

HOME RANGE SIZE AND DAILY MOVEMENTS OF MIDLAND PAINTED TURTLES (*CHRYSEMYS PICTA MARGINATA*) IN RELATION TO BODY SIZE, SEX, AND WEATHER PATTERNS

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Abstract.—To gain potential insights into energy acquisition of the ectothermic Midland Painted Turtles (*Chrysemys picta marginata*), we studied influences of weather patterns, habitat structure, sex, and body size on activity patterns. Shell temperature (T_s) cycled on a diel basis and movement was relatively low during the 0000–0400 h time period, possibly indicating thermal or daylight limitations on activity. Mean daily T_s and daily distance moved were lower on cloudy days relative to sunny days and did not vary among intra-specific classes (juveniles with 2–5 completed activity seasons and adult males and females). Juveniles and adult males and females moved similar mean daily distances, occupied similar-sized home range areas, and established single or multiple core areas of activity. Variations in weather patterns, and therefore, available thermal energy, apparently affect activity similarly across a range of body sizes. Core area use in both juveniles and adults presumably reflects familiarity with resource distributions that is established early in life. Males and females apparently expended similar energy on movements, even during the nesting season when movements of females might exceed those of males, or during other times when males searched for sexually receptive females. Despite the potentially greater mobility of large relative to small turtles, adults and juveniles showed similar spatial ecologies, perhaps because of small marsh size restrictions on movements, or because of compensatory locomotor capacities of juveniles (e.g., greater rate of limb movement). Therefore, when scaled to body size, juveniles probably invested more energy to movements than did adults.

Key Words.—*Chrysemys picta marginata*; home range size; Midland Painted Turtles; movements; thermal ecology

INTRODUCTION

In reptiles, variations in the thermal environment and microhabitat use affect activity, and therefore, energy acquisition and fitness (Huey 1982; Congdon 1989). The rates of physiological processes, such as digestion and muscle activity, are strongly temperature-dependent (Huey 1982). Variation in weather conditions, and the use of microhabitats with variable water depths, can significantly affect body temperature (T_b) variation and foraging activity of freshwater turtles (Rowe and Dalgarn 2009). Reduced solar radiation levels on overcast days can reduce T_b (Spotila et al. 1990) resulting in less-variable T_b variation and diminished movements in adult Midland Painted Turtles, *Chrysemys picta marginata* (Rowe and Dalgarn 2009). The use of densely-vegetated and shallow marsh edge microhabitat by *C. picta marginata* can result in variable T_b and reduced movements relative to individuals that use deeper, open-water microhabitats thus imposing a potential cost in terms of T_b stability and mobility (Rowe and Dalgarn 2009). Relative to large-bodied adults, variation in daily weather conditions and use of relatively shallow water microhabitats could have greater effects on T_b variation and activity in relatively small-bodied juvenile freshwater turtles, which would

warm up and cool down quickly (Spray and May 1972; Costanzo 1982; Lefevere and Brooks 1995).

Within an aquatic ecosystem, individual turtles may utilize habitat differently depending on habitat structure, age, or sex (Congdon et al. 1992; Lindeman 2003). Within freshwater turtle home ranges (i.e., inclusive areas used by individuals during their daily activity), individuals may establish core areas (intensively used areas) that could indicate patchy distributions of resources (Hall and Steidl 2007) or familiarity with basking sites (Lefevere and Brooks 1995), cover, and foraging areas (de Solla et al. 1999; Rowe 2003). Changes in dietary habits, body size, locomotor ability (Zani and Claussen 1994, Elnitsky and Claussen 2006), and vulnerability to predation influence habitat use by differing size and age-classes (Pluto and Bellis 1986; Lindeman 2003). In riverine turtle species that are strongly sexually size dimorphic, such as map turtles (*Graptemys*), juveniles and relatively small adult males may be highly vulnerable to predation or lack the energy reserves for long distance travel when compared to large adult females (Bodie and Semlitsch 2000). Congdon et al. (1992) found that *Chrysemys picta marginata* used shallower microhabitats as juveniles, which may have facilitated efficient foraging on animal prey (Sexton 1959). Older individuals, however, used deeper waters as their swimming ability improved and as they began to

forage on plant matter, decreasing predation risk. Shallow areas also provide a warmer microclimate and could promote rapid growth of juveniles (Congdon et al. 1992). Because shallow water microhabitats attain higher temperatures than deepwater microhabitats during the daylight hours (Rowe and Dalgarn 2009), age differences in habitat use suggest that juveniles and adults have different preferred T_b (the T_b set point range around which T_b is behaviorally or physiologically regulated; Hertz et al. 1993). Ontogenetic differences in habitat use presumably result in greater daily distances traveled and home range size in adults relative to juveniles. For instance, juvenile *C. picta* in riverine populations apparently do not travel as far as adults (MacCulloch and Secoy 1983). In *C. picta* in lentic habitats, however, it is not clear how mobility and microhabitat use impact daily distances moved and home range size in juveniles relative to adults.

Inter-sexual differences in activities and movements in freshwater turtles seem to be related to differences in reproductive ecology. Because allocation of energy to ovaries is temperature-dependent (Huey 1982), female *C. picta* may bask more frequently and longer than males during the nesting season (Krawchuk and Brooks 1998; Carriere et al. 2008). Male *C. picta* maintain higher T_b during the early morning hours (Rowe and Dalgarn 2009) and may bask more than females during early spring (Grayson and Dorcas 2004). In some north temperate freshwater turtle species, inter-sexual differences in movements are related to nesting activity of females during late spring and early summer (Litzgus and Mousseau 2004) or to mate searching by adult males (Morreale et al. 1984; Hall and Steidl 2007). According to the reproductive strategies hypothesis (Morreale et al. 1984; Litzgus and Mousseau 2004), male *C. picta* move greater mean distances both daily (Rowe and Dalgarn 2009) and seasonally (MacCulloch and Secoy 1983). In populations where female *C. picta* nest on land in close proximity to their aquatic home range (Rowe et al. 2005), females and males move similar daily aquatic distances.

