As juveniles preferentially used areas with moist soils and rarely left humid, shaded regions of the island (Hamilton, 2000), they may not be as dependent on rain as are adults. Adults were frequently encountered resting on dry, sandy soils and made frequent movements outside of shaded areas to exploit fluctuating seasonally abundant food resources in other habitat types (Dodd et al., 1994; Hamilton, 2000). Although adult box turtles on Egmont Key appear to be more active during and following rain, juveniles may be less vulnerable to water loss given their habitat preferences, extensive use of moist soil and leaf litter as cover, and avoidance of open areas with dry soils (Hamilton, 2000).

The results of the principal components analysis suggest that temperature is more important in regulating activity of juvenile box turtles at this site than either precipitation or RH. Again, the frequent use of cool moist substrates (Hamilton, 2000) emphasizes the importance of temperature regulation to juvenile turtles and is congruent with these results. Activity in other terrestrial turtle species is strongly influenced by temperatures as well. Temperature had a significant effect on activity in *Testudo kleinmanni*, while neither precipitation nor RH was correlated with activity in this species (Geffen and Mendelssohn, 1988). It is possible that precipitation and RH may be important to juvenile box turtles, but as the humidity was consistently high on Egmont Key during this study period, especially within the habitat used by juvenile box turtles at this site, the significance of these factors may have been masked. The relative importance of moisture and temperature variables may shift seasonally, and juveniles may respond more strongly to environmental conditions in different seasons, as in *Testudo graeca* (Diaz-Paniagua et al., 1995). The relative importance of environmental variables to members of this species changed seasonally, with no correlations found between movement of *T. graeca* and any environmental variables recorded during the summer and fall months, but during spring, female tortoise movement was highly correlated with maximum and minimum temperatures, RH, rainfall, and radiation.

Factors Influencing Activity. — Although time of day significantly influenced the level of activity in juvenile box turtles on Egmont Key, it did not significantly influence the types of activity in which juveniles were engaged. However, T_a did significantly affect the type of activity undertaken by juvenile box turtles. At a median T_a of 28°C, juvenile box turtles were generally resting; as the temperatures at capture locations increased, juveniles were either walking or inactive, suggesting that juveniles were resting at a preferred temperature, but retreated when temperatures became too high. These findings are congruent with previous work with *T. ornata* in which turtles basked at relatively low temperatures, moved at slightly higher temperatures, and burrowed as the temperatures increased further (Ellner and Karasov, 1993). Juvenile turtles found inactive on Egmont Key generally were covered with leaf litter or moist soil and were resting on cool damp soils, suggesting a retreat from higher temperatures or lower humidities.

Movement. — An increase in the mean distance moved occurred during September, and was caused by unusually large movements made by five subadult individuals. The impetus for these movements is unclear; they may reflect a seasonal shift in home range or the exploitation of seasonal food resources as observed for adults. Large scale movements of juvenile *T. carolina* were observed by Stickel (1950), who hypothesized that juveniles may be more itinerant than adults, and that this lack of site fidelity may make them more difficult to relocate. This idea is supported by low recapture success during the study period (Hamilton, 2000), as most marked juveniles were never re-captured. However, several juvenile turtles were re-captured near their original capture location. A subadult individual (CL = 117 mm), was captured in August and again in November within 200 m of its original location, and a smaller juvenile (CL = 77 mm) was recaptured within 1000 m of its initial location after one year. Additionally, some juvenile turtles marked during this study were relocated between the years of 1998 and 2000 in the vicinity of their original capture (C.K. Dodd, Jr., *pers. comm.*).

Information regarding the ecology of juvenile members of the population is necessary to develop appropriate conservation plans that incorporate the needs of this age class, as well as to ensure accurate censuses. Behavioral and physiological differences between juvenile and adult box turtles on Egmont Key, as well as differences reported in the literature for other species, suggest the impacts of management practices on adults may not necessarily be identical for juveniles. The data presented in this paper should aid in development of more appropriate management plans, accurate census techniques, and understanding of box turtle ecology.

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