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Movement and Overwinter Survival of Released Captive-raised Juvenile American Alligators (*Alligator mississipiensis*) in Southeastern Oklahoma, USA

Alligator mississipiensis (American Alligator) occurs throughout the southeastern United States, and it has been postulated that its northern distribution is limited largely by severe or prolonged periods of freezing temperatures (Hagan et al. 1983; Lee et al. 1997). Several studies have characterized the thermoregulatory behavior, activity patterns, and mortality of American alligators during cold winter weather (Chabreck 1966; Goodwin and Marion 1979; Brisbin et al., 1982; Hagan et al. 1983; Brandt and Mazzotti 1990; Joanen and McNease 1990; Lee et al. 1997; Asa et al., 1998). For example, Joanen and McNease (1990) described alligator deaths across a variety of size classes associated with a severe freezing event in Louisiana. As another example, Elsey et al. (2015) showed that freezing of tissues in alligators can result in necrosis of dermal tissue, which may lead to mortality some time after the freezing event. However, few studies have examined the overwintering ecology and survival of juveniles. Brandt and Mazzotti (1990) and Lee et al. (1997) focused on the ability of juvenile alligators (< 1 m total length; TL) to withstand freezing conditions and hypothesized that the northern range of the American alligator is limited by the inability of juvenile alligators to withstand extended periods of ice formation. Brandt and Mazzotti (1990) reported on the responses of nine juvenile alligators to two cold weather events. Two individuals in their study were able to survive brief periods of ice formation by utilizing a submerged breathing posture in which only the tips of their snouts were kept out of water. Lee et al. (1997) observed the wintering behavior of nine hatchling alligators, eight of which also used the submerged breathing posture observed by Brandt and Mazzotti (1990) to survive air temperatures as low as -9.5°C. Hagan et al. (1983) originally termed this behavior the "icing response" after observing it in adult alligators. Brandt and Mazzotti (1990) and Hagan et al. (1983) both suggest that alligators use this behavior to maintain a breathing hole during short periods of ice formation. While these studies provide the basis for what is known about winter survival of juvenile American Alligators, both were conducted in enclosed artificial ponds with limited sample sizes.

In addition to using the icing response to withstand ice formation in shallow water, utilization of deep-water refugia may also play a role in the overwinter survival of alligators. Brandt and Mazzotti (1990) and Brisbin et al. (1982) reported that adult and juvenile alligators were able to survive overnight exposure to low air temperatures by seeking out deep-water reservoirs. Furthermore, Mazzotti et al. (2016) suggest that this behavior helped prevent alligator mortality during a recent cold spell in Florida, whereas a record number of American Crocodiles (*Crocodylus acutus*), which bask rather than seek deep-water refugia (Lang 1987), were found dead during this same time period. At the northern boundaries of the American Alligator's range, deeper water refugia may function as heat sources or sinks and could serve similar purposes to subterranean dens in shallow-water marshes (Brisbin et al. 1982). This function may be especially important for juvenile alligators that have recently dispersed from their natal ponds, thereby making their natal dens unavailable as cold-weather refugia.

While selection pressures associated with overwinter survival of juvenile American Alligators are likely to be most pronounced at the northern margins of the range, no previous studies have addressed winter effects where freezing temperatures and ice-over are relatively common. Southeastern Oklahoma has a small but persistent population of alligators that are mostly restricted to McCurtain County (Heck 2006; Patton et al. 2010), the southeastern-most county in Oklahoma. This population represents the northwestern-most reported population of American Alligators. Freezing temperatures and ice formation are common in this region, and McCurtain County experiences on average > 60 days/year with minimum temperatures < 0°C. Such temperatures are likely contributing factors in limiting population growth. Consequently, understanding how freezing conditions impact juvenile survival and recruitment would facilitate the conservation of alligators in southeastern Oklahoma and may provide insight into how the American Alligator's distribution could be impacted by climate change.