We studied the influences of weather conditions, microhabitat use, and intra-specific class (juveniles and adult females and males) on daily movements and home range size of *C. picta marginata* at Miller's Marsh on Beaver Island, Michigan, USA using radio telemetric techniques. The marsh has sparsely vegetated and deep, open-water regions with shallow-water, heavily vegetated microhabitats on its periphery (Rowe and Dalgarn 2009). We expected that juvenile *C. picta marginata* would use the shallower, heavily vegetated, edge microhabitats more than adult males and females (Congdon et al. 1992). Because adults have longer stride and more rapid voluntary locomotor capabilities than juveniles (Zani and Claussen 1994) and may require more food than relatively small individuals (Perry and

Garland 2002), we assumed that daily distance moved would scale to body size and so we expected that adults would move greater mean daily distances than juveniles. Based on the fact that juveniles of some pond turtle species frequently bask (Janzen et al. 1992; Lindeman 1993), we expected that juvenile shell temperature (T_s) would show diel cycling similar to the T_s and T_b of adults (Grayson and Dorcas 2004; Edwards and Blouin-Demers 2007; Rowe and Dalgarn 2009). Due to relatively low solar radiation and thus available thermal energy on overcast days, we anticipated that mean daily T_s and mean daily distances moved would be greater on sunny days than on overcast days (Rowe and Dalgarn 2009). The relatively small juveniles would likely have less stable body temperature than adults (Spray and May 1972; Costanzo 1982) and so, relative to adults, we predicted that juveniles would move less than adults on overcast days. Because we anticipated that juveniles would have lower mean daily distances moved relative to adults, it would follow that home range size would be small relative to adults. Because male *C. picta marginata* are sexually active throughout the summer months (Ernst and Lovich 2009), we expected that males would move greater daily distances than females.

MATERIALS AND METHODS

Study site.—Miller's Marsh is a natural, north temperate wetland (46° 35' 46" N 85° 35' 29" W) that varies in maximal depth (1–2 m) within and among years. Common emergent vegetation includes various sedge species (*Carex* spp.), cattails (*Typha* sp.), bulrush (*Scirpus* sp.), and grasses and submergent vegetation including Yellow Lilies (*Nuphar variegatum*), pondweeds (*Potamogeton* spp.), and Water Shield (*Brasenia schreberi*). The marsh exists as two separate bodies of water, North Marsh and Main Marsh, and total surface area of the marsh varies annually (< 1–8 ha).

Radio telemetry.—We collected turtles in funnel traps, baited with sardines or chicken livers, or by hand beginning in early May, 2004 and 2006, and late May, 2005, and uniquely marked each individual by shell-notching. We obtained straight-line carapace length (CL) using calipers and body mass using spring scales (Table 1). We used epoxy to adhere calibrated, temperature-sensitive radio transmitters (1.5 g; Advanced Telemetry Systems Inc., Isanti, Minnesota, USA) to the dorsal margins of the carapaces of 24 juvenile Midland Painted Turtles (Table 2). The age of turtles varied between 2 and 5 completed activity seasons (Table 1), as estimated by counting abdominal scute annuli (Rowe et al. 2003). Radio transmitters were calibrated (1–45° C, $\pm 0.12^\circ$ C) to collect T_s . For some juveniles, we attached radio transmitters relatively late in the summer to replace turtles that had lost their radio

Herpetological Conservation and Biology

TABLE 1. Numbers of individual turtles (*n*) equipped with radio transmitters and dates of radio transmitter application for juvenile and adult *C. picta marginata* at Miller's Marsh, Beaver Island, Michigan.

Year	Juveniles		Adults	
	<i>n</i>	Dates of Application	<i>n</i>	Dates of Application
2004	6	2–28 May	6	2–26 May
	2	12 July		
2005	8	1–12 June	6	2–30 June
	1	15 July		
2006	5	10 May–2 June	5	6 May–22 June
	2	23 June		

transmitters due to scute shedding or radio transmitter failure. Although data obtained using carapace-mounted radio transmitters (T_s) do not exactly equal T_b (Edwards and Blouin-Demers 2007), T_s data should represent environmental temperatures experienced by the individual and should be reasonable estimates of T_b (Grayson and Dorcas 2004), particularly in relatively small turtles. All adult turtles received surgically implanted radio transmitters (2.8 g) with coiled antennae (Table 2). In 2006, we attached carapace-mounted radio transmitters to adults in addition to implanted transmitters to facilitate comparisons of T_s between adults and juveniles. Average adult carapace length and body mass at capture were 1.8 and 4.3 times that of juveniles, respectively (Table 2).

In each year, we constructed a grid of labeled nylon flags with wire stems ($n = \text{ca. } 300\text{--}500$) at distances of 2.5–5 m apart, and anchored floats at distances of 10–25 m apart throughout the marsh. We used variable numbers of flags among years because surface area of Main Marsh varied annually (2004: 6.5 ha; 2005: 4.1 ha; 2006: 2.8 ha). We prepared maps of the grid using a handheld Trimble GPS (Trimble Inc., Sunnydale, California, U.S.A.) unit and ArcMap 8.0 (ESRI, Redlands, California, U.S.A.). Radio telemetry was conducted from a small boat using a handheld radio receiver and antenna. During radio telemetry, we obtained radio signals from at least three directions and attempted to maintain a distance of approximately 5 m such that we did not disturb the turtle. Using the numbered flags as spatial reference points, we plotted a turtle's approximate location on a hardcopy map of the study site. Each turtle was located three times per day (0900, 1300 and 1900 ± 1 h), four to seven days per week. We plotted turtle locations on a hard copy map and later transferred the locations to a Geographic Information System (GIS; ArcView 3.2; ESRI, Redlands, California, U.S.A.). We then calculated the distances between successive locations for each individual to determine the total daily distance moved ($D1 + D2 = \text{TDDM}$). Daily weather condition type

(overcast- mostly cloudy to entirely overcast or sunny- partly cloudy to entirely sunny) was recorded by direct observation and from data obtained from the National Climatic Data Center (www.ncdc.noaa.gov/oa/ncdc.html). We scored each 12 h radio telemetry period as “overcast all day” (0800–2000), “overcast during the morning (0800–1300) and sunny during the afternoon (1300–2000)”, “sunny-mostly sunny during the morning and overcast during the afternoon”, or “sunny all day.”

We assessed diel variation in turtle movements using an intensive sampling regimen in which turtles were located seven times per day ($n = 2\text{--}4$ days for 5 adults, $n = 1\text{--}4$ days for 11 juveniles). We measured D_i between successive locations for a total of six movement distances per individual per day. The total daily distance moved for each individual over the 24 h sampling period was calculated as the summation of the six distances.

