American Alligator Nesting Ecology in Impounded Marsh Habitat, Louisiana.

Steven Richard Reagan
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AMERICAN ALLIGATOR NESTING ECOLOGY
IN
IMPOUNDED MARSH HABITAT, LOUISIANA

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
in
The School of Forestry, Wildlife and Fisheries

by
Steven Richard Reagan
B.S., University of Massachusetts, 1987
M.S., The University of Tennessee, 1991
May 2000
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Abstract

The goal was to monitor a large number of female alligators over a 3-year period to obtain information on alligator nesting ecology. This dissertation, although designed to estimate annual nesting rates, provides additional meaningful information on methods of capture, tag retention rates, nest spacing patterns, segregation of size classes, nest site fidelity, the relationship between attendance and nest success, the effects of fire ants on alligator nest success, the relationship between hatchling alligators and their mother, and hatchling dispersal. Passive integrated transponder (PIT), monel web, and cranial mounted reflector tags were evaluated for marking and identifying alligators. Use of harmonic radar for relocating marked alligators was tested. A total of 368 adult and 2,674 hatchling alligators were captured and individually marked between May, 1997 and October, 1999. Methods describe innovative techniques for capturing adult alligators from dens and with baited lines. A total of 378 nests were located. Nest locations were clustered and clusters were not stationary among years. Females of the largest size class nested together away from the marsh edge. Approximately 66% of nests found without eggs were not paired with nests with eggs. The percent of alligators nesting annually ranged from an estimated 6.34% to 15.60%. Average nest site reuse was 3.7%. There were no cases of reuse at a previous nest site by the same female. Fire ants negatively affect alligator nest success by possibly killing hatchlings in the nest, and deterring the opening of nests by the maternal alligator. Attendance by the female alligator did not have an effect on nest success until it was time for the nest to be opened. A field experiment also demonstrated that ants reduce alligator nest success,
and that adult activity prior to hatch was unaffected by fire ant presence. Hatchlings alligators that successfully escaped the nest started moving and mixing with other pods within days after hatch. Newly released hatchlings moved distances up to 1,000 m from the natal nest site. Hatchlings appeared to move both as individuals and groups. Some hatchlings may disperse immediately after hatch and require no parental care.
Introduction

The reproductive ecology of the American alligator (*Alligator mississippiensis*) possibly consists of four distinct components including courtship, nesting, hatchling release, and brooding. Courtship is thought to involve 90% of adult males and 75% of adult females within any given year (Vliet 1989). Annual nesting has been estimated to occur for < 10% to 68.1% of wild adult females (Joanen and McNease 1980, Taylor 1984, Lance 1989, Taylor et al. 1991, Walthers and Ivy, Sabine National Wildlife Refuge, Louisiana, unpublished data, Wilkinson, South Carolina Wildlife and Marine Resources Department, unpublished data). Although observation of hatchling self-release have been reported (Joanen 1969), nest opening by the maternal alligator is the commonly reported way by which hatchlings escape the nest (McIlhenny 1935, Joanen 1969, Herzog 1975, Deitz and Hines 1980, Hunt and Watanabe 1982). Once out of the nest, hatchlings are thought to remain near the nest from the time of hatching, through winter and until the next breeding season (McIlhenny 1935, Chabreck 1965, Deitz 1979, Woodward et al. 1989).

Courtship begins in April and peaks in May (Vliet 1989). The May peak is correlated with ovulation (Joanen and McNease 1975, 1980). Male alligators establish secluded sites from which to display (Vliet 1989). Garrick and Lang (1975) and Vliet (1989) describe the alligator’s social displays. Head slapping and bellowing are used by both sexes to elicit approaches by the opposite sex. Females move among the male territories in search of suitable mates (Garrick and Lang 1975). Females may terminate courtship with unsuitable males (Garrick and Lang 1975) and kill males and rival females.
Males monitored with telemetry have often been associated with canals, bayous, and deep water ponds during this period. Females demonstrate the most movement during courtship (Rootes 1989), but do not necessarily move out of the marsh interior (Taylor 1984). Joanen and McNease (1970) found female yearly home range size to vary between 2.3 ha and 15 ha. None of their 5 female home ranges overlapped canals but each did contain a marsh pool. It was not determined if these marsh pools served as male display areas during courtship.

Annual nesting rates for wild and captive alligators are estimated at < 10% to 80% (Joanen and McNease 1970, 1971, 1975, 1980, Lance 1989, Taylor 1984, Taylor et al. 1991). Reproductive female alligators are categorized within 3 size classes based on total body length: 1.83-2.12 m, 2.13-2.42 m, and > 2.42 m (Taylor et al 1991). The larger reproductive females appear to have higher annual nesting rates, but this relationship is not consistent (Taylor et al 1991). There is no published information relating alligator condition and nesting rates. Peak periods of nest initiation occur within a two-week period and are positively correlated with warm April air temperatures (Joanen and McNease 1989). Nesting occurs from June to early September (Joanen and McNease 1975, Taylor 1984). Solitary female alligators form mound-like nests (McIlhenny 1934, Joanen 1969, Deitz and Hines 1980) from material found adjacent to the site including soil and vegetation (Joanen 1969, Taylor 1984). The nest is frequently associated with a previously established den or depression within the marsh (McIlhenny 1934, Joanen 1969, Kushlan 1973, Hunt and Ogden 1991). Eggs are deposited within a hollow created in the top center of the nest and covered (McIlhenny 1935, Joanen 1969).
Nests without eggs are frequent (Joanen 1969, Deitz and Hines 1980, Platt et al. 1995) and are assumed to be failed nest building attempts and generally assumed associated with a nest with eggs.

Nest site selection does not appear to be based on stable optimal habitat (Woodward et al. 1984). Instead, nests locations change yearly although habitat may remain unchanged. Alligator nests are clustered (Woodward et al. 1984, Jennings et al. 1987). Nest clustering may be caused by mutual attraction among nesting females (Woodward et al. 1984). In an apparent conflict, however, females are suspected of keeping minimum distances between nests. Multiple nests found within 30.5 m of each other are thought to be produced by the same female (Chabreck 1966). Rootes and Chabreck (1993), however, do report a single case of 2 nests with eggs being found within 30 m of each other. McIlhenny (1935) suggests site selection is due to site fidelity.

Adult female alligators are hypothesized as caring for nests during incubation (McIlhenny 1935, Deitz and Hines 1980, Kushlan and Kushlan 1980, Joanen and McNease 1989), however, this conclusion is based on retroductive logic. Following the completion of the nest, the female reportedly attends and guards the nests from a nearby den (Joanen 1969, Kushlan 1973, Hunt and Ogden 1991). A high of 33% of nests, however, ever receive protection from nest predation (Hunt and Ogden 1991), and nest attendance occurs at only 14.9% to 66% of nests (Deitz and Hines 1980, Hunt and Ogden 1991). The amiant air and decomposing plant material combine to provide the heat needed for incubation within the nest itself (McIlhenny 1935, Joanen 1969, Chabreck 1973). The female provides no direct role in incubation of eggs. Females
repair damaged nests and cover exposed eggs but only for up to 30 days following nest completion (Joanen and McNease 1989, Hunt and Ogden 1991). The variation associated with this behavior has not been described. Flooding and predation are cited as the two major causes of nest failure (Joanen 1969, Deitz and Hines 1980, Joanen and McNease 1989). The raccoon (*Procyon lotor*) is considered the most frequent nest predator (Joanen 1969, Deitz and Hines 1980, Joanen and McNease 1989, Fleming et al. 1976). Protection of nests by alligators is considered a subset to attendance of nests. Nests with adult protection have been associated with increased nest success (Metzen 1977, Deitz and Hines 1980, Hunt and Ogden 1991).

Hatching occurs 60-65 days after laying (McIlhenny 1934, Joanen 1969, Goodwin and Marion 1978). Hatchlings begin to produce grunting sounds just prior to hatching, which may synchronize hatch (Lee 1968) and signal to the attending female to open the nest (Joanen 1969, Hunt 1987). Alligators are documented opening nests (McIlhenny 1934, Joanen 1969, Herzog 1975, Kushlan 1973, Goodwin and Marion 1978, Deitz and Hines 1980, Platt et al. 1995, Joanen and McNease 1989) and transporting hatchlings from the nest within their mouths (Kushlan and Simon 1981, Hunt 1987). It has not been documented, however, that these are always the maternal females.

