

SURVIVAL OF YOUNG AMERICAN ALLIGATORS ON A FLORIDA LAKE

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Abstract: A capture-recapture study was conducted on Orange Lake, Florida, from 1979 through 1984 to estimate survival rates of young in an American alligator (*Alligator mississippiensis*) population. Hatchlings remained together in sibling groups (pods) for at least their 1st year and then began to disperse during their 2nd spring and summer. Mortality through mid-November of their 1st year was negligible. Jolly-Seber (JS) survival estimates of hatchlings for 6 and 12 months were 76 and 41%, respectively. The 2-year JS estimate for the 1980 cohort was 8%. Minimum-Known-Alive (MKA) survival values were 72 and 46% of JS estimates for 6 months and 1 year of age. Survival during the 2nd 6 months of life (spring-summer) tended to be lower than survival during the 1st 6 months (fall-winter).

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Generally, crocodylians are secretive; they quickly learn to avoid humans and frequently inhabit areas that are difficult to access. These factors render them difficult subjects for survival studies. Therefore, most references to survival rates have been based on casual observations (Neill 1971), small samples (McIlhenny 1935, Modha 1967, Murphy 1977, Webb et al. 1977), or interpretation from population size structures (Chabreck 1966, Graham 1968, Nichols et al. 1976, Webb et al. 1983, Taylor and Neal 1984). Recent mark-recapture studies have attempted to estimate survival rates, using MKA estimates, for American alligators (Deitz 1979) and salt-water crocodiles (*Crocodylus porosus*) (Messel et al. 1981:390-394) <2 years of age. The MKA survival rate estimator is used extensively by crocodylian researchers because of its simplicity. However, as its name implies, MKA estimates are biased (Nichols and Pollock 1983).

Survival rates are an important component of population models (Nichols 1987), especially when models are intended for use in predicting population responses to harvest strategies. Furthermore, growing emphasis on early age-class harvest will make juvenile survival rates increasingly important when evaluating the suitability of various alligator populations for egg or hatchling removal.

Our work on Orange Lake, Florida, provided an opportunity to conduct long-term mark-recapture studies on a relatively abundant and accessible population of alligators. Our primary

objectives were to estimate survival rates of juvenile alligators using the JS estimator (Jolly 1965, Seber 1965) and to determine the relationship between the JS and MKA estimators.

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METHODS

Study Area

Orange Lake, in northcentral Florida, is a 5,140-ha mesotrophic lake fringed with an extensive marsh characterized by floating islands and mats (Reid 1952). These islands are colonized by arrowhead (*Sagittaria* spp.), pickerelweed (*Pontederia lanceolata*), water pennywort (*Hydrocotyle umbellata*), maidencane (*Panicum hemitomon*), and cattail (*Typha* spp.) during their early development and change successional to stationary tree islands dominated by sweet gum (*Liquidambar styraciflua*), willow (*Salix* spp.), wax myrtle (*Myrica cerifera*), and button bush (*Cephalanthus occidentalis*). Other emergent marsh is dominated by sawgrass (*Cladium jamaicense*) and cattail. The open water is generally fringed with spatterdock (*Nuphar luteum*) and, to a lesser extent, American lotus (*Nelumbo lutea*). In some years, extensive areas of the limnetic zone are covered with hydrilla (*Hydrilla verticillata*), and waterhyacinth (*Eichhornia crassipes*) has become a major vegetational component since 1982.

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Field Methods

Alligator nests were initially located by airplane or helicopter in mid-July 1979–82 and marked on aerial photographs. Airboat crews ground-marked nests for subsequent visits. Nest status was monitored through early September. Apparently successful nests were revisited at night to capture newly hatched alligators by searching the immediate area around the nest with a low intensity (15,000 candle power) spotlight. If hatchlings could not be found, the search pattern was expanded to cover accessible marsh and open water in the general vicinity of the nest. Hatchlings were captured by hand or with Pilstrom tongs (Pilstrom Tong Co., Ft. Smith, Ark.). (Reference to trade names and companies does not imply endorsement by the Fed. Gov. or the State of Fla.) During the tagging process, additional siblings, previously missed, often appeared. These hatchlings were collected, and the entire process was repeated until no more untagged animals were sighted. Hatchlings were marked with sequentially numbered #1 Monel tags (Nat'l. Band and Tag Co., Newport, Ky.) inserted through the web between the 2nd and 3rd digits of the right rear foot. Tags were inserted $\frac{3}{4}$ of the tag length into the web for maximum retention. All animals were released at their original capture sites.