To record thermal data, we placed an omni directional antenna and a radio receiver with data logging capabilities (TR5, Telonics Inc., Mesa, Arizona, USA) at a central location in the marsh. We programmed the data-logging radio receiver to record pulse intervals (durations of time between pulses; ms) for each turtle every 15 min for a maximum of 96 observations per individual per day. Pulse intervals were converted to T_s values for each individual using fourth order polynomial regression equations ($R^2 > 0.99$). We determined hourly temperatures per individual to reduce biases throughout the day when four temperature values per hour were not determined for each individual.

Home range size.—We estimated an individual's home range size by plotting a sequence of single daily locations per individual over the summer activity season. Home range size was measured using minimum convex polygons (MCPs) and fixed 50% and 95% kernels (Worton 1989) using the Animal Movements Extension (Hooge and Eichenlaub 2000) for ArcView 3.2. Minimum convex polygons include the area formed by the outermost locations of an individual (Hayne 1949). Kernel analysis is a non-parametric technique (Worton

TABLE 2. Body size dispersion statistics (mean \pm SE, min.–max.) of adult female and male and juvenile radio-tagged *Chrysemys picta marginata* at Miller’s Marsh, on Beaver Island, Michigan, 2004–2006.

	Adults		Number of Growing Seasons Completed by Juveniles			
	Females (<i>n</i> = 11)	Males (<i>n</i> = 7)	2 (<i>n</i> = 13)	3 (<i>n</i> = 10)	5 (<i>n</i> = 1)	2–5 (<i>n</i> = 24)
CL (mm)	151.9 \pm 4.53	139.1 \pm 2.01	76.7 \pm 2.17	87.8 \pm 2.79	99.0	82.2 \pm 2.10
	144–157	130–146	60–92	70–101		60–101
Mass (g)	418.7 \pm 15.69	291.0 \pm 13.02	73.6 \pm 6.01	98.6 \pm 5.63	128.0	86.3 \pm 5.01
	353–525	233–345	45–126	70–130		45–130

1989) that can reveal core areas of activity as evidenced by clusters of an individual’s location points (Blundell et al. 2001; Row and Blouin-Demers 2006). The use of 50% kernels ($K_{50\%}$) has the advantage of minimizing the inclusion of areas that were not occupied by individuals, thus $K_{50\%}$ may better estimate areas regularly occupied by individuals (Donaldson and Echternacht 2005). We chose smoothing factors (*h*) for kernel determination in two ways to facilitate comparisons with other published studies. First, we used least-squares cross validation (LSCV) for optimum bandwidth selection (Bowman 1984) because an individual’s locations were often highly clustered (Gitzen et al. 2006). However, the use of LSCV for *h* value selection can render more variable results in home range size among individuals than do MCP estimates (Row and Blouin-Demers 2006). Therefore, we also determined $K_{50\%}$ and $K_{95\%}$ based on *h* values that resulted in equivalent $K_{95\%}$ and MCP area sizes for each individual (Row and Blouin-Demers 2006).

The estimation of home range size can be biased by autocorrelation if insufficient time between radiolocations is allowed for individuals to travel to any one location within the home range (Swihart and Slade 1985). We observed both juvenile and adult turtles traversing the length of the marsh within several hours, and so using locations that were obtained 24–48 hours apart should have minimized serial autocorrelation that was due to variation in sampling increments. When marsh water levels were relatively high (i.e., 2004), some individuals tended to temporally frequent different microhabitats such that open-water areas were used in the morning and early evening and edge areas were used during the afternoon. Therefore, on sequential radio telemetry days, we plotted one morning, one afternoon, or one evening location per day so that our plots included approximately equal numbers of daily points in edge and open-water microhabitats over time. To determine an appropriate number of locations required to adequately evaluate home range size, we sequentially and incrementally plotted daily locations of each individual turtle to determine an asymptotic home range size (Rose 1982; Stone and Baird 2002). We estimated

home ranges as MCPs, $K_{50\%}$, and $K_{95\%}$ areas at three-day cumulative increments (3, 6, 9, 12 etc. with each three-day segment comprised of a daily 0900, 1300, and 1900 location). On average, home range sizes of both adults and juveniles (MCP, $K_{50\%}$, and $K_{95\%}$) that were plotted at three-day, cumulative increments, attained an asymptote between 42 and 51 radiolocation days. However, due to radio transmitter failure or loss through scute shedding in juveniles, some individuals were not monitored throughout the entire summer. Differences in sampling duration among individuals can bias home range size estimates (Rose 1982; Stone and Baird 2002), particularly when some autocorrelation of data exists (de Solla et al. 1999). Therefore, we maximized sample sizes, but minimized duration of monitoring differences among individuals, by basing comparisons of home range size among juveniles, adult females and males, on plots of 36 radio telemetry days. Our home range size estimates therefore represent relative measures of the areas occupied by turtles, during a standardized time period, throughout the summer rather than estimates of home range size over the entire year.

Statistical analyses.—Shell temperature was normally distributed (Shapiro-Wilk $W = 0.96$, $P > 0.05$) as was TDDM after *ln* transformation (Shapiro-Wilk $W = 0.99$, $P > 0.05$). Home range size as measured by MCP, $K_{50\%}$, and $K_{95\%}$ areas were not normally distributed (Shapiro-Wilk $W = 0.72–0.83$, $P > 0.05$ in all tests). To analyze variation in TDDM and hourly T_s , averaged per individual per day, we determined mean daily T_s and TDDM values for each individual in each year overall and under each of the four daily weather condition types, and three daily microhabitat use types. We analyzed variation in TDDM by ANOVA with intra-specific class (juvenile, male, and female), microhabitat type, and daily weather condition type terms as main effects and with all possible two and three-way interaction terms included in the model. Variation in T_s in juveniles was analyzed by ANOVA with microhabitat type, daily weather condition type, and microhabitat \times daily weather condition type terms included in the model. In both

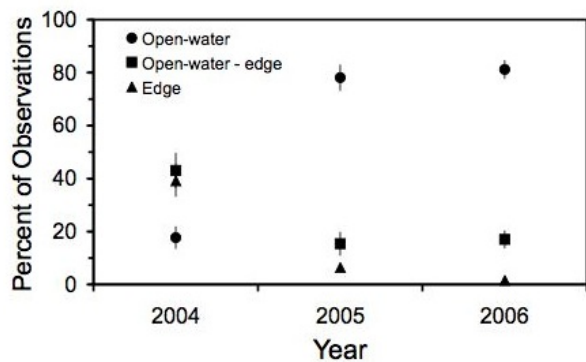


FIGURE 1. Mean (\pm 1 SE) proportional daily microhabitat use for juvenile ($n = 24$), adult female ($n = 12$) and, adult male ($n = 7$) *Chrysemys picta marginata*, 2004–2006, at Miller’s Marsh, Beaver Island, Michigan.

