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MORTALITY OF AMERICAN ALLIGATORS ATTRIBUTED TO CANNIBALISM

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Abstract: Mortality of juvenile (<122 cm total length; TL) American Alligators (*Alligator mississippiensis*) attributed to cannibalism on Orange Lake, Florida was examined. Alligator web tags used in mark–recapture studies were found in 12% of 267 stomachs sampled from alligators ≥168 cm TL. Captive alligators retained 76% of force-fed tags during a 588-d tag-retention trial. Models relating the probability of tag recovery to the annual probabilities of juvenile survival, cannibalism, tag retention, adult survival, and adult harvest suggested that cannibalism may on average remove 6–7% of the juvenile alligator population annually. Vulnerability continued to 140 cm TL (age 6–8 yr). Cannibalism of juveniles may serve to regulate the alligator population on Orange Lake. Alligator cannibalism may vary widely among populations, depending on demography and environmental conditions. The role and importance of cannibalism in alligator population dynamics should be more fully assessed and environmental and population factors that influence cannibalism identified to better evaluate management programs.

Key words: American Alligator; *Alligator mississippiensis*; Band recovery models; Cannibalism; Florida; Mortality; Stomach contents; Survival

Cannibalism occurs among a wide range of taxa and can have important ecological implications (Elgar and Crespi, 1992). Consumption of conspecifics can sustain a population by providing an alternative food if other sources are scarce, remove potential competitors, and serve to regulate population size and age structure (Dong and Polis, 1992; Fox, 1975; Polis, 1981; van den Bosch et al., 1988). Although usually considered facultative and beneficial at the individual predator and population levels, cannibalistic behavior has some implicit costs. Cannibals may sustain injury during predation, lose inclusive fitness if they consume relatives, and risk increased exposure to pathogens and parasites (Dong and Polis, 1992; Fox, 1975; Polis, 1981). Cannibalism appears to occur opportunistically during predatory behavior of reptiles (Polis and Myers, 1985) and may be density dependent (Mitchell, 1986).

The magnitude and influence of cannibalism in crocodilian populations is difficult to assess (Cott, 1961; Messel and Vorlicek, 1986; Neill, 1971; Richards and Wasilewski, 2003). The occurrence of American Alligator (*Alligator mississippiensis*) remains and marking tags in alligator stomachs may evince intraspecific predation (Delany and Abercrombie, 1986; Rootes and Chabreck, 1993), consumption as carrion (Giles and Childs, 1949), ingestion after agonistic encounters (Valentine et al., 1972), or oophagy after nest opening (McNease and Joanen, 1977). Cannibalism among American Alligator populations may be demographically important. For example, Nichols et al. (1976*a*) predicted annual mortality rates of 2–6% due to cannibalism among alligators in Louisiana, and Rootes and Chabreck (1993) estimated that cannibalism accounted for ≥50% of the total annual mortality of alligators on their study area in Louisiana.

Cannibalism was suspected as a cause of some mortality of juvenile (<122 cm total length; TL) alligators on Orange Lake, Florida, USA (Woodward et al., 1987). Our objective in this study was to estimate the rate of cannibalism among American Alligators on Orange Lake, Florida by analyzing the recovery probabilities of marking tags from alligator stomachs sampled during harvests.

Materials and Methods

Tag Occurrence in Stomachs of Wild Alligators

Data were collected at Orange Lake, Alachua County, Florida. The 5140-ha lake

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is shallow (1.8 m average depth) and mesotrophic. Reid (1952) described the vegetational components of the lake's extensive perimeter marshes and floating islands. During 1975–1987, 3851 alligators were captured on Orange Lake, marked with serially numbered 10–15-mm Monel tags in the webbing of the right foot, and released. Tagging methods were described by Woodward et al. (1987). Tags were generally retained for several years and holes created in the webbing appeared to be permanent. The right rear feet of captured alligators were inspected for the presence of tags or holes during 1981–1987. We found that less than 1% of recaptured alligators ≤0.9 m total length (TL) and only 2% of alligators 0.9–1.8 m TL showed evidence of tag loss. We therefore considered tag loss to be negligible for alligators ≤1.8 m TL.

Stomachs were collected from 267 hunter-harvested wild alligators during 1981–1987 and examined for tags. Of those, Delany and Abercrombie (1986) examined 146 stomachs collected during 1981–1983. Of those, 76 were subadults (122–183 cm TL), and the stomach of only one (168 cm TL) of them contained evidence of cannibalism. Therefore, only stomachs of adult alligators (≥183 cm TL) were analyzed. We used mark–recapture records for the total number of alligators tagged, year of tagging, pod (sibling group) affiliation, and TL at last capture. Alligator populations on Orange Lake were estimated from annual night-light counts during 1981–1987 and adjusted for the estimated proportion of the lake surveyed (this ranged between 70% and 85%, depending on water level-related accessibility of marsh), reduction in visibility due to survey conditions (0–40% reduction in counts due to wave action, fog, and insects; Woodward et al., 1992) and estimated proportion of alligators visible at the surface of the water during an average alligator survey with good conditions (19%; Woodward et al., 1996).

Tag Retention in Stomachs of Captive Alligators

Ten alligators were maintained at a commercial alligator farm from 15 July 1986 through 23 February 1988. TL was 150–180 cm ($\bar{X}$ = 170 cm) when the study was initiated. At last measurement, on 14 August 1987, TL was 170–210 cm ($\bar{X}$ = 190 cm). Alligators were housed in indoor (July 1986–June 1987) and outdoor (July 1987–February 1988) facilities (4.6-m × 5.5-m concrete tanks) and fed commercially available fish. Care of captive animals complied with state and local standards. On 15 July 1986, each alligator was force-fed five #1 Monel web tags identical to those used in mark–recapture studies and recovered from stomachs. To simulate natural digestion, tags were attached to hatchling alligator feet removed from carcasses. Experimental alligators were restrained and force-fed using methods similar to those described by Taylor et al. (1978). Alligators were then marked with a numbered web tag and returned to the holding facility. Alligators were radiographed nine times at 16- to 108-d intervals to examine stomachs for the presence of tags; the last radiographs were taken 588 d after the start of the experiment.

