

Movements, Activity, and Spacing of Sonoran Mud Turtles (*Kinosternon sonoriense*) in Interrupted Mountain Streams

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We quantified movements, spacing, and activity of Sonoran Mud Turtles (*Kinosternon sonoriense*) in interrupted mountain streams of southern Arizona over an 18-year period using capture–recapture sampling and radiotelemetry. Movement and activity patterns of turtles depended on water availability and varied by their sex and size. Although considered almost entirely aquatic in Arizona, mud turtles estivated terrestrially during periods of extreme drought. After the onset of summer rains, turtles increased the frequency with which they moved between pools and to nesting sites. Movements (average distance moved [AvD] \pm SE) of all turtles were shorter during drought years (males = 26 ± 1.3 m, females = 19 ± 1.3 m) than non-drought years (males = 153 ± 1.2 m; females = 41 ± 1.2 m). Adult male turtles made longer movements (93 ± 1.2) and had longer home-range lengths (206 ± 1.2 m) than did adult females (AvD = 38 ± 1.2 ; home range = 40 ± 1.2 m). Younger adult females (carapace length [CL] 100–118 mm) made longer movements (52 ± 1.2 m) and had longer home ranges (80 ± 1.9 m) than did older females (>118 CL mm; AvD = 38 ± 1.2 m; home range = 26 ± 2.2 m). Males made movements >500 m more frequently (8%) than females (2%) and moved as far as 7.2 km as measured along drainage bottoms. Large turtles used pools exclusively, only rarely sharing pools with other large individuals of the same sex. Degradation and losses of interior wetlands in the southwestern U.S. have reduced the potential for long-distance movements of turtles among disjunct, remnant populations, which has consequences for conservation of turtles and other aquatic species in the region.

THE distribution of resources can profoundly influence patterns of movements, activity, and spacing behaviors within a species (Swingland, 1983; McIntyre and Wiens, 1999; Maher and Lott, 2000). Populations that inhabit areas where resources are distributed patchily or vary temporally can exhibit movement and spacing patterns that differ from those where resources are available consistently (Waser and Wiley, 1979; Wiens et al., 1995). Consequently, insights into the effects of resource distribution and abundance on behavior can be gained by studying populations in areas where resources vary spatially or temporally.

Movements and spacing of freshwater turtles vary in response to changes in resource levels (Stone, 2001), to changes caused by the onset of adverse environmental conditions (Cagle, 1944; Gibbons et al., 1983; Morales-Verdija and Vogt, 1997; Stone, 2001), and to changes in season (Sexton, 1959; Bennett et al., 1970). Movements also vary with life-history stages, including nesting (Moll and Legler, 1971; Congdon et al., 1983) and natal dispersal (Parker, 1984; Tuberville et al., 1996), and due to fundamental differences in behavioral strategies of males and females thought to maximize reproductive output (Morreale et al., 1984; Gibbons, 1986). Home ranges of freshwater turtles generally overlap (Obbard

and Brooks, 1981; Doody et al., 2002; Litzgus and Mousseau, 2004), and although agonistic behaviors dictate spacing in many other taxa, behavioral spacing in freshwater turtles has been difficult to document (Galbraith et al., 1987; Kaufmann, 1992).

The Sonoran Mud Turtle (*Kinosternon sonoriense*) inhabits rivers, streams, and impoundments in the southwestern U.S. and Sonora, Mexico. Although individuals from all populations have adaptations necessary for inhabiting environments that dry periodically, behavioral and physiological responses to water stress vary among populations (Peterson and Stone, 2000; Lignon and Peterson, 2002). Within populations, variation in frequency and length of terrestrial movements by mud turtles vary with water availability (Stone, 2001). Therefore, temporal and spatial variation in water availability at both regional and local scales may be an important factor influencing the physiology and behavior of Sonoran Mud Turtles.

We investigated movements and spacing of Sonoran Mud Turtles in small interrupted mountain streams of southern Arizona between 1983 and 2001. The wetlands we studied were small, discrete, and sparsely distributed throughout the landscape, and were isolated seasonally by large inhospitable areas of dry stream bed.

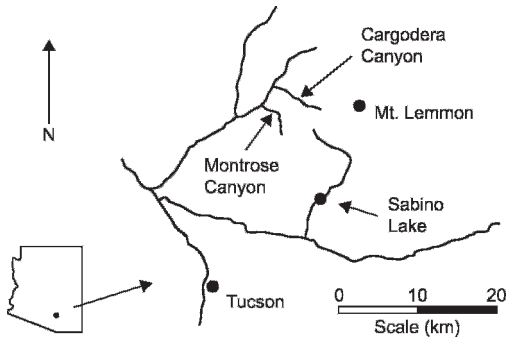


Fig. 1. Map of three study sites in the Santa Catalina Mountains, Pima Co., Arizona.