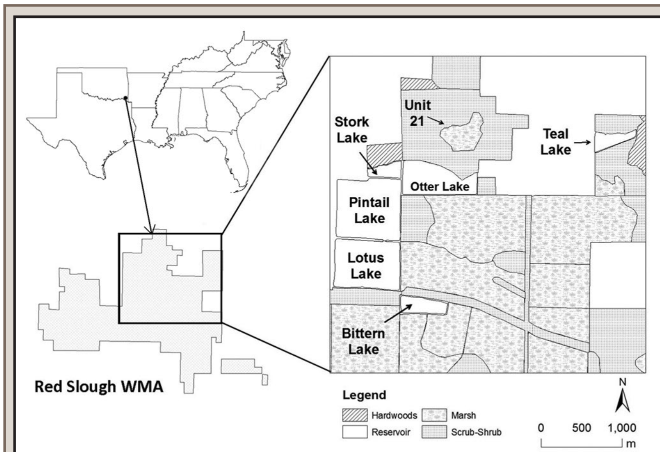

Fig. 1. Map showing the position of Red Slough Wildlife Management Area within the southeastern US and the specific lakes and habitats in which alligators were released.

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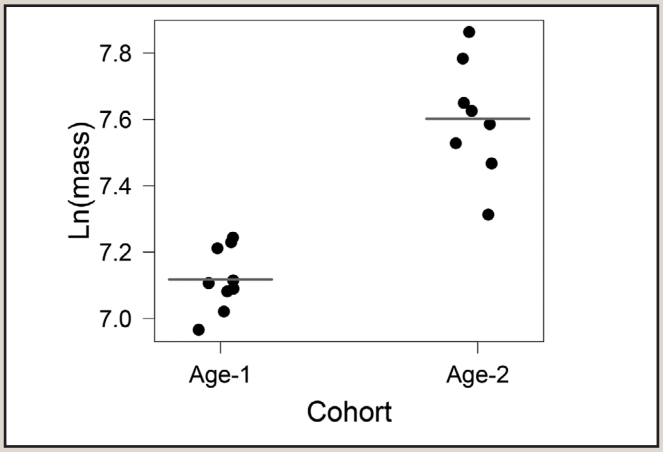

Fig. 2. Stripchart showing the natural logarithm of body mass at time of release in age-1 and age-2 alligators. The gray horizontal bars represent the mean for each of the two age classes (t = -7.00, df = 10.55, $p < 0.001$).

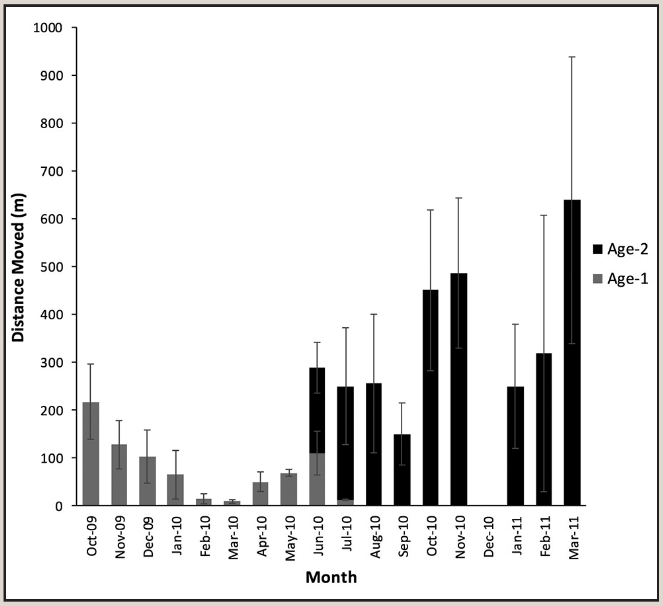

Fig. 3. Mean distances (m) ± SE between monthly locations of age-1 and age-2 radio-telemetered American Alligators on Red Slough Wildlife Management Area in southeastern Oklahoma, October 2009–March 2011. Movement data were not collected in December 2010.