Statistical Analysis

Tag retention in stomachs.—Results from the captive alligator experiment were used to estimate tag retention, or annual probability that an ingested tag remains in an alligator. Observations were treated as failure time data and were analyzed using parametric survival regression methods with the S-PLUS *survReg* function (Harrell, 2001; Insightful Corporation, 2005). If a tag disappeared from a stomach between two radiographic checks, its failure time was interval censored (it was known only that the tag had been passed sometime between two dates); if a tag was present in any subsequent radiographic check, it was considered to have survived to that date in the stomach. A tag remaining in a stomach at the end of the study represented a right censored failure time (Harrell, 2001).

Parametric failure time modeling requires choosing a survival distribution. Weibull and exponential model distributions of tag retention data were compared. Because fates of tags within the same alligator stomach might not have been independent, models were estimated with a random Gaussian effect for individual alligators.

Models were compared using the *extractAIC.survReg* function in the MASS library

for S-PLUS (Venables and Ripley, 2002) and corrected for sample size by Akaike information criterion (AIC_c; Burnham and Anderson, 2002). Retention probabilities for the tags were predicted for 12 yr by using the *predict.survReg* S-PLUS function and averaged over the 10 alligators. Median retention times were estimated with percentile confidence intervals on the basis of 10,000 bootstrap resamples (Insightful Corporation, 2002).

Cannibalism rate.—To estimate juvenile mortality due to cannibalism, we built a probability structure for modeling the number of tags recovered in stomachs of wild adult alligators. We developed these models in the band recovery framework outlined by Brownie et al. (1985). Derivation of the probability structure is described in Appendix I. Multiple assumptions were required to address this complex situation; essential assumptions are as follows:

(1) Tag recoveries in any given year from cannibalized juvenile alligators that had been released in a previous year were assumed to be complete (i.e., no released tagged juveniles had lost their tags before cannibalism by a recovered adult) and to follow a multinomial distribution.
(2) A release (as used above) was the final live capture and release of an alligator in a mark–recapture study.
(3) Total risk (i.e., average annual probability) of cannibalism was a constant annual probability for age classes 0 (hatchlings) to 3 yr and was insignificant among older animals. (Fewer than 10% of recovered tags of juveniles were from individuals ≥0.9 m TL, approximately 4 yr old, when released.)
(4) Vulnerability to cannibalism could be dependent on age or year of release, following one of three scenarios:
    (a) One-year-old vulnerability case: One-year-olds are at greater relative risk to cannibalism than other age classes because of their movement away from the protection of the maternal alligator, shallow water, and dense vegetation (Deitz, 1979; Woodward et al., 1987).
    (b) Equal vulnerability case: Juveniles of each age class are cannibalized in proportion to their abundance (i.e., no dependence on age or year of release).
    (c) Release vulnerability case: All risk of cannibalism occurs in the year of release, regardless of age. In most cases, however, released, tagged juveniles were hatchlings.
(5) Annual survival rates were constant and specific for hatchlings, 1-yr-olds, and alligators older than 1 yr. Survival rates for hatchlings and 1-yr-olds were fixed at values reported by Woodward et al. (1987; see Appendix I).
(6) Recovery of adults by hunters could be either constant or variable among years.
(7) The time window in which activities (release, cannibalism, and recovery) occurred was sufficiently narrow to be essentially instantaneous.
(8) All adults that cannibalized juveniles in a given year were equally likely to survive, retain cannibalized victim tags, and be recovered a given number of years later. The size distribution of harvested alligators was similar to those observed during night-light surveys (Woodward et al., 1992). However, the likelihood of an adult to cannibalize may not be independent of its survival fitness or its exposure to harvest.
(9) Upon release of a pod of tagged juveniles, the probability that any individual's tag would be recovered either varied independently for each individual or was the same for all members of a pod. The latter condition is possible because pods are "cohesive units and [remain] together throughout their 1st year" (Woodward et al., 1987).
(10) The probability that a tag would be retained in the stomach of a cannibal was treated in three alternative ways:
    (a) as quantified in the captive force-feeding experiments using the Weibull distribution with random individual alligator effects;
    (b) as quantified in the captive force-feeding experiments using the ex-

ponential distribution with random individual alligator effects; or

(c) as a constant estimated directly (by the SURVIV program referenced below) from Orange Lake tag-recovery data.

We compared 18 models, assuming that recovery units were either individuals or pods (assumption 9, above). These resulted from the three alternative assumptions about tag retention in stomachs (exponential, Weibull, or estimated as a constant), three alternative assumptions about juvenile vulnerability to cannibalism (1-yr-old, equal, or release), and two alternative assumptions about variation in annual adult recovery (year-specific or year-invariant harvest rate). We used program SURVIV (White, 1983, 1986) with modifications by Hines (1999) to estimate cannibalism rate, adult recovery (harvest) rate(s), adult survival rate, and in some cases (assumption 10c, above) rate of tag retention in stomachs. An example SURVIV program is presented in Appendix II. AIC_c was used to compare models within recovery-unit sets and to compute Akaike weights upon which model-averaged parameter estimates, standard errors, and 95% confidence intervals (CI) were based. Evaluations of goodness of fit and overdispersion followed recommendations by Burnham and Anderson (2002). We could not use AIC_c to compare models between recovery-unit sets because response data differed.