These environmental conditions, in concert with our relatively long-duration study, allowed us to assess how patterns of movements, activity, and spacing of turtles varied with sex, body size, drought, season, and the presence of conspecifics. We compared patterns observed in Sonoran Mud Turtles to other kinosternids that inhabit more mesic environments to assess how movement patterns of mud turtles vary across a range of environmental conditions. Because habitat of Sonoran Mud Turtles has been reduced drastically by human activities, we address how these reductions affect conservation strategies for the species.

MATERIALS AND METHODS

Study areas.—We studied Sonoran Mud Turtles in three areas of the Santa Catalina Mountains, Arizona (Fig. 1). Two populations inhabited smaller canyons on the west flank of the range, Cargodera Canyon ($32^{\circ}26'27''\text{N}$, $110^{\circ}51'42''\text{W}$) and Montrose Canyons ($32^{\circ}25'15''\text{N}$, $110^{\circ}53'26''\text{W}$), and one inhabited a larger canyon on the south flank of the range, Sabino Canyon ($32^{\circ}18'54''\text{N}$, $110^{\circ}48'37''\text{W}$). We studied Cargodera Canyon an average of 26 days per year (range = 14–35) in 1983–1984, 1990, 1992–1993, 1995–1999, and 2001. We studied Montrose Canyon for 55 days in 2000 and Sabino Lake in Sabino Canyon for 24 days between 1999 and 2001. We visited sites from late March through October.

Canyon bottoms were comprised of combinations of large rocks, cobble, gravel, sand, and bedrock. Vegetation bordering streams was interior riparian deciduous forest (Minkley and Brown, 1994) dominated by ash trees (*Fraxinus velutina*), with scattered mesquite (*Prosopis velutina*), sycamore (*Platanus wrightii*), hackberry (*Celtis reticulata*), walnut (*Juglans major*), willow (*Salix gooddingii*), and cottonwood (*Populus fre-*

montii) trees. Some pools supported small stands of cattail (*Typha* sp.), bulrush (*Scirpus* sp.), and spike rush (*Carex* sp.).

Cargodera Canyon is 11.7-km long, begins at an elevation of 2,476 m, ends at 874 m, and drains an area 9.5 km². The study reach was a 1.9-km-long section of stream containing 58 perennial pools where the stream gradient averaged 90 m/km. Average (\pm SE) size of perennial pools in this reach was 16 ± 2.6 m² with maximum depth of 1.5 m. Pools were concentrated into nine complexes where pools were <50 m apart, with an average complex length of 0.11 ± 0.02 km and an average of 7.0 ± 0.8 pools per complex. Montrose Canyon is 9.5-km long, begins at an elevation of 2,286 m, ends at 810 m, and drains an area 10.5 km². The study reach was a 2.2-km-long section containing 41 perennial pools where the stream gradient averaged 89 m/km. Average size of perennial pools in this reach was 49 ± 11.2 m² with a maximum depth of 2.5 m. Pools were concentrated into three complexes with an average complex length of 0.31 ± 0.05 km and an average of 12.8 ± 2.40 pools per complex. Sabino Canyon drains an area 93.2 km² within which we studied Sabino Lake, a small impoundment built in the lower reaches of the stream in 1936. Surface area of Sabino Lake varied seasonally between 50–1000 m², and its depth ranged between 1–2 m.

Water levels in canyons fluctuated considerably because of seasonal and annual variation in rainfall. Some stream reaches dried completely during late spring and early summer, with surface water remaining only in small, scattered runs and perennial pools carved in bedrock with steep sides and little soil-bank development. In a typical year, most stream reaches and ephemeral pools dried before the onset of summer rains in July, with water remaining only in a few reaches and in perennial pools. In Cargodera Canyon, for example, the number of pools retaining water decreased annually by an average of 53%, with water typically persisting in only one or two stream reaches between pools. In drought years, all stream reaches dried, with water remaining only in a few spring-fed perennial pools. In the driest years, almost all perennial pools dried, although a small amount of surface water usually persisted until the rains begin. During heavy summer rains, stream levels rise dramatically and scour pools free of rocks, gravel, sand, and vegetation, and fill other pools with debris. Although sometimes called “intermittent,” these streams are more accurately defined as “interrupted” because they contain both perennial and intermittent water (American Meteorological Society, 2000).