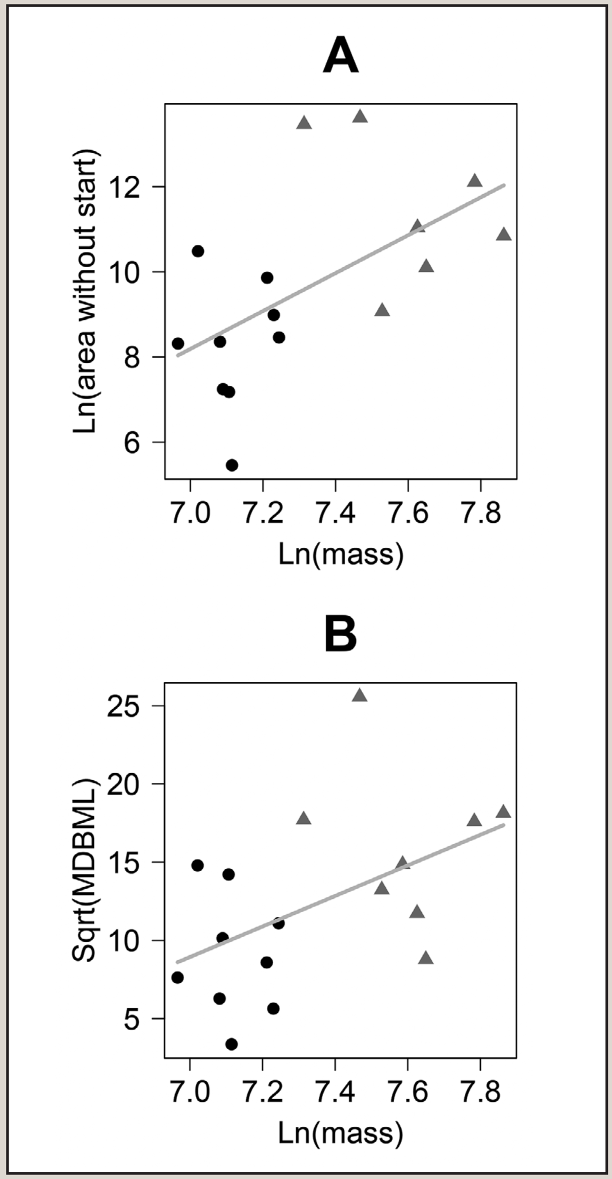

Fig. 4. Relationship between the natural logarithm of mass at release and the natural logarithm of area without start (A) and the square root of mean distance between monthly locations (MDBML) (B). Age-1 animals are depicted as black circles and age-2 animals are depicted as gray triangles.

We used radio-telemetry to assess several aspects of juvenile (age-1 and age-2) alligator overwinter ecology. Our primary objectives were to examine the relationships between overwinter survival and body size, movement, and patterns of habitat utilization.

Methods

Study site, study animals, and husbandry.—We conducted this study at Red Slough Wildlife Management Area (RSWMA) located in McCurtain County (Fig. 1). This 3157-ha area is in the Gulf Coastal Plain ecoregion and is comprised of bottomland hardwoods, riparian zones, wet prairies, scrub-shrub, emergent marshes, and reservoirs (Fig. 1). Though surveys for alligators and nests in RSWMA have been limited and no rigorous population estimate has been made, 1–2 nests/year and 10's of adults have been observed since 2005 (Arbour and Bastarache 2006; Robison 2015). In 2008, a nest that was periodically monitored was determined to have been abandoned by the mother. Monitoring continued and after eggs hatched on 8 September, 20 hatchlings (21.5–24.3 cm TL) were excavated from the nest by state wildlife officials and moved to Southeastern Oklahoma State University (SOSU) in Durant, Oklahoma to be raised in captivity.

At SOSU, hatchlings were evenly divided into two large tanks housed indoors that provided aquatic areas deep enough for them to submerge and terrestrial basking sites. A diet consisting of pelletized Crocodilian Diet (45% protein), mealworms, and fish was provided daily. A combination of 160-W active UV mercury vapor lamps and 100-W ceramic infrared heaters were used to maintain a basking site of 32°C and ambient day and night temperatures of approximately 29 and 24°C, respectively. In addition, lamps were kept on timers to achieve a 12:12 light:dark

Table 1. Comparison of parametric failure time models using Akaike's information criterion (AIC).

Distribution	Model type	Model structure	AIC
Exponential	Full model	Time = Intercept + Mass + Area no start + MDBML	53.68
Weibull	Full model	Time = Intercept + Mass + Area no start + MDBML	51.92
Log-normal	Full model	Time = Intercept + Mass + Area no start + MDBML	51.95
Log-logistic	Full model	Time = Intercept + Mass + Area no start + MDBML	51.86
Exponential	Minimum adequate	Time = Intercept	50.03
Weibull	Minimum adequate	Time = Intercept + MDBML	49.06
Log-normal	Minimum adequate	Time = Intercept	48.11
Log-logistic	Minimum adequate	Time = Intercept	47.92

Minimum adequate models were identified via comparison of nested models using likelihood ratio tests. During this procedure, the term with the largest p-value was removed and the resulting simpler model was compared with the prior more complicated model. This procedure was repeated until no non-significant terms remained. This backward selection procedure was performed independently for all four distributions that were considered.

cycle. To accommodate their increasing size, alligators that were not released with the first cohort were transferred to the Durant State Fish Hatchery in Durant, Oklahoma and housed in large indoor runways designed for fish. Feeding, lighting, and heating regimes remained the same.