Hatchlings are documented to remain near the natal site through the following spring (Deitz 1979, Woodward et al. 1989), however, reports conflict on when hatchlings begin dispersal. Hunt and Watanabe (1982) report mothers form nursery areas and stay in close proximity to hatchling alligators for up to 2 years after hatch. However, hypotheses of hatchlings dispersing immediately following escape from the nest have

The goal of this project was to monitor a large number of female alligators over a 3-year period to obtain information on alligator nesting ecology. The project's objectives were to describe nest spacing patterns, annual nesting rates, the influence of female attendance on nest success, and the effects of fire ants on alligator nest success using a designed field experiment. An additional objective was to observe and describe post-hatching alligator movements.
Chapter 1. Capturing and Marking American Alligators

As research needs demand more long-term studies, the needs for tags being of long-life and high reliability increase. Tag loss on alligators (Alligator mississippiensis) remains an unidentified and potentially serious problem. Significant variation reported between species, years, and studies preclude reliable extrapolation from studies reporting tag retention rates to alligators (Bjorndal et al. 1996).

Methods of tagging alligators include toe clipping, tail-scute notching, and placement of monel tags. Studies marking American alligators as part of life history research have used the methods of toe clipping and tail-scute notching as originally described by Chabreck (1963). The combination of these 2 marks can provide identification of over 3,000 individuals. Researchers, however, are increasingly marking alligators using individually numbered monel tags placed on webbing located between the toes (Goodwin and Marion 1979, Jacobson and Kushlan 1989, Rootes et al. 1991, Rootes and Chabreck 1993). The use of numbered monel tags provides for an unlimited number of alligators to be marked and later identified. Anecdotal comments suggest that none of these tags provide permanent marks, but no one has quantified retention rates.

The objective was to evaluate the use of 3 individual identification tag types (cranial mounted reflectors, monel web tags, and passive integrated transponders) and a harmonic radar relocation system on American alligators.

STUDY AREA

Sabine National Wildlife Refuge is located in southwestern coastal Louisiana. The study area encompassed two impoundments on the refuge and contained vegetative...
types consistent with fresh (8 km²) and intermediate (21 km²) marsh (Chabreck and Linscombe 1988). The main source of water for the impoundments was rainfall. Dense marshhay cordgrass (*Spatina patens*) dominated the habitat. A marsh lake and canals bordered the dense marsh. The border levees of the impoundments were vegetated with Chinese tallow-tree (*Sapium sebiferum*), sea-myrtle (*Baccharis halimifolia*), and clumps of roseau cane (*Phragmites communis*). The marsh was interspersed with shallow, open water pools many of which were being colonized by bullwhip (*Scirpus californicus*) and cattail (*Typha* spp.). Each unit had at least one public access point used by recreationalists and alligator hunters.

**METHODS**

Alligators targeted for capture included hatchlings and adults. Adult alligators were captured throughout the two impoundments starting during the courtship period (April and May) and continuing through the nesting season (June through September). Hatchling alligators were initially captured near natal nest sites immediately following their hatch in September. Alligators of or under 1.5 m total length were hand-grabbed at the neck. Alligators over 1.5 m were noosed using an Aldrich style snare. A 0.95 cm diameter snare cable was clamped to a 2.54 cm diameter pole of 3 m length using of a flexible PVC hose of compatible diameter. The noose was attached by swivel to a rope. The noose was slipped over the head of the alligator and tension applied by the alligator allowed the snare cable to separate from the pole. Alligators were allowed to spin freely until they tired and rotation slowed. Adult alligators were restrained by first controlling the mouth. As described by McIlhenny (1935), noosed alligators were pulled onto the
side of the boat and while applying a pulling force on the noose cable, the top jaw was pressed downward against the floor of the boat using a pole or foot. Once closed the mouth was kept shut with approximately 10 size-64 rubber bands. Alligators were moved to stable locations (i.e., the deck of the boat or flat ground) for processing. During processing tags were applied, body measurements taken, sex identified and notes made of condition and physical abnormalities. Alligators were restrained by applying downward pressure to the top of the head and when necessary to the area over the pelvis; eyes were covered during processing. Alligators over 3 m total length were restrained in shallow water due to the weight of the animal. Adult alligators were categorized within 4 size classes based on total lengths: Small (1.52-1.82 m), Medium (1.83-2.12 m), Large (2.13-2.42 m), and Very Large (> 2.42 m). Alligators were released at the site of capture and rubber bands removed by pulling an attached cord. Hatchling alligators were placed in a bucket with 8 cm water while awaiting marking. They were restrained with one hand and released on site. A two person team captured, handled, and marked all alligators. Only animals marked with cranial reflectors were anesthetized.

Alligator dens were checked for the presence of alligators using a 1.27 cm diameter black-iron pole of 3 m length. The pole was pushed down through the roof systematically until the entire den was searched. The approximate dimensions of each den were recorded. When alligators were found, the pole was used to irritate the alligator with the purpose of causing increased activity (i.e., oxygen consumption);
alligators were easily made active by a simple touch. Alligators were noosed when they surfaced to breathe at the den entrance.

In addition to free noosing alligators within the marsh or out of dens, alligators were captured using baited lines. The baited lines were similar in appearance to that used in the harvest of alligators; however, a wooden dowel was used in place of a barbed hook. Approximately 20 cm of white nylon seine twine (twine size 30) was attached to the two ends of a 1.27-cm diameter wooden dowel of 10 cm length. A grocers chicken leg was attached with rubber bands to the wood dowel. The 20-cm piece of twine was attached to enough twine of the same size to reach from an anchor to deep water habitat (i.e., the middle of a canal or deep pool). Objects not easily uprooted, such as bushes and artificial stakes, were used to anchor the twine. Using a clothes pin, attached to a 3-m pole of 2.54 cm diameter pushed into the ground at a 30-degree angle, the baited dowel was hung approximately 61 cm above water level. Alligators that swallowed a baited dowel were carefully raised toward the water's surface and noosed prior to surfacing with a large diameter snare loop. Once the alligator was noosed, the twine was cut.

All alligators were marked with a non-unique tail notch and an uniquely coded Passive Integrated Transponder (PIT) tag. Alligators captured during the 1999 field season and of at least 1.52 m total length, received a web tag in addition to a PIT tag. For alligators marked previous to and handled during 1999, a second PIT tag was placed within the left ear flap along with the web tag on the foot. Web tags consisted of an individually numbered self-piercing monel tag (Style 1005-4, National Band and Tag...
The tag was placed between the third and forth toes on the left front foot of alligators.

The tail notch was created by removing the third single tail scute near the base. The removal of this scute created a distinct gap within the symmetry of the tail and was spotted easily on recapture. This mark ("C" notch) was used as a general identifier of study animals. Adults were injected with 12 mm x 2 mm (American Veterinary Identification Devices [AVID], Norco, CA) or 11 mm x 2 mm (Destron-Fearing Corp, St. Paul, MN) PIT tags subcutaneously within the right earflap. Hatchling were injected with 11 mm x 2 mm PIT tags with BioBond (Destron-Fearing Corp, St. Paul, MN) into the right neck with the tag resting subcutaneously above the sternomandibularis muscle. BioBond provided true anti-migration characteristics to the PIT tag. A Standard Reader and water resistant probe (American Veterinary Identification Devices [AVID], Norco, CA) was used to identify PIT tags.

Only 18 adult alligators received cranial mounted reflectors. The mounting of the cranial reflector was based on descriptions provided by Smith (1972) and Yerbury (1977). This mark was used to identify individual alligators. A 5 cm by 3.5 cm by 3.5 cm reflector plate was used and consisted of clear epoxy poured around a flat aluminum plate of 0.6 cm thickness with mounted reflector flags. The aluminum extended out of the epoxy resin and served as a point of connection to the skull. The tag was attached to the skull using #8 stainless steel screws. Holes measuring 2.38 mm were drilled through the plate and 5 mm deep into the posterior end of each squamosal bone. A 6 mm space was left under the plate and filled with all-purpose acrylic to prevent necrosis of the skin.
The acrylic pad hardened after the attachment was made. Anesthetic (tiletamin-zolazepam) was administered previous to tag application (Clyde et al. 1994).

