Small Scale-High Resolution Terrestrial Activity of *Trachemys scripta elegans*, Harvest Intensity, and Immediate Movement Responses Following Harvest Events

Author(s): Ivana Mali , Floyd W. Weckerly , Thomas R. Simpson , and Michael R. J. Forstner
Source: Copeia, 104(3):677-682.
Published By: The American Society of Ichthyologists and Herpetologists
DOI: http://dx.doi.org/10.1643/CH-15-367
URL: http://www.bioone.org/doi/full/10.1643/CH-15-367

Copeia 104, No. 3, 2016, 677–682

Small Scale-High Resolution Terrestrial Activity of *Trachemys scripta elegans*, Harvest Intensity, and Immediate Movement Responses Following Harvest Events

Ivana Mali[1,2], Floyd W. Weckerly[2], Thomas R. Simpson[2], and Michael R. J. Forstner[2]

Overland movement is an important aspect of freshwater turtle ecology. Turtles make overland excursions searching for mates, to find new aquatic habitats, in response to drought, or during nesting. Here, we tested how environmental factors may influence the excursion events of adult Red-eared Sliders (*Trachemys scripta elegans*). We found that 85% of turtles made overland movements at least once, which is higher than previously reported, and some turtles made multiple movements (2–6) during a single season. Rain and drought events were significant predictors of overland movements. While sex did not appear to be a significant factor, there was an indication that movement may depend on seasonal temperatures. In addition, we showed that turtles immigrated to depopulated ponds in a short period of time after a simulated harvest event. However, after a second harvest simulation, our experimental pond was not repopulated to its original abundance. Our results call for caution when implementing spatially controlled harvest regimes. Ponds depleted by harvesting might not be repopulated by immigrating turtles if source population sizes also decrease due to the regular dispersal to sink populations and subsequently slows overall reproduction rates.

FRESHWATER turtles are dependent on pond ecosystems and surrounding landscapes for maintaining regional population stability (Harrison, 1991; Thomas et al., 1999; Joyal et al., 2001; Pittman and Dorcas, 2009). Turtles make overland movements during nesting events, in search for mates, and in response to drought conditions although other reasons may exist (Parker, 1984; Tuberville et al., 1996; Doody et al., 2002; Bowne et al., 2006; Steen et al., 2012). An increasing number of studies have examined the patterns of overland movements to improve our understanding of habitat requirements and to establish buffer zones for conservation management strategies.

Research has shown that the proportion of turtles moving across the landscape varies among species, sex, and size. For example, the proportion of Snapping Turtles (*Chelydra serpentina*) that moved among a network of ponds ranged from 5% (Congdon et al., 1994) to 12% (Patrick and Gibbs, 2010), whereas the Eastern Long-necked Turtle (*Chelodina longicollis)* had higher movement rates of 33% (Roe et al., 2009). In regards to sex, a fraction of studies found that there were no movement differences between males and females (House et al., 2010; Rasmussen and Litzgus, 2010; Mali and Forstner, 2014), while others found females (Aresco, 2005; Carriere et al., 2009) or males (Morreale et al., 1984) moved more frequently. Additional studies found that small and immature turtles were more likely to make overland movements (Roe et al., 2009; House et al., 2010), contrary to the prediction that smaller turtles would make fewer movements due to a higher probability of desiccation.

Terrestrial activity is also influenced by environmental factors like seasons, hydroperiod, distances among water bodies, and landscape composition. In general, overland movement is diurnal (Rowe, 2003; Mali and Forstner, 2014). Movement usually increases during drought conditions as turtles search for more suitable water bodies (Bowne et al., 2006). However, some turtles have exhibited both quiescent and dispersal behaviors in response to drying (Roe and Georges, 2008). Distance to the nearest wetland is generally inversely correlated to movement rates (Roe and Georges, 2008; Roe et al., 2009), and habitat quality is an important factor for female immigrants selecting a new habitat (Bowne et al., 2006). Males are generally more active and move more during the mating season, whereas females are more active and move more during the nesting season (Morreale et al., 1984; Gibbons, 1990). Yet, there are exceptions (Litzgus et al., 2004).