Results

Radiographs of captive alligators indicated that after 588 d, 38 tags (76%) remained in nine stomachs. The first tag was passed between days 43 and 106 postingestion. One alligator passed all five tags between days 287 and 395. Four alligators each retained all five tags. For the exponential survivorship model, median retention time was estimated at 3768 d (10.32 yr), 95% CI = 2906 (7.96 yr)–infinity. The Weibull model was apparently greatly influenced by increased tag passage toward the end of the study, as it estimated median tag retention at 715 d (1.96 yr), 95% CI = 598–1012 d (1.64–2.77 yr). Average annual tag retention probability was 0.94 for the exponential model and was 0.96, 0.50, 0.05, and 0 for years 1–4 for the Weibull model. AIC_c favored the exponential model over the Weibull model (110.68 vs. 144.41).

Fifty-six tags were found in 33 stomachs (12%) from 27 male and 6 female wild alligators caught at Orange Lake. TL of alligators whose stomachs contained tags ranged from 168 cm to 370 cm ($\bar{X}$ = 275 cm). One stomach contained 14 tags from members of two pods; one contained six tags from members of two pods; two contained three tags each, all individuals from different pods; and one contained two tags from members of different pods. Twenty-eight stomachs contained one tag each. Mark–recapture records available for 54 of the recovered tags revealed that they were from alligators that measured 26–140 cm TL at last release ($\bar{X}$ = 43.7 cm, SD = 27.3). For most (91%) TL was ≤85 cm, and these individuals were estimated to be no more than 3 yr old (Woodward et al., 1992). No alligator remains were observed in stomachs. Alligator populations at Orange Lake during 1981–1987 were estimated to contain 4100 juveniles, 950 subadults, and 1800 adults.

SURVIV model fits are summarized in Appendices III and IV. Estimated overdispersion parameters were in general greater for individual recovery unit models (Appendix III) than for pod recovery unit models (Appendix IV), and *P* values for the pooled chi-square goodness-of-fit statistics were in general less for the individual recovery unit models than for the pod recovery unit models (which suggests a poorer fit). However, goodness of fit was adequate for best models in both recovery unit sets. Therefore, AIC_c (rather than quasi-AIC_c) could be used for comparison within sets (Burnham and Anderson, 2002).

SURVIV models using the tag-retention rates from the captive study and based on a Weibull distribution fared poorly in comparison with those based on the exponential distribution or with those for which annual tag-retention rate was estimated as a fixed constant from tag recoveries in the wild. Models based on Weibull survivorship had 0 Akaike weight and thus did not influence model-averaged parameter estimates. For both recovery unit sets, models with the

TABLE 1.—Parameter estimates, standard errors, and confidence limits (lower and upper, LCL and UCL, respectively) from model-averaged SURVIV program results for American Alligators (*Alligator mississippiensis*).

Recovery unit	Parameter	Estimate	SE	95% LCL	95% UCL
Individual	Cannibalism	0.07	0.02	0.03	0.11
	Adult survival	0.84	0.05	0.74	0.94
	Recovery 1981	0.10	0.03	0.05	0.16
	Recovery 1982	0.02	0.01	0.00	0.05
	Recovery 1983	0.09	0.03	0.04	0.15
	Recovery 1984	0.15	0.04	0.06	0.24
	Recovery 1985	0.10	0.04	0.03	0.18
	Recovery 1986	0.08	0.03	0.01	0.15
	Recovery 1987	0.04	0.02	0.00[a]	0.08
Pod	Cannibalism	0.06	0.02	0.02	0.10
	Adult survival	0.85	0.05	0.75	0.96
	Recovery 1981	0.11	0.03	0.06	0.17
	Recovery 1982	0.03	0.02	0.00	0.06
	Recovery 1983	0.10	0.03	0.04	0.17
	Recovery 1984	0.07	0.03	0.02	0.12
	Recovery 1985	0.11	0.04	0.03	0.19
	Recovery 1986	0.09	0.04	0.01	0.16
	Recovery 1987	0.04	0.03	0.00[a]	0.09

[a] Negative value truncated.

release vulnerability assumption and annually varying recovery rates were superior by AIC_c ($\geq$0.56 of total model weight accounted for by these two models).

Point estimates for parameters in the best models with either recovery unit assumption differed little from model-averaged estimates (Table 1); CIs for model-averaged estimates were slightly greater than those for the best models alone. Model-averaged point estimates of cannibalism rates for individual and pod recovery data sets were 0.07 and 0.06, respectively; the corresponding model-averaged 95% CIs were 0.03–0.11 and 0.02–0.10, respectively. Over all 18 models within each type of recovery unit, the range of point estimates of cannibalism rate was 0.06–0.10 for analyses based on individual recovery units and was 0.04–0.08 for analyses based on pod recovery units. Model-averaged estimates were 0.84–0.85 for annual adult survival rate and were 0.03–0.15 for annual adult harvest rates. For both recovery unit data sets, estimates of cannibalism and survival rates were slightly less with release-vulnerability models than with 1-yr-old and equal-vulnerability models, whereas mean recovery rates were slightly greater with release-vulnerability models.

When SURVIV estimated the annual tag-retention rate, it was 1.0 in both sets of recovery unit models, i.e., there was no tag loss from stomachs. This estimate was independent of the results of the captive tag-retention study and was much closer to the exponential than to the Weibull-based tag retention estimates of that study.

DISCUSSION

The rate (12%) of recovery of alligator-marking tags from stomachs of hunter-harvested alligators suggested that cannibalism was a major source of mortality on Orange Lake. However, the persistence of tags in stomachs may explain the disparity between the prevalence of tags in stomachs and our estimate of cannibalism. Under captive conditions, marking tags remained in stomachs for 43 to at least 588 d, and the better-fitting exponential model estimated median tag retention for over 10 yr. Rootes and Chabreck (1993) assumed that tags found in stomachs represented predation within the preceding 12 mo and calculated a small annual probability of retention (0.32). This assumption may partially explain why their estimate of annual mortality by cannibalism ($\geq$22–42%) was greater than ours (6–7% annually). Our estimate is closer to the range (2–6%) predicted by Nichols et al. (1976*a*) in their population model. Estimates of cannibalism rates vary with the time tags are retained in

stomachs. Conditions in captivity can affect crocodilian food conversion rates (Webb et al. 1991) and may have influenced tag retention in stomachs during our study. The low incidence of tag loss for marked juvenile alligators in Orange Lake probably had a negligible effect on our estimate of cannibalism.

