
CONSERVATION IMPLICATIONS OF MALE-BIASED MOVEMENTS IN SONORAN MUD TURTLES (*KINOSTERNON SONORIENSE*) INHABITING INTERMITTENT AQUATIC HABITATS

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Abstract.—Defining core areas for conservation of semi-aquatic species requires data on habitat requirements and space use. Many freshwater turtles use multiple bodies of water and intervening terrestrial habitat, and there are often sex differences within populations. We use 19 years of mark-recapture data from Sonoran Mud Turtles (*Kinosternon sonoriense*) to evaluate core area requirements and examine intersexual differences in movements. Our study area was in the Peloncillo Mountains of southwestern New Mexico, USA, a complex desert landscape characterized by variable hydroperiods. The primary study canyon included an intermittent impoundment and 3.75 km of canyon bed where ephemeral pools formed during wet periods. Linear home ranges in the primary study canyon were over twice as long for males than females, and males were over five times more likely to undergo long-distance movements outside the primary study canyon. Apparent mortality was nearly three times greater for males, indicating that many males were transients. Catchability was low and did not differ between sexes. Both sexes underwent seasonal migrations corresponding to water availability in canyon pools. Core areas for conservation of Sonoran Mud Turtles should include impoundments connected to extensive runs of canyon pools. A core area that included the primary study canyon would encompass the known movements of 88% of the adults we encountered. To encompass 100% of known movements, maintaining connectivity of aquatic habitats on a range-wide scale is needed. In particular, likely dispersal pathways along drainages and over low points along ridges should be included in core areas.

Key Words.—apparent mortality; catchability; core area conservation; long-distance movements; seasonal migrations

INTRODUCTION

Terrestrial movements by semi-aquatic organisms have a variety of functions that are important to individual fitness and population viability. For example, freshwater turtles often migrate between seasonally flooded wetlands and more permanent aquatic habitats (Wygoda 1979; Kennett and Georges 1990; Rödel 1999; Stone 2001; Congdon et al. 2011), sometimes with a positive effect on growth and reproduction (Kennett and Georges 1990). Movement among water bodies promotes gene flow among populations (Shoemaker and Gibbs 2013) and disrupting these movements can adversely affect population structure, population density, and sex ratio (Gibbs and Shriver 2002; Marchand and Litvaitis 2004; Aresco 2005). Successful conservation of semi-aquatic species requires protection of core areas that often include multiple bodies of water and intervening expanses of land (Semlitsch and Bodie 1998; Foster and Soluk 2006; Congdon et al. 2011). Data on space use are needed to define core areas and understand differences in habitat requirements among age and sex classes. In particular, sex differences in terrestrial

movements are common in semi-aquatic organisms and must be considered in conservation plans (Foster and Soluk 2006).

Among freshwater turtles, males often move more frequently and over greater distances than females (Morreale et al. 1984; Tuberville et al. 1996; Chelazzi et al. 2007; Hall and Steidl 2007). Male-biased movements have been explained using a cost-benefit argument where mate-limited males disperse in search of females despite costs including increased energy expenditure and increased predation risk (Morreale et al. 1984). Conversely, resource-limited females often aggregate in areas with dense resources (Morreale et al. 1984), but have their own movement challenges associated with nesting.

Sonoran Mud Turtles, *Kinosternon sonoriense*, occur in aquatic habitats ranging from permanent springs to intermittent pools (Hulse 1974; van Loben Sels et al. 1997; Stone 2001; Hall and Steidl 2007; Hensley et al. 2010). In permanent aquatic habitats, turtles have poorly developed desiccation tolerance (Ligon and Peterson 2002) and are not known to engage in terrestrial activity other than nesting (Hulse 1974; Emslie 1982; Rosen

1987). In contrast, Sonoran Mud Turtles in intermittent aquatic habitats use terrestrial habitat in various contexts (van Loben Sels et al. 1997; Stone 2001; Hall and Steidl 2007; Hensley et al. 2010; Stone et al. 2011). Turtles aestivate on land during drought (Ligon and Stone 2003; Hall and Steidl 2007) and have the physiological capacity to withstand long periods without water (Peterson and Stone 2000; Ligon and Peterson 2002). Individuals routinely move long distances across land within and between drainages (Ligon and Stone 2003; Hall and Steidl 2007; Hensley et al. 2010), including seasonal migrations between intermittent impoundments and ephemeral canyon pools (Stone 2001). Documentation of populations in intermittent aquatic habitat contributed to the recent uplisting of Sonoran Mud Turtles on the IUCN Red List from Vulnerable to Near Threatened (IUCN. 2013. Available from <http://www.iucnredlist.org> [Accessed 12 April 2014]). However, little is known about intersexual or interpopulational variation in terrestrial habitat use in these populations, and we lack sufficient data to define core areas in intermittent aquatic habitats. Conserving populations that use intermittent aquatic habitats will require incorporation of terrestrial habitat and ephemeral wetlands into conservation plans, and it will be impossible to do this without a better understanding of mud turtle movements.