All adult females received a harmonic radar tag. Commercially produced harmonic radar tags (Recco AB, Lidingo, Sweden) measuring 6.5 cm by 2.2 cm by 0.8 cm were placed subdermally under the bony neck scutes. This tag was used to locate alligators and numbers etched within the tag's surface served as a backup identifier of individuals. A 3-cm incision was made posterior to the rear-most neck scute and the tag was inserted through the incision. The tag was pressed forward into place under the leading bony neck scutes. The skin was sealed using tissue glue. The tags were relocated using a hand-held sending/receiving unit (Model R5P1) produced by the same company.

The retention rates of the 3 tags and tail notch were estimated using a binomial distribution and a 0.05 probability level in association with the number retained and functional out of tagged animals reexamined. Percentages used to calculate the mean and 95% Confidence Intervals (95% CI) were transformed in order to achieve uniform variance using the arcsin of the square root of the estimate. Linear regression was used to describe the detection range for 60 artificially placed harmonic radar tags. Twenty tags were manually placed at each the following heights compared to water level: -2.54 cm, 2.54 cm, and 91.44 cm. Half of the tags at each of the heights were oriented so to be parallel to the sending/receiver unit; remaining tags were oriented to be perpendicular. The predictor variables included within the model were height of tag compared to water level and orientation of the tag. The response variable was the maximum distance at which the tag was detected.
RESULTS

Individual alligators (2,674 hatchlings and 368 alligators over 1.52 m) were captured between May, 1997 and October, 1999. The adult sex ratio for captures was 1 male to 5.24 females. Small, Medium, Large, and Very Large alligators made up 8.5%, 27.1%, 8.5%, and 55.9% of male captures, respectively. Small, Medium, Large, and Very Large alligators made up 5.8%, 22.3%, 43.1%, and 28.8% of female captures, respectively. Average workup time for adult alligators not receiving a cranial reflector was 14.02 minutes (SE = 0.83). Workup time was significantly longer when cranial reflectors were being applied ($F_{1,312} = 15.50$, $P = 0.001$) and averaged 31.36 minutes (SE = 2.84), excluding time for recovery from anesthesia.

Approximately 31% of males and 54% of females were captured out of dens, and 9% of alligators were captured using baited lines. The average dimensions of the 75 dens measured were the same size regardless of the adult’s sex or size class. The average den had a 2.4 m (SD = 1.0) long tunnel that ended in a 0.9 m (SD = 0.2) diameter rear chamber. The longest den tunnel measured was 7 m and the largest diameter chamber recorded was 1.5 m. Tunnels were generally straight and chambers slightly offset to one side of the tunnel. Dens were at least 60 cm underground. All dens examined ($n = 232$) had only 1 entrance. Dens were identified using a pole to feel the bottoms of shallow marsh ponds and by looking for muddied water within isolated pools. Most alligators captured at dens (89%) were not seen prior to investigation of the den. Alligators left the den after an average of 36 minutes of harassment (range: 1 - 186 minutes). All harassment times over 60 minutes were at dens where alligators were seen
prior to searching the den. Additionally, alligators appeared less likely to leave dens a second time after a failed noose attempt. For 4 alligators harassed within the den, missed, and then re-harassed and captured, the first attempt took an average 15 minutes of harassment and the second attempt took an average 80 additional minutes of harassment. No instances of tail-notches being lost were recorded for hatchlings (n = 204) or adults (n = 117). Fifteen (4%) and 101 (27%) adult alligators were naturally missing parts of, or entire, feet and various lengths of tail, respectively. Hatchlings handled had the following abnormalities: missing parts of tail (0.26%), damaged eyes (0.07%), and missing feet (0.03%).

PIT tags used on alligators ≥ 1.52 m total length had a mean yearly retention rate of 0.836 (95% CI: 0.683, 0.946) (Table 1). Gun shots to the head of the alligators during harvest caused 45% of the losses. The remaining missing tags had apparently backed out of the injection hole soon after application. Monel web and PIT tags were placed simultaneously on 100 alligators of which 37 were recaptured within 60 days. No alligators were missing web tags. Using a binomial distribution and a 0.05 probability level in association with 0 cases of missing tags and 37 cases of retained tags, the retention rate up to 60 days was estimated to be no less than 0.922. Three of these same alligators were missing PIT tags. PIT tag retention averaged 0.919 (95% CI: 0.831, 1.000).

A total of 204 previously marked hatchlings (i.e., alligators < 1 m total length) were reexamined over the 3-year study and yearly PIT tag retention was estimated at 0.972 (95% CI: 0.781, 1.00) (Table 1). All of these losses were for hatchlings handled within
the first year of the study. Hatchlings marked and recaptured during 1999 (n = 23) also retained 100% of PIT tags, however, there were only a few weeks between recaptures.

Table 1. Probability of an alligator retaining a passive integrated transponder (PIT) tag between recaptures from 1997 through 1999, Sabine National Wildlife Refuge, Louisiana. Size is the total length of alligators; Year is the year in which the alligator was originally tagged; year 1999 includes alligators tagged with both web and PIT tags and were excluded from the 1999 sample; r* is the number of alligators reexamined within interval i; l* is the number of alligators missing a PIT tag at interval i; K* is the probability of tag retention during the recapture interval i.

<table>
<thead>
<tr>
<th>Size</th>
<th>Year</th>
<th>i ≤ 1 Yr</th>
<th>1 Yr &lt; i ≤ 2 Yrs</th>
<th>2 Yrs &lt; i ≤ 3 Yrs</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>rᵢ</td>
<td>lᵢ</td>
<td>rᵢ</td>
<td>lᵢ</td>
</tr>
<tr>
<td>≥1.52 m</td>
<td>1997</td>
<td>21</td>
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<td>0.857</td>
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<tr>
<td></td>
<td>1998</td>
<td>12</td>
<td>1</td>
<td>0.917</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>23</td>
<td>3</td>
<td>0.870</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>21</td>
<td>4</td>
<td>0.810</td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>77</td>
<td>11</td>
<td>0.857</td>
</tr>
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</tr>
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</tr>
<tr>
<td></td>
<td>All</td>
<td>149</td>
<td>10</td>
<td>0.933</td>
</tr>
</tbody>
</table>

Forty-nine of 77 adults were relocated under natural conditions and identified using the PIT tag only. Of these adults, 15 alligators were identified without handling using the water resistant probe and 3 of these were identified while still underground within the den. One alligator with a cranial reflector was observed and re-identified using the reflective tag; this occurred 3 days after the original capture. Of the 18 alligators fitted with this tag type, 6 were rehandled at least 90 days after application and no evidence of
the tag or its placement remained. Using a binomial distribution and a 0.05 probability level in association with the 6 cases of missing tags and no cases of retained tags, the estimated retention rate after 90 days was no more than 39.3%.

The detection distance for harmonic radar tags used to relocate alligators was under 15 m when the tag was less than 2.54 cm from or below water level, and tag orientation effected signal strength. Overall, the tags detection range (m) was equal to 0.2717 times the height (cm) of the tag above water level (n = 60) but was reduced by 8.6 m when parallel to the receiver ($F_{2,7} = 239.42, P < 0.001, R^2 = 0.89$).

DISCUSSION

When marking alligators for later identification there is no perfect tag available. Within this study only web and hatchling PIT tags had retention rates approaching 100%. Monel tags used on sea turtles also have demonstrated excellent short-term retention, however 100% of tags are suspected lost after a 10-year period (Limpus 1992). Alligators may possibly live well over 50 years (Hutton 1991), and farm-raised alligators are routinely harvested without web tags (Sabine National Wildlife Refuge, unpublished data). Additionally, monel tags that are appropriate for adults are not suitable for use on newly hatched alligators that are only 5% of adult size. If an animal retains a PIT tag after the injection wound is healed, the probability it retains the PIT tag should be relatively high and stable over time (Schooley et al. 1993).

Adult alligators have been marked routinely using what are considered permanent body marks consisting of toe clipping and notched tail scutes. Alligators, however, naturally lose various body parts including parts of feet and segments of tails. Our
cranial reflectors, even when mechanically attached to the skulls of alligators, demonstrated very low retention rates; these tags were apparently sheared off leaving no indication of their presence.