The absence of alligator remains (other than tags) in our sample and their infrequency (<1% occurrence) in other studies (Barr, 1997; Delany and Abercrombie 1986; Delany et al., 1999; McNease and Joanen, 1977; Valentine et al., 1972) may not accurately reflect the incidence of cannibalism. Alligator digestion of prey is rapid (Barr, 1997; Delany and Abercrombie, 1986), and compared with other prey taxa (especially turtles and mammals), alligators may be underrepresented in stomach contents. Tags, however, were perduring evidence of ingestion (Rootes and Chabreck, 1993; this study). Because several pod cohorts were represented (as identified by tags) in some stomachs, it seems unlikely that they had all been available as carrion. Furthermore, because only a small proportion of juvenile alligators was tagged, cannibalistic alligators would have had to eat thousands of dead alligators (untagged and tagged) as carrion to achieve the prevalence of tags in stomachs that we observed during this study; that much mortality probably would have required a major disease event that we would have observed during the course of this study. Rootes and Chabreck (1993) also believed alligators were cannibalized and "not scavenged after dying of other causes."

Smaller individuals are usually more vulnerable to cannibalism by large conspecifics (Fox, 1975; Polis, 1981), and cannibalized alligators in our study were probably small enough to pose little risk of injury to cannibal alligators during capture. Alligators on Orange Lake apparently remained vulnerable to cannibalism until they had reached 140 cm TL or 6–8 yr of age. In contrast, Rootes and Chabreck (1993) found cannibalism mortality distributed proportionately among all size classes. Our results support models of cannibalism (Stenseth, 1985; van den Bosch et al., 1988) that assume size difference between cannibals and their prey and a differential use of food resources between size classes (see Delany, 1990).

Adult alligators (>183 cm TL) made up 26% of the population on Orange Lake but accounted for 97% of the cannibalism. Our sample excluded smaller size classes of alligators because only 1 of 76 subadults (122–182 cm TL) showed evidence of cannibalism (Delany and Abercrombie, 1986). Rootes and Chabreck (1993) also reported that large alligators (>273 cm TL) were more cannibalistic, but did find evidence of cannibalism by smaller size classes (122–182 cm TL). The alligator population estimated at Orange Lake (6850) was smaller than the Louisiana population (14,866) examined by Rootes and Chabreck (1993); however, the size class structures were similar in both populations.

Cannibalism is more common among euryphagous predators and may be induced by starvation (Polis and Myers, 1985). It can allow individuals to maintain metabolic stability when other food resources are scarce (van den Bosch et al., 1988). Small individuals may be acceptable prey, providing a net energetic benefit (Dong and Polis, 1992). Food resource limitations may affect alligator diet at some locations in Florida (Delany et al., 1999), and cannibalism of juveniles may help to maintain a stable population of alligators of larger size classes.

The rate of cannibalism is usually considered a function of population density (Fox, 1975; Polis, 1981), with intraspecific predation consistent with the predictions of optimal foraging theory (Dong and Polis, 1992). Nichols et al. (1976*a*) assumed that cannibalism mortality among alligators was a function of water depth and alligator population density, accounting for 2–6% of the annual mortality of the species in Louisiana. They assumed cannibalism mortality rates as great as 15% for populations at carrying capacity, with 60% of the mortality suffered by 1-yr-olds. Rootes and Chabreck (1993) estimated high rates of cannibalism (42.0% mortality of hatchlings and 22.1% of alligators ≥11 mo old) in a population in Louisiana believed to be at or near carrying capacity. Compared with those at other lakes in Florida, the alligator population on Orange Lake is rela-

tively dense, with 21.4 individuals/km of shoreline (Wood et al., 1985). However, Orange Lake provides more vegetative escape cover than do many aquatic habitats in Florida. Consequently, cannibalism rate may be considerably different at other locations.

The incidence of cannibalism may be influenced by environmental cues (Polis, 1981). Juvenile mortality, for example, is thought to increase during warmer months (April–October) when water levels are low and alligators are concentrated during their most active feeding period (Hayes-Odum and Jones, 1993; Woodward et al., 1987). The average TL at last recapture of cannibalized alligators (47.3 cm) on Orange Lake may be apposite to reduced survival rates reported for this size class (Woodward et al., 1987). One-year-old (approximately 50 cm TL) alligators disperse from marsh areas associated with the nest to the interface of the marsh and open water (Deitz, 1979), where contact with larger alligators is more likely (Goodwin and Marion, 1979). Size class separation and differences in structure of aquatic habitats and hence access to refuges (Fox, 1975) may affect cannibalism rates in other areas.

On Orange Lake, cannibalism appears to be an appreciable source of mortality for juvenile alligators and may help regulate the population. In alligator mark–recapture studies on Orange Lake, individuals were released at the site of capture, and efforts were made to minimize disturbance (M. F. Delany, personal observation). Our release-year models may be superior to the others because the presence of tags on juveniles increases the frequency of encounters that might end in cannibalism, and hence our estimates of the rate of cannibalism may be too large. However, given that the majority of alligators that we tagged were hatchlings, their greater vulnerability may be a more feasible explanation. Because the fates of tagged juvenile siblings are probably not independent, using the pod as the recovery unit was a conservative approach to the estimation of cannibalism, and such models had a better fit than when individual tag recoveries were modeled. The smaller sample of recovered pods (39) than of individual tags (56), and consequent lesser power, may also have contributed to the better fit of pod-based models.