Capturing turtles.—We searched for turtles at all times of day but mostly between evening and mid-morning. Each visit consisted of 1–2 passes through a study reach. We captured turtles by hand or with nylon net hoop-traps (single throat, 76-cm diameter) and smaller wire-mesh traps (single throat, 30-cm diameter) baited with canned sardines or cat food, placing at least one trap in one pool within each pool complex. At Sabino Lake, we placed 8–10 nylon net hoop-traps at 10–40-m intervals around the perimeter of the impoundment.

We marked each turtle by filing notches in marginal scutes (Cagle, 1939) and used dial calipers to measure carapace length (CL). We determined sex by presence or absence of male secondary sexual characteristics (Ernst and Barbour, 1972), which males developed before reaching 80 mm CL. Therefore, we classified turtles <80 mm CL that were not clearly male as juveniles and turtles ≥ 80 mm CL that could not be classified as male as females; we found no misclassified individuals in subsequent recaptures. We palpated 100 females (67 from Cargodera Canyon, 33 from Montrose Canyon) 202 times to determine if eggs were present.

Movements and space use.—We quantified movements based on recaptures and radiotelemetry. We used capture–recapture data to assess whether capture frequency, maximum distance moved, and number of days between successive captures differed among female, male, and juvenile turtles. We used average distance moved between successive captures (AvD) as an index to movements (Slade and Swihart, 1983; Slade and Russell, 1998). To assess the effects of drought conditions on AvD, we used Palmer drought severity index (Palmer, 1965) averaged between May and September to classify years as drought (index ≤ -2.5 , $n = 3$ years) or non-drought (index > -2.5 , $n = 9$ years). To assess the effects of turtle size on AvD, we used data for each turtle captured >2 times and that had not grown >2 mm CL between captures. We excluded between-watershed movements from AvD calculations and weighted AvD by the number of recaptures per turtle.

We used size as a proxy for maturity of females and classified female turtles >100 mm CL as sexually mature adults. For Sonoran Mud Turtles in Arizona, minimum age at maturity is 5–6 years, which corresponds to a minimum CL of approximately 90 mm (Rosen, 1987). In our study areas, body size of females aged 5–6 years averaged 97 ± 1.5 mm CL ($n = 19$), however only females >103 mm CL carried eggs, which is similar to the minimum of 106 mm CL reported elsewhere in

southern Arizona (van Loben Sels et al., 1997). Average distance moved for females also increased markedly after they reached a CL of approximately 100 mm (Hall, 2002); therefore, we placed female turtles into three size classes based on CL: small (80–99 mm) that were not yet sexually mature, medium (100–118 mm) that likely had reached sexual maturity recently, and large (>118 mm) that had been sexually mature for years and were approaching maximum size for female turtles in this area.

We radio-tracked 29 turtles between 1996 and 2000. In 1996, we tracked eight turtles in Cargodera Canyon (four females, CL = 124–135 mm, four males, CL = 112–131 mm) at least once per week for an average of 29 locations per turtle (range = 24–35) from late April until late October. In 1997, we tracked seven turtles in Cargodera Canyon (three females, CL = 125–135 mm, four males, CL = 119–131 mm) twice per week for an average of 24 locations per turtle (range = 22–24) from April until February, with most locations between May–October. In 1998, we tracked four turtles in Cargodera Canyon (two females, CL = 120, 128 mm, two males, CL = 120, 123 mm) at least once per week for an average of 23 locations per turtle (range = 21–26) from April until mid-October. In 2000, we tracked ten female turtles in Montrose Canyon (six with CL = 108–115, four with CL = 120–136 mm) twice weekly for an average of 42 locations per turtle (range = 35–46) from late April until late September.

Transmitters (<5% of body mass) were attached to the posterior marginal scutes with epoxy and a nylon tie fastened through a small hole drilled through the shell at the margin. We used radiotransmitters manufactured by Wildlife Materials (model SOPI, Holohil (model BD-2GH), or that were homemade. Transmitters generally lasted three months and were replaced after failure. Turtles were captured, radio-marked, and returned to the field within 24 h of capture. Turtles were not handled after they were radio-marked except to replace a failing transmitter.

We quantified home-range length, site fidelity, directionality of movements, spacing, and association for radio-marked turtles. We defined home range as the distance between farthest upstream and downstream locations during one year (Plummer and Shirer, 1975). We quantified home-range overlap as the percentage of home ranges that overlapped for pairs of turtles in a single pool complex.