From 1994 to 2012, we collected data on movements of Sonoran Mud Turtles from aquatic habitats in the Peloncillo Mountains, New Mexico, USA (Stone 2001; Ligon and Stone 2003). The aquatic habitats vary in hydroperiods, and even the most persistent dry completely on occasion (Stone 2001; Ligon and Stone 2003). Our data provide an opportunity to elucidate core area requirements and explore sex differences in movements of turtles inhabiting intermittent aquatic habitats. Under the hypothesis that movements by Sonoran Mud turtles are male-biased, we predict that males will: (1) make longer movements within a drainage; (2) make more frequent seasonal migrations; (3) have lower recapture probabilities; (4) have higher apparent mortality rates, and; (5) make more frequent movements among drainages than females.

MATERIALS AND METHODS

Study area.—The Peloncillo Mountains are a north-south oriented range (110 × 20 km) along the southern border of New Mexico and Arizona, USA. The Peloncillo Mountains are near the eastern edge of the Madrean Sky Islands, a cluster of about 40 small, isolated ranges that connect the much larger ranges of the Mogollon Rim to the north and Sierra Madre Occidental to the south (Warshall 1995). Climate in the region is typical of the Chihuahuan Desert, with a distinct dry season (April-June) and wet season (July-

September), variable winter precipitation, high annual variation in precipitation, and frequent drought (Neilson 1986; Moir et al. 2000; Bodner et al. 2003).

We collected the majority of data from Blackwater Canyon, a 3.75 km canyon with an elevational gradient of about 50 m (Fig. 1A). During 1994–2012, Blackwater Canyon dried completely at least six times and became a flowing stream about 10 m wide for brief periods in most years. During dry seasons, 15 canyon pools were most persistent (Ligon and Stone 2003), and total surface area of canyon pools ranged from 0–375 m² (Stone 2001; Stone et al. 2011). During wet seasons, many more pools formed and total pool surface area increased approximately 10-fold (Stone 2001; Stone et al. 2011). A concrete dam constructed 0.75 km from the top of the Blackwater Canyon formed Blackwater Hole, the largest and most persistent body of water in the canyon (maximum surface area = 375 m², maximum depth = 2 m, 1,700 m elevation; Fig. 1A). During dry seasons Blackwater Hole was completely dry during at least seven years from 1994–2012, and reduced to a puddle ≤ 10 m² during three other years. During wet seasons Blackwater Hole was full during at least 13 years from 1994–2012.

We gradually expanded the areas sampled to include 25 additional sites within a 200 km² area (Stanila 2009). The new sites included four reaches of canyon pools and two impoundments in Clanton Draw, the drainage that includes Blackwater Canyon (Fig. 1A). We also sampled 19 sites including impoundments and canyon reaches in three adjacent drainages (Stanila 2009, Fig. 1B). Drainages were separated by terrestrial habitat that included mountain ridges that required turtles to make long, steep movements between drainages. Because our use of capture data from outside Blackwater Canyon is limited to long-distance movements (see below), we avoid a detailed description of the other sites here, but instead refer readers to Stanila (2009).

Data collection.—We captured turtles using baited hoop nets set overnight in impoundments with water deeper than about 0.5 m and by hand in shallower pools (Stone 2001; Stone et al. 2011). Once captured, turtles were processed immediately and released at the site of capture. We marked turtles with a unique series of notches in the marginal scutes, measured midline carapace length (MCL) to the nearest mm with dial calipers, and determined sex based on sexually dimorphic traits and body size (MCL < 86 mm was considered juvenile unless obviously male; Stone 2001).

During 1994–2012 we sampled Blackwater Canyon (Stone 2001; Stone et al. 2011). In most years we took two sampling trips of 1–2 weeks each, one during May (dry season) and one during August (wet season). In 1999 and 2007, we camped in the study area for 2.5 and