High rates of alligator nest failure (Goodwin and Marion, 1978) and the assumption of high juvenile mortality are used to justify the removal of as much as 50% of the annual production from some lakes in Florida. Estimates of cannibalism's effect on juvenile survival may be useful in the development of population models that evaluate alligator harvest strategies and restocking programs (Nichols et al., 1976*a*,*b*). Even the seemingly low rate of juvenile mortality attributed to cannibalism reported here may be an important factor in population regulation (Fox, 1975). The role and importance of cannibalism in alligator population dynamics needs to be more fully assessed and environmental and population factors that influence cannibalism identified to evaluate management programs.

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Appendix I

We developed models within the band recovery framework outlined by Brownie et al. (1985). Tag recoveries in year j of N_i juvenile alligators released in year i were assumed to follow a multinomial distribution. A release was the last live capture and release of an alligator in mark–recapture operations. Harvest recoveries of alligators released as adults (≥122 cm total length [TL]) provided inference on adult survival and annual recovery rate.

Complicating the models was the possibility that cannibalism might take place at any time between the release and recovery years. In addition, juveniles released in any year were of varying ages and probably subject to age-specific survival rates. Thus, recovery probabilities are affected not only by i and j but also by the year of cannibalism h ($i \leq h \leq j$) and by the age class k of the animal in year i. Of recovered tags of juveniles (whose TL was recorded at release), only 9% were ≥0.9 m TL, approximately 4 yr old, when released. Although this percentage would have been greater had it been possible to record TL at death, we judged that cannibalism of individuals older than 3 yr was insignificant. Therefore, we restricted values of k to age classes 0–3. We assumed age-class-specific annual survival rates for hatchlings (S', age class 0), 1-yr-olds (S''), and >1-yr-olds (S). Models in which adult survival was allowed to vary annually were also considered but were never superior and are not presented here. We did not model sex-specific survival rates in either the juvenile or adult population.

We let the symbol $\pi_{h|\,ij,k}$ represent the probability that a juvenile had been cannibalized in year h given that it was age k when released in year i and its tag was recovered in year j. The subscript notation $h|ij,k$ was chosen to reflect both the conditional nature of h on levels of i, j, and k and the independence of k and levels of i and j. The probability structure adopted for $\pi_{h|ij,k}$ was

$$\pi_{h|ij,k} = CR_{h|\,j} S^{j-h} f_j \times \begin{cases} S'^{I(h>1)} S''^{I(h>i+1)} S^{(h-i-2)I(h>i+2)}, & k=0 \\ S''^{I(h>i)} S^{(h-i-1)I(h>i+1)}, & k=1 \\ S^{(h-i)I(h>i)}, & k>1 \end{cases}$$

where S', S'', and S are parameters described above; C is the average annual probability that an alligator in age class 0–3 is cannibalized; f_j is the probability that a hunter will recover the cannibal in year j; $R_{h|\,j}$ is the probability that a tag will remain in a cannibal's stomach given recovery in year j after cannibalism in year h; and $I(x)$ is an indicator function resulting in a value of 1 if the expression x is true and 0 if x is false. The part of the probability expression preceding the brace is the cannibal recovery component. If the probability that a tag will be retained in the stomach is described with an annualized constant R_a, then the probability that a cannibal both lives and retains an ingested tag over $j - h$ years is $(R_a S)^{j-h}$. The remainder of the expression is the victim survival component, which describes survival of a juvenile from its release to its cannibalism. Note that as k increases, parameters S' and S'' are successively eliminated. For a given value of k, appropriate survival probabilities are multiplied in sequence for $h - i$ years.

For a fixed recovery span of $j - i$ years, we can write a $4 \times (j - i + 1)$ matrix of $\pi_{h|ij,k}$ expressions as k ranges from 0 to 3 and h ranges from 0 to $j - i$. Calculating the expectation (over h and k) of $\pi_{h|ij,k} = \pi_{i.j.}$ involves determining with what probability each of these matrix cells will occur relative to one another. When these probabilities, $g(k,h - i|j - i)$, are known, it follows that

$$\pi_{i.j.} = \sum_{h=i}^{j} \sum_{k=0}^{3} \pi_{h|ij,k} g(k,h-i|\,j-i).$$

Multiplying each of these probabilities for a fixed i by N_i provides the expected number of tag recoveries in adult stomachs.

Conditional on the time between release and recovery ($j - i$), $g(k,h - i|j - i)$ is the joint probability density function of juvenile age (k) and years of juvenile survival ($h - i$). Because we ignored cannibalism of juveniles older than 3 yr, we could disregard distinct values of $j - i > 3$ yr. Thus, $g(k,h - i\,|j - i)$ was defined for $j - i = \{0,1,2,3+\}$, $h - i = \{0,\ldots,j - i\}$, and $k = \{0,1,2,3\}$ as the product of $a(k)$, the age class proportions of released juveniles, and $d(k + h - i|k,j - i)$, the probability density function of the victim's age at cannibalism ($k + h - i$) given that it was age k at time of release. The former distribution was estimated from the last-live-capture data by averaging each of the four annual age-class proportions over 12 yr of capture information (1975–1986). Juvenile ages were based on TL, approximated with the formula

$$\text{age} = \frac{\text{TL m}}{0.1524 \text{ m yr}^{-1}} - 2.0 \text{ yr}.$$

Age classes were assigned by truncating the decimal portion of age.