ANOVA models, we included turtle identification number as a random variable to account for autocorrelation such that the assumption of data independence was met (Zar 2009). We also included year (2004, 2005, and 2006) as a random variable to account for any variations in environmental conditions or annual differences in sampling periods. Test statistics were considered significant at the 95% significance level.

RESULTS

Microhabitat use.—During the 0800–2000 radio telemetry period, juveniles and adult females and males used both edge and open-water microhabitats similarly but microhabitat use depended on the year of

measurement. Significant terms in the ANOVA of proportional daily microhabitat use that were square root transformed (open-water for the entire day, open-water and edge during a single day, or edge all day) expressed as a percentage of each daily type per individual per year included daily microhabitat type ($F = 27.1$, $df = 2,102$, $P < 0.0001$, $R^2 = 0.28$) and year \times daily microhabitat type ($F = 21.8$, $df = 4,102$, $P < 0.0001$). The intra-specific class (juvenile, adult female, and adult male), year, and all two and three-way interaction terms were not significant ($P > 0.05$). Overall and in 2006, least square (LS) means multiple t-test *post hoc* comparisons of mean daily proportional microhabitat use indicated that the use of open-water microhabitat represented the highest proportional use by individuals, and the use of the edge microhabitat all day had the lowest proportional use ($P < 0.05$; Fig. 1). In 2005, turtles used the open-water microhabitat significantly more often than the edge or both the edge and open-water habitats throughout the day ($P < 0.05$; Fig. 1). In 2004, turtles used the open-water microhabitat proportionally less than edge and open-water, or edge only, during a single day ($P < 0.05$; Fig. 1).

Diel variation in T_s and movement distances.—Shell temperature (T_s) of adults and juveniles varied significantly throughout the course of the day and did not vary among intra-specific classes. Monotonic T_s declines during the early morning hours were followed by rapid elevation in T_s during late morning or early afternoon (Fig. 2). Mid-afternoon T_s oscillations terminated in a monotonic T_s decline during the late evening hours. Mean annual T_s averaged per individual

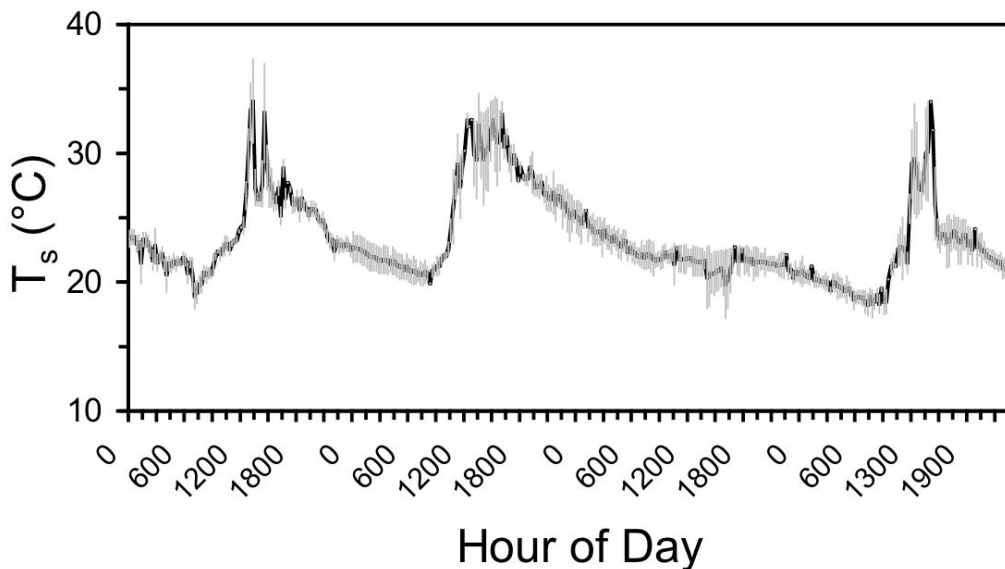


FIGURE 2. Mean (solid line) and \pm 1 SE (vertical lines) shell temperature (T_s) of five juvenile *Chrysemys picta marginata* recorded at 15 min intervals over a four-day period (16–19 June, 2006) at Miller’s Marsh, Beaver Island, Michigan.

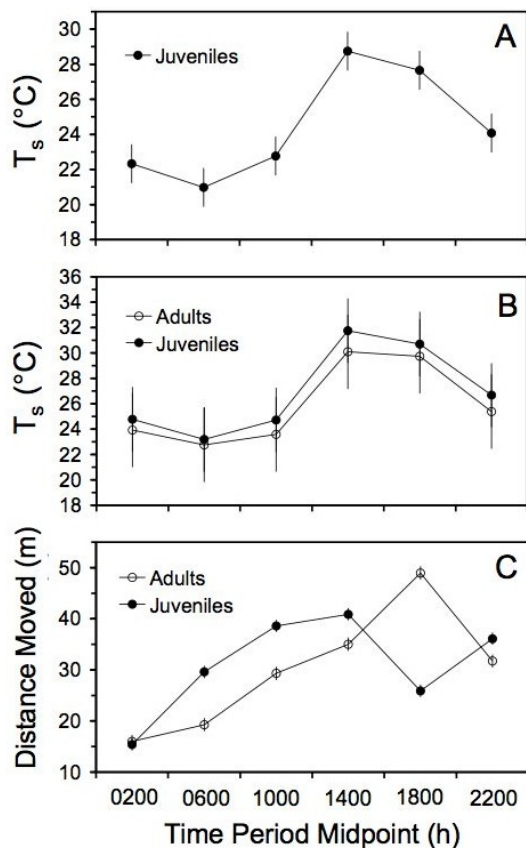


FIGURE 3. Diel variation in mean (\pm SE) shell temperature (T_s) averaged per individual during six, four-hour time periods in A) 24 juvenile *Chrysemys picta marginata* monitored on 268 days during 2004–2006, and B) juveniles ($n = 7$) and adult females ($n = 40$ and adult males ($n = 2$) measured on 100 days in 2006. C) Total distance moved during six, four-hour time periods measured in juveniles ($n = 7$), adult females ($n = 4$), and adult males ($n = 2$) on six days during 2006 at Miller’s Marsh, Beaver Island, Michigan.