Subsequent attempts to recapture marked hatchlings were made in the spring (Mar–May) and fall (Sep–Nov) of each year (1980–84). Although we attempted to revisit pods at regular intervals, changes in water levels, vegetation densities, and equipment capabilities limited accessibility to certain areas. Therefore, recapture efforts were not equal for all pods or all years.

Statistical Methods

Animals used in the following analyses were distributed throughout Orange Lake and initially captured in the late summer and fall (23 Aug–11 Nov) of their 1st year. Initial capture and tagging occurred from 1979 to 1982 and recaptures from 1980 to 1984.

Juvenile Survival.—The JS model was used to estimate 6-month and 1-year survival probabilities for each marked cohort of hatchlings. Data permitted computation of survival estimates to 2 years for the 1980 cohort. Data with adequate sample size and regular capture effort were available from 3 cohorts, representing alligators hatched in the summers of 1979, 1980,

and 1981. Separate JS analyses were conducted for each of these cohorts. In addition, we pooled animals from 1979–82 cohorts for a single JS analysis. In this latter analysis we ignored calendar year and pooled animals captured at the same ages. For example, all initial captures were pooled to define a single composite cohort. All animals captured in the spring following initial tagging were pooled to form a composite group of alligators captured 6 months after hatching, and similar pooled groups were used for recaptures at ages 1, 1.5, and 2 years. In all analyses we used the bias-adjusted survival rate estimator of Seber (1982:204). The estimated standard errors included both sampling variation or "error of estimation" (Jolly 1965) and binomial non-sampling variation associated with the death process. Goodness-of-fit was assessed whenever possible, using the test suggested by Pollock et al. (1985).

All survival estimates, $\hat{\phi}_i$, correspond to approximate 6-month intervals. The probability of a young alligator tagged in its 1st fall surviving to the 2nd fall was estimated as:

$$\hat{\phi}^* = \hat{\phi}_1 \hat{\phi}_2,$$

where $\hat{\phi}_1$ corresponds to the survival probability from initial fall to the following spring, and $\hat{\phi}_2$ extends from the 1st spring to the 2nd fall. The standard error of $\hat{\phi}^*$ was estimated as:

$$\widehat{SE}(\hat{\phi}^*) = \sqrt{(\hat{\phi}^*)^2 \left(\sum_{i=1}^2 \frac{\widehat{VAR}(\hat{\phi}_i)}{\hat{\phi}_i^2} + \frac{2 \widehat{COV}(\hat{\phi}_1, \hat{\phi}_2)}{\hat{\phi}_1 \hat{\phi}_2} \right)},$$

where \widehat{SE} , \widehat{VAR} , and \widehat{COV} denote estimates of standard errors, variances, and covariances, respectively. We tested for age- and time-specific variation in survival and capture probabilities using both Z-statistics (Brownie et al. 1985:180–182) and constant-parameter models B and D of Brownie et al. (1986). Model B assumes constant survival/unit time over all sampling periods but incorporates temporal variation in capture probability. Model D assumes constant survival and capture probabilities. Likelihood ratio tests between pairs of models (B, D, and A [the standard JS model]) were used to test hypotheses about variation in capture and survival probabilities (Brownie et al. 1986). Marked and unmarked pods were assumed to have similar survival probabilities.