The density function $d(k + h - i|k,j - i)$ is the likelihood that the cannibalism victim was eaten in year $k + h - i$ after its release. We guessed at values of this function on the basis of age-specific movement and behavior patterns of juveniles as they pertain to relative risk of cannibalism under three scenarios. One we called the 1-yr-old vulnerability case. It reflects a situation in which 1-yr-olds are placed at higher risk to cannibalism than other classes because of their movement away from the protection of the nest into deeper water and greater concentrations of adult alligators (Deitz, 1979). In this case, we assigned the values 0.20, 0.40, 0.28, and 0.12 to $d(k + h - i|k = 0,j - i = 3+)$, for $h - i = 0$, 1, 2, and 3, respectively. Note that the cannibalism risk for a 1-yr-old is twice that for a hatchling. Values of $d(k + h - i|k,j - i)$ for other settings of k and $j - i$ are obtained from the above vector of probabilities through the formula

$$d(k+h-i|k,j-1) = \frac{d(k+h-i|0,3+)}{\sum_{m=k}^{\min(j-i,3-k)+k} d(m|0,3+)}.$$

For the equal vulnerability case,

$$d(k+h-i|k,j-i)=\frac{1}{\min(j-i,3)+1}.$$

All values of $k+h-i$ for a given level of k and $j-i$ occur with equal probability. For the release vulnerability case,

$$d(k+h-i|k,j-i)=\begin{matrix}1, h=i\\ 0, h>i\end{matrix}.$$

In other words, all cannibalism risk occurs in the year of release ($h = i$).

Parameters S, C, and f_j in the expression defining $\pi_{h|ij,k}$ were estimated in the program SURVIV model. $R_{h|j}$ was either predicted from the force-feeding experiment and depended only on $j-h$ and on which survival distribution was assumed, or it was estimated by SURVIV as an annualized constant R_a in the model so that $R_{h|j} = R_a^{j-h}$. S' was fixed at 0.41 (Woodward et al., 1987) and S'' was fixed at 0.65, a reasonable intermediate value between 0.41 and a greater estimated adult survival rate of 75–90% (Nichols et al., 1976*a*). We assumed that all activities (release, cannibalism, and recovery) recurred at the same time each year and that each adult cannibalizing in year h was equally likely to survive, retain victim tags, and be recovered $j-h$ years later. This assumption is imposed on all band recovery models that operate on an annual time step.