It is understood that anthropogenic modifications of the landscape can alter terrestrial movement behaviors as well (Aresco, 2005; Gibbs and Steen, 2005). Dispersal rates are known to be lower in urbanized and fragmented habitats (Bennett et al., 2010; Patrick and Gibbs, 2010). However, it is unclear how human harvests affect density dependent movement responses. This is an issue because some harvest regimes rely directly on the assumption that turtles in non-harvested waters will migrate and repopulate harvested regions (TPWD, 2007). Studies on whether or not a harvested population can recover through immigration, or how quickly that might occur, are lacking. There is indirect evidence that turtles do colonize ponds as males have been shown to settle in new aquatic habitats (Tuberville et al., 1996).

To address this question, we applied a relatively new method of monitoring freshwater turtle movement using a stationary PIT tag reader (Mali and Forstner, 2014). Our goals were twofold. Our first goal was to determine environmental variables that correlated with terrestrial activity of adult male and female Red-eared Sliders (*Trachemys scripta elegans*) under anthropogenically undisturbed conditions. Second, we aimed to monitor movement following significant depletion in population size by simulated harvests. Here, we defined a turtle population as individuals that inhabit an identifiable aquatic habitat pond, while those individuals that are outside a circumscribed aquatic habitat are extrapopulational. This definition is used in studying much of what we know about life history of Red-eared Sliders (Gibbons, 1990). In addition, studies that examined overland movement often times did so in light of interpond movement with interpond distances

[1] Department of Biology, 1500 S Avenue K Station 33, Eastern New Mexico University, Portales, New Mexico 88130; Email: ivana.mali@enmu.edu. Send reprint requests to this address.
[2] Department of Biology, 601 University Drive, Texas State University, San Marcos, Texas 78666; Email: (FWW) fw11@txstate.edu; (TRS) R_Simpson@txstate.edu; and (MRJF) MF@txstate.edu.
Submitted: 2 November 2015. Accepted: 26 January 2016. Associate Editor: M. J. Lannoo.
 DOI: 10.1643/CH-15-367 Published online: 22 August 2016

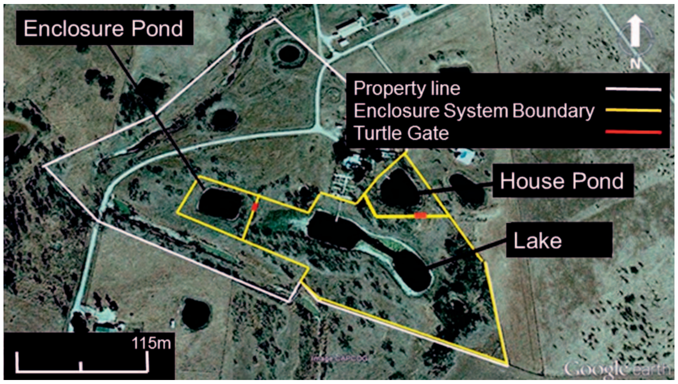

Fig. 1. Aerial view of the study system showing the ponds and location(s) of the movement monitoring system, turtle gate, consisting of the game camera and the PIT tag reader. The first turtle gate was installed between the Enclosure Pond and the Lake in July 2011. The main focus of the experiment was the Enclosure Pond for which the exact number of resident turtles was known at any given time. The second turtle gate was installed between the House Pond and the Lake in 2013 and was only used for comparison of overall activity between the two gates.

varying from very small (~100 m) to large (several kilometers; i.e., Bowne et al., 2006; House et al., 2010). We elaborate more on implications of using such a definition in the Discussion. In addition, because our study was short term in comparison to turtle longevity, we focused specifically on the adult males and females. Adults are harvested most frequently, and adults also have the greatest impact on turtle population growth (Congdon et al., 1994).

MATERIALS AND METHODS

Study site and data collection.—We conducted the study from July 2011 to October 2013 in a complex of ponds within a private property parcel in Guadalupe County, Texas. The study system applied the methods to monitor freshwater turtle movement that were detailed in Mali and Forstner (2014). Briefly, the study site contains a closed complex of three permanent water bodies: Enclosure Pond, Lake, and House Pond (Fig. 1). In non-drought conditions, the Enclosure and House Ponds have perimeters of 96 m and 87 m, respectively. The Lake is the largest and has a 270 m perimeter. But in drier months, the Lake turns into a shallow 5 m wide and 45 m long canal. The distances between the ponds are relatively short, 85 m between the Enclosure and the Lake and 50 m between the Lake and House Pond.