PIT tags are a viable alternative to toe clipping and tail notching for identifying individuals of all size classes. Both methods provide for the possible long-term identification of alligators, however, only PIT tags allow for unlimited numbers of individuals to be marked. Retention of 100% may be possible if care is taken where the PIT is applied. The placement in the earflap of adults made the tags susceptible to loss by migration and gunshot damage. The style of tag (i.e., true anti-migration characteristics) may also protect against tag loss. Alligators have a less sophisticated inflammatory response to foreign bodies than mammals and little swelling occurs following injection; the earflap and its restricted size allowed movement toward the injection site. Most preventable losses of PIT tags appear to occur prior to the healing of the injection wound, after this time minimal natural loss should occur. Sealing the injection wound prior to release may additionally help reduce PIT tag loss.

The lack of information on tag retention rates made planning a long-term nesting ecology study difficult. The goal of monitoring large numbers of individual female alligators and their young over successive years meant dependency on reliable tags. The amount of time alligators spent in a subterranean environment had affects on the ease of identifying individuals. For example, web tags proved to be an excellent tag for adults, however, alligators were required to be handled to read tags and identify individuals. Every handling involves risks of injury to researchers and alligators. PIT tags were the
only tags tested that provided for the identification of all size classes of alligators under various field conditions. PIT tags allowed the identification of individuals without handling or even seeing the animal, even with the limited range (< 7.5 cm) of the water resistant probe.

Harassment of alligators out of dens, although time consuming, proved to be highly successful and allowed the capture of animals that would otherwise have been overlooked. Care should be taken to harass the alligator only to induce greater activity and not to harass through the den entrance. Alligators appear to become more obstinate as they become aware of the consequence of leaving the den. Baited lines allowed capture of alligators that would have otherwise escaped capture. Alligators within deep water habitat easily out maneuver the noose. The baited line allowed some control prior to noosing. Care should be taken to use a weak enough twine to prevent drowning, due to the line becoming entangled underwater, but strong enough to provide a noosing opportunity while the alligator is still underwater.

MANAGEMENT IMPLICATIONS

There are no long-term estimates on tag retention for alligators. Estimates of life history characteristics based on mark-recapture techniques will be underestimated without correction for tag loss. Web tags are a commonly used mark for identifying individuals. All of Louisiana’s farm-raised alligators are web tagged prior to release into natural habitats (Elsey et al. 1992). This study provides a web tag retention rate estimate of at least 92.2%, but only over a 60 day period. Based on estimates from sea turtles, it should not be unexpected that many of web tags placed on young alligators may be lost.
by the time they reach sexual maturity at 10-years of age. PIT tags are a good alternative to the traditional web tag in marking alligators. It is not unrealistic to expect extremely high retentions for PIT tags when these tags have true anti-migration characteristics and are placed in areas where tags cannot easily back out of the injection wound, such as the neck. A single PIT tag placed within the neck will provide identification of individuals of all life stages, hatchling through adult. Additional reports of the probability of tag loss in alligators are needed, however, for ranking the available tags and selecting tags that best meet proposed projects goals.
Chapter 2. Spacing Patterns of Alligator Nest Sites

Peak periods of nesting have been positively correlated to warm air temperatures during March, April, and May (Joanen 1969). Female alligators (*Alligator mississippiensis*) select nest sites based on undefined criteria. The bulk of nesting within Louisiana occurs within coastal marshland and the intermediate marsh type contains the highest alligator densities (McNease and Joanen 1978). McIlhenny (1935) suggests site selection is due to site fidelity. However, even if his hypothesis was correct, he does not provide information on why original sites were selected. The only descriptions of requirements for nesting arise from propagation of alligators in captivity. Joanen and McNease (1971, 1975) indicate the following 6 factors are necessary for females to nest successfully: fresh water and food for consumption, den habitat for rest and thermoregulation, a breeding male that is acceptable to the particular female, deep water areas for copulation, a small pool for the female to use as a refuge, and natural marsh vegetation for use as nest material. Numerous habitat variables including shade, height of nest above water level, vegetation density, distance to nearest high ground, and distance to nearest open water provide no insight into nest site selection (Jennings et al. 1987).

Although it is not known why a female alligator chooses a particular site, several studies address spatial distribution of alligator nests. Nests within 30.5 m of each other have been reported as being produced by the same female with only one nest having eggs (Chabreck 1966). Goodwin and Marion (1978) found that their data supported this conclusion; no nests were constructed within 160 m of another nest. Rootes and
Chabreck (1993), however, found a single occurrence of 2 nests with eggs within 30 m of each other. Additionally, Woodward et al. (1984) and Jennings et al. (1987) report alligator nests within Florida are clustered. They suggest that clustering is possibly due to a mutual attraction among females. The ideas that alligator are both attracted to each other, and yet territorial around their nests appears to conflict. To gain insights into alligator nest site selection, a large number of alligator nests were monitored at Sabine National Wildlife Refuge in southwestern coastal Louisiana. The objectives were to describe alligator nest distribution patterns, segregation of nests within the habitat based on the size class of nesting females, and minimum distances between nests with eggs.

STUDY AREA

The study area encompassed two impoundments on the refuge and contained vegetative types consistent with fresh (8 km²) and intermediate (21 km²) marsh (Chabreck and Linscombe 1988). The main source of water for the impoundments was rainfall. Monthly rain amounts averaged 13.53 cm (SD = 5.72), 15.19 cm (SD = 10.18), and 11.22 cm (SD = 8.99) for the 1997, 1998, and 1999 summer seasons, respectively (Sabine National Wildlife Refuge, unpublished data). Water levels within the 2 impoundments varied among years; the 1999 study year had significantly less water during the period of May through August. Dense marshhay cordgrass (Spartina patens) dominated the habitat. A marsh lake and canals bordered impoundments. The border levees were vegetated with Chinese tallow-tree (Sapium sebiferum), sea-myrtle (Baccharis halimifolia), and roseau cane (Phragmites communis). The marsh was interspersed with shallow open water pools, many of which were being colonized by

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bullwhip (*Scirpus californicus*) and cattail (*Typha* spp.). Giles and Childs (1949) provide historic information on alligator management at Sabine National Wildlife Refuge.

**METHODS**

Adult females were located systematically and captured throughout the two impoundments starting during the courtship period (April and May) and continuing through the period of egg incubation (June through September). In addition, all untagged alligators caught at nest sites were tagged. Adults with total length $\geq 1.52$ m were marked with a non-unique tail notch and an uniquely coded Passive Integrated Transponder (PIT) tag. Adults were injected with 12 mm x 2 mm (American Veterinary Identification Devices [AVID], Norco, CA) or 11 mm x 2 mm (Destron-Fearing Corp, St. Paul, MN) PIT tags subcutaneously within the right earflap. Alligators were categorized within the following 4 size classes based on total body length: Small ($< 1.83$ m), Medium (1.83-2.12 m), Large (2.13-2.42 m), and Very Large ($> 2.42$ m).

With no information available on assessing alligator condition, relative condition of alligators was assessed using tail girth divided by the total body length. Tail girth was measured at the base of the tail.

Nests were located systematically using an airboat during the 1997 and 1998 nesting seasons, and by helicopter and airboat during the 1999 nesting season. Alligator nests were marked with poles and numbered tags. Universal Transverse Mercator (UTM) coordinates were determined for nest sites using a Global Positioning System (GPS) with real time correction. All marked nest sites were visited yearly to assess reuse of sites.
Nesting patterns were compared to 160 randomly generated nest locations. Additionally, each generated nest was randomly assigned an artificial female from the four size classes. The proportions of females among the size classes were assigned to match those observed at alligator nests. All areas with any component of *Spartina patens* and border levees were assumed potential nesting habitat, only open water areas were excluded. Distances to edge of marsh were compared between alligator and generated nests using Kruskal-Wallis Test with an alpha of 0.05. Distances to edge of marsh among nests for the four size classes of alligators were examined using Bonferroni (LSD) Test with an alpha of 0.05. Segregation of alligator nests among females of the different size classes were evaluated by comparing female size classes of nearest neighboring nests. The number of females with nearest neighbors of the same size class was compared to that randomly expected using Cochran-Mantel-Haenszel Test with an alpha of 0.05. Analysis of variance with an alpha of 0.05 was used to compare condition measurements between nesting and non-nesting females for each year.