While in captivity, all alligators were weighed and measured monthly to monitor growth and overall health. Of the 20 hatchlings raised in captivity, one died within the first week of being moved to SOSU, presumably from natural causes. A second alligator drowned at approximatively six months of age after getting its head lodged in its tank's drainage pipe; a design flaw that was quickly resolved. Of the 18 surviving alligators, 17 alligators served as the study animals for this assessment, and one alligator was kept in captivity at the Durant State Fish Hatchery for educational demonstrations.

Radio telemetry.—We used radio telemetry on a monthly basis to locate each alligator through winter and spring, with additional tracking efforts being made to determine survival following severe freezing events. On 24 September 2009, we randomly selected nine alligators to be released as the age-1 cohort (72.0–78.6 cm TL). Prior to release, alligators were weighed, measured, and affixed with radio transmitters. All animals were released at RSWMA into suitable habitat consisting of shallow reservoirs and marshes with abundant emergent and submergent vegetation. Furthermore, each alligator was released individually in a unique site to minimize competition. We tracked surviving age-1 individuals until October 2010. On 25 June 2010, we released the remaining eight age-2 alligators (77.0–90.0 cm TL) and tracked survival until March 2011. Age-2 alligators were also weighed, measured, and individually released in unique sites that differed in location from the sites where age-1 alligators were released.

We used Advanced Telemetry Systems® (ATS) model R1860 (19g) transmitters on age-1 alligators and ATS model A2930B (62g) transmitters on age-2 alligators. All transmitters were equipped with a mortality signal that activated after 24 hours of inactivity. Transmitters had wire loops to facilitate attachment, and were affixed to the dorsal surface of the base of the tail using steel wire run subcutaneously and spanning the width of the tail. The use of steel wire allowed for transmitters to detach as wires eventually corroded, with the intent that detachment would occur after termination of the study. We used an ATS R2000 receiver (148–149.999 Mhz) and a hand-held yagi antenna for locating radio-tagged alligators (within 2m in shallow water; within 5–10 m in deeper water), and tracking was conducted by walking during daylight hours. Locations were recorded using a handheld Garmin eTrex Global Positioning System unit (accuracy: < 15 m) and analyzed for area traveled and straight-line distance between monthly locations in ArcGIS 9.3 using Hawth's Analysis Tools (Beyer 2004).

When alligators were found (alive or dead) we made note of the general habitat characteristics, including water versus land, water depth (within 2.5 cm), approximate distance to shore (within 1 m), the presence of ice cover, and vegetation. Additionally, for dead alligators, we noted indication of use of the icing position, and whether remains had been scavenged.

Statistical analyses.—We used Pearson's product moment correlation coefficient to examine associations among several continuous variables including: snout–vent length (SVL) at release, total length (TL) at release, body mass at release (mass), area traveled with start point, perimeter around area with start point, area traveled without start point, perimeter around area traveled without start point, and mean distance between monthly locations (MDBML). Because there were no visually verified encounters with one of the age-2 alligators after five days post-release (DPR), there were not enough data points to calculate area traveled for this individual; accordingly, this alligator was not included in our exploratory correlation analysis or other analyses involving area traveled. In addition to investigating relationships among continuous variables, we used Welch's t-test (one-tailed; H_{Alt} ln(mass) of age-2 alligators > ln(mass) of age-1 alligators) to assess whether age-1 and age-2 alligators differed in ln(mass).

During the course of exploring our data, we fit ANCOVA models that used ln(mass) and cohort (age-1 vs. age-2) to predict ln(area traveled without start) and the square root of MDBML. However, deletion test-based model simplification (see Crawley 2013) always identified minimum adequate models containing only the cohort term. Because our study confounds cohort with time of year at release and year-specific ecological effects, the interpretation of cohort-only models is precarious (see below for additional discussion of this issue). As such, we present simple linear regression models in which ln(mass) is the sole predictor of ln(area traveled without start) and the square root of MDBML.