In 2009, the Enclosure Pond was fenced off from the rest of the system and pumped dry in order to remove all turtles (Mali and Forstner, 2014). On 4 June 2011, we manually repopulated the pond with PIT (Passive Integrated Transponders) tagged individuals prior to the beginning of the experiment (Mali and Forstner, 2014). Some turtles were original Enclosure Pond animals, while some were captured from the surrounding areas, not the study system. For each PIT tagged turtle, we recorded the sex, carapace length (CL), and weight. We repopulated the Enclosure Pond with 29 female and 24 male adult Red-eared Sliders. Because the Enclosure Pond was manually repopulated, we kept the gates closed and gave turtles an adjustment period of 33 days, specifically seeking to avoid recording any movement events caused by displacement itself. After the adjustment period, we opened a single turtle gate between the Enclosure Pond and the Lake. Movement was monitored with a stationary ISO-2001 Biomark© PIT tag reader and RECONYX© game camera (Mali and Forstner, 2014). The reader recorded PIT tagged turtles crossing the gate, and the game camera recorded non-PIT tagged turtles originally residing in the Lake or the House Pond. Based on preliminary testing of the PIT tag reader and the camera together, frequent visits to the study site to make sure the system is operational, and the sync results between the reader and the camera, we believe that the recording system errors were trivial. Our Enclosure Pond monitoring system provided an opportunity to follow the number of adults in the Enclosure Pond from day to day and to evaluate the parameters affecting movement into and out of the pond. By the end of 2011, an additional 19 Red-eared Sliders, found on land outside of but in proximity to our system, were captured, equipped with PIT tags, and released to the Lake.

We monitored movement from July 2011 to May 2012. We assessed which environmental factors and periods of the day individuals were more likely to make excursions among ponds and whether movements were related to turtle size. Second, we simulated two harvest events in the Enclosure Pond in May 2012 and June 2013. Simulated harvest consisted of trapping turtles using 76.2 cm diameter hoop nets baited with canned sardines, the traditional method used by commercial harvesters. The first harvest event lasted from 18 May 2012 to 26 May 2012 with a total of 140 trap days. After the harvest event, we continued to monitor the interpond movement with the chip reader and the game camera for the following 12 months. The second simulated harvest event occurred between 9 June and 16 June 2013, again with a total of 140 trap days. We continued to monitor the system for the following six months. Our goal was to assess the short-term recovery speed of the Enclosure Pond by immigration from the Lake. Harvested individuals were measured, unmarked individuals were PIT tagged, and all harvested turtles were placed in the House Pond.

Data analyses.—To correlate activity events to environmental factors, we used logistic Generalized Linear Mixed Effects Modeling (GLMM; Zuur et al., 2009). For this analysis, we used only the 53 adult PIT tagged Red-eared Sliders that were used to repopulate Enclosure Pond. This allowed us to treat each individual PIT tag ID as a random effect since the movement events by the same turtle may not be independent. For each day of the year, we recorded a response variable of 1 or 0 if an animal was recorded on the chip reader or not, respectively.

The full model included the following factors: turtle size (CL) measured in millimeters, sex, maximum daily temperature, season, rain event, and the number of days since the last rain event. Maximum daily temperatures were obtained from the National Oceanic and Atmospheric Administration (NOAA) weather station, located 13 km from the study site (29.704N, –98.029W). Rainfall data were obtained directly from an on-site rain gauge. In the model, we presented the rain event as a binary variable with values 0 (no rain) and 1 (rainfall greater than 1 mm). The factor "season" included calendar seasons: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). The models also included an interaction term between the season and maximum daily temperature and an interaction term between sex and season. We compared the models using Akaike's information criteria and calculated the Akaike weights for each model (AIC; Burnham and Anderson, 1998). To estimate models, we used the glmmML function in