The methods of Woodward et al. (1984) were used to evaluate nest and capture spacing patterns. Instead of a third party assigning quadrats, however, 464 quadrats, each measuring 6.25 ha, were developed using U.S. Geological Survey mapped UTM grid blocks. Quadrats were formed by sectioning each grid block evenly every 0.25 km over the entire study area. Unlike Woodward et al. (1984), all quadrats vacant of nests during all three years of the study were not dropped. Instead, all areas with any component of *Spartina patens* and border levees were assumed potential habitat for alligator activity and nesting. The mean-to-variance ratios were examined for each
annual distribution. Regression analysis and the associated coefficients of determination were used to determine if quadrats contained similar numbers of nests among the years.

RESULTS

A total of 309 (128, 96, and 85 in 1997, 1998, and 1999, respectively) adult females among the specified size classes (6% Small, 23% Medium, 42% Large, and 29% Very Large) were captured. During 1997, 1998, and 1999, 77%, 59%, and 42% of the females, respectively, were caught prior to the nesting season. One hundred sixty-seven of females were captured out of dens and 67% of the denned females were captured at nest sites. Relative condition was significantly different between nesting and non-nesting females ($F_{1,344} = 7.75$, $P = 0.006$). Nesting and non-nesting adult female alligators had an average relative condition of 0.209 and 0.204, respectively. Alligator captures, excluding captures at nests, were not clustered during all years (Table 2). Alligators within capture clusters were not segregated and contained mixtures of all size classes.

The total number of nests identified within the study area was 121, 102, and 155 for 1997, 1998, and 1999, respectively. During the same years, females were associated with 40, 43, and 70 nests. Small, Medium, Large, and Very Large females were associated with nests in the following proportions: 4%, 13%, 41%, and 42%, respectively. Only during 1998 were false nests (i.e., nests appearing complete but containing no eggs) significantly less likely to have females captured at the site ($\chi^2 = 7.99$, 1 df, $P = 0.005$). A total of 13 females were captured at false nests during each of the following years: 1997 (2 of 9 nests), 1998 (2 of 21 nests), and 1999 (9 of 20 nests).
Table 2. Mean, variance, and significance levels for nests, randomly generated and alligator, and alligator capture distributions, 380 quadrats, Sabine National Wildlife Refuge, Louisiana, 1997-99.

<table>
<thead>
<tr>
<th>Group</th>
<th>Sample</th>
<th>Mean number per quadrat</th>
<th>Variance</th>
<th>Alpha for rejecting null hypothesis that entire distribution is Poisson</th>
<th>Pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td>Captures</td>
<td>1997</td>
<td>0.2105</td>
<td>0.2668</td>
<td><em>P &lt; 0.001</em></td>
<td>Clustered</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>0.1447</td>
<td>0.1557</td>
<td><em>P = 0.19</em></td>
<td>Random</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>0.0868</td>
<td>0.1006</td>
<td><em>P = 0.07</em></td>
<td>Random</td>
</tr>
<tr>
<td>Nests</td>
<td>Generated</td>
<td>0.4211</td>
<td>0.4661</td>
<td><em>P = 0.759</em></td>
<td>Random</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>0.3158</td>
<td>1.0082</td>
<td><em>P &lt; 0.001</em></td>
<td>Clustered</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>0.2526</td>
<td>0.5112</td>
<td><em>P &lt; 0.001</em></td>
<td>Clustered</td>
</tr>
<tr>
<td></td>
<td>1999</td>
<td>0.3947</td>
<td>0.6981</td>
<td><em>P &lt; 0.001</em></td>
<td>Clustered</td>
</tr>
</tbody>
</table>

Approximately 2,375 ha (82%) of the study area were considered suitable for alligator nesting. Minimum nest densities for the three years were as follows: one nest per 19.69 ha (1997), one nest per 23.28 ha (1998), and one nest per 15.32 ha (1999). The distribution of nests within quadrats varied from Poisson expectations (Table 3). The mean-to-variance ratio for all years was less than 1.0 (Table 2). As expected, there was insufficient evidence to reject the null hypothesis that random nest locations were collected from a Poisson distribution.

Quadrats were not observed having the same relative number of nests each year, and all coefficients of determination for nesting distributions were not significant. Quadrats were reused but numbers of nests within quadrats varied yearly. Approximately 31%,
33%, and 63% of quadrats received some level of reuse between 1997 and 1998, 1997 and 1999, and 1998 and 1999, respectively.

No difference was detected between alligator and randomly assigned nests in reference to marsh edge both within and among years. Alligator nests were an average of 364 m (SE = 22) from the marsh edge. Nesting females of different size classes were not distributed significantly different from randomly generated females of different size classes in reference to the edge of the marsh. Among alligator nests, however, nests of Very Large females were significantly farther from the edge of the marsh than nests of either Small or Medium females (Table 4). Segregation occurred among size classes of nesting alligators with neighboring nests of Very Large alligators occurring more than randomly expected (Table 5).

A total of 64 (17.6%) of the 364 nests both with and without eggs were located within 30.5 m of each other, and 47 of these nests contained eggs. Of the 47 nests with eggs, 34 nests were located within 20 m, 22 nests within 10 m, and 12 nests within 5 m of another nest. Females were captured at 6 pairs of these 47 nests and in all cases the adjacent females were of the same size class. A total of 50 false nests were found during the 3-year project and 66% did not have a paired nest within 30.5 m. The proportion of false nests did not vary among years ($\chi^2 = 1.03, 1$ df, $P = 0.31$) with 0.076 in 1997, 0.208 in 1998, and 0.131 in 1999. In 7 cases, females associated with the false nests were relocated later the same year at nests with eggs. The associated female’s real nest was the closest neighboring nest in 5 of these cases. Average distance between these female’s false and real nests was 67 m (SD = 34).
Table 3. Distribution of randomly generated and alligator nests within quadrats, Sabine National Wildlife Refuge, Louisiana, 1997-99.

<table>
<thead>
<tr>
<th>Number Nests per Quadrat</th>
<th>Proportion of Quadrats</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Generated</td>
</tr>
<tr>
<td>0</td>
<td>0.663</td>
</tr>
<tr>
<td>1</td>
<td>0.274</td>
</tr>
<tr>
<td>2</td>
<td>0.047</td>
</tr>
<tr>
<td>3</td>
<td>0.011</td>
</tr>
<tr>
<td>4</td>
<td>0.005</td>
</tr>
<tr>
<td>5</td>
<td>0.000</td>
</tr>
<tr>
<td>6</td>
<td>0.000</td>
</tr>
<tr>
<td>12</td>
<td>0.000</td>
</tr>
</tbody>
</table>

DISCUSSION

Using systematic searches, alligators were found to be randomly distributed in the same year nests sites were clustered. Segregation of the female size classes occurred at nests but not at capture locations. The largest size class of female alligators nested near other Very Large females. Size class appears to determine where and how close the different size classes nest. Females may seek, or create, isolation from other size classes of nesting females. Additionally, alligators did not maintain minimum distances between nests, but seem to exclude smaller females within minimum distances.
Table 4. Distance from marsh edge for nests of females of different size classes, Sabine National Wildlife Refuge, Louisiana, 1997-99. Comparisons non-significant at the 0.05 level are indicated by same letter grouping.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>No. Nests</th>
<th>Distance to Marsh Edge</th>
<th>Mean (meters)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>6</td>
<td></td>
<td>146 a</td>
<td>107</td>
</tr>
<tr>
<td>Medium</td>
<td>20</td>
<td></td>
<td>246 a</td>
<td>240</td>
</tr>
<tr>
<td>Large</td>
<td>63</td>
<td></td>
<td>353 a, b</td>
<td>258</td>
</tr>
<tr>
<td>Very Large</td>
<td>64</td>
<td></td>
<td>449 b</td>
<td>281</td>
</tr>
</tbody>
</table>

Table 5. Number of nests with the nearest neighbor being of the same size class for randomly generated and alligator nests, Sabine National Wildlife Refuge, Louisiana, 1997-99.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Nest</th>
<th>Yes</th>
<th>No</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>Generated</td>
<td>0</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Alligator</td>
<td>2</td>
<td>4</td>
<td>0.154</td>
</tr>
<tr>
<td>Medium</td>
<td>Generated</td>
<td>3</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Alligator</td>
<td>2</td>
<td>18</td>
<td>0.589</td>
</tr>
<tr>
<td>Large</td>
<td>Generated</td>
<td>31</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Alligator</td>
<td>33</td>
<td>30</td>
<td>0.724</td>
</tr>
<tr>
<td>Very Large</td>
<td>Generated</td>
<td>16</td>
<td>32</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Alligator</td>
<td>38</td>
<td>26</td>
<td>0.006</td>
</tr>
</tbody>
</table>

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One hypothesized mechanism is that natural nest locations are based on a breeding hierarchy with high ranking females obtaining the best habitat, and all others getting suboptimal habitat (Platt et al. 1995). If nest dispersion is determined by a female based hierarchy, it seems sensible to expect the hierarchy to be based on size of the alligator. Larger females should dominate the optimal nesting habitats and smaller females should be pushed toward the suboptimal. Alligator nests should cluster around that optimal habitat with large animals dominating clusters. The largest nesting female alligators within this study were found farther from marsh edge than smaller females. Additionally, alligator nests were clustered and the largest females dominated the clusters. Both of these findings support the concept of a female based hierarchy. Since nest clustering, however, was not in the same area from year to year, clustering was not based on a stationary optimal habitat; it is associated with a non-stationary characteristic. No dramatic changes occurred within the study area’s vegetation during the sample period. It is possible that water levels varied within the interior marsh pools and these changes were not readily detectable.