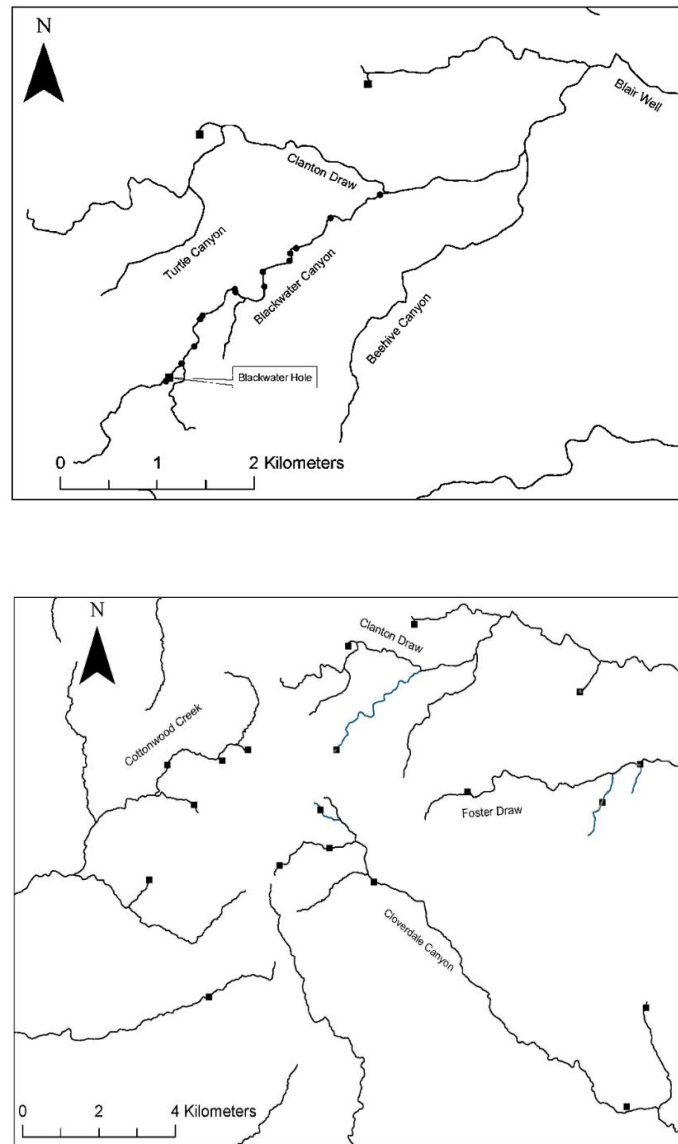


FIGURE 1. Map of study area. Top) Map of Clanton Draw, New Mexico, USA. Closed circles are the most persistent pools in Blackwater Canyon. Closed squares are impoundments where we sampled with hoop nets. Labeled canyons are areas where we hand sampled canyon pools. Bottom) Map of the study area. Closed squares indicate sampled impoundments.

3.5 months, respectively, and sampled more intensively. Except for seven trips when water levels were exceptionally high, we sampled all canyon pools in Blackwater Canyon on each trip. During the study, we sampled approximately 128 km of canyon bed in Blackwater Canyon. We set hoop nets in Blackwater Hole whenever water levels permitted, for a total of 242 trap nights.

Compared to Blackwater Canyon, we sampled less consistently in Clanton Draw and the other drainages. We hand sampled 12 canyon reaches outside Blackwater

Canyon. With multiple samples from many of these reaches, the total distance hand sampled outside of Blackwater Canyon was approximately 165 km. In addition, we trapped in 18 impoundments other than Blackwater Hole a total of 787 trap nights. Most sampling outside of Blackwater Canyon occurred after 2006.

We mapped Blackwater Canyon in 1996 using a compass and measuring tape, painting numbered points at 50 m intervals on prominent rocks in the canyon (Stone 2001). The map was subsequently ground-

truthed using topographic maps and later confirmed using global positioning system (GPS) units (E-trex Vista C, Garmin, Olathe, Kansas, USA). Prior to 2007, trapping was restricted to Blackwater Canyon and impoundments that were evident from topographic maps, and we recorded capture locations relative to mapped points. In 2007, we expanded trapping in canyons surrounding Blackwater Canyon and began using GPS units to collect locality data. Regardless of collection method, all locality data were georeferenced as x-y coordinates (UTM Zone 12N) so that movements of individuals could be calculated using Euclidean distance.

Prior to analyses, we edited the data in several ways. Any individual that remained a juvenile throughout the study was eliminated from the data set. All captures of individuals that became adults during the study were included in the analyses. For turtles that were recovered dead during the study, we discarded the location of the carcass because it could have been moved by high water, predators, or scavengers. For turtles that were captured more than once during a 1–2 week sampling trip, we only used the location of the first capture. For turtles caught more than once during the extended trips to the study area in 1999 and 2007, we only included pairs of locations that were at least six days apart. Because of the richness of capture histories and the consistency of sampling, we restricted analyses of small-scale movements to turtles with all captures in Blackwater Canyon; whereas, analysis of long-distance movements included data from all sites.

We also evaluated the potential correlation between sample size and distance moved in the Blackwater Canyon population. In many systems, there is a positive correlation between sample size and distance moved and it is necessary to estimate the minimum sample size at which this correlation disappears and then eliminate animals with fewer samples than the minimum (Rose 1982). We used linear regression to evaluate the effect of sample size on distance moved.

Movements within Blackwater Canyon.—For each individual, we calculated linear home range and average distance moved. Linear home range was the greatest straight-line distance between any two locations of an individual, a conservative measurement with no assumptions about how much tortuosity occurred during movement. Average distance moved was the average of straight-line distances between chronological pairs of locations. Using both metrics facilitated comparison with other studies and included both average and maximum distances moved for each turtle. Because the data were not normally distributed, we used Wilcoxon rank sum tests with continuity correction to evaluate the prediction that males in Blackwater Canyon had longer linear home ranges and greater average distances moved

than females. For this and all subsequent analyses, $\alpha = 0.05$.

Seasonal movements.—We also tested the prediction that seasonal movements between Blackwater Hole and canyon pools were male-biased by further editing the data set to include only individuals that were captured on consecutive May–August or August–May sampling occasions. We expected turtles captured in May–August to move from Blackwater Hole to canyon pools, whereas turtles captured in August–May were expected to move from canyon pools to Blackwater Hole. We used mixed-effects logistic regression (glmer in R package lme4 fit with adaptive Gauss-Hermite quadrature) to predict the binary response variable that indicated whether or not an individual turtle had moved (with fixed effects indicated in Table 2). To account for repeated measurements of some individuals within the data set, we modeled individuals as random effects. We used this analysis to ask whether turtle movements between Blackwater Hole and canyon pools were predictable based on the fixed effects sex, season, site, or interactions among these factors (Bates et al. 2015). The seasonal migrations described by Stone (2001) would be confirmed with a larger sample size if a significant interaction between season and site occurred, whereas a significant sex effect would indicate sex-biased movements.