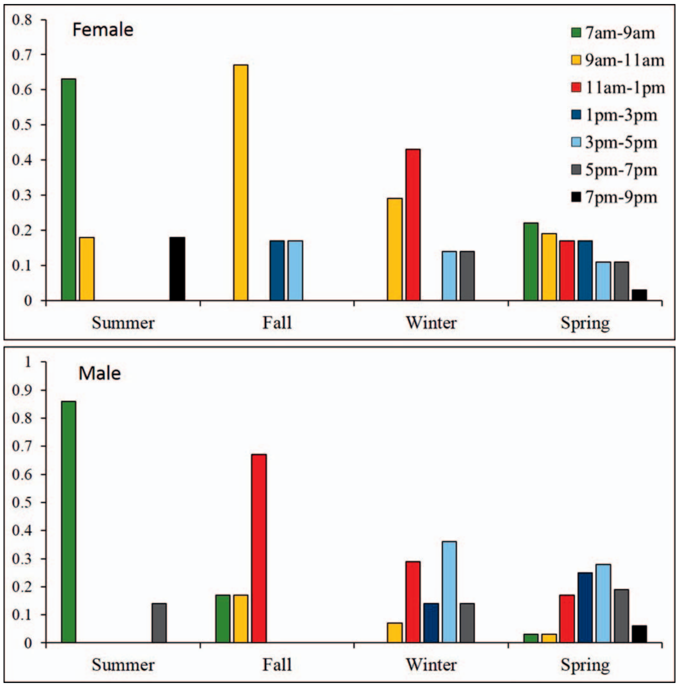

Fig. 2. Daily activity peaks of Red-eared Sliders (*Trachemys scripta elegans*) per season. All turtles showed diurnal activity. Turtles were active throughout the day during spring, but only early in the morning during summer. In winter months, they tend to be more active during midday.

R which uses maximum likelihood estimators and allows AICs to be calculated (Zuur et al., 2009). For model parameters, we inferred statistical significance at $\alpha = 0.05$.

For the second portion of the experiment, we evaluated the number of PIT tagged and non-PIT tagged turtles present throughout the experiment in the Enclosure Pond. Unfortunately, based solely on the game camera images, it was not possible to distinguish every individual non-PIT tagged turtle. Therefore, we estimated the daily number of non-PIT tagged turtles entering/exiting the Enclosure Pond as the difference between the number of turtles entering and the number of turtles exiting the pond, which yielded either a positive (net gain) or negative (net loss) number. We calculated the Enclosure Pond population size at the end of every month pre- and post-harvest, based on the number of known PIT tagged and estimated number of non-PIT tagged turtles. We used segmented regression in R (Muggeo, 2003, 2008; Ricca et al., 2014) to describe population growth patterns within the 12 months following the first harvest simulation event. We conducted the model selection approach by using the Akaike Information Criterion corrected for small sample size to test a linear (single-slope) and two-slope model (AICc; Burnham and Anderson, 1998). The significance of each slope was based on 95% confidence intervals. The CIs that do not overlap zero indicate that there is a significant change in population size, while CIs that overlap zero indicate that there is no significant change in population size.

RESULTS

Terrestrial activity.—Of 53 PIT tagged adult Red-eared Sliders, 45 (85%, 23 females and 22 males) moved during the first nine months of the study period. It is important to note that many individual movements were recorded on multiple occasions during a single season as well as over multiple seasons. Daily activity peaks varied by season (Fig. 2). Turtles were active throughout the day during spring, but only early in the morning during summer. In winter months, turtles tended to be more active during midday (1100 to 1300 h daylight savings time), especially females.

The best fit model included season, maximum daily temperature, rain, the number of days since the last rain event, and the interaction between the season and temperature as explanatory variables ($w_i = 0.49$; Table 1). While rain had significant positive effect on movement ($P < 0.01$) number of days since the last rain event had a significant negative effect ($P = 0.02$). There was a significant positive interaction between the winter season and temperature ($P = 0.03$), indicating that seasonality of the movement is temperature related. Interestingly, turtle size and sex did not significantly correlate with movement.

Harvest intensity and post-harvest immigration.—Prior to the first harvest event, the number of adult Red-eared Sliders in the Enclosure Pond was 42 (22 originally PIT tagged turtles, two PIT tagged after the experiment started, and 18 non-PIT tagged turtles). The first harvest event yielded 16 Red-eared Sliders (6 PIT tagged and 10 non-PIT tagged turtles), resulting in harvest intensity of 38.1% and 0.11 capture per unit effort (CPUE). Of these, six were the original stock turtles and the rest were non-PIT tagged turtles. Prior to the second harvest event, the number of adult Red-eared Sliders in the Enclosure Pond was 49 (25 PIT tagged and 24 non-PIT tagged turtles). The second harvest event yielded 24 Red-eared Sliders (six PIT tagged, 18 non-PIT tagged), resulting in 49.0% harvest intensity and 0.19 CPUE.