Woodward et al. (1984) suggests nesting is limited by the following three associations: physical limitations on nest construction material or space, reduced fecundity due to poor nutrition, and agonistic behavior that restricts mating opportunity. In this study area *Spartina patens* appears readily available, and alligators do not have minimum distances between nests. Nest densities were not excessively high compared to others reported within Louisiana (McNease and Joanen 1978, Taylor et al. 1991) and are much lower than those of alligators bred in captivity (Joanen and McNease 1975).
Therefore, physical limitations on material or space do not seem to limit nest construction. The relative condition of alligators was different between nesting and non-nesting adult females, but captures were randomly distributed during the same years that nests were clustered. Assuming our index of condition is representative, nutrition does seem to play some role in limiting the number of females nesting within this study area, but not where they build nests. The final suggestion of agonistic behavior restricting mating opportunity may best explain the observations of clustering and segregation seen within this study.

Joanen and McNease (1971, 1975) stated that six biological requirements need to be met before females can be expected to reproduce. It is the interaction of these requirements that should determine where alligators build nests. However, there is no qualitative or quantitative information on how these requirements affect reproduction among populations of wild alligators. In this study area food appears to limit the number of reproducing females. However, capture locations being randomly distributed implies food is available throughout the marsh. There is no evidence to suggest water, den or female refuge habitat, or natural marsh vegetation are limited. Habitat that is not used for nesting in any single year is often acceptable nesting habitat in other years. These together suggests that nesting may be limited locally due to local conditions and agonistic behavior among females at those sites.

Quality of nesting sites appears to differ with distance from marsh edge (Taylor 1984), and access to quality males in breeding pools may become limited within the interior marsh due to males preferring the external deep water habitats (Joanen and
McNease 1972). Competition for males within the limited deep water habitats may cause non-stationary clustering and segregation among the reproductive size classes. Female alligators will discontinue courtship with unacceptable males (Garrick and Lang 1977). Joanen and McNease (1971) describe having to present three males, which they perceived as quality, to a particular female before finding an acceptable mate. Additionally, they report females killing rival females and substandard males during the courtship period. If quality males are limited due to few deep water habitats within the marsh interior, larger better conditioned females should logically out compete the smaller females and be the predominate nesters within those areas. There is no information on characteristics of quality males or whether quality males become limited. However, if male display areas are limited, the artificial placement of breeding pools within the marsh interior should stimulate clustering around those pools.

**MANAGEMENT IMPLICATIONS**

As part of the nest-to-population extrapolation method used to manage Louisiana's alligators (McNease and Joanen 1978, Taylor et al. 1991), nest distribution patterns are assumed random and alligator nests found within 30.5 m of each other are counted as one (Chabreck 1966). Both of these assumptions are incorrect, however, the removal of expected false nests causes a more immediate bias to the statewide survey. The majority of false nests were found not paired with any nests and 15% of nests with eggs were produced in very close proximately to each other.

The clustering pattern of nests within the heavily vegetated marsh may additionally affect Louisiana's survey if clusters coincide with the sampling interval or some multiple
of the interval. If transect lines tend to pass through clusters then the estimates will be too high and if they tend to pass between clusters then the estimates will be too low. In both of these instances the variances associated with the estimates will be too small and would give the biologist/manager a false sense of security about the estimates. If clusters tend to fall on the line one time and between the lines the next time, the mean estimate may be correct but the variance would be too high. This would lead the biologist/manager to think that they needed a larger sample than really necessary. The patterns noted are unlikely to persist across an area as large as the southwest coast of Louisiana but may be present on smaller areas like a single refuge or management area. This may be particularly true on areas where manmade features such as levees, roads, and canals occur at systematic intervals across an area. Although much simpler to implement, a systematic sample is equivalent to a random sample of the same size only if the population units are randomly distributed. The use of random starting points for all transects may eliminate effects of periodicity within nest cluster patterns.
Chapter 3. Annual Nesting Rates

Louisiana estimates the annual alligator (Alligator mississippiensis) population and develops harvest quotas using nest-to-population extrapolation factors (Chabreck 1966, McNease and Joanen 1978, Taylor et al. 1991). The factors used for the calculation include annual nests counts and 3 constants: annual nesting rate, percent alligators over 1.83 m total length, and percent females among the alligators over 1.83 m total length (McNease and Joanen 1978, Joanen et al. 1984, Taylor and Neal 1984). The estimates of percent alligators over 1.83 m total length and percent females within this group were developed from a single study based on harvested alligators (Taylor and Neal 1984) and probably are not constant or representative of the population. Harvest methods are designed to be biased away from small alligators and nesting females (Joanen et al. 1984). Annual nesting rate estimates have been estimated using a variety of methods and for several wild American alligator populations (Table 6). These annual nesting rates vary greatly from <0.1 to 0.681 (Joanen and McNease 1980, Taylor 1984, Lance 1989, Rootes and Chabreck 1989, Taylor et al. 1991, Walthers and Ivy, Sabine National Wildlife Refuge, Louisiana, unpublished data, Wilkinson, South Carolina Wildlife and Marine Resources Department, unpublished data). This variation suggests that reproductive rates may be unique to the time and place of the study (Woodward et al. 1984). The use of differing annual nesting rates within the model yields very different population estimates and harvest quotas.

Female alligators are commonly assumed to nest at the same site with each reproductive effort. Rates of site reuse, however, have not been integrated for the
Table 6. Reported annual nesting rates and methods of estimation for American alligators.

<table>
<thead>
<tr>
<th>Source</th>
<th>Location</th>
<th>Annual Nesting Rate</th>
<th>Method of Data Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Walthers and Ivy, Sabine National Wildlife</td>
<td>Louisiana</td>
<td>0.681</td>
<td>Females (n = 69) collected in one year's harvest and examined for eggs.</td>
</tr>
<tr>
<td>Refuge, Louisiana, unpublished data</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joanen and McNease 1980</td>
<td>Louisiana</td>
<td>0.63</td>
<td>Females (n = 28) collected during one year using an undefined method of collection and examined for eggs.</td>
</tr>
<tr>
<td>Kushlan and Jacobsen 1990</td>
<td>Florida</td>
<td>0.29</td>
<td>Monitored an unknown number of individual females over a 7-year project.</td>
</tr>
<tr>
<td>Taylor 1984</td>
<td>Louisiana</td>
<td>0.28</td>
<td>Monitored 9 females over a 1-year period.</td>
</tr>
<tr>
<td>Taylor et al. 1991</td>
<td>Louisiana</td>
<td>0.253</td>
<td>Collected 1,715 females using experimental harvests over a 4-year period and examined reproductive tracts for corpora lutea.</td>
</tr>
<tr>
<td>Wilkinson, South Carolina Wildlife and Marine</td>
<td>South Carolina</td>
<td>0.25</td>
<td>Monitored 32 females over a 3-year period.</td>
</tr>
<tr>
<td>Resources Department, unpublished data</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lance 1989</td>
<td>North Carolina</td>
<td>&lt;0.10</td>
<td>Measured plasma calcium for an unknown number of female alligators that were collected in an unknown manner.</td>
</tr>
<tr>
<td>Rootes and Chabreck 1993</td>
<td>Louisiana</td>
<td>0.33</td>
<td>Monitored 15 females over a 1-year period.</td>
</tr>
</tbody>
</table>
improvement of understanding alligator nest ecology. McIlhenny (1935) made some of the first detailed descriptions on alligator nest site fidelity, and observed that the same females were frequently using the same location year after year. Joanen (1969) monitored 315 nests over a 4-year period and found the majority of nests were located within 182 m of an old nest site, but only 1.3% of the nests were located immediately adjacent to the same nest site. Carboneau (1987) and Platt et al. (1995) have reported 4.1% and 5.3% of nest sites, respectively, were reused annually. Those studies that report site reuse do not document that reuse was by the same female and, thus, can not address fidelity rate. With the inherent bias associated with harvest and alternative estimates of annual nesting rates being based on few individuals over short time periods, the goal of this study was to monitor a large sample of systematically captured individual females over a 3-year period and develop estimates of annual nesting and nest site fidelity rates use females recaptured at systematically located samples of nests.