Because our data are clearly interval censored, we used the 'interval' package for R (Fay and Shaw 2010) to estimate generalized Kaplan-Meier survival curves for age-1 and age-2 animals via non-parametric maximum likelihood. The interval

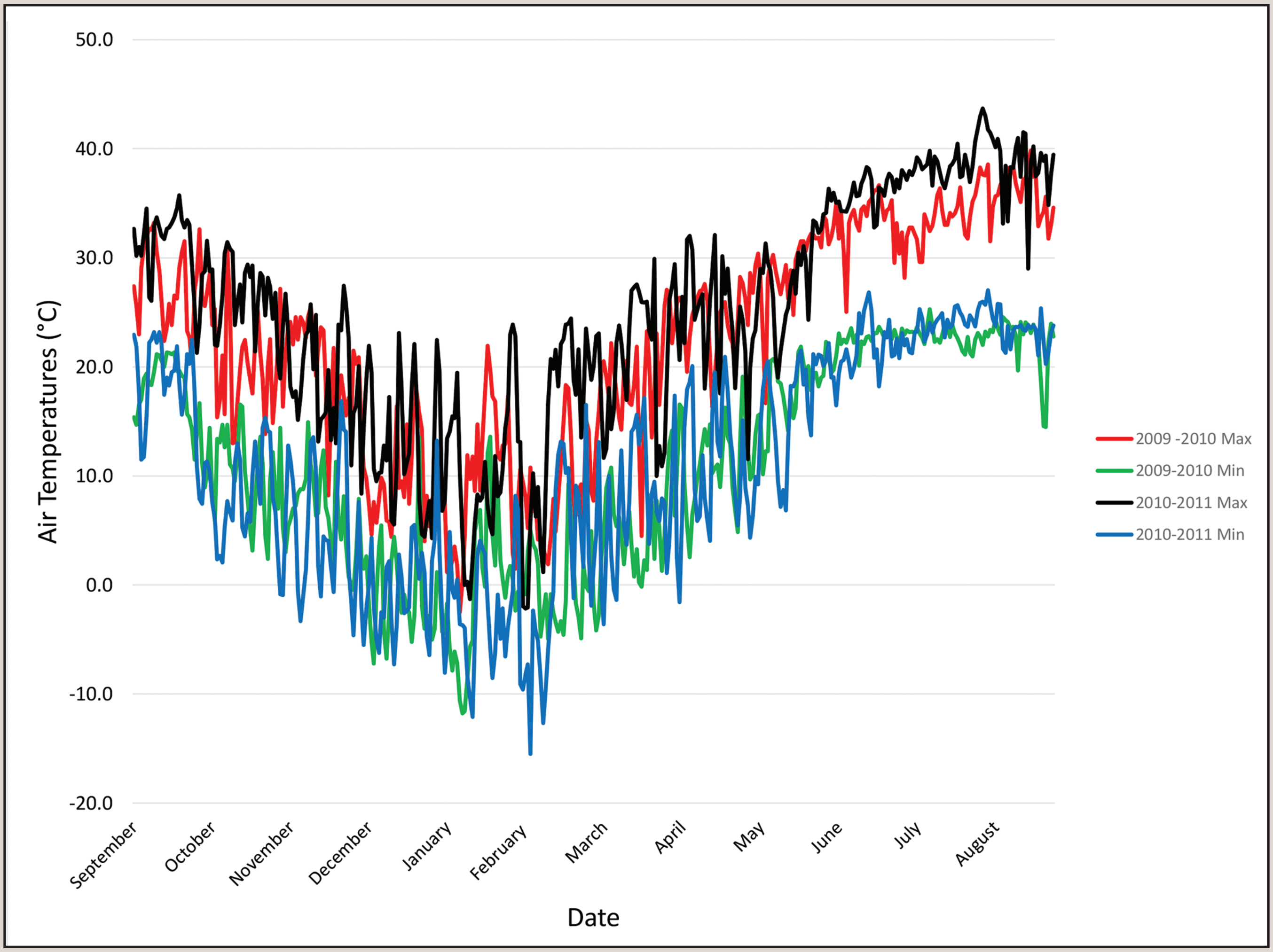

Fig. 5. Maximum and minimum air temperatures at Red Slough Wildlife Management Area in southeastern Oklahoma from September 2009 (first release) through August 2011.

package was then used to perform an exact log-rank test of the null hypothesis that the two age classes have identical survival curves (S(t)). Finally, we used parametric failure time regression models to assess the influence of mass, area traveled without start point, and MDBML on survival of age-1 alligators. We chose to employ parametric survival models on age-1 animals because all seven deaths recorded in our study were among age-1 individuals and because software capable of extending the Cox regression framework to interval censored data is largely lacking (see Fay and Shaw 2010). When fitting parametric failure time models, we considered a variety of distributions (exponential, Weibull, log-normal, log-logistic) and decided among competing distributions using Akaike's information criterion (AIC). All statistical analyses were performed using the R environment for statistical computing (R Core Team 2016).