After the first harvest event, the depleted population ($n = 26$) grew to 47 individuals by the end of September, which was six individuals higher than just before the first harvest event. For the period between the two harvest events, the relationship between the population size and month was described by a two-slope model rather than a single slope model (AICc = 68.12 and 89.87, respectively). Significant population growth occurred within the first four months

Table 1. Results from a model selection analysis using Akaike Information Criterion (AIC) to test the influence of turtle size, sex, and various environmental factors on overland activity of Red-eared Sliders (*Trachemys scripta elegans*). The model containing season, temperature, rain event, days since the last rain event, and the interaction between temperature and season as predictors ranked the highest.

Predictor	# of parameters	AIC	ΔAIC	AIC weight
Size+Sex+Season+MaxT+RainDay+DaysSinceRain+Sex:Season	9	1250	9	0.005
Size+Sex+Season+MaxT+RainDay+DaysSinceRain	8	1247	6	0.025
Sex+Season+MaxT+RainDay+DaysSinceRain	7	1245	4	0.069
Sex+Season+MaxT+RainDay+DaysSinceRain+Season:MaxT	8	1242	1	0.300
Season+MaxT+RainDay+DaysSinceRain+Season:MaxTemp	7	1241	0	0.49
Season+MaxT+RainDay+DaysSinceRain	6	1244	3	0.110

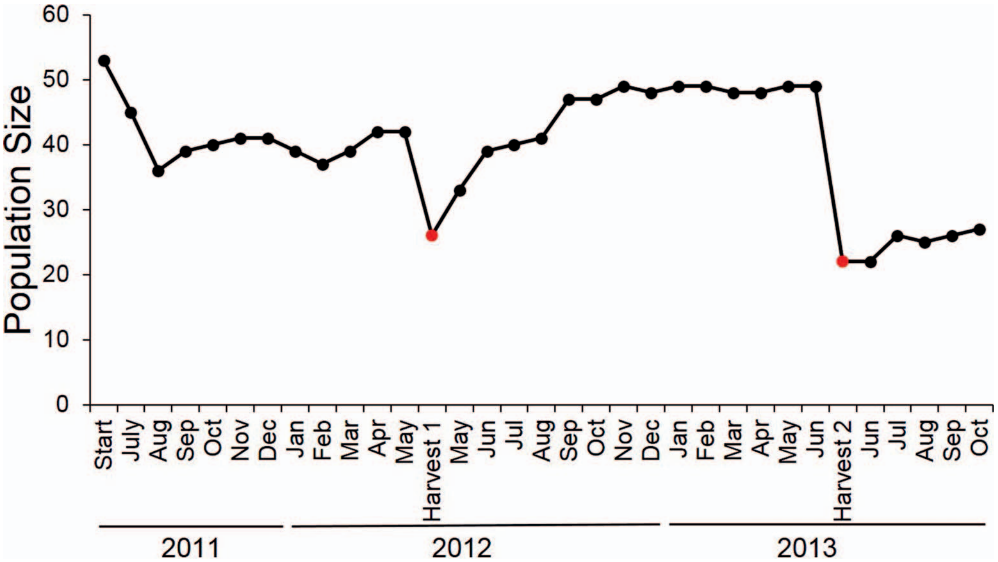

Fig. 3. The number of Red-eared Sliders (*Trachemys scripta elegans*) in the Enclosure Pond at the end of each month from July 2011 to October 2013. The population size was calculated based on the chip reader data and the game camera data recording the movement. Two harvest simulations took place, in May 2012 and June 2013, and the graph also presents the number of turtles immediately after harvest events (red circles).

after the harvest ($r = 0.47$, 95% CI = 2.86–4.92). For the rest of the period, population was considered stable ($r = 0.25$, 95% CI = –0.42–0.66; Fig. 3). On the other hand, the second post-harvest immigration period generated different results. Although there was evidence of population recovery in the following four months, the population increased to only 27 individuals, which is approximately 55.0% of the pre-second harvest population size and 64.3% of the pre-first harvest population size.

Prior to the first harvest, some level of exchange between PIT tagged and non-PIT tagged turtles occurred between the Enclosure and the Lake. However, after both harvest events, most of immigrants were non-PIT tagged turtles, which could be considered as novel turtles moving into the system and being responsible for population growth (Fig. 3). It is also worth noting that even during population stabilizing months, turtle activity was still observed with an approximately even number of immigrants and emigrants detected.