was $24.2 \pm 0.5^\circ\text{C}$ ($20.6\text{--}28.9^\circ\text{C}$) based on an average of 1088.8 ± 121.5 observations per individual across 1,059

observation days (mean = 50.2 ± 4.8 d per individual). Mean hourly T_s for juveniles varied among the six, four-hour time periods varied among time periods ($F = 294.7$, $df = 5,519$, $P < 0.0001$, $R^2 = 0.83$; $P < 0.05$ in all *post hoc* comparisons). Least square (LS) mean T_s was lowest during the 0400–0800 time period ($P < 0.05$ in all comparisons), similar during the 0000–0400 and 0800–1200 time periods ($P > 0.05$), and highest, and significantly different, among the three time periods between 1200 and 0000 ($P < 0.05$ in all comparisons; Fig. 3a).

Mean T_s values of adults and juveniles were similar and both intra-specific classes cycled throughout the day. In 2006, T_s was measured for seven juveniles and six adults (due to the small number of males, $n = 2$, data

were pooled with those of females). Mean T_s averaged per individual varied among the six, four-hour time periods ($F = 293.8$, $df = 5,267$, $P < 0.0001$, $R^2 = 0.901$; Fig. 2a), but neither intra-specific class, nor intra-specific class \times time period effects, were significant ($P > 0.05$; Fig. 3b).

Both juvenile and adult turtles maintained movements during all hours of the day with a slight, but significant, decrease in activity during the early morning hours. The time period term in the ANOVA of natural log transformed distance traveled during six, four-hour time periods ($n = 6$ days) was significant ($F = 5.1$, $df = 5,84$, $P = 0.0004$, $R^2 = 0.36$) but intra-specific class and intra-specific class \times time period terms were not significant ($P > 0.05$). Mean distance moved was significantly shorter during the 0000–0400 time period relative to other time periods ($P < 0.05$ in all comparisons; Fig. 3c).

Mean daily T_s and TDDM.—Mean daily T_s was relatively low on days with cloud cover and microhabitat use did not affect T_s . Analysis of variance of daily T_s measured in juveniles during the daily 0800–2000 radio telemetry period averaged per individual per summer, indicated significant effects of weather ($F = 23.1$, $df = 3,135$, $P < 0.0001$, $R^2 = 0.57$). Microhabitat use and weather conditions \times microhabitat use terms were not significant ($P > 0.05$ in both cases). Least square mean T_s was significantly lower on days that were overcast all

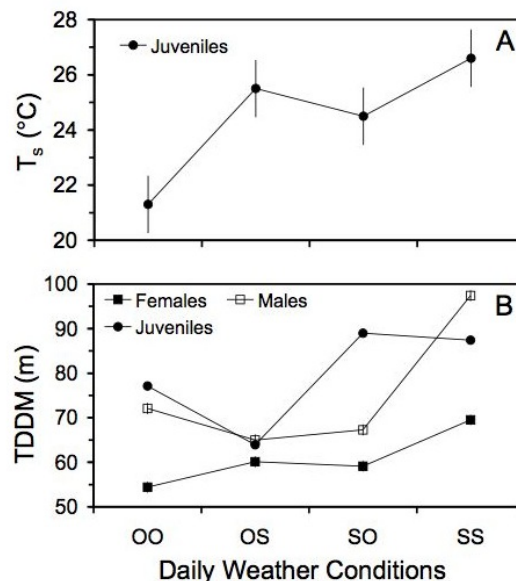


FIGURE 4. A) Shell temperature (T_s) of 24 juvenile *Chrysemys picta marginata* under four daily weather condition types (OO- overcast between 0800–2000 h, OS- overcast between 0800–1200 h and sunny between 1200–2000 h, SO- sunny between 0800–1200 h and overcast between 1200–2000 h, and SS- sunny between 0800–2000 h) measured on 268 days between 2004–2006, and B) total daily distance moved (TDDM) by juveniles ($n = 24$), females ($n = 12$), and adult males ($n = 7$) measured on 191 days in 2004–2006 at Miller’s Marsh, Beaver Island, Michigan.

TABLE 3. Home range size (ha) as measured by minimum convex polygons (MCP), $K_{50\%}$, and $K_{95\%}$ with smoothing factors (h) adjusted by least squares cross validation (LSCV; Bowman 1984) and for the area of the MCP (Row and Blouin-Demers 2006) for juveniles ($n = 17$), females ($n = 9$), and males ($n = 4$).

Intra-specific class	MCP	$K_{50\%}$ (h adjusted by LSCV)	$K_{50\%}$ (h adjusted to MCP)	$K_{95\%}$ (h adjusted by LSCV)	$K_{95\%}$ (h adjusted to MCP)
Juveniles	1.5 ± 0.2	0.3 ± 0.1	0.2 ± 0.1	2.0 ± 0.4	1.5 ± 0.2
	0.3–4.5	0.2–1.6	0.1–0.6	0.4–7.1	0.3–4.4
Females	1.8 ± 0.4	0.3 ± 0.1	0.2 ± 0.1	2.1 ± 0.5	1.8 ± 0.4
	0.5–4.4	0.1–1.1	0.1–0.4	0.1–4.9	0.6–4.2
Males	2.9 ± 1.2	0.8 ± 0.4	0.4 ± 0.2	4.2 ± 1.7	2.9 ± 1.2
	0.7–5.6	0.2–1.6	0.1–1.0	0.9–7.9	0.6–5.5

day than on days that were sunny during at least part of the day ($P < 0.05$ in all comparisons) and significantly greater on days that were sunny all day than on days that were sunny only in the morning ($P < 0.05$; Fig. 4a). Sample sizes were not sufficient in 2006 for comparisons among intra-specific classes, daily microhabitat use, daily weather conditions and their interactions. However, a t -test of mean T_s averaged per individual between juveniles (mean $T_s = 25.6 \pm 0.9^\circ \text{C}$, 22.7 – 28.9°C , $n = 7$) and adults (mean $T_s = 24.9 \pm 0.7^\circ \text{C}$, 22.5 – 26.2°C , $n = 5$) was not significant ($T = 0.90$; $df = 40$; $P > 0.05$).