Appendix II

Example SURVIV program for estimating rate of cannibalism of juvenile American Alligators (S[1]), adult recovery (harvest) rate (S[2],S[4–9], and adult survival (S[3],S[10–19]). This example assumes probabilities of tag retention in stomachs as estimated under the exponential distribution model (with random alligator effects) and release-year vulnerability. Annual adult survival is assumed constant by the constraint that S(3) = S(10–19). Annual adult recovery is assumed either to vary annually (model VFF) or to be constant (model FFF) by the constraint that S(2) = S(4–9).

```
PROC TITLE Survival & cannibalism rates;
PROC MODEL NPAR=19;
COHORT=17;
1:S(18)*S(17)*S(16)*S(15)*S(2);
1:S(18)*S(17)*S(16)*S(15)*S(14)*S(4);
0:S(18)*S(17)*S(16)*S(15)*S(14)*S(13)*S(5);
1:S(18)*S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(6);
0:S(18)*S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(7);
0:S(18)*S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*
S(8);
0:S(18)*S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*
S(10)*S(9);
COHORT=25;
2:S(17)*S(16)*S(15)*S(2);
1:S(17)*S(16)*S(15)*S(14)*S(4);
2:S(17)*S(16)*S(15)*S(14)*S(13)*S(5);
0:S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(6);
0:S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(7);
0:S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*S(8);
0:S(17)*S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*S(10)*
S(9);
COHORT=25;
1:S(16)*S(15)*S(2);
2:S(16)*S(15)*S(14)*S(4);
2:S(16)*S(15)*S(14)*S(13)*S(5);
2:S(16)*S(15)*S(14)*S(13)*S(12)*S(6);
3:S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(7);
0:S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*S(8);
0:S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*S(10)*S(9);
COHORT=36;
4:S(15)*S(2);
1:S(15)*S(14)*S(4);
2:S(15)*S(14)*S(13)*S(5);
1:S(15)*S(14)*S(13)*S(12)*S(6);
1:S(15)*S(14)*S(13)*S(12)*S(11)*S(7);
0:S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*S(8);
0:S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*S(10)*S(9);
COHORT=45;
5:S(2);
0:S(14)*S(4);
3:S(14)*S(13)*S(5);
3:S(14)*S(13)*S(12)*S(6);
3:S(14)*S(13)*S(12)*S(11)*S(7);
2:S(14)*S(13)*S(12)*S(11)*S(3)*S(8);
1:S(14)*S(13)*S(12)*S(11)*S(3)*S(10)*S(9);
COHORT=5;
0:S(4);
0:S(13)*S(5);
0:S(13)*S(12)*S(6);
0:S(13)*S(12)*S(11)*S(7);
1:S(13)*S(12)*S(11)*S(3)*S(8);
0:S(13)*S(12)*S(11)*S(3)*S(10)*S(9);
COHORT=5;
2:S(5);
0:S(12)*S(6);
0:S(12)*S(11)*S(7);
0:S(12)*S(11)*S(3)*S(8);
0:S(12)*S(11)*S(3)*S(10)*S(9);
COHORT=3;
0:S(6);
0:S(11)*S(7);
1:S(11)*S(3)*S(8);
0:S(11)*S(3)*S(10)*S(9);
COHORT=2;
0:S(7);
0:S(3)*S(8);
0:S(3)*S(10)*S(9);
COHORT=192 /* released 1976 */;
0:S(1)*S(2)*.6955*S(19)*S(18)*S(17)*S(16)*S(15) {PR=
S(19)*S(18)*S(17)};
0:S(1)*S(4)*.6511*PR*S(16)*S(15)*S(14) {PR=PR*S(16)};
0:S(1)*S(5)*.6105*PR*S(15)*S(14)*S(13) {PR=PR*S(15)};
0:S(1)*S(6)*.5731*PR*S(14)*S(13)*S(12) {PR=PR*S(14)};
1:S(1)*S(7)*.5387*PR*S(13)*S(12)*S(11) {PR=PR*S(13)};
0:S(1)*S(8)*.5068*PR*S(12)*S(11)*S(3) {PR=PR*S(12)};
0:S(1)*S(9)*.4773*PR*S(11)*S(3)*S(10);
COHORT=388 /* released 1977 */;
0:S(1)*S(2)*.7443*S(18)*S(17)*S(16)*S(15) {PR=S(18)*
S(17)*S(16)};
0:S(1)*S(4)*.6955*PR*S(15)*S(14) {PR=PR*S(15)};
1:S(1)*S(5)*.6511*PR*S(14)*S(13) {PR=PR*S(14)};
0:S(1)*S(6)*.6105*PR*S(13)*S(12) {PR=PR*S(13)};
3:S(1)*S(7)*.5731*PR*S(12)*S(11) {PR=PR*S(12)};
0:S(1)*S(8)*.5387*PR*S(11)*S(3) {PR=PR*S(11)};
0:S(1)*S(9)*.5068*PR*S(3)*S(10);
COHORT=182 /* released 1978 */;
1:S(1)*S(2)*.7982*S(18)*S(16)*S(15);
0:S(1)*S(4)*.7443*S(18)*S(16)*S(15)*S(14);
```

```
0:S(1)*S(5)*.6955*S(18)*S(16)*S(15)*S(14)*S(13);
0:S(1)*S(6)*.6511*S(18)*S(16)*S(15)*S(14)*S(13)*S(12);
0:S(1)*S(7)*.6105*S(18)*S(16)*S(15)*S(14)*S(13)*S(12)*
S(11);
0:S(1)*S(8)*.5731*S(18)*S(16)*S(15)*S(14)*S(13)*S(12)*
S(11)*S(3);
0:S(1)*S(9)*.5387*S(18)*S(16)*S(15)*S(14)*S(13)*S(12)*
S(11)*S(3)*S(10);
COHORT=327 /* released 1979 */;
3:S(1)*S(2)*(.8580)*(S(16)*S(15));
0:S(1)*S(4)*(.7982)*(S(16)*S(15)*S(14));
0:S(1)*S(5)*(.7443)*(S(16)*S(15)*S(14)*S(13));
0:S(1)*S(6)*(.6955)*(S(16)*S(15)*S(14)*S(13)*S(12));
0:S(1)*S(7)*(.6511)*(S(16)*S(15)*S(14)*S(13)*S(12)*S(11));
0:S(1)*S(8)*(.6105)*(S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*
S(3));
0:S(1)*S(9)*(.5731)*(S(16)*S(15)*S(14)*S(13)*S(12)*S(11)*
S(3)*S(10));
COHORT=506 /* released 1980 */;
2:S(1)*S(2)*(.9248)*(S(15));
0:S(1)*S(4)*(.8580)*(S(15)*S(14));
3:S(1)*S(5)*(.7982)*(S(15)*S(14)*S(13));
0:S(1)*S(6)*(.7443)*(S(15)*S(14)*S(13)*S(12));
1:S(1)*S(7)*(.6955)*(S(15)*S(14)*S(13)*S(12)*S(11));
0:S(1)*S(8)*(.6511)*(S(15)*S(14)*S(13)*S(12)*S(11)*S(3));
0:S(1)*S(9)*(.6105)*(S(15)*S(14)*S(13)*S(12)*S(11)*S(3)*
S(10));
COHORT=305 /* released 1981 */;
2:S(1)*S(2);
0:S(1)*S(4)*(.9248)*S(14);
0:S(1)*S(5)*(.8580)*(S(14)*S(13));
1:S(1)*S(6)*(.7982)*(S(14)*S(13)*S(12));
1:S(1)*S(7)*(.7443)*(S(14)*S(13)*S(12)*S(11));
1:S(1)*S(8)*(.6955)*(S(14)*S(13)*S(12)*S(11)*S(3));
1:S(1)*S(9)*(.6511)*(S(14)*S(13)*S(12)*S(11)*S(3)*S(10));
COHORT=496 /* released 1982 */;
0:S(1)*S(4);
1:S(1)*S(5)*(.9248)*S(13);
0:S(1)*S(6)*(.8580)*(S(13)*S(12));
1:S(1)*S(7)*(.7982)*(S(13)*S(12)*S(11));
3:S(1)*S(8)*(.7443)*(S(13)*S(12)*S(11)*S(3));
0:S(1)*S(9)*(.6955)*(S(13)*S(12)*S(11)*S(3)*S(10));
COHORT=429 /* released 1983 */;
3:S(1)*S(5);
3:S(1)*S(6)*.9248*S(12);
1:S(1)*S(7)*(.8580)*(S(12)*S(11));
0:S(1)*S(8)*(.7982)*(S(12)*S(11)*S(3));
0:S(1)*S(9)*(.7443)*(S(12)*S(11)*S(3)*S(10));
COHORT=222 /* released 1984 */;
0:S(1)*S(6);
0:S(1)*S(7)*.9248*S(11);
2:S(1)*S(8)*(.8580)*(S(11)*S(3));
2:S(1)*S(9)*(.7982)*(S(11)*S(3)*S(10));
COHORT=84 /* released 1985 */;
1:S(1)*S(7);
1:S(1)*S(8)*.9248*S(3);
0:S(1)*S(9)*(.8580)*(S(3)*S(10));
COHORT=136 /* released 1986 */;
0:S(1)*S(8);
0:S(1)*S(9)*.9248*S(10);
LABELS;
S(1)=Cannibalism 1976;
S(2)=Recovery, 1981;
S(3)=Survival 1986;
S(4)=Recovery, 1982;
S(5)=Recovery, 1983;
S(6)=Recovery, 1984;
S(7)=Recovery, 1985;
S(8)=Recovery, 1986;
S(9)=Recovery, 1987;
S(10)=Survival 1987;
S(11)=Survival 1985;
S(12)=Survival 1984;
S(13)=Survival 1983;
S(14)=Survival 1982;
S(15)=Survival 1981;
S(16)=Survival 1980;
S(17)=Survival 1979;
S(18)=Survival 1978;
S(19)=Survival 1977;
PROC ESTIMATE NAME=VFF MAXFN=3000;
INITIAL;
S(1)=.05; S(2)=.1; S(3)=.8;
S(4)=.1; S(5)=.1; S(6)=.1; S(7)=.1; S(8)=.1; S(9)=.1;
S(10)=.8; S(11)=.8; S(12)=.8; S(13)=.8; S(14)=.8; S(15)=.8;
S(16)=.8; S(17)=.8; S(18)=.8; S(19)=.8;
CONSTRAINTS;
S(19)=S(3); S(18)=S(3); S(17)=S(3); S(16)=S(3); S(15)=S(3);
S(14)=S(3);
S(13)=S(3); S(12)=S(3); S(11)=S(3); S(10)=S(3);
PROC ESTIMATE NAME=FFF MAXFN=3000;
INITIAL;
RETAIN=VFF;
CONSTRAINTS;
S(4)=S(2); S(5)=S(2); S(6)=S(2); S(7)=S(2); S(8)=S(2);
S(9)=S(2);
S(19)=S(3); S(18)=S(3); S(17)=S(3); S(16)=S(3); S(15)=S(3);
S(14)=S(3);
S(13)=S(3); S(12)=S(3); S(11)=S(3); S(10)=S(3);
PROC TEST;
PROC STOP;
```