Results

Associations among variables and movement.—As expected, the three measures of body size at release (mass, SVL, and TL) were strongly correlated (minimum r = 0.845; maximum r = 0.939) with one another. Similarly, all measures of movement (area with start, perimeter with start, area without start, perimeter without start, MDBML) were highly correlated (minimum r = 0.811; maximum r = 0.993). However, MDBML was more weakly correlated with area and perimeter (r = 0.811 for MDBML and area without start; r = 0.836 between MDBML and perimeter without start) than measures of area and perimeter were with one another (r = 0.928 between area without start and perimeter without start). In general, mass was the measure of body size that was most strongly correlated with the various measures of movement. In particular, mass and perimeter without start point (r = 0.373) and mass and MDBML (r = 0.422) were the body size and movement variables that exhibited the strongest correlations. As expected, age-2 animals had significantly larger body masses at time of release than the age-1 animals (Fig. 2).

Among age-1 alligators, MDBMLs were highest (217 m; N = 9) in October and decreased through winter to 8 m (N = 4) in March (Fig. 3). MDBMLs increased to 110 m (N = 2) by June 2010 (Fig. 3). However, among age-2 alligators, MDBMLs were relatively consistent from June through September (range = 150–255 m; N = 7–8) and increased to > 450 m (N = 7) in October and November before decreasing to 249 m (N = 5) in January. By March, MDBMLs had increased to 638 m (Fig. 3). It is important to note that only three of the five remaining age-2 alligators could be located in March due to faint signals. However, we were able to detect the lack of any mortality signals. Thus, we

TABLE 2. Parameter estimation and model selection for log-logistic failure time models on age-1 alligator survival.

Parameter/quantity	Full model	Step 1[a]	Step 2[b]	Minimum adequate model[c]
Intercept	3.660	5.300	5.316	4.913
Std. error	2.330	4.35×10^{-1}	4.51×10^{-1}	2.34×10^{-1}
z-value	1.575	12.177	11.790	21.02
P-value	0.115	4.12×10^{-34}	4.27×10^{-32}	3.95×10^{-98}
Mass	1.28×10^{-3}	N/A	N/A	N/A
Std. error	1.82×10^{-3}	N/A	N/A	N/A
z-value	0.705	N/A	N/A	N/A
P-value	0.481	N/A	N/A	N/A
Area without start	1.35×10^{-5}	1.31×10^{-5}	N/A	N/A
Std. error	1.82×10^{-5}	1.87×10^{-5}	N/A	N/A
z-value	0.743	0.698	N/A	N/A
P-value	0.456	0.485	N/A	N/A
MDBML	-4.00×10^{-3}	-4.43×10^{-3}	3.40×10^{-3}	N/A
Std. error	3.41×10^{-3}	3.52×10^{-3}	3.23×10^{-3}	N/A
z-value	-1.171	-1.258	-1.050	N/A
P-value	0.241	0.209	0.293	N/A
Log(scale parameter)	-1.050	-1.020	-0.981	-0.913
Std. error	3.32×10^{-1}	3.31×10^{-1}	3.31×10^{-1}	3.29×10^{-1}
z-value	-3.158	-3.066	-2.960	-2.770
P-value	0.002	0.002	0.003	0.005
Log-likelihood of model	-20.90	-21.2	-21.4	-22
Overall model χ^2	2.06	1.57	1.08	N/A
df	3	2	1	N/A
P-value	0.560	0.46	0.30	N/A

[a]Likelihood ratio test comparing the full model and step 1: Deviance = 0.489, df = 1, P = 0.485

[b]Likelihood ratio test comparing step 1 and step 2: Deviance = 0.490, df = 1, P = 0.484

[c]Likelihood ratio test comparing step 2 and the minimum adequate (null) model: 1.082, df = 1, P = 0.298

N/A = parameter/quantity not estimated

considered all five alligators to be alive. With respect to area traveled (area without start), there was a great deal of variability among each age class (Fig. 4A), and several individuals within each age class made a very large initial movement upon release. Accordingly, we determined area traveled with and without the initial starting point, and statistical analyses were restricted to data in which the initial movements were excluded. Linear regression revealed that both the natural logarithm of area without start (slope = 4.453, Std. Error = 1.746, t = 2.551, df = 14, P = 0.023; R^2 = 0.317; Fig. 4A) and the square root of MDBML (slope = 9.764, Std. Error = 4.448, t = 2.195, df = 15 P = 0.044, R^2 = 0.243; Fig. 4B) had slopes that significantly differed from zero when regressed against ln(mass).