To quantify space use within a home range, we used the distribution of movements from each turtle's activity center or home pool, which we

defined as the mode of all pool locations for each individual each year. We quantified site fidelity as the percentage of times that a turtle was found in its home pool and an index of activity as the proportion of times that a radio-marked turtle had moved to another pool between successive locations. To assess directionality in movements, we compared the number of movements each turtle made upstream and downstream from their home pool. We classified turtles as estivating when we found them dormant in terrestrial locations (Seidel, 1978; Lignon and Stone, 2003).

Spacing and association.—To assess patterns of spacing, we used locations of radio-marked males and medium and large females from a single year and pool complex. We compared the spatial arrangement of turtles in pools to the probability that the spatial arrangement of turtles in pools was a random assortment (P_r) within a complex.

$$P_r = \binom{k}{n} P^k (1 - P)^{n-k}$$

To compute this probability, we treated each group of locations as a Bernoulli trial that we modeled with a binomial distribution for each sex and size group, where n was the number of sampling events and k was the number of events where turtles were found together in any combination of turtles and pools. P is the probability of finding turtles together in a pool during one sampling event and was computed as the number of ways turtles could be assigned to pools together divided by the total number of ways turtles could be arranged in pools without restriction. We assumed that all pools were equally available to each turtle in a complex.

We quantified the degree of association among turtles in a complex by calculating a coefficient of association based on the number of instances in which two or more turtles were found in the same pool at the same time (White and Garrott, 1990:139). We calculated the coefficient for each possible pair of radio-marked turtles within a pool complex.

Immigration.—To estimate immigration rate, we removed all turtles captured in Sabino Lake beginning in June 1999. By October 1999, capture success had declined to zero. We then trapped 70 days over the next 18 months to determine the number and characteristics of turtles that entered the impoundment. Turtles captured during this period were marked, measured, and released. Turtles that were removed were held in captivity until July 2001 when they were returned to their initial capture location.

Statistical analyses.—We used ANOVA to assess variation in AvD, home-range length, frequency of capture, and time and distance between successive captures for turtles of different sexes and sizes. We used linear regression to assess relationships between AvD, home-range length, and pool fidelity versus CL, and the distance moved by a turtle versus the number of days since last recapture. When assessing AvD versus CL for females, we gauged the need for CL² as an additional explanatory variable (AvD = intercept + CL + CL²) to account for curvature evident in the AvD-CL relationship. We used Poisson regression to determine if the number of radio-marked females per pool varied with the number of pools available, which declined during dry summer months. We used Student's t -tests to assess differences in AvD between sexes and between drought and non-drought years for each sex separately. We used a one-sample t -test to assess directionality of movements by comparing the difference in number of movements upstream and downstream from a turtle's home pool with zero. We used Fisher's Exact tests to compare activity levels between sexes by month, differences in frequency of long-distance movements (>500 m) between sexes, and differences in size classes of females captured during the immigration experiment. We log-transformed AvD, home-range length, and time between captures because their distributions were skewed; therefore, we report back-transformed estimates for these measures. We report estimates ± 1 SE unless otherwise noted.

RESULTS

Movements and space use.—We captured 215 individual turtles 607 times between 1983 and 2001, 81 females, 62 males, and 72 juveniles. Number of captures per individual averaged 2.7 ± 0.17 , was similar for females (3.0 ± 0.11) and males (2.8 ± 0.16), and was lower for juveniles (1.6 ± 0.27 ; $F_{2,604} = 29.2$, $P < 0.0001$). Time between successive captures averaged 184 ± 1.1 days and was similar for females (198 ± 1.1), males (174 ± 1.2), and juveniles (147 ± 1.2 ; $F_{2,384} = 0.62$, $P = 0.54$). Distance moved between successive captures did not vary with time between captures for females (slope = 1.1 ± 1.06 m/day, $t_{230} = 1.32$, $P = 0.19$) but increased slightly for juveniles (slope = 1.2 ± 1.13 m/day, $t_{37} = 1.74$, $P = 0.090$) and increased consistently for males (slope = 1.3 ± 1.10 m/day, $t_{114} = 3.32$, $P = 0.002$).