**STUDY AREA**

Sabine National Wildlife Refuge is located in southwestern coastal Louisiana. The study area encompassed two impoundments on the refuge and contained vegetative types consistent with fresh (8 km²) and intermediate (21 km²) marsh (Chabreck and Linscombe 1988). The main source of water for the impoundments was rainfall. Monthly rain amounts averaged 13.53 cm (SD = 5.72), 15.19 cm (SD = 10.18), and 11.22 cm (SD = 8.99) for the 1997, 1998, and 1999 summer seasons, respectively (Sabine National Wildlife Refuge, unpublished data). Water levels within the 2 impoundments varied among years; the 1999 study year had significantly less water
during the period of May through August (Sabine National Wildlife Refuge, unpublished data). Dense marshhay cordgrass (*Spartina patens*) dominated the habitat. A marsh lake and canals bordered the dense marsh. The border levees of the impoundments were vegetated with Chinese tallow-tree (*Sapium sebiferum*), sea-myrtle (*Baccharis halimifolia*), and clumps of roseau cane (*Phragmites communis*). The marsh was interspersed with shallow open water pools many of which were being colonized by bullwhip (*Scirpus californicus*) and cattail (*Typha spp.*). Giles and Childs (1949) provide historic information on alligator management at Sabine National Wildlife Refuge.

**METHODS**

Starting during courtship and continued through the period of incubation, adult females were captured systematically throughout the study area using handling methods similar to those described by Chabreck (1963). Additional untagged alligators found at nest sites were tagged each year. Adults captured were marked with a non-unique tail notch ("C" notch) and a uniquely coded Passive Integrated Transponder (PIT) tag. Adults were injected with 12 mm x 2 mm (American Veterinary Identification Devices [AVID], Norco, CA) or 11 mm x 2 mm (Destron-Fearing Corp, St. Paul, MN) PIT tags subcutaneously within the right earflap. Reproductive female alligators were categorized within 4 size classes based on total length: Small (1.52-1.82 m), Medium (1.83-2.12 m), Large (2.13-2.42 m), and Very Large (> 2.42 m) (Taylor et al., 1991).

Nests were located, using systematic searches across the study area, from an airboat during the 1997 and 1998 nesting seasons, and by helicopter and airboat during the 1999 nesting season. Alligator nests were marked with poles and numbered tags. Nest sites...
were assigned Universal Transverse Mercator (UTM) coordinates using a Global Positioning System (GPS) with real time correction. All marked nest sites were visited yearly to assess reuse of sites.

During the 1999 nesting season, pots were placed at random UTM coordinates throughout the intermediate marsh. The pots were used to estimate the proportion of alligator nests found during airboat searches. Knowing total number of nests within the study area was necessary to calculate the probability of detecting previously marked females at nest sites. Persons not associated with the airboat searches placed the pots. Three-dimensional plant pots were assumed to provide similar detection difficulty to that of an alligator nest. The 68 pots were constructed from 18.5 L black plastic nursery pots. The pots were mounted on 1.9 cm diameter PVC poles and placed at a height above the ground surface of 76 cm, the approximate height of the average nest. The vegetation around the pots was left standing. Pots were found in conjunction with alligator nests.

Yearly nest site reuse rates (i.e., the proportion of nests reused by any female) were calculated using the number of sites reused divided by the number of nests identified in a previous year. Nests had to be within 10 m of a previous nest site to be considered as reused. For example, if 1 nest was within 10 m of a previous year’s nest site and there were 10 nests at known locations during that previous year, then the estimated reuse rate would equal 10%. The probability of detecting previously marked females at nests was calculated using the yearly number of nests with associated females divided by the estimated total number of nests for that same year. For example, if females were
associated with 40 of an estimated 170 nests during a given year, the probability of detecting a previously marked female within that year would be 0.235. The variance was calculated under the assumption that probability of detection could be represented as a binomial distribution. Annual nesting rates were calculated using the estimated number of previously marked females nesting within a year divided by the number of females captured prior to that year’s nesting season. The estimated number of marked nesting alligators was calculated using the number of marked alligators identified at nests during a given year divided by that year’s probability of detecting a previously marked female at a nest. For example, if 3 previously marked females were identified at nests and the probability of detection was 0.235 for that year, an estimated 12.77 females nested. If 98 females were marked prior to that nesting season, the estimated annual nesting rate would be 0.1303 (i.e., 12.77 / 98).

Yearly levels of nest site fidelity (i.e., the proportion of nest sites reused by the same female) were calculated by dividing the number of females renesting within 10 m of the same site by the total number of nests sites with associated females in the previous year and the annual nesting rate for that year. For example, if 1 female was found nesting within 10 m of her previous nest site, 55 nests from the previous year had females associated, and the annual nesting rate was 9.45%, the estimated nest site fidelity would be 0.1924 (i.e., 1 / [55 x 0.0945]). Prior capture was assumed to have no impact on the chance of nesting and also assumed to have no impact on the probability of detecting a female given that it had nested. It was also assumed no adult female alligators within the
study nested outside of the study area. Furthermore, it was assumed that combining information gathered within the 2 impoundments did not bias the results.

RESULTS

A total of 309 (128, 96, and 85 in 1997, 1998, and 1999, respectively) adult females were captured among the specified size classes (6% Small, 23% Medium, 42% Large, and 29% Very Large). During 1997, 1998, and 1999, approximately 77%, 56%, and 41% of the females handled, respectively, were caught prior to nesting. A total of 121, 102, and 155 nests were located during 1997, 1998, and 1999, respectively.

Airboat searches found 71% of pots. The estimated total number of nests within the study area was 170 and 143 for 1997 and 1998, respectively. Pots proved not to be visible from the helicopter, but the helicopter was used to locate 147 alligator nests during 1999. The airboat search found an additional 8 alligator nests immediately after the completion of the helicopter search. Based on the estimate that airboat searches find an estimated 71% of nests, there appeared to be 11 alligator nests left undetected by the helicopter; the helicopter found 93% of the alligator nests within the study area. Total number of nests within the study area were estimated to be 158 during 1999.

Females were associated with 40, 43, and 70 nests during 1997, 1998, and 1999, respectively. Small, Medium, Large, and Very Large females were associated with these 153 nests in the following proportions: 4%, 13%, 41%, and 42%, respectively. Fewer Medium ($\chi^2 = 6.35, \text{1 df, } P = 0.012$) and more Very Large ($\chi^2 = 7.43, \text{1 df, } P = 0.006$) alligators were caught at nests than captured prior to nesting. An estimated 62 marked
females nested during the 3-year study. The 95% confidence interval for the estimated mean annual nesting rate across years was bounded between 9.97% and 14.75% (Table 7). Estimated nest densities for the three years were as follows: one nest per 19.69 ha (1997), one nest per 23.28 ha (1998), and one nest per 15.32 ha (1999).

The average nest site reuse rate was 3.7% (SE = 1.6) during the 3-year study. A total of 12 reused sites were documented; unidentified females reused 9 sites and different marked females 3 sites. No nest sites were used a second time by the same female. Six females were documented nesting twice during the 3-year study and in all cases fresh unmarked nest sites were selected (i.e., not fidelity). Using a binomial distribution and a 0.05 probability level in association with the 9 cases of non-fidelity and no cases of fidelity, we estimated annual nest site fidelity to be no greater than 28.3%.