Survival of age-1 alligators.—In 2009, minimum air temperatures began to fall below freezing in mid-November (Fig. 5). The first mortality was found scavenged on the shore on 10 December 2009, and the second mortality was found intact on the shore on 5 January 2010, both following several days of sub-freezing temperatures (Fig. 5A). Between 5 January and 12 January 2010, the most severe freezing events of that winter occurred with maximum and minimum air temperatures as low as -2.5 and -11.8°C, respectively (Fig. 5A), and most of the aquatic habitat available had substantial ice covering. Three additional mortalities were located on 12 January 2010, including two animals that were found dead in the icing position in shallow water near the shore (one with its snout frozen in the ice, the other with its snout surrounded by a small pocket of water). On the same date, of the four alligators remaining alive, two were observed in the icing response, and another was trapped under 4 cm of ice and giving a mortality signal indicating it had not moved in at least 24 h. This individual did not respond to our presence but its status was determined as alive in a subsequent tracking event—a result that demonstrates the importance of following up on ambiguous mortality signals. One study animal was found dead in March 2010, and another in April 2010. In summary, two of the nine (22%) age-1 alligators remained alive after winter. We noted that age-1 alligators were consistently found in shallow water (<1 m deep) and near shore during cold events, or basking on the shore on warm days.

Survival of age-2 alligators.—Eight alligators were released in June 2010, but by the onset of winter, three of the eight transmitters had become detached or failed. Consequently, we were only able to monitor five age-2 alligators through winter. However, animals that were lost from the study were included as censored observations in our survival analysis (see below). Air temperatures began to fall below freezing in early November 2010. We found all five alligators alive each month, and noted that, unlike age-1 alligators, they generally moved into deeper water as winter progressed. The minimum air temperature average for a two-week period starting on 1 February 2011 was -7.2°C with a minimum temperature of -15.5°C observed on 5 February 2011 (Fig. 5). We located all five alligators alive on 12 February 2011. At this time,

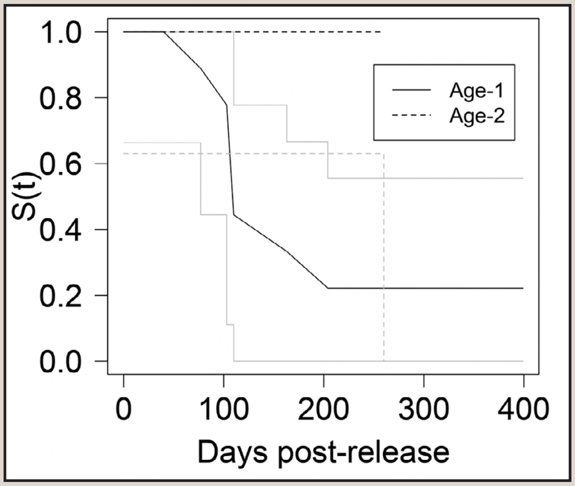

FIG. 6. Non-parametric maximum likelihood estimates (NPMLE) of survival as a function of time, S(t), for age-1 animals (solid black line) and age-2 animals (dashed black line). Ninety-five percent confidence intervals of the NPMLEs based on 10,000 bootstraps are shown as solid gray lines for age-1 animals and dashed gray lines for age-2 animals.

there was significant ice cover extending approximately 4.0 m from the shore. Each alligator was submerged at a depth of > 1 m, 10–50 m from the shore in open water. By the final tracking event on 12 March 2011, minimum and maximum air temperatures remained above freezing, and all five remaining alligators were alive and responsive to our disturbance. All had moved back to shallow areas with abundant emergent vegetation. Thus, 100% of the alligators with functional transmitters survived, and at least 62.5% of the eight age-2 alligators survived the winter.