Movement distances (AvD) varied among sex and size classes of turtles ($F_{4,121} = 15.16$, $P < 0.0001$), with males moving farther than females

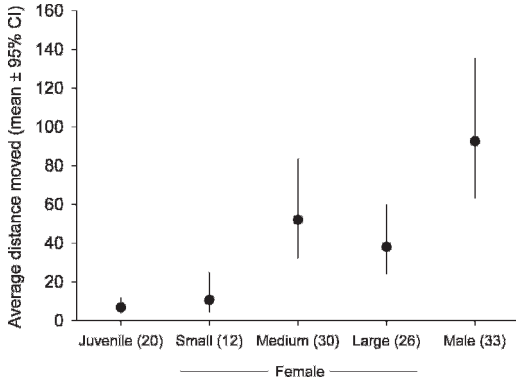


Fig. 2. Movement distances by sex and size class of mud turtles. Numbers in parentheses are the sample sizes of unique turtles used to generate each estimate.

and adults moving farther than juveniles (Fig. 2). Average distance moved did not vary with body size for males ($t_{31} = 0.52, P = 0.61$) or juveniles ($t_{18} = 0.22, P = 0.83$) but varied in a curvilinear way for females (Fig. 3; test for quadratic term: $t_{65} = -2.80, P = 0.0067$). For large females, the relationship between AvD and body size was corroborated by radiotelemetry data; AvD decreased as body size increased for females between 120 and 135 mm CL (slope = -0.13 ± 0.03 m/mm, $t_{17} = -4.23, P = 0.0006$). Average distance moved was shorter during drought than non-drought periods for both sexes, although the effect was larger for males (non-drought = 153 ± 1.2 m, drought = 26 ± 1.3 m, $t_{37} = 5.23, P < 0.0001$) than for females (non-drought = 41 ± 1.2 , drought = 19 ± 1.3 , $t_{77} = 2.25, P = 0.027$).

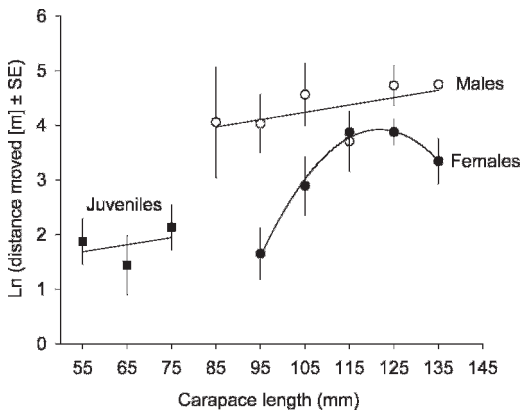


Fig. 3. Relationship between average distance moved and average carapace length for female ($n = 69$), male ($n = 34$), and juvenile ($n = 20$) mud turtles. Y-axis is natural-log transformed.

TABLE 1. ACTIVITY MEASURED AS THE PROPORTION OF TIMES THAT RADIO-MARKED TURTLES MOVED BETWEEN POOLS ON SUCCESSIVE RELOCATIONS. *P*-values from Fisher's Exact Tests comparing activity between sexes.

	Females		Males		<i>P</i>
	<i>n</i>	Proportion	<i>n</i>	Proportion	
May	18	0.16	25	0.38	0.003
June	20	0.12	49	0.19	0.104
July	15	0.12	41	0.19	0.128
August	31	0.23	57	0.26	0.528
September	30	0.22	31	0.42	0.007
October	6	0.23	13	0.30	0.588

Movements of radio-marked turtles between pools separated by dry stream reaches were common for males ($58 \pm 6.9\%$, $n = 266$), less common for medium females ($28 \pm 6.4\%$, $n = 246$), and rare for large females ($9 \pm 5.3\%$, $n = 452$). Although long-distance movements >500 m were rare (4% of 391 recaptures), adult males made these more frequently (8% of 118 recaptures, 2 made by the same male; distances = 500–7,200 m) than adult females (2% of 233 recaptures, 2 made by the same medium female; distances = 669–854 m; $\chi^2 = 3.1, P = 0.01$; Fisher's Exact Test). We observed movements between drainages by male turtles twice. One male (CL = 102 mm) moved 7.2 km as measured along drainage bottoms (2.7 km straight-line distance) from where it was marked one year earlier to the location where it was subsequently captured. Another male (CL = 79 mm) moved 3.1 km as measured along drainage bottoms (2.4 km straight-line distance) from where it was marked three years earlier to the location where it was subsequently captured. Juveniles never moved >500 m (0% of 40).

Home ranges of male turtles (206 ± 2.0 m) averaged more than two times longer than those of medium females (80 ± 1.9 m) and eight times longer than large females (26 ± 2.2 m; $F_{2,27} = 23.2, P < 0.0001$). For females, but not males ($P = 0.76$), home-range length decreased as CL increased (slope = $-0.95 \pm 1.023, t_{17} = -2.19, P = 0.043$). Home-range length of two males was considerably shorter during a drought year (157 ± 1.1 m) compared to a subsequent non-drought year (435 ± 1.3 m). There was no directionality in movements of turtles away from their home pool; the average difference between the number of upstream and downstream movements was nearly zero ($0.25 \pm 0.27, t_{27} = 0.92, P = 0.36$).