Apparent mortality and catchability.—We used a Cormack-Jolly-Seber (CJS) model with maximum likelihood estimation (using “optim” in R for maximization) to estimate per sampling occasion probability of capture conditional on presence (catchability) and constant per day probability of disappearance (apparent mortality rate) for turtles captured in Blackwater Canyon during 32 sampling occasions distributed between dry season ($n = 15$ sampling occasions) and wet season ($n = 17$) samples (R Core Team 2015). We used a two-parameter model to estimate catchability and apparent mortality for males, females, and both sexes combined. We estimated confidence intervals for parameter estimates (in the CJS model) by computing the parameter values that reduced the log-likelihood by 2.0 in either direction (Edwards 1972; Hilborn and Mangel 1997). We hypothesized that the predicted differences in space use by males and females would lead to increased apparent mortality in males because males were more likely than females to permanently emigrate, and decreased catchability in males because males were more likely to temporarily emigrate. Because of marked seasonal differences in water levels, we also used a three-parameter model to estimate seasonal variability in catchability with a single value for apparent mortality for males, females, and both sexes combined.

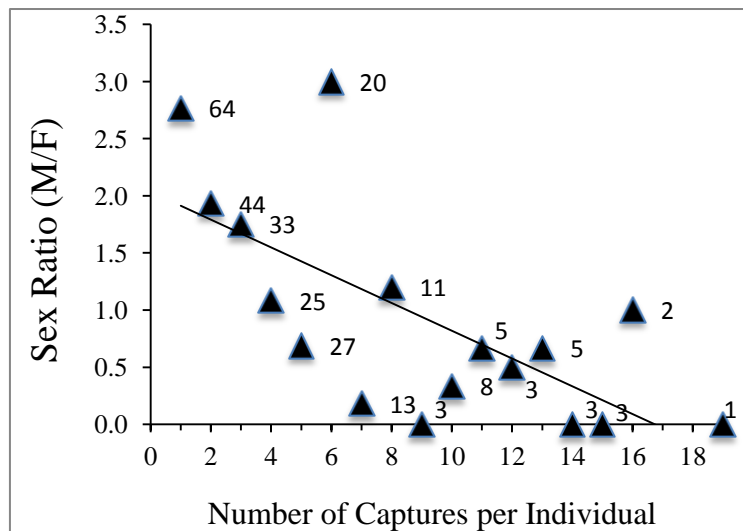


FIGURE 2. Sex ratio vs. number of captures for Sonoran Mud Turtles (*Kinosternon sonoriense*) in Blackwater Canyon, New Mexico, USA. Symbols indicate sex ratio of turtles with a specific number of total captures. Numbers beside symbols are number of individuals (males and females combined) in x-axis categories.

Long-distance movements.—We identified long-distance movements as movements from Blackwater Canyon to another part of Clanton Draw or movements between two drainages. Movements within Clanton Draw could be accomplished without leaving the canyon bed whereas movements between drainages involved steep climbs over mountain ridges. For movements within Clanton Draw, we included all adults with at least one capture in Blackwater Canyon and one capture in another part of Clanton Draw. For each movement, we used the Ruler and Elevation Profile tools in Google Earth (Google Inc., Mountain View, California, USA) to measure distance moved and total elevation change for two paths that best represented the trade-off between distance and elevation: a straight-line path between the two capture locations that define the long-distance movement (minimum distance path); and a curved path that followed the Clanton Draw drainage between these capture locations (minimum elevation path). For movements among drainages, we included all instances of adults moving between drainages, even if there were no captures within Blackwater Canyon. For each movement, we calculated the straight-line distance moved and the total elevation change over that distance. Curved paths for movements among drainages were not quantified because they were less obvious and alternative paths more numerous. To evaluate the prediction that males were more likely than females to make long-distance movements, we combined both types of long-distance movement and used a one-tailed binomial test. No turtle was included in both the

‘movements within Blackwater Canyon’ and ‘long-distance movements’ analyses.

RESULTS

During 1994–2012, we recorded 1,712 captures of 692 individuals in Blackwater Canyon and 291 (42.1%) were adults at last capture. Of 1,180 captures of adults that exclusively used Blackwater Canyon, 672 captures (57%) were from Blackwater Hole. Males outnumbered females in Blackwater Canyon ($m/f = 170/121 = 1.40$, $X^2 = 8.25$, $df = 1$, $P = 0.004$). However, many males were captured only once, and others emigrated from Blackwater Canyon, so that as the number of captures per individual increased there were relatively fewer males in each category (Fig. 2). Among individuals with two or more captures and all captures within Blackwater Canyon, the sex ratio did not differ from unity ($m/f = 105/101 = 1.04$, $X^2 = 0.078$, $df = 1$, $P = 0.780$). Among all adults, the modal number of captures was one, and the maximum number of captures was 19. Home range length did not increase with number of captures per individual ($r^2 = 0.001$, $F_{1,204} = 0.270$, $P = 0.604$, Fig. 3). Indeed, the trend was opposite the prediction: the largest home ranges were observed in turtles with few captures (Fig. 3). Therefore we included all turtles with two or more captures in further analyses.