We also computed MKA survival rate "esti-

Table 1. Six-month interval and cumulative survival rates estimated by the Jolly-Seber model for young American alligators at Orange Lake, Florida.

| Year hatched | No. of alligators | Period | 6-month intervals | | | | | | | |
|----------------------|-------------------|------------|-----------------------------|-----------------|---------------------------------|------|---------------------------------|------|---------------------------------|------|
| | | | Fall (i)- spring (i + 1) | | Spring (i + 1)- fall (i + 1) | | Fall (i + 1)- spring (i + 2) | | Spring (i + 2)- fall (i + 2) | |
| | | | \bar{x} | SE ^a | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE |
| 1979 | 166 | 6-month | 0.55 | 0.05 | 0.69 | 0.11 | | | | |
| | | Cumulative | 0.55 | 0.05 | 0.38 | 0.06 | | | | |
| 1980 | 359 | 6-month | 0.82 | 0.14 | 0.50 | 0.30 | 0.85 | 0.56 | 0.23 | 0.12 |
| | | Cumulative | 0.82 | 0.14 | 0.41 | 0.23 | 0.35 | 0.12 | 0.08 | 0.04 |
| 1981 | 222 | 6-month | 0.82 | 0.05 | 0.46 | 0.10 | | | | |
| | | Cumulative | 0.82 | 0.05 | 0.38 | 0.08 | | | | |
| 1979-82 ^b | 921 | 6-month | 0.76 | 0.04 | 0.54 | 0.09 | | | | |
| | | Cumulative | 0.76 | 0.04 | 0.41 | 0.06 | | | | |

^a SE estimates include both sampling error (or "error of estimation," Jolly 1965) and binomial nonsampling variation associated with the death process.

^b All animals in the 4 annual cohorts were combined to provide overall estimates for the 1st year of life.

mates" for hatchling alligators tagged and recaptured during the study period (1979-84). MKA survival rates represent the proportion of tagged animals known to survive to a certain age from an initial sample of tagged animals.

August-November Mortality Within Pods.—JS analyses do not account for mortality occurring prior to initial capture. Therefore, we conducted an ad hoc analysis to gain some insight into mortality during the period from 23 August through 11 November. We plotted the natural logarithm of the number of hatchlings caught in each pod against the date of capture for the pod. If several assumptions are met, then the resulting plot should be linear, and the negative of the estimated slope of the regression should estimate the instantaneous daily mortality rate of hatchlings within pods. (Note that losses of entire pods will not be included in this mortality rate estimate.) We then used analysis of covariance to determine if the slopes for individual cohorts were significantly different. If yearly slopes were not different, we combined all years and used simple linear regression methods (Steel and Torrie 1960:161-182) to estimate the overall slope (SAS Inst., Inc. 1982). Tests of the hypothesis that the resulting regression slopes equalled 0.0 constituted crude tests of the hypothesis of no mortality from 23 August to 11 November.

RESULTS

Pod Behavior

As described by Deitz (1979), we found that pods remained near the nest until the spring following hatching if adequate pools of water

were available. Pods were occasionally observed to move >200 m from the original nest site during their 1st year, usually in search of permanent water. We confirmed Deitz's (1979) observations that hatchling pods began as cohesive units and remained together throughout their 1st year. Pod integrity was less conspicuous by the 2nd summer, and after 4 years, Orange Lake alligators showed no obvious attachment for specific nest sites or siblings. Most hatchlings showed little or no avoidance behavior when encountered at night on the 1st and 2nd capture events as hatchlings; however, after their 1st year, they appeared to become more wary with age and each subsequent capture attempt.

Juvenile Survival

Capture histories from a total of 921 alligators were used in our analyses. There were no recaptures for the 1982 cohort in the 3rd sampling period (fall of 1983), so we were not able to obtain estimates or test models for this cohort alone; however, we used data from all 4 cohorts in our combined analysis. Table 1 presents survival rate estimates computed by the JS model.