DISCUSSION

In this study, we attempted to answer several questions essential to the management and conservation of freshwater turtles by examining overland activity patterns. We would like to emphasize that although this study examines movement behavior on a high resolution, our study represents a single small scale replicate. Therefore, conclusions drawn here should be taken cautiously and replication of this study on a larger scale may be of future interest. In general, the study shows that adult Red-eared Sliders made overland movements more frequently than other species of freshwater turtles (Congdon et al., 1994; Roe et al., 2009; Patrick and Gibbs, 2010), with 85% making overland excursions at least once. Our first goal was to correlate these excursion events to environmental factors on a much finer scale than what has previously been reported, i.e., which environmental factors trigger turtles to leave their aquatic habitats. Although our recording system did not identify turtles immediately upon their excursion, the relatively small system allowed us to assume that turtles did not spend an extensive amount of time on land before being recorded. We speculated that time to be approximately two hours based on our anecdotal daily observations of the system prior to the beginning of the experiment-gate opening. Movement was strictly diurnal, which is consistent with previous reports (Gibbons, 1990; Rowe, 2003). The timing of movement throughout the day seemed to be closely related to season, with the hotter summer activity peaked in the morning hours whereas in the cooler winter, activity peaked at midday.

Many studies provide evidence that overland movement is stimulated by drought, as turtles will search for more suitable habitat. Our study indicated that rain had a positive effect on movement. However, number of days since the last rain event had an inverse effect on movement. This does not necessarily indicate that these turtles will exhibit quiescent behavior in response to drying. Although our study was conducted during exceptionally dry years for Texas, none of the ponds in our study system dried, with the shallowest pond dropping to ~3 m of water at maximum depth during the first ten months of the study. Our future studies may examine whether there is a drought/hydroperiod threshold beyond which turtles begin to leave the environment.

Due to the small scale of the study system and based on home range sizes for Red-eared Sliders, some could argue that the movements in our experiment are considered intrapopulational (short-range) rather than extrapopulational (long-range) movements. However, consistent with the definition of Gibbons (1990), we treated Enclosure Pond immigration and emigration as extrapopulational. We, however, realize that other studies have shown that the distance between the ponds can be an important factor influencing dispersal (Roe and Georges, 2008; Roe et al., 2009). Thus, the high overland activity we document could be due to the close proximity of water bodies.

Our study demonstrated the ability of turtles to invade and repopulate harvest depleted ponds in a relatively short period of time. This was particularly evident after the first harvest event. However, after the second harvest, the recovery was much less. Unfortunately, we only monitored population size in the Enclosure Pond and did not estimate the population size across time for the rest of the system. Hence, it is difficult to discuss how the entire metapopulation was distributed over time. Although harvested individuals stayed in the system (House Pond), only two of these individuals were recorded again by the chip reader near the Enclosure Pond, suggesting that few individuals moved from the House Pond. This was later confirmed by installing the second monitoring system, the PIT tag reader and the game camera, between the Lake and the House Pond in 2013. Although not specifically tested, Enclosure Pond and the Lake were similar in their appearances and characterized by clear waters, while the House Pond is both more shaded and had steeper banks. Based on previous research, we speculate that landscape itself might play an important role for movement in turtle metapopulations (Roe and Georges, 2008; Patrick and Gibbs, 2010).

It is important to note the environmental context of our study. Turtles in our study system did not experience human altered habitats such as urbanization or a landscape intersected by roads. Natural predators were scarce in our study due to fencing. Across the two years of study only three turtle shells were recovered and no raccoon (as predators) activity was observed. In an unfenced system, raccoon predation might be influential. Nonetheless, this study significantly contributes to our understanding of turtle movement behavior, especially in terms of fine scale movement patterns. Moreover, this may be the first study seeking to directly test the effects of harvest on movement. Given that Red-eared sliders can disperse great distances (Ernst and Lovich, 2009; Steen et al., 2012), future studies should include a variety of landscapes and larger spatial scales to estimate source-sink dynamics of harvested turtle populations. This may also lead to specifically designing management units for different species of turtles (i.e., a single pond vs. a system of ponds) depending on species vagility.

ACKNOWLEDGMENTS

We thank A. Villamizar, D. Brown, and M. Jones for their help with turtle trapping and marking. We also thank Z. Adcock, L. Schumacher, A. Parandhaman, D. Preston, and D. Wallace for their help with fence construction. This work was done under Texas Parks and Wildlife Scientific Permit SPR-0102-191 and IACUC Permits 0417_0513_2016 and 1012_0501_11.