Movements within Blackwater Canyon.—As predicted, males had longer linear home ranges ($W = 6430$, $P = 0.004$) and greater average distances moved ($W = 6572$, $P = 0.001$) than females (Fig. 4). By either

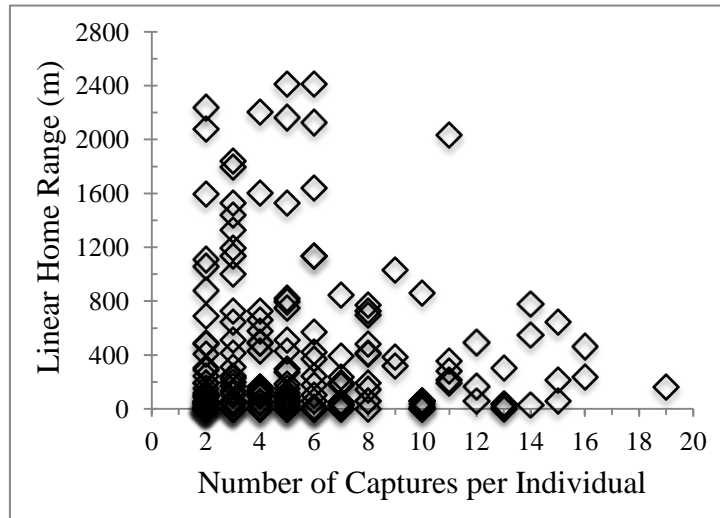


FIGURE 3. Linear home range length vs. number of captures for Sonoran Mud Turtles (*Kinosternon sonoriense*) from Blackwater Canyon, New Mexico, USA.

metric, males moved more than twice as far as females (Fig. 4). About half of all turtles with two or more captures used

both Blackwater Hole and canyon pools, whereas the other half were equally distributed, either exclusively captured in Blackwater Hole or exclusively captured in canyon pools, with no obvious sex differences in pool or impoundment occupancy (Table 1).

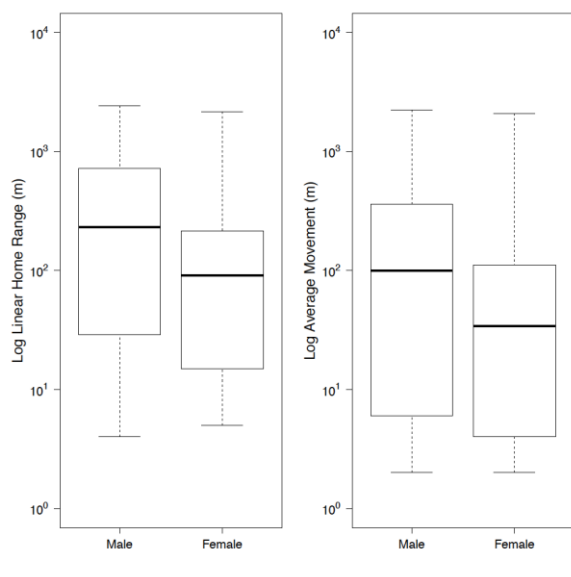


FIGURE 4. Linear home range length and average movement distances for male and female Sonoran Mud Turtles (*Kinosternon sonoriense*) from Blackwater Canyon, New Mexico, USA. Thick lines indicate medians, box edges indicate upper and lower quartiles, and brackets defined by dashed lines indicate ranges. The Y-axis was \log_{10} transformed to enhance viewing.

Seasonal movements.—Turtle movements showed the same seasonal pattern described from a smaller data set by Stone (2001). Turtles migrated from Blackwater Hole downstream to canyon pools during the monsoon season and returned from canyon pools to Blackwater Hole during the dry season. This pattern is evident from the significant site by season interaction ($Z = 2.448$, $P = 0.014$) in the mixed-effects logistic regression analysis (Table 2) combined with the predictable directionality of movements between Blackwater Hole and canyon pools (Fig. 5). Contrary to the prediction, seasonal migrations were not sex-biased ($Z = 1.092$, $P = 0.275$), nor were any other factors in the model significant (Table 2). Movement probabilities indicated that during the wet season, turtles of both sexes were nearly ten times more likely to have moved in the predicted direction than in the opposite direction (Fig. 5). This pattern was not as pronounced during the dry season, particularly for males (Fig. 5), leading to the marginally significant season effect in the model (Table 2).

Apparent mortality and probability of recapture.—As predicted, apparent mortality was almost three times higher for males than females (Table 3). Using apparent mortality rates, the average tenure of an adult male in the study area was estimated at 7.8 y, compared to 20.6 y for study area was estimated at 7.8 y, compared to 20.6 y for an adult female. However, contrary to the prediction, catchability did not vary between sexes (Table 3). The combined catchability for males and females of 0.25 (Table 3) suggests it would take two years to encounter the average turtle, assuming two sampling trips to the study area per year. The three-parameter model that allowed for seasonal variability in catchability offered no

TABLE 2. Mixed-effects logistic regression estimates of the Sonoran Mud Turtle (*Kinosternon sonoriense*) in New Mexico, USA. Estimates are log odds-ratios. Intercept is the log-odds ratio for the probability that a male captured in Blackwater Hole in the dry season was captured in a canyon pool during the previous wet season. Subsequent factors show the effect of manipulating these default conditions in the indicated way. An asterisk (*) indicates significance.