Results of relevant model tests are summarized in Table 2. The goodness-of-fit tests provided no evidence that the JS model (Model A) did not fit the data for the 3 separate cohorts although the power of this test is not expected to be high for these sample sizes (Pollock et al. 1985). However, this test provided strong evidence that the combined cohort data did not fit Model A. The Model D vs. A tests were significant for all 3 cohorts, providing strong evidence that capture and/or survival probabilities varied

Table 2. Results of goodness-of-fit and between-model tests for survival models A, B, and D of Brownie et al. (1986) for young American alligators at Orange Lake, Florida.

| Cohort | Sampling periods | Model A goodness-of-fit | | | Model D vs. A | | | Model B vs. A | | |
|---------|------------------|-------------------------|----|-------|-----------------|----|-------|-----------------|----|------|
| | | χ^2 | df | P | χ^2 | df | P | χ^2 | df | P |
| 1979 | 5 | 0.01 | 1 | 0.91 | 9.72 | 4 | 0.05 | NA ^a | | |
| 1980 | 7 | 0.01 | 1 | 0.93 | 91.15 | 7 | <0.01 | 4.72 | 2 | 0.09 |
| 1981 | 6 | 1.85 | 1 | 0.17 | 114.82 | 4 | <0.01 | NA ^a | | |
| 1979-82 | 5 | 17.93 | 2 | <0.01 | NA ^b | | | NA ^b | | |

^a Insufficient data for test.

^b Model A did not fit data, so subsequent tests are inappropriate.

with age and/or time. There were sufficient data for the Model B vs. A test only for the 1980 cohort. The test provided some evidence ($P = 0.09$) of variation in 6-month survival probabilities from 1 age and time period to the next.

Model A estimates of capture probability are presented in Table 3. In each of the 3 cohorts, point estimates of capture probability are higher in the 1st spring than in subsequent periods. This is consistent with field observations that alligators become more difficult to capture after they grow beyond the hatchling stage. The Model D vs. A test results (Table 2) and the Model D vs. B results (highly significant for each cohort, $P < 0.01$) provide statistical evidence of time and/or age variation in capture probability. The point estimates of capture probability for specific sampling periods (e.g., spring [$i + 1$] and fall [$i + 1$]) show substantial variation among the 3 cohorts (Table 3) and are probably largely responsible for the poor fit of Model A to the 1979-82 combined-cohort analysis (Table 2).

The decrease in capture probabilities, and thus in data, with time since initial tagging led to progressively poorer estimates of survival. The 1st 2 survival estimates had relatively low standard errors and coefficients of variation, and are thus reported for all 3 cohorts and for the combined cohort (Table 1). We present the 1st 4 survival estimates for the 1980 cohort, which had the largest initial sample size of tagged individuals. The Model B vs. A test provided evidence of variation in survival associated with age and/or time for the 1980 cohort, the only group for which this test could be run. The fall-spring survival estimate appeared larger than the spring-fall estimate for the 1980 and 1981 cohorts and for combined cohorts, 1979-82 (Table 1). The difference was significant ($Z = 2.98$, $P < 0.01$) for the 1980 animals.

MKA survival rates were calculated to 4 years of age and are presented in Table 4. These are

poor estimates of survival and are presented solely for comparison with JS estimates in order to approximate the bias of MKA "estimators."

August-November Mortality Within Pods

Initial capture dates for animals used to compute survival estimates varied from 23 August to 11 November. Although exact hatching dates were not known for most clutches, it is likely that pods were 1st captured from 1 to 90 days after hatching.

After concluding that yearly slopes of $\ln(\text{pod size})$ and initial capture date were not significantly different ($F_{3,30} = 0.24$, $P = 0.87$), we pooled observations from all years. The estimated common slope was -0.0015 but was not significantly different from 0 ($F_{1,33} = 0.11$, $P = 0.74$). Therefore, we concluded that mortality was minimal during that period.

DISCUSSION

The JS model permitted estimation of survival rates from recapture data. However, 4 caveats are necessary:

1. Capture periods were long, and therefore, heterogeneity in survival may have been introduced. Examination of a band recovery model closely related to the JS model has shown that the relevant estimators are relatively robust to this violation of assumptions (Nichols et al. 1982, Pollock and Raveling 1982).
2. In the combined-year analysis, we introduced heterogeneity in capture probabilities for animals in different cohorts. Evidence that such heterogeneity is present is found in the goodness-of-fit test statistic for combined cohorts (Table 2) and in the different \hat{p}_i associated with the different cohorts (Table 3). Survival estimates are extremely robust to