Statistical analyses of survival.—The non-parametric maximum likelihood estimates of generalized Kaplan-Meier curves for age-1 and age-2 alligators are shown in Fig 6. The estimates for age-1 and age-2 animals statistically differed from one another (n Score Statistic for age-1 alligators = 3.671, n Score Statistic for Age-2 alligators = -3.671, $P = 0.004$), with age-2 alligators having significantly higher survival than age-1 animals. Out of the distributions that we considered for our parametric failure time analyses of age-1 alligators, the log-logistic best fit the data (Table 1). As can be seen in Table 2, neither area without start, MDBML, nor mass significantly explained variation in survival among age-1 animals. Consequently, step-wise removal of non-significant terms resulted in a minimum adequate model consisting of only an intercept term (Table 2).

DISCUSSION

Movement.—All but one age-2 alligator traveled between multiple wetland units, whereas, no age-1 alligators traveled between wetland units. Differences in area traveled between age-1 and age-2 alligators could be associated with a reduced activity season because of our decision to release the first age group after the summer instead of during summer as we did with the age-2 alligators. However, age-2 alligators did not restrict winter movements whereas age-1 alligators did. It is possible that age-1 alligators were at a thermal disadvantage due to smaller body size and lower thermal inertia. As such, age-1 animals may not have been able to maintain body temperatures high enough for unrestricted winter movements (Lee et. al. 1997). Thus, increased movement may have enabled age-2 alligators to find habitat that provided thermal refugia, which in turn may have contributed to their higher survival rates. While we cannot rule out the possibility that differences in survival between age-1 and age-2 animals trace to differences in release conditions, it is clear that body size at release influenced movement, as ln(mass) explained approximately one-third of the variation in ln(area without start) and approximately one-quarter of the variation in sqrt(MDBML).

Survival and habitat use.—Although our sample sizes are modest, the exact log-rank test that we conducted suggests that age-2 animals had higher survivorship than age-1 animals. While it is important to note that this cohort effect is strongly confounded with year-specific ecological effects and potentially important differences in release conditions (see above), it is unlikely that the difference in survival between age-1 and age-2 animals is entirely a result of climatological differences between the first and second years of our study. Of particular relevance to this view is that the harshest temperatures during our study were observed in 2011 when age-2 animals were experiencing their first winter in the wild. In addition, we also observed clear differences in behavior between age-1 and age-2 animals, with age-2 animals tending to favor open water during freezing periods and age-1 animals tending to stay closer to shore. In particular, age-2 alligators were always observed in deeper water >10 m away from the shore during freezing events. In contrast, all of the age-1 deaths that we observed occurred out of water, or in shallow areas that had frozen over. These results support the idea that deep water may provide refugia in the form of heat sources (Brisbin et. al. 1982). Brisbin et. al. (1982) reported that an adult alligator that submerged in deeper portions of a lake survived ambient air temperatures as low as -8.4°C, whereas a similarly sized alligator that remained immobile in shallow water died. Collectively, our results are consistent with the view that age-1 and age-2 animals differed in their behavioral responses to freezing temperatures and that these differences in behavior affected survival.

Finally, while our data suggest that body size and movement were important factors underlying differential survival between age-1 and age-2 alligators, we were unable to find evidence that these factors explained variation in survival among age-1 animals. Consequently, the primary inference we can draw about survival in the age-1 cohort is that the risk of death (i.e., the instantaneous hazard) increased sharply until approximately 110 DPR (mid-January 2010; steeply decreasing region of the solid black line in Fig. 6) and then decreased.

CONCLUSIONS

Juvenile American Alligators in this study withstood up to two weeks of ice formation and ambient air temperatures as low as -15.5°C by utilizing the icing response and deep-water refugia. This temperature was the lowest recorded temperature during our study and to our knowledge, is the lowest air temperature ever recorded at which alligator survival has been documented. Our results support the hypothesis that the northern distribution of American Alligators is more limited by the severity and duration of freezing periods than the inability to withstand ice formation (Lee et. al. 1997). Arbour and Bastarache (2006) suggested that recruitment at RSWMA is low, and our results suggest that the low rate of overwinter survival of age-1 alligators contributes to low recruitment. Repatriation programs for alligators have been suggested by Temsiripong et. al. (2006) as an option for increasing recruitment in areas where predation rates are high and/or flooding is common. Elsey and Kinler (2012) provide a rationale as to why captive-raised alligators in Louisiana should be at least 91 cm TL upon release, and although the alligators in our study were smaller than 91 cm TL upon release, our results do support the idea that size and age are important considerations when designing captive-release programs. As such, when repatriating or subsidizing populations with captive-raised juveniles in areas where temperatures are similar to those at RSWMA, we recommend releasing alligators that are at least two years of age.

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