Factor	Estimate	S.E.	Z Value	P
Intercept	-1.092	0.534	-2.045	0.041*
Sex (female)	0.765	0.700	1.092	0.275
Site (pool)	-0.270	0.882	-0.306	0.760
Season (wet)	-1.562	0.822	-1.899	0.058
Sex:Site	-1.794	1.629	-1.101	0.271
Sex:Season	-0.754	1.115	-0.677	0.499
Site:Season	3.145	1.285	2.448	0.014*
Sex:Site:Season	2.559	2.010	1.273	0.203

improvement over the two-parameter model, suggesting no seasonal differences in catchability. Despite the added parameter, log-likelihoods for the two models were nearly identical and confidence intervals overlapped greatly.

Long-distance movements.—As predicted, males ($n = 24$) were more likely than females ($n = 5$) to undergo long-distance movements (one-tailed binomial test, $P < 0.001$). Eight turtles (six males, two females) were captured in both Blackwater Canyon and another part of Clanton Draw. Straight-line paths for these moves were 2.5 times shorter but involved 1.7 times greater changes in elevation than paths along drainage bottoms (Table 4). Another 21 turtles (18 males, three females) changed drainages during the study, including two movements by males that exceeded 7 km and crossed the main pass in the Peloncillos, from east-flowing to west-flowing drainages. Straight-line distances and elevation changes for these movements were nearly twice as large as straight-line paths in Clanton Draw (Table 4).

DISCUSSION

Movements of adult Sonoran Mud Turtles in our study were consistent with the pattern observed in many species: greater movements of males compared to females. Males moved on average over twice as far as females within Blackwater Canyon, males were five times more likely to move among drainages than females, and apparent mortality in males was nearly three times higher than in females. Hall and Steidl (2007) also reported male-biased movements in Sonoran Mud Turtles from the Santa Catalina Mountains, another range in the Madrean Sky Islands. However, two other

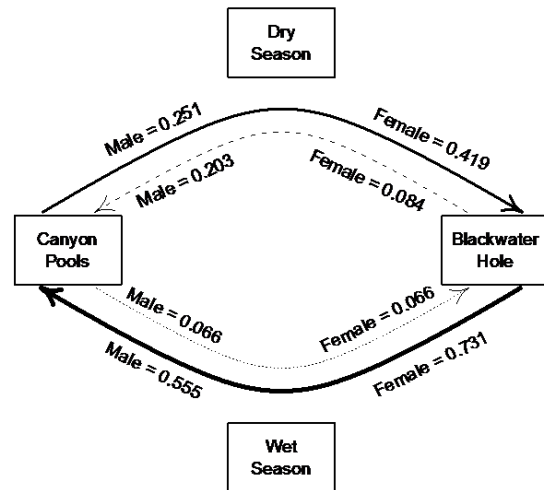


FIGURE 5. Movement probabilities computed from General Linear Mixed Model estimates given in Table 3 for Sonoran Mud Turtles (*Kinosternon sonoriense*) from Blackwater Canyon, New Mexico, USA. Each value printed on an arrow gives the predicted probability that a given turtle (male or female) captured at a particular site during the indicated season had moved to the new site from the alternate site in the previous season. For example, we predict a 73% chance that a female captured in 'Canyon Pools' during Wet Season sampling had moved from Blackwater Hole (where she was captured during the previous Dry Season sampling). Solid arrows indicated expected movements in line with the hypothesis, while dashed lines indicated unexpected movements that are counter to the hypothesis. The line thickness roughly corresponds to the magnitude of predicted probabilities (thinnest line, which illustrates probabilities of 0.066 each, up to the thickest line, which illustrates probabilities of 0.555–0.731).

studies of Sonoran Mud Turtle movements reported trends of female bias in movement distances (Emslie 1982; Hensley et al. 2010). Variation among populations in relative movement rates of males and females has also been reported for Sliders, *Trachemys scripta* (Morreale et al. 1984; Parker 1984; Rose and Manning 1996; Bodie and Semlitsch 2000), Painted Turtles, *Chrysemys picta* (Sexton 1959; Gibbons 1968; MacCulloch and Secoy 1983; Tuberville et al. 1996; House et al. 2010), and box turtles, *Terrapene* spp. (reviewed by Bernstein et al. 2007). In each case there were no obvious environmental correlates, such as elevation or habitat permanence, to explain the differences among populations.

Movements within Blackwater Canyon.—Blackwater Hole was the focal point for turtle activity in Blackwater Canyon. Almost 57% of all captures were from Blackwater Hole, and 75% of turtles were captured there at least once. High capture success at other impoundments in our study area (Stanila 2009) and elsewhere in the Madrean Sky Islands (van Loben Sels et al. 1997) provide further evidence of the importance of

TABLE 3. Estimates for per sampling occasion probability of capture conditional on presence (catchability) and constant per day probability of disappearance (apparent mortality rate) of the Sonoran Mud Turtle (*Kinosternon sonoriense*) in New Mexico. Confidence limits (lower, upper) are given below each parameter estimate. The log-likelihood values ($\log(L)$) for the estimated parameters are given for each model below the column heading.