Total daily distance moved (TDDM) during the 12-hour radio telemetry period was affected by daily weather conditions but not by microhabitat use or by intra-specific class. Daily weather conditions were significant for both juveniles ($n = 24$) and adults ($n = 11$ females, $n = 7$ males) over all three years of the study ($F = 4.6$, $df = 3,305$, $P < 0.01$, $R^2 = 0.47$). Intra-specific class, microhabitat use, and two-way and three-way interaction terms were not significant ($P > 0.05$). Individuals moved significantly greater distances on days that were sunny during the morning only, or sunny all day, than on days that were sunny in the afternoon only ($P < 0.05$; Fig. 4b). Analysis of variance of $\ln\text{TDDM}$, with intra-specific class as a main effect and year as a random effect, indicated no significant differences among juveniles (mean = 89.8 ± 4.7 m, 42.3 – 134.8 m, $n = 24$, $n = 905$ total observation days, mean = 37.7 ± 3.5 , 11 – 67 observation days per individual) and adults (mean_{female} = 81.2 ± 12.1 m, 19.3 – 155.8 m, $n = 11$; mean_{male} = 96.5 ± 11.0 m, 59.0 – 139.4 m, $n = 7$; $n = 717$ total observation days, mean = 39.8 ± 4.4 days, 18 – 76 observation days; $F = 1.29$; $df = 2, 39$; $P > 0.05$). In data combined for both juveniles and adults, Spearman rank correlation analyses indicated no significant relationships between annual $\ln\text{TDDM}$ averaged per individual and body size (Spearman Rank Correlations: $\ln\text{CL}$ vs. $\ln\text{TDDM}$, $\rho = -0.12$, $t = -0.76$,

$df = 41$, $P > 0.05$; $\ln\text{BM}$ vs. $\ln\text{TDDM}$, $\rho = -0.16$, $t = -1.03$, $df = 41$), further indicating that adults and juveniles traveled similar daily distances.

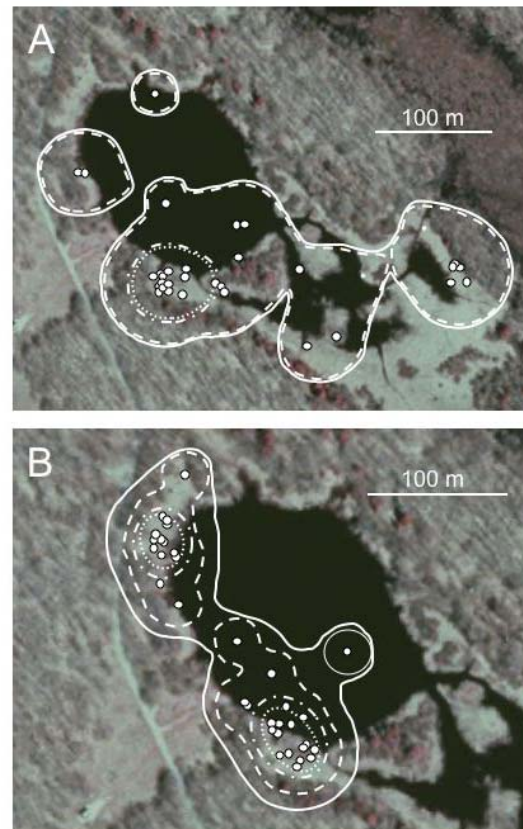


FIGURE 5. Daily locations (solid circles) measured over 36 radio telemetry days in 2004 and associated kernels with smoothing factors adjusted by least squares cross validation (LSCV; Bowman 1984; $K_{50\%}$ - dot-dashed lines and $K_{95\%}$ - solid lines) and $K_{95\%}$ adjusted for the area of the MCP (Row and Blouin-Demers 2006; $K_{50\%}$ - dotted lines and $K_{95\%}$ - dashed lines) in A) a single representative female *Chrysemys picta marginata* with a single core area ($K_{50\%}$) and B) a single representative juvenile *C. picta marginata* with two distinct core areas in Miller's Marsh, Beaver Island, Michigan.

Home range size.—During the summer months, most turtles established contiguous home ranges within Main Marsh throughout the summer (Fig. 5), with the exception of one adult male that established disjunct home ranges in Main and North Marshes. Generally, home range size as estimated using 36 radio telemetry days did not vary among juveniles, adult females, and males. Kruskal-Wallis tests for the differences in home range size as measured by MCP, $K_{50\%}$, and $K_{95\%}$ (h determined by LSCV and adjusted for MCP) were not significant (MCP: $H = 0.78$, $df = 2$, $P > 0.05$; $K_{95\%}$: $H = 1.47$, $df = 2$, $P > 0.05$; $K_{50\%}$: $H = 2.28$, $df = 2$, $P > 0.05$; Table 3). Home range size as estimated by $K_{95\%}$ (LSCV) was larger than using MCP (mean difference = -0.6 ± 0.2 , $n = 30$; Wilcoxon matched-pairs signed-ranks $T = 154.5$, $n = 30$, $P = 0.0006$) or $K_{95\%}$ adjusted for MCP area (mean difference = 0.6 ± 0.2 ha, $T = 156.0$, $P = 0.0005$; Fig. 5; Table 3). Similarly, $K_{50\%}$ (LSCV) area was significantly larger than $K_{50\%}$ area adjusted to MCP area (mean difference = 0.1 ± 0.1 ha, $T = 167.50$, $P = 0.0001$; Fig. 5; Table 3).

Within home ranges, juveniles and adults used similar numbers of core areas as identified by $K_{50\%}$ (Donaldson and Echternacht 2005) and, when edge microhabitat was available, turtles appeared to establish core areas mainly in the edge microhabitat rather than in open-water. Using smoothing factors as determined by LSCV and by adjusting $K_{95\%}$ for MCP, the average number of core areas as determined by $K_{50\%}$ was 1.9 ± 0.2 (1–6 core areas per individual) and 2.0 ± 0.2 ha (1–4 core areas per individual) respectively. Chi-square contingency analyses indicated that there were no significant differences among intra-specific classes in the number of core areas established at 36 radio telemetry days. In 2004, more than 50% of each individual's radio location points within the core area occurred on the edge microhabitat; whereas, less than 25% were located in the edge microhabitat.