LITERATURE CITED

Aresco, M. J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37–44.

Bennett, A. M., M. Keevil, and J. D. Litzgus. 2010. Ecology and population genetics of northern map turtles (*Graptemys geographica*) in fragmented and continuous habitats in Canada. Chelonian Conservation and Biology 9:185–195.

Bowne, D. R., M. A. Bowers, and J. E. Hines. 2006. Connectivity in an agricultural landscape as reflected by interpond movements of a freshwater turtle. Conservation Biology 20:780–791.

Burnham, K. P., and D. R. Anderson. 1998. Model Selection and Inference: A Practical Information-theoretic Approach. Springer Verlag, New York.

Carriere, M. A., G. Bulte, and G. Blouin-Demers. 2009. Spatial ecology of northern map turtles (*Graptemys geographica*) in a lotic and lentic habitat. Journal of Herpetology 43:597–604.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long lived organisms. American Zoology 34:397–408.

Doody, J. S., J. E. Young, and A. Georges. 2002. Sex differences in activity and movements in the pig-nosed turtle, *Carettochelys*, in the wet-dry tropics in Australia. Copeia 2002:93–103.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. The John Hopkins University Press, Baltimore, Maryland.

Gibbons, J. W. 1990. Life History and Ecology of the Slider Turtle. Smithsonian Institution Press, Washington, D.C.

Gibbs, J. P., and D. A. Steen. 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. Conservation Biology 19:552–556.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73–88.

House, W. J., I. M. Nall, and R. B. Thomas. 2010. Interpond movements of western painted turtles (*Chrysemys picta*) in east-central Kansas. Southwestern Naturalist 55:403–410.

Joyal, L. A., M. McCullough, and M. L. Hunter, Jr. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15:1755–1762.

Litzgus, J. D., T. A. Mousseau, and M. J. Lannoo. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. Copeia 2004:804–817.

Mali, I., and M. R. J. Forstner. 2014. Use of stationary microchip reader for monitoring interpond movement of freshwater turtles. Herpetological Review 45:22–25.

Morreale, S. J., J. W. Gibbons, and J. D. Congdon. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). Canadian Journal of Zoology 62:1038–1042.

Muggeo, V. M. R. 2003. Estimating regression models with unknown break-points. Statistics in Medicine 22:3055–3071.

Muggeo, V. M. R. 2008. Segmented: an R package to fit regression models with broken-line relationships. R News 8:20–25.

Parker, W. S. 1984. Immigration and dispersal of slider turtle (*Pseudemys scripta*) in Mississippi farm ponds. American Midland Naturalist 112:280–293.

Patrick, D. A., and J. P. Gibbs. 2010. Population structure and movements of freshwater turtles across a road-density gradient. Landscape Ecology 25:791–801.

Pittman, S. E., and M. E. Dorcas. 2009. Movements, habitat use, and thermal ecology of an isolated population of bog turtles (*Glyptemys muhlenbergii*). Copeia 2009:781–790.

Rasmussen, M. L., and J. D. Litzgus. 2010. Habitat selection and movement patterns of spotted turtles (*Clemmys guttata*): effects of spatial and temporal scales of analyses. Copeia 2010:86–96.

Ricca, M. A., D. H. Van Vuren, F. W. Weckerly, J. C. Williams, and A. K. Miles. 2014. Irruptive dynamics of introduced caribou on Adak Island, Alaska: an evaluation of Riney-Caughley model predictions. Ecosphere 5:Art 94.

Roe, J. H., A. C. Brinton, and A. Georges. 2009. Temporal and spatial variation in landscape connectivity for a freshwater turtle in a temporarily dynamic wetland system. Ecological Applications 19:1288–1299.

Roe, J. H., and A. Georges. 2008. Terrestrial activity, movements and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*, in a temporally dynamic wetland system. Austral Ecology 33:1045–1056.

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

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

Texas Parks and Wildlife Department (TPWD). 2007. Texas turtle regulations. Title 31, Part 2, Chapter 65. Subchapter O. Texas Register, Austin, Texas.

Thomas, B. R., N. Vogrin, and R. Altig. 1999. Sexual and seasonal differences in behavior of *Trachemys scripta* (Testudines: Emydidae). Journal of Herpetology 33:511–515.

Tuberville, T. D., J. W. Gibbons, and J. L. Greene. 1996. Invasion of new aquatic habitats by male freshwater turtles. Copeia 1996:713–715.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.