	Male $\log(L) = -1075.973$	Females $\log(L) = -1293.561$	Combined $\log(L) = -2386.589$
Apparent Mortality	0.000351 (0.000309, 0.000437)	0.000133 (0.000057, 0.00021)	0.000232 (0.000184, 0.000276)
Catchability	0.246179 (0.222399, 0.271111)	0.251242 (0.231476, 0.272377)	0.249062 (0.233587, 0.265056)

impoundments as turtle habitat. However, many impoundments in our study area are failing due to siltation or dam failures (Stone et al. 2014). Maintenance and restoration of existing impoundments should therefore be a priority for Sonoran Mud Turtle conservation (Riedle et al. 2012; Stone et al. 2014). Given the precarious status of impoundments in our study area, the recent uplisting of Sonoran Mud Turtles on the IUCN Red List (IUCN. 2013. *op cit.*), based in large part on the discovery of populations in intermittent aquatic habitats, seems premature at best.

Despite the importance of Blackwater Hole, a core area that only included Blackwater Hole would encompass the known home ranges of just 23% of the adults captured in Blackwater Canyon. Over 77% of turtles were captured at least once in canyon pools, and 25% were captured exclusively there. A core area that included all of Blackwater Canyon would include 88% of known home ranges. All major concentrations of turtles we have documented in the study area are associated with impoundments that are proximate to extensive runs of canyon pools (Stanila 2009). Maintaining connectivity between impoundments and canyon pools is therefore important, and any management activities that enhance this connectivity or increase hydroperiod of pools should benefit turtles.

In addition to core area requirements described above, Sonoran Mud Turtles use terrestrial habitat for estivation and nesting, activities that should be considered in conservation plans. Based on small samples, terrestrial estivation sites were within 79 m of canyon beds (Ligon and Stone 2003); whereas, nesting sites were within 52 m of canyon beds (Hollelt 2002). While more data are needed on both types of activity, if we assume these small samples are representative, protection of terrestrial habitat in a 100 m zone on either side of canyon beds, particularly those located near impoundments, should accommodate the majority of individuals engaged in terrestrial estivation or nesting. Within the protection zone, management activities such as controlled burning or removal of invasive shrubs should be avoided during dry periods, typically May and June, when large numbers of aestivating turtles will likely be encountered (Ligon and Stone 2003). Likewise, management

activities should be minimized during wet periods in July and August when most nesting activity occurs (van Loben Sels et al. 1997).

Seasonal movements.—Males and females used Blackwater Hole and canyon pools at similar frequencies, and also responded similarly to seasonal changes in water availability. Seasonal movements between Blackwater Hole and canyon pools increased the length of home ranges in both sexes. The pattern of seasonal movements was consistent with that described from a smaller sample by Stone (2001). After ephemeral pools filled during the wet season, turtles dispersed into pools from Blackwater Hole. As ephemeral pools evaporated during the dry season, turtles returned to Blackwater Hole. Other studies have shown a similar pattern of turtles moving into seasonal wetlands when those habitats became available (Wygoda 1979; Kennett and Georges 1990; Chelazzi et al. 2007; Luiselli et al. 2011). Such movements are likely associated with exploiting periodically abundant resources in seasonal wetlands (Kennett and Georges 1990; Rödel 1999). Tadpoles of Canyon Treefrogs (*Hyla arenicolor*) and Red-spotted Toads (*Bufo punctatus*) are abundant during the wet season in ephemeral pools in our study area, and in other systems mud turtles are known to undergo seasonal movements to ephemeral pools to feed on tadpoles (Newman 1987). Opportunities to feed on tadpoles could motivate seasonal movements of Sonoran Mud Turtles from Blackwater Hole to canyon pools.

Apparent mortality and probability of recapture.—The large number of rarely captured animals contributed to the high apparent mortality, particularly in males, revealed by the Cormack-Jolly-Seber model. We interpret the high apparent mortality in males as evidence of a greater frequency of emigration in males, rather than evidence of a greater rate of actual mortality, based on the observed movement data and the pattern of recovery of dead turtles. We routinely find shells of dead turtles in our study area. However, turtles recovered dead are typically juveniles (Stone 2001) and there is no obvious sex bias in the adult shells we have recovered. If actual mortality rates were nearly three

TABLE 4. Comparison of straight-line and curved distances travelled and total elevation changes (mean \pm SE, range in parentheses) for long-distance movements of Sonoran Mud (*Kinosternon sonoriense*) in Clanton Draw and among drainages in New Mexico.

Site	Straight-Line Distance (m)	Curved Distance (m)	Straight Elevation	Curved Elevation
Clanton Draw	1,783 \pm 384 (583–4,060)	4456 \pm 672 (1,140–7,590)	288 \pm 40 (142–476)	169 \pm 26 (48–296)
Drainages	3,094 \pm 453 (1,513–8,876)		521 \pm 101 (181–2,034)	

times higher in males than females we would expect a male bias in recovered shells.