Males were always more active than females, especially during May and September (Table 1). Except for males in May, activity of both males

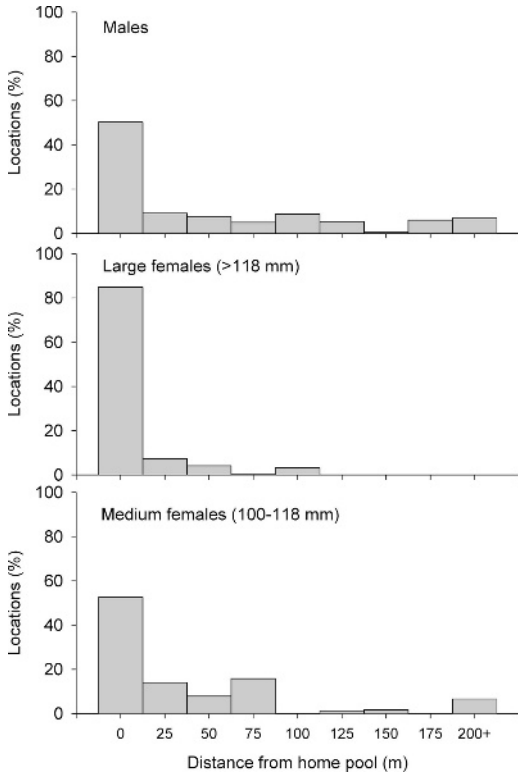


Fig. 4. Distribution of movements measured as the distance from home pool for males, large females, and medium female mud turtles.

and females was highest from August through October following the onset of summer rains. We observed nesting once in July, six times in August, and twice in September. We observed mating three times in June and once in each other month when turtles were active (April through October).

During drought years, turtles estivated terrestrially before the onset of summer rains when canyons were driest. In June and July of drought years, females were found estivating during 45% of telemetry locations ($n = 71$) and males during 55% of locations ($n = 55$). We never observed a turtle estivating in any other month of drought years ($n = 203$) or at any time during non-drought years ($n = 497$). In the 62 instances where we classified a turtle as estivating, 64% of locations were under vegetation, soil, or organic matter, and 36% were in crevices of boulder piles.

Site fidelity and spacing.—Males occupied their home pool only $37 \pm 3.9\%$ of the time (Fig. 4), and fidelity to their home pool varied little with body size (slope = $0.7 \pm 0.62\%$ fidelity/mm, $t_{11} = 1.12$, $P = 0.29$). In contrast, large females

occupied their home pool $74 \pm 6.3\%$ of the time and medium females $47 \pm 8.8\%$ of the time ($t_{18} = -2.95$, $P = 0.009$); fidelity of all females to their home pool increased with body size (slope = $2.2 \pm 0.61\%$ fidelity/mm, $t_{16} = 3.62$, $P = 0.0023$). Males and medium females traveled farther from their home pools than did large females (Fig. 4).

Home ranges of four radio-marked male turtles from a single pool complex overlapped $81 \pm 4.8\%$ in space but did not overlap in time (coefficient of association = 0.04 ± 0.02); their distribution among pools in the complex was not random ($P = 0.004$). Two males occupied the same pool in only 13% of samples ($n = 179$), all of which occurred during two drought events when few pools (4 of 58) held water. This pattern was corroborated with hand-capture sampling of which only 5% ($n = 114$) included two males occupying the same pool at the same time. Males occupied a pool with a medium or large female in 10% ($n = 114$) of hand-capture samples.

The amount of overlap among home ranges of females in the same pool complex varied with body size. Home ranges of six medium females overlapped $40 \pm 5.3\%$ in space and somewhat in time (coefficient of association = 0.12 ± 0.02); their distribution among pools was indistinguishable from random ($P = 0.17$). In contrast, home ranges of four large females did not overlap in either time or space (overlap = 0%, coefficient of association = 0); their distribution among pools was not random ($P < 0.0001$). Although we commonly found two medium females occupying the same pool at the same time (34% of 245) or one large female occupying a pool with a medium female (8% of 426), large females almost never shared a pool with another large female (1% of 181). Similarly, two large females occupied the same pool in $<1\%$ of hand-capture samples ($n = 228$). The frequency with which medium and large female turtles shared pools decreased as the availability of pools increased after the onset of summer rains (slope = -0.23 ± 0.039 turtles/pool, $\chi^2 = 40.8$, $P < 0.0001$; Poisson regression).