Table 3. Capture probability estimates (\hat{p}) of young American alligators for the 1st 3 sampling periods after hatching at Orange Lake, Florida.^a

| Cohort (fall, <i>i</i>) | Spring (<i>i</i> + 1) | | Fall (<i>i</i> + 1) | | Spring (<i>i</i> + 2) | |
|-----------------------------|------------------------|-------------------|----------------------|-------------------|------------------------|--------------------------------|
| | \hat{p}_i | SE(\hat{p}_i) | \hat{p}_i | SE(\hat{p}_i) | \hat{p}_i | SE(\hat{p}_i) ^b |
| 1979 | 0.72 | 0.064 | 0.61 | 0.097 | 0.24 | |
| 1980 | 0.30 | 0.056 | 0.04 | 0.028 | 0.29 | 0.097 |
| 1981 | 0.85 | 0.050 | 0.41 | 0.093 | 0.16 | |

^a Estimates are based on Model A, the Jolly-Seber model.

^b Blanks indicate that quantities could not be estimated.

heterogeneity of capture probabilities (Carrothers 1973, 1979; Nichols and Pollock 1983). Nevertheless, although the point estimates are probably reasonable, the standard error estimates may not be, so we chose not to conduct Z-tests using these combined-year estimates.

- The fate of a marked individual is probably not independent of the fate of other marked individuals within the same pod. This should not affect survival estimates but may cause variance estimates to be biased low (Pollock and Raveling 1982). If they occurred, such biases would affect Z statistics and their associated probability levels.
- Pod-to-pod variation in survival and/or capture probabilities may have existed. However, the goodness-of-fit tests provided no indication of heterogeneity for the single-cohort analyses. Also, as noted before, JS survival rate estimators have been found to be relatively robust to such heterogeneity (Carrothers 1973, 1979; Nichols et al. 1982; Pollock and Raveling 1982; Nichols and Pollock 1983). In general, we believe that the JS estimator provided an approximately unbiased estimate of survival rates.

Six-month and 1-year survival estimates were 76 and 41%, respectively, for the JS analysis and 53 and 19%, respectively, for the MKA analysis. A comparison of these values gives an indication of the magnitude of bias associated with MKA estimates. The ratio of MKA/JS estimates was 72% for 6 months (estimated relative MKA bias = 28%) and 46% for 1 year (estimated relative MKA bias = 54%).

Deitz (1979) found similar 6-month MKA survival rates on both Orange Lake (52%) and Lake Griffin (47%) in central Florida. Deitz also reported 1-year MKA survival rates of 35% on Orange Lake and 30% on Lake Griffin, which

Table 4. Minimum-Known-Alive (MKA) survival estimates of alligators tagged 1979–82 on Orange Lake, Florida.

| Age | Marked animals in pop | MKA | MKA survival rate |
|-----|-----------------------|-----|-------------------|
| 0.0 | 921 | 921 | 1.000 |
| 0.5 | 921 | 489 | 0.531 |
| 1.0 | 921 | 176 | 0.191 |
| 1.5 | 921 | 122 | 0.133 |
| 2.0 | 747 | 31 | 0.042 |
| 2.5 | 747 | 22 | 0.030 |
| 3.0 | 525 | 4 | 0.008 |
| 3.5 | 525 | 3 | 0.006 |
| 4.0 | 166 | 0 | 0.000 |

were substantially higher than our MKA rate. However, Deitz recaptured pods much more frequently and followed their movements throughout their 1st year, which probably increased his recapture efficiency and, thus, MKA survival rates. Messel et al. (1981:390–394) reported that MKA 1-year survival of saltwater crocodiles in Australia was 38% and speculated that actual survival was probably 46%, which was close to our estimates.

For the 1980 cohort, we were able to estimate the probability of surviving to the fall of the 2nd year (8%). As noted earlier, pod integrity declined after the 1st year and many of the losses indicated in the 2nd year likely represent emigration from the immediate sampling area, rather than mortality. Therefore, as the JS survival estimate represents a combination of emigration and mortality, true survival can be expected to be higher than 8%.