In contrast to differences in apparent mortality, catchability was low and independent of sex. Combined catchability for males and females was 0.25, which is consistent with previous measures in Blackwater Canyon (Stone 2001). Given the low surface area of aquatic habitats and thorough sampling in Blackwater Canyon, we previously argued that low catchability was not related to inefficient sampling, but was more likely related to temporary absences from the study area associated with movements into terrestrial aestivation (Stone 2001; Ligon and Stone 2003). Freshwater turtles inhabiting seasonal wetlands often enter terrestrial aestivation in response to a decline in aquatic habitat quantity or quality. Movements into terrestrial aestivation are often synchronized with a predictable environmental cue (Wygoda 1979; Iverson 1991; Morales-Verdeja and Vogt 1997) but can occur asynchronously with weaker environmental correlates (Roe and Georges 2008). In our study area, many Sonoran Mud Turtles emerged synchronously from terrestrial aestivation following a period when the habitat completely dried and then filled (Ligon and Stone 2003). However, when water is present in our study area turtles appear to move between aquatic and terrestrial habitat at unpredictable times (Stone 2001), perhaps because of vulnerability to predation in shallow aquatic habitats (Stone et al. 2011). Asynchronous aquatic activity likely has a large effect on per capita resource availability, potentially reducing competition among mud turtles foraging in shrinking aquatic habitats and potentially reducing the attractiveness of shrinking aquatic habitats to predators of mud turtles.

Long-distance movements.—We found that 21 turtles changed drainages during the study, moving mostly across terrestrial habitat that included mountain ridges. Long-distance movements over land by Sonoran Mud Turtles have been documented in other populations (Hall and Steidl 2007; Hensley et al. 2010). Hensley et al. (2010) used circumstantial evidence, long absences from the study area by individuals (low catchability) and the appearance of unmarked adults (presumed immigrants) in the study area after years of intensive sampling, to argue that long-distance movements were more common

than observed. The lack of correlation between home range length and number of captures in our study also supports this argument. Many turtles captured regularly over long periods displayed site fidelity whereas turtles with the largest home ranges were rarely captured. It is likely that turtles with large home ranges and few captures moved out of Blackwater Canyon and were not encountered afterward in less intensively sampled areas. A similar explanation seems likely for the 47 males and 17 females that were captured once and never recaptured. We argue that turtles captured once and not encountered again were transients, moving through the study area too quickly to be encountered twice. Kiester et al. (1982) described a similar pattern among Three-toed Box Turtles (*Terrapene carolina*) in which there were frequently encountered residents with stable home ranges and transients moving in a linear fashion through and out of the study area. All transients described by Kiester et al. (1982) were males. Other studies have noted high variation in individual movement rates characterized by a portion of an animal population moving long distances while another portion remains relatively sedentary (Swingland and Lessells 1979; Sheppard et al. 2006; Roshier et al. 2008).

Dispersal across drainages can reduce reproductive isolation and lower the probability of extirpation of subpopulations. The frequency and scope of interdrainage movements suggest high gene flow and little population structure in Sonoran Mud Turtles in our study area. Male biased movements suggest males are the primary agents of gene flow. Therefore, nuclear DNA, which is biparentally inherited, should show less genetic structure compared to maternally inherited mitochondrial DNA (Monsen and Blouin 2003). However, the predicted pattern of genetic diversity and structure in nuclear vs. mitochondrial genomes of populations outside our study area will likely depend on degree of habitat isolation and relative movement rates of males and females. Compared to our study area, little gene flow is expected among populations that occur in isolated patches of aquatic habitat, such as Quitobaquito Spring (Riedle et al. 2012). Likewise, female biased gene flow is likely in populations where movement rates are female biased, as has been suggested in two studies (Emslie 1982; Hensley et al. 2010).

The frequency and magnitude of long-distance movements by Sonoran Mud Turtles, coupled with historical variability of aquatic habitats in our study area, suggests that maintaining connectivity of aquatic habitats on a range-wide scale is needed. In addition to impoundments and canyon pools, likely dispersal pathways along drainages and over low points along ridges should be included in core areas of Sonoran Mud Turtles. During the past century aquatic habitats in our study area were greatly modified by humans. Most of the natural springs were capped, with water diverted to troughs and holding tanks for livestock, greatly reducing aquatic habitat for wildlife. Meanwhile, impoundments were constructed in many canyons, mitigating the loss of springs by creating new aquatic habitats. Historically, there must have been large changes in local abundance of Sonoran Mud Turtles within our study area, with individuals concentrated around natural springs before ranching began but shifting to impoundments and canyon pools after impoundments were built and springs were modified. The long-term survival of Sonoran Mud Turtles in the isolated ranges of the Madrean Sky Islands may depend on range-wide connectivity of aquatic habitats that prevent the isolation of subpopulations.

Acknowledgments.—We thank 59 individuals, mostly undergraduate students from the University of Central Oklahoma (UCO), for assistance in the field. We thank the Gault, Hadley, and McDonald families for providing access to their private property or encouraging our activities on their Forest Service leases. We thank Justin Congdon for thoughtful comments on a draft of the manuscript. Partial funding was provided by the UCO Office of Research and Grants. This research was conducted under permits issued by the New Mexico Department of Game and Fish (2905), the Arizona Game and Fish Department (SP621273) and the US Forest Service (SUP0080–01), and under an IACUC protocol from the University of Central Oklahoma.

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