DISCUSSION

The proportional use of edge and open-water microhabitats was similar between the juveniles and adult *C. picta marginata* in our study. Our results contrast with those of Congdon et al. (1992) who found that juveniles in their first few growing seasons used shallower water than the larger adults. In our study, it is possible that the difference in depth between edge and open-water microhabitats was not sufficient to cause differential microhabitat use between adults and juveniles. If, however, juvenile *C. picta marginata* avoid relatively deep water because of the presence of piscine predators (Congdon et al. 1992), the lack of piscine predators at Miller's Marsh may have allowed juveniles to use both shallow and deep water. Our annual differences in microhabitat use by *C. picta*

marginata might be explained by microhabitat availability among years. The greatest proportional use of the edge microhabitat occurred in the year with the highest annual water levels (i.e., 2004) when flooded grass-sedge areas were expansive.

Diel variation in T_s of both juveniles and adults in our study resembled T_s profiles in *C. picta* from North Carolina (Grayson and Dorcas 2004) and T_b profiles obtained using body cavity-implanted radio transmitters of adult *C. picta marginata* at Miller's Marsh (Rowe and Dalgarn 2009). Mid-day spikes and afternoon oscillatory declines presumably result from aerial or aquatic basking activities (Grayson and Dorcas 2004; Plummer et al. 2005) and monotonic declines during the late evening and early morning presumably reflect declining environmental temperatures (Rowe and Dalgarn 2009). Adult male *C. picta marginata* are capable of thermoregulating (Edwards and Blouin-Demers 2007) and we assume at least some thermoregulatory capabilities by the turtles of our study. We suspect that our T_s measurements were reasonable estimates of T_b as mean values were similar to mean daily T_b of adults with body cavity-implanted radio transmitters (24°C; Rowe and Dalgarn 2009; Rowe and Grace In press). Because we found no significant difference in mean T_s between adults and juveniles, we have no reason to believe that thermal preference, or any other aspects of thermoregulatory behavior, changed ontogenetically (Congdon et al. 1992) in the *C. picta marginata* of our study.

Consistent with our *a priori* expectations, movement of individuals continued throughout the 24-h daily period. However, distances moved during the 0000–0400 time period were significantly lower than during other times of the day. We suggest that, because T_s did not vary significantly among the three, four-hour time periods between 0000–1200, insufficient daylight, rather than low environmental temperatures, limited movements and foraging activity during the early morning hours. Similarly in north-temperate Stinkpot Turtles (*Sternotherus odoratus*), reduced movements during the early morning hours relative to movements during the late morning and afternoon seemed to be related more to diminished light levels than to low environmental temperatures (Rowe et al. 2009). Study of the ability of individuals to forage under low illumination might aid in determining why reduced activity occurs during some nocturnal hours in *C. picta marginata*. Alternatively, activity levels may not be limited by light levels or thermal energy directly but rather thermal and photic cycling could interact to determine a circadian locomotor rhythm (Ellis et al. 2009; Gopar-Canales 2010).

We assume that the relatively low T_s of both juveniles and adults on cloudy days resulted from the limited thermal radiation on those days (Spotila et al. 1990).

Similarly, T_b of adult turtles at Miller's Marsh has been shown to be low on cloudy days relative to days that were sunny during the morning, afternoon, or both (Rowe and Dalgarn 2009). We found that mean daily TDDM was diminished on overcast days and it is possible that activity was limited by thermal energy available for muscle activity. Alternatively, or additionally, thermal influences on neurological mechanisms could reduce appetitive behavior and ultimately activity (Gianopulos and Rowe 1999; Rowe and Dalgarn 2009). Contrary to our expectations, the degree of T_s and movement reduction on overcast days was not greater in juveniles than in adults. Apparently, although relatively small turtles would have lower thermal inertia than larger turtles (Spray and May 1972; Costanzo 1982), turtles of various sizes have similar and broad T_b ranges over which activity is possible. Similarly, Ben-Ezra et al. (2008) found that locomotor performances of hatchling and adult north-temperate Northern Map Turtles (*Graptemys geographica*) were similar over a broad range of T_b values.

That we did not find relatively small mean daily distance moved by turtles that used densely vegetated edge microhabitat relative to movements in the open-water microhabitat contrasts with previous work on our population (Rowe and Dalgarn 2009). However, we believe that limited availability of edge microhabitat in two of three years of the study resulted in a low occurrence of turtles in the edge microhabitat, thus precluding detection of microhabitat use effects. Regardless of microhabitat use, and contrary to our expectations, relatively large turtles did not move greater mean daily distances than small turtles. While larger turtles can attain greater burst speeds relative to smaller juveniles (Zani and Claussen 1994; Elnitsky and Claussen 2006), it is not always clear how laboratory-determined locomotor performance measures are related to the performance of organisms in the field (Irschick and Garland 2001; Irschick 2003). Speeds of individuals may vary during different activities, such as foraging, predator escape, or inter-specific interactions (Irschick and Garland 2001) and so maximal locomotor performance cannot always be assumed (Hertz et al. 1988). In *C. picta marginata* at Miller's Marsh, daily movements may be slow and circuitous and punctuated with periods of inactivity (Irschick and Garland 2001; Dubois et al. 2009) that could obscure the detection of differences among intra-specific size classes. Similar mean daily distances moved by juveniles and adults might also be affected by compensatory locomotor mechanisms of juveniles (Irschick and Garland 2001; Herrel and Gibb 2006). The relative and absolute speeds of juveniles might be enhanced through the circular shape of juvenile turtle shells relative to the more elongate shells of adults (Myers et al. 2007) or through relatively rapid limb locomotion that reduces the

advantage of long stride length of adults (Zani and Claussen 1994; Irschick 2003). We would expect that very small hatchlings that occupy the very shallow (< 25 cm) edge microhabitat of Miller's Marsh (pers. obs.), would have more restricted daily movements than juveniles and adults. Regardless, it would seem reasonable to conclude that relative energy expenditure would be greater in the smaller individuals than in larger individuals when individuals of different sizes move similar daily distances and have similar thermal physiology (Nagy 2005).