APPENDIX III.—Akaike's information criterion corrected for sample size (AIC_c), difference in AIC_c from best model in set Δ_i, Akaike weight w_i, estimated overdispersion parameter $\hat{c}$ (= χ^2/df), and probability of larger chi-square (goodness of fit) for models based on individual tag recoveries from American Alligators (*Alligator mississippiensis*). Vulnerability to cannibalism was assumed to be greatest for 1-yr-olds, equal for all ages according to abundance, or greatest in the year of release. Tag-retention rates in the model were estimated from the captive study (assuming exponential or Weibull distribution with random alligator individual effects) or as a fixed annual parameter by the SURVIV program. Annual recovery rate was estimated individually for each year in the study or was assumed to be constant.

Vulnerability model	Tag retention	Recovery estimate	AIC_c	Δ_i	w_i	$\hat{c}$	$P(>\chi^2)$
Release	Exponential	Variable	255.38	0.00	0.52	1.20	0.22
Release	Constant	Variable	256.55	1.17	0.29	1.22	0.17
Equal	Exponential	Variable	259.36	3.98	0.07	1.13	0.29
1-yr-old	Exponential	Variable	259.78	4.40	0.06	1.16	0.27
Equal	Constant	Variable	261.21	5.83	0.03	1.33	0.12
1-yr-old	Constant	Variable	261.65	6.27	0.02	1.35	0.11
Release	Exponential	Constant	268.18	12.80	0.00	1.22	0.18
Release	Constant	Constant	269.45	14.07	0.00	1.19	0.22
Equal	Exponential	Constant	272.50	17.12	0.00	1.48	0.04
1-yr-old	Exponential	Constant	273.04	17.66	0.00	1.49	0.03
Equal	Constant	Constant	274.44	19.06	0.00	1.52	0.03
1-yr-old	Constant	Constant	274.99	19.61	0.00	1.54	0.03
Equal	Weibull	Variable	296.05	40.67	0.00	1.51	0.05
1-yr-old	Weibull	Variable	296.42	41.04	0.00	1.52	0.05
Equal	Weibull	Constant	307.53	52.15	0.00	1.77	0.00
1-yr-old	Weibull	Constant	308.02	52.64	0.00	1.61	0.02
Release	Weibull	Variable	444.00	188.62	0.00	3.72	0.00
Release	Weibull	Constant	451.38	196.00	0.00	2.67	0.00

APPENDIX IV.—Akaike's information criterion corrected for sample size (AIC_c), difference in AIC_c from best model in set Δ_i, Akaike weight w_i, estimated overdispersion parameter $\hat{c}$ (= χ^2/df), and probability of larger chi-square (goodness of fit) for models based on pod tag recoveries from American Alligators (*Alligator mississippiensis*). Vulnerability to cannibalism was assumed to be greatest for 1-yr-olds, equal for all ages according to abundance, or greatest in the year of release. Tag-retention rates in the model were estimated from the captive study (assuming exponential or Weibull distribution with random alligator individual effects) or as a fixed annual parameter by the SURVIV program. Annual recovery rate was estimated individually for each year in the study or was assumed to be constant.

Vulnerability model	Tag retention	Recovery estimate	AIC_c	Δ_i	w_i	$\hat{c}$	$P(>\chi^2)$
Release	Exponential	Variable	234.56	0.00	0.36	0.77	0.76
Release	Constant	Variable	235.73	1.17	0.20	0.92	0.57
Equal	Exponential	Variable	236.69	2.13	0.12	0.70	0.85
1-yr-old	Exponential	Variable	236.74	2.18	0.12	0.69	0.85
Equal	Constant	Variable	237.92	3.36	0.07	0.72	0.82
1-yr-old	Constant	Variable	238.00	3.44	0.06	0.76	0.77
Release	Exponential	Constant	239.71	5.15	0.03	0.82	0.72
Release	Constant	Constant	240.71	6.15	0.02	0.87	0.66
Equal	Exponential	Constant	242.16	7.60	0.01	0.88	0.66
1-yr-old	Exponential	Constant	242.27	7.71	0.01	0.88	0.66
Equal	Constant	Constant	243.33	8.77	0.00	0.91	0.60
1-yr-old	Constant	Constant	243.48	8.92	0.00	0.84	0.70
Equal	Weibull	Variable	276.77	42.21	0.00	1.23	0.21
Equal	Weibull	Constant	279.59	45.03	0.00	1.48	0.04
1-yr-old	Weibull	Variable	280.49	45.93	0.00	1.34	0.13
1-yr-old	Weibull	Constant	283.90	49.34	0.00	1.51	0.04
Release	Weibull	Variable	368.50	133.94	0.00	2.36	0.00
Release	Weibull	Constant	370.35	135.79	0.00	2.94	0.00