Immigration.—Over 48 trap days, we removed 22 turtles from Sabino Lake: 4 juveniles, 1 medium female, 7 large females, and 10 males. We estimated that these 22 turtles comprised the entire resident population (removal estimator in program CAPTURE, White et al., 1982), suggesting that we had removed all resident individuals. During the subsequent 18 months, we captured 15 turtles that had entered the lake: 2 juveniles, 5 medium females, and 8 males. The size distribution of turtles entering the lake after removal of residents was smaller than individuals in the pre-

TABLE 2. AVERAGE DISTANCE MOVED AND HOME-RANGE LENGTH OF TURTLES FROM THE FAMILY KINOSTERNIDAE.

Environment	Species	Sex	Average distance moved (m)	Home-range length (m)
Lentic	<i>Kinosternon flavescens</i> ^a	Female	213	
		Male		
Lentic	<i>K. leucostomum</i> ^b	Female		112.5
		Male		83.3
Lotic	<i>K. sonoriense</i> ^c	Female, 100–118 mm CL	98.1	19.4
		Female, >118 mm CL	57.6	104.1
		Male	127.1	297.7
Lotic	<i>K. subrubrum</i> ^a	Female	61.9	
		Male	52.1	
Lotic	<i>Sternotherus depressus</i> ^d	Female	19.2	87.0
		Male	31.2	88.8
Lotic	<i>S. carinatus</i> ^a	Female	17.4	
		Male	38.6	
Lotic	<i>S. odoratus</i> ^a	Female	44.5	

^a Mahmoud, 1969.

^b Morales-Verdeja and Vogt, 1997.

^c This study; we report arithmetic means here for consistency with other studies.

^d Dodd et al., 1988.

removal population ($\chi^2 = 11.9$, $P = 0.001$; Fisher's Exact Test) primarily because no large females entered the lake after removal. None of the immigrants was ever recaptured, suggesting they did not establish residency.

DISCUSSION

Movements of Sonoran Mud Turtles can be viewed hierarchically at four spatial scales: within a pool, between pools in a complex, between complexes, and between drainages. The majority of movements by turtles in our study areas were within a single pool or complex, with occasional movements between complexes and only rare movements between drainages. This pattern reflected low availability of surface water during much of the year in the arid environment we studied, where turtles were often restricted to perennial pools separated by dry reaches of stream bed. Even when surface water was continuous between pools, however, pools remained the center of almost all activities by turtles, especially for juveniles and older females that restricted their activities to a single pool or pool complex. In contrast, juvenile turtles in mesic environments move readily throughout systems of continuous streams, routinely traveling distances over 1 km (Moll and Legler, 1971; MacCulloch and Secoy, 1983; Pluto and Bellis, 1988). In environments where water is scarce, the number of terrestrial movements by turtles should be relatively high as turtles may need to move to ephemeral pools when they become available and to more permanent pools or to estivation sites when ephemeral pools dry (Stone, 2001).

Home-range length and movement distances for female Sonoran Mud Turtles are among the longest reported within the Kinosternidae (Table 2). Movements and distribution of female turtles among pools changed with their life stage. Younger, recently mature females moved longer distances and had longer home ranges than did older females, especially in drought years when distances moved by older females were much shorter than in non-drought years. Younger females also were distributed among pools within a complex in a pattern that was effectively random whereas older females were distributed uniformly because they did not share pools with other older females. Only younger females entered a pool where all residents had been removed, further indicating that younger females moved farther and more frequently than older females. Lastly, unmarked turtles captured at sites where all residents had been marked were either juveniles <55 mm CL that hatched locally or were young females and males that had likely immigrated into the area. These patterns all suggest that young mature females were highly mobile and had not yet established residency at this stage in their life history.

Male Sonoran Mud Turtles had the longest home ranges and second longest movement distances reported for the family Kinosternidae (Table 2). Movements by males are likely influenced by mating opportunities, thus spacing of females likely affected movement patterns of males. Because large females were relatively sedentary and widely spaced compared to mud turtles in regions with more perennial water, males likely moved farther to increase encoun-

ters with females and mating opportunities. Male turtles may restrict their movements to areas that support concentrations of females during the mating season (Obbard and Brooks, 1981; Bodie and Semlitsch, 2000; Litzgus and Mousseau, 2004).