Both juvenile and adult *C. picta marginata* established one or more core areas of activity during our study. That juvenile *C. picta marginata* in their third or fourth growing seasons showed multiple core area use suggests that familiarization with specific areas of an aquatic habitat can occur over a relatively short period of time during the life of a turtle. If core areas indicate that familiarity with refugia sites, foraging areas, basking sites, and aquatic thermal patches are important (Rowe 2003), the ability to establish core areas quickly might be important when water depth, and therefore habitat structure, varies annually and seasonally. The frequent use of the edge microhabitat, as opposed to the open-water microhabitat, resulted in the concentration of core areas mainly in the edge microhabitat by turtles in 2004. If the frequent use of the densely vegetated edge microhabitat by turtles in 2004 reflected a preference over the open-water microhabitat, then we suggest that core area distribution could be used to elucidate habitat preference in some years (i.e., 2004 when both edge and open-water microhabitats were available) but not in others (i.e., 2005 and 2006 when mainly the open-water microhabitats were available).

At Miller's Marsh, we found no differences in home range size among different intra-specific classes at 36 radio telemetry days. Home range size estimates (MCPs and kernels) of *C. picta marginata* in our study were probably heavily influenced by the size and shape of Miller's Marsh (Rowe 2003). Indeed, in a riverine population of *C. picta marginata*, mean maximal seasonal distances moved by males exceeded 5 km whereas females and juveniles averaged about 4 and 0.6 km, respectively (MacCulloch and Secoy 1983). The "reproductive strategies hypothesis" states that male freshwater turtles may move farther than females during the mating season and females may move farther than males during the nesting season (Morreale et al. 1984; Litzgus and Mousseau 2004). In previous studies at Miller's Marsh, greater mean daily distances traveled by male relative to female *C. picta marginata* were either undetectable (Rowe 2003) or the effect was weak (Rowe and Dalgarn 2009). It may be that our summer monitoring occurred when males were not intensively searching for receptive females. While males might move farther than females during the spring mating

season, there are no inter-sexual differences in daily movements throughout the fall (Rowe and Dalgarn 2009). Alternatively, our methodology may not have had sufficient resolution to detect inter-sexual differences in daily movements. Similar to the data for daily distances traveled, inter-sexual differences in summer activity range size have not been detected in *C. picta marginata* at Miller's Marsh (Rowe 2003 and this study). It seems likely that females are not so widely spatially dispersed so as to bias home range size between sexes in our small marsh population. Apparently, the locomotor capacity of juveniles was sufficient to meet their ecological requirements within our relatively small marsh system. Detection of differences in home range size among intra-specific classes at Miller's Marsh might require year-round monitoring of both sexes as well as the inclusion of data on both hatchlings and yearlings.

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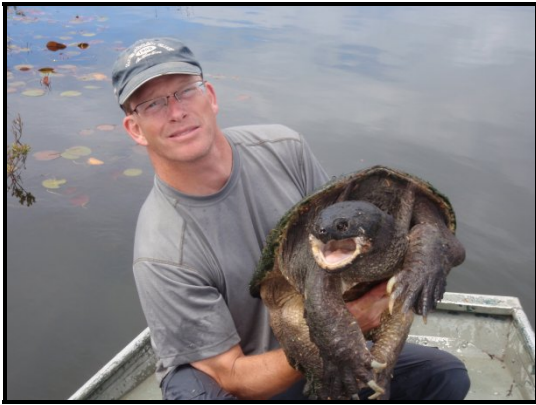
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APPENDIX A. Home range size (ha) as measured by minimum convex polygons (MCP), $K_{50\%}$, and $K_{95\%}$ with smoothing factors (h) adjusted by least squares cross validation (LSCV; Bowman 1984) and for the $K_{95\%}$ area equivalent to the MCP (Row and Blouin-Demers 2006) for juveniles ($n = 17$), females ($n = 9$), and males ($n = 4$).

Turtle ID number	Intra-specific class	Year	MCP	LSCV			Adjusted to area of MCP		
				$K_{50\%}$	$K_{95\%}$	h	$K_{50\%}$	$K_{95\%}$	h
832	J	2004	2.5	0.6	3.3	33	0.4	2.5	26
1309	J	2006	1.6	0.2	2.0	17	0.2	1.6	14
1311	J	2004	1.3	0.4	2.0	22	0.2	1.2	14
1312	J	2006	1.4	0.2	1.5	14	0.2	1.4	12
1316	J	2004	4.5	1.1	7.1	38	0.6	4.4	24
1317	J	2004	0.6	0.1	0.7	11	0.1	0.6	9
1318	J	2004	2.5	0.4	2.8	21	0.3	2.5	18
1331	J	2004	0.6	0.2	0.6	8	0.1	0.5	7
1336	J	2005	1.8	0.1	1.5	16	0.2	1.8	21
1378	J	2005	0.6	0.3	1.6	18	0.1	0.6	7
1382	J	2005	1.5	0.3	1.9	25	0.2	1.4	19
1384	J	2005	0.3	0.1	0.4	10	0.0	0.3	6
1387	J	2005	1.3	0.1	1.4	13	0.1	1.2	11
1432	J	2006	1.5	0.2	2.2	15	0.1	1.4	10
1437	J	2006	0.6	0.1	0.8	10	0.1	0.7	8
1481	J	2006	1.1	0.1	0.8	11	0.2	1.1	18
1556	J	2006	1.8	0.7	2.9	17	0.2	1.7	10
18	F	2006	1.1	0.2	1.2	12	0.1	1.0	10
66	F	2004	0.5	0.0	0.1	7	0.0	0.6	5
69	F	2004	2.3	0.2	1.8	18	0.3	2.2	23
163	F	2006	0.8	0.2	0.9	12	0.2	0.7	10
204	F	2005	1.0	0.2	1.2	15	0.2	1.0	13
260	F	2005	2.1	0.3	1.9	26	0.3	2.1	28
390	F	2004	4.3	0.4	4.4	31	0.4	4.3	30
442	F	2006	1.9	0.7	4.9	33	0.1	1.9	16
649	F	2004	1.9	0.2	2.3	17	0.1	1.9	14
139	M	2005	1.1	0.3	1.8	14	0.1	1.2	9
151	M	2004	4.1	1.3	6.2	32	0.5	4.4	23
308	M	2006	0.7	0.2	0.9	12	0.1	0.6	9
957	M	2004	5.6	1.6	7.9	39	1.0	5.5	27

Herpetological Conservation and Biology



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