Our test for declining pod size during August–November provided an indirect means of testing for early mortality. The relatively constant pod sizes we observed suggested that mortality prior to initial tagging was minimal and that the JS estimates we present in Table 1 are representative of survival from hatching.

Little is known about the causes of mortality in alligators. Nichols et al. (1976) believed that cannibalism was the major density-dependent factor and speculated that cannibalism may account for 2–6% of the annual mortality. Cannibalism has not been well documented in alligators. However, on Orange Lake, Delany and Abercrombie (1986) found indirect evidence of cannibalism through the recovery of web tags from stomachs of harvested alligators. Delany (unpubl. data) also found that mortality appears to be highest on alligators in the 40–80-cm total

length range, which corresponds approximately with the size at which alligators begin dispersing and occupying deep pools and marsh fringe (Deitz 1979).

There was some evidence that spring-fall survival was lower than fall-spring survival (evidence was strongest for the 1980 cohort). This suggests that mortality increased during the warmer months, which represent the major feeding period for alligators. In Florida annual water levels are lowest during the March-July period; this concentrates alligators in the remaining water and makes them more vulnerable to cannibalism as well as to heat, disease, and restricted food supply. Webb and Smith (1984:344-345) suggested that hatchling survivorship of Johnstone's crocodiles (*C. johnstoni*) is greatly enhanced by early moderate rains, which lead to an abundance of food and increased availability of wet habitats. Although our data were insufficient to demonstrate this phenomenon on Orange Lake, it is likely that years with low rainfall increase stress on alligators by limiting available water and food in the protective marsh and, thereby, increase mortality.

High early survival may occur only in habitat types (such as the dense emergent and floating marsh found on Orange Lake) that provide many small pools and water trails for hatchlings to inhabit during their 1st few months. These areas are not commonly used by larger alligators (TL > 1.8 m), except for adult females (Goodwin and Marion 1979), and therefore provide a refuge for hatchlings. As pods disperse during their 1st summer (Deitz 1979), they begin to use larger pools and deeper water areas that are inhabited by larger alligators, thereby increasing their chances of being preyed upon.

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ACCURACY OF DAILY POINT RELOCATIONS IN ASSESSING REAL MOVEMENT OF RADIO-MARKED ANIMALS

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Abstract: Correlation coefficients were calculated for the straight line distances between telemetry relocations taken at 24-hour intervals and the sum of the distances between relocations taken more frequently over 24 hours for pronghorns (*Antilocapra americana*), coyotes (*Canis latrans*), bobcats (*Felis rufus*), and mallards (*Anas platyrhynchos*). In only two of 8 comparisons was there a statistically significant correlation between "perceived" and "real" distance travelled. This suggests that using daily relocation data as a measure of real or relative movement for comparisons between subsets of a population (e.g., M vs. F or ad vs. juv), or seasonal comparisons within a subset, may not be a valid practice.

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Before the widespread use of radio telemetry in wildlife research, the time span between relocations of individually marked animals was variable and uncontrollable. Nonetheless, a large body of information was accumulated regarding home ranges and movements of individuals and demographic groups, such as juveniles, pregnant females, or adult males. The advent of reliable telemetry equipment allowed researchers more control over the frequency with which marked animals were located. In many telemetry studies radio-collared animals were relocated once daily at approximately 24-hour intervals. The distance between these resulting consecutive point locations was calculated and

used by many researchers as an index of the total daily movement for an individual (Bailey 1974, Kitchings and Story 1979, Steigers and Flinders 1980, Taylor and Guthery 1980, Springer 1982, Young and Ruff 1982, Whiteside and Guthery 1983, Hemker et al. 1984, Lawhead 1984, Riley and Dood 1984, Knowles 1985, Hines 1986). These distances, which we call perceived daily movements, were usually reported as daily movement or mobility. Perceived movements were often compared relative to various factors (e.g., sex, age, or season), and conclusions were drawn concerning effects these factors have on movement. For these comparisons to be meaningful and conclusions to be valid, perceived daily movement must have a consistent relationship with the distance actually travelled in 24 hours by the animal; i.e., the real movement.

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