Movements of turtles increased with the onset of sexual maturity. Unlike females, however, movement distances of males did not change as they increased in size. Pond Sliders (*Trachemys scripta*) in a lentic environment also traveled longer distances after becoming sexually mature (Moll and Legler, 1971). Movements of male turtles during non-drought years averaged six times longer and were more frequent between pools than during drought years. In contrast to females, males often moved among pools within a complex. Males also occasionally moved across dry stream reaches that separated pool complexes; we observed 23% of males with CL >110 mm occupy a single pool complex for 3 to 10 years then move to another pool complex 0.15 to 1.5 km from their original complex.

Although activities of all turtles were centered on a single pool, fidelity to this pool was strongest in females, especially for large females. One large female, for example, occupied the same home range for 19 years and was almost always captured in the same pool (35 of 36 captures, 97%). Movements of large females away from home pools occurred only to abandon a drying pool or to move to an estivation or nesting site. Once nesting activity was completed or a drought ended, females returned to their home pool. Terrestrial movements away from drying environments has been documented in Sonoran Mud Turtles (Stone, 2001) and in other kinosternids (Wygoda, 1979; Gibbons et al., 1983; Morales-Verdeja and Vogt, 1997).

All turtles were consistently more active after the onset of summer rains when surface water increased and facilitated movements by turtles through wetted reaches. This period of increased activity also coincided with nesting. Male mud turtles were more active than females early in the year, perhaps because males were actively seeking mates as observed for other freshwater turtles (Morreale et al., 1984). Males also remained active during nesting, which contrasts with other turtles where males were less active than females during nesting (Morreale et al., 1984; Gibbons, 1986; Doody et al., 2002).

Simultaneous occupancy of a pool by two males or two older females was rare except during drought when water was extremely limited. This pattern may be maintained through some form of agonistic behavior as reported occasionally for other turtles. For example, male

Wood Turtles (*Clemmys insculpta*) form dominance hierarchies over access to mates (Kaufmann, 1992). Despite this dominance behavior, male Wood Turtles of all ranks moved freely throughout the population. In contrast, male and large female Sonoran Mud Turtles maintained nearly exclusive use of pools, suggesting they may be territorial as postulated by Emslie (1982). Territorial behavior may be more likely to manifest in the environment we studied relative to others inhabited by mud turtles because pools are small and discrete, making it possible for adults to defend these limited resources.

As in other populations inhabiting areas with intermittent water (Lignon and Stone, 2003), turtles in the population we studied estivated in years of extreme drought when their home pools dried. Although Sonoran Mud Turtles may prefer environments with permanent water that requires fewer terrestrial movements and allows them to avoid estivation, they readily inhabit areas that periodically dry. Like most kinosternids, they can tolerate water deprivation for extended periods (Stone, 2001). The extent to which Sonoran Mud Turtles tolerate drought varies considerably among populations, however, from <30 days in a population from southern Arizona (Lignon and Peterson, 2002) to >80 days in a population from New Mexico near the eastern extent of the species' geographic range (Peterson and Stone, 2000). This regional difference in drought tolerance reflects regional differences in water availability that may drive different selection regimes for behavioral and physiological adaptations to drought (Lignon and Peterson, 2002). The selection regime for Arizona turtles may have intensified recently because the wetlands they inhabit have diminished to 10% of their former size, principally from activities associated with urbanization and agriculture (Laney, 1991; Tellman and Shaw, 1991). Although Sonoran Mud Turtles readily inhabit impoundments, these may not be ideal environments because they are often inhabited by nonnative species such as American Bullfrogs (*Rana catesbeiana*) and crayfish (Astacidae) that may be detrimental to turtle populations (van Loben Sels et al., 1997; Schwendiman, 2001) and because these small impoundments require periodic dredging that can kill turtles (DHH, unpubl. data).

A conservation challenge for this and other aquatic species in this region is to maintain habitat connectivity at the largest scales. Historically, the interrupted streams we studied flowed into perennial streams and wetland complexes that almost certainly supported the vast majority

of turtles and other aquatic species in the region. These persistent wetlands once linked what are now isolated pools in mountain canyons. Because these former wetland complexes no longer hold permanent water, perennial pools in mountain canyons have become increasingly important as habitat for turtles and other aquatic species. Because these remnant habitat patches are small and isolated, their inhabitants are increasingly vulnerable to impacts from human activities and stochastic events. Any force that reduces the number of perennial pools or the duration of seasonal surface water will reduce the potential for movements of individuals within populations. Therefore, large-scale conservation strategies for mud turtles and other aquatic species must address restoration of perennial, lowland wetland complexes, which provide a source of colonizers after local extinctions and facilitate movements and gene flow among populations.

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