Females nested an average of 257 m (SD = 195) away from their previous nest site. Movement between nest sites was also seen within years. A total of 50 false nests were located during the 3-year project. False nests appeared normal except no eggs were deposited. An average of 66% of false nests were not located within 30.5 m of a nest with eggs. When false nests were paired (within 30.5 m) with nests with eggs, the average distance between nests was 11 m (SD = 9). In 7 cases, the females associated with the false nests were relocated later during the same year at other nest sites with eggs. Average distance between these female’s false and real nests was 67 m (SD = 34).

DISCUSSION

Estimation of annual nesting rates have been made using harvested alligators and few individuals monitored over short periods. Harvests are designed, however, to be male

<table>
<thead>
<tr>
<th>Year</th>
<th>Cumulative No. Captured Prior to that Year's Nesting Season</th>
<th>95% Confidence Interval for Probability of detection</th>
<th>No. Marked Nesters Recaptured</th>
<th>Estimated No. of Marked Nesters</th>
<th>95% Confidence Interval for Percent Nesting Annually</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>98</td>
<td>(0.245, 0.415)</td>
<td>3</td>
<td>(07.23, 12.24)</td>
<td>(7.37, 12.49)</td>
</tr>
<tr>
<td>1998</td>
<td>182</td>
<td>(0.324, 0.520)</td>
<td>6</td>
<td>(11.54, 18.52)</td>
<td>(6.34, 10.18)</td>
</tr>
<tr>
<td>1999</td>
<td>224</td>
<td>(0.372, 0.532)</td>
<td>13</td>
<td>(24.43, 34.94)</td>
<td>(10.91, 15.60)</td>
</tr>
</tbody>
</table>
biased and favor the capture of non-nesting alligators (Joanen et al 1984). Samples
based on small samples are inherently biased toward the characteristics of those few
individuals. This study, however, systematically captured many individuals prior to the
nesting season and then examined nests for previously marked female alligators. Very
Large alligators nested in higher proportion than that found for captures and made up a
largest proportion of the nesting females within the marsh. Taylor et al. (1991) suggests
these Very Large females also have higher annual nesting rates. Within this study area,
annual nesting rates were low compared to those reported for other areas and may be a
reflection of different methods or unique site characteristics.

Sabine National Wildlife Refuge was established in 1935 and has offered alligators
within the study area long-term protection. The alligator population was beginning to
recover by 1945 (Giles and Childs 1949) and this study occurred over 50 years later.
The 2 marsh impoundments sampled during this project have a mature and dense
alligator population with a low annual nesting rate. The high proportion of Large and
Very Large females reflects the maturity, and the low recapture rate the density. Despite
this, the nest densities at Sabine National Wildlife Refuge are low in comparison to those
reported at other sites in Louisiana (McNease and Joanen 1978, Taylor et al. 1991),
including those reported for alligators bred in captivity (Joanen and McNease 1975).
This supports the hypothesis that a negative relationship exists between percent nesting
and population density (Woodward et al 1984).

Alligators within the study area could not be shown to practice nest site fidelity as
suggested by McIlhenny (1935). Although annual nesting rates appear low, nest site
fidelity could not be validated as occurring for any individual female alligators that did reproduce twice during the 3-year study. Instead, alligators moved from the old nest site to a fresh site. The distances moved were on average greater than that described by Joanen (1969). Different females were found using previous sites and renesting females were found at fresh unmarked sites. Without seeing nest site fidelity, the expected link between nest site fidelity and annual nesting rates could not be demonstrated.

Nesting rates within the study area are lower than those reported within the literature, and even those reported from the same area. Walthers and Ivy (Sabine National Wildlife Refuge, unpublished data) reported an annual nesting rate 5.5-times higher than the rate reported on the same area 36 years later. Estimated annual nesting rates appear area and time specific, possibly due to site specific factors. Annual nesting rates were consistent during this study, but are highly variable among studies. Percent nesting may be inversely related to population density (Woodward et al. 1984).

MANAGEMENT IMPLICATIONS

Aerial counts of nests have been conducted annually over 1.2 million ha of coastal marsh habitat within Louisiana. Nest-to-population extrapolation factors have been used as a basis to estimate alligator populations (Chabreck 1966, Taylor et al. 1991) and to develop harvest quotas (McNease and Joanen 1978). During extrapolation the annual nesting rates, percent of alligators over 1.83 m total length, and percent females among the alligators over 1.83 m total length are assumed constant across all areas and years (McNease and Joanen 1978, Joanen et al. 1984, Taylor 1984). Annual nesting rates, however, vary with study or site (Joanen and McNease 1980, Wilkinson, South Carolina
Chapter 4. David and Goliath Retold: Fire Ants and Alligators

McIlhenny's (1934) description of alligator (Alligator mississippiensis) nesting ecology was 30 years prior to the infestation of red imported fire ants within Louisiana (Callcott and Collins 1996). Fire ants build colonies in recently disturbed ground (Tschinkel 1988). Alligator nests, as described by McIlhenny (1934) and others (Joanen 1969, Deitz and Hines 1980, Taylor 1984), provide such disturbed ground and protection from flooding within the marsh environment. Female alligators form mound-like nests from adjacent soil and vegetation. Eggs are deposited and covered with nest material within a hollow created in the top center of the nest (McIlhenny 1935, Joanen 1969). Nests without eggs are frequent (Joanen 1969, Deitz and Hines 1980, Platt et al. 1995) and of similar appearance to nests with eggs. Ants colonize the new high ground during or after construction.

Ants are mentioned in several papers discussing alligator nesting ecology, but most authors suggest that these opportunistic generalists (Tschinkel 1988) do not affect nest success (Joanen 1969, Goodwin and Marion 1978, Taylor 1984, Platt et al. 1995). Though the effects of ants on adult alligators have not been documented, Allen et al. (1997) in a laboratory experiment demonstrated the ability of fire ants to cause the mortality of hatchlings, and the possible effects of ant stings on the long-term survival of hatchlings after exposure.

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The aggressive nature of fire ants and their relentless defense of alligator nests that they inhabited was observed. The ability of female alligators to carry out their duties of nest maintenance and hatchling release was questioned if she too received frequent and repeated stings at the nest. This study hypothesized that nests with fire ants would receive less maintenance by female alligators, and thus nests would be less likely to succeed.

STUDY AREA

Sabine National Wildlife Refuge is located in southwestern coastal Louisiana. The study area encompassed two impoundments on the refuge and contained vegetative types consistent with fresh (8 km²) and intermediate (21 km²) marsh (Chabreck and Linscombe 1988). The main source of water for the impoundments is through rainfall. Monthly rain amounts for 1997-98 calendar years averaged 13.59 cm (SD = 7.01). Monthly rain amounts averaged 9.9 cm (SD = 3.28) and 18.36 cm (SD = 7.92) for the 1997 and 1998 nesting seasons, respectively (Sabine National Wildlife Refuge, unpublished data). An alligator nesting season runs from June to October.

METHODS

During the period of incubation, nests were examined for adult alligator attendance, the presence of fire ants, and nest success. Evidence for adult attendance included the presence of an adult female, or fresh alligator tracks or tail drag within the mud on or within 3 m of the nest. The presence of fire ants was determined by brushing and prodding only the surface of the nest with a pole to stimulate the ants defense response of swarming. Fire ant colony distribution at observed alligator nests was compared to
that expected randomly within 107 randomly numbered 20-ha quadrats. The number of
ant colonies assigned randomly equaled those observed within the field. Numbers of ant
colonies per quadrat were then compared using Chi-squared tests. Nest success was
recorded after opening of the nest by a female alligator or when all hatchlings were
believed dead within the nest cavity. Researchers attempted to minimize interference
with the nesting process and did not open any nests until the end of the nesting season.
Visits to the nest were limited to an initial examination of a nest, semimonthly visits to
determine hatching status, and a final visit when nesting was considered complete. Adult
alligator attendance and presence of fire ants were recorded as present or absent at each
visit.

Nests were categorized as empty, eggs, pipped hatchlings, and successful. Empty
nests appear normal but contain no eggs, and are sometimes called false nests (Deitz and
Hines 1980). Nests categorized as eggs contained unhatched eggs only. Nests with
pipped hatchlings produced at least one live hatchling and all hatchlings died within the
nest cavity. Successful nests produced at least one hatchling that escaped the nest alive
with or without the females assistance. Data were analyzed using logit models for count
data (Agresti 1996). Only nests categorized as pipped hatchlings or successful were
used for the statistical model; nests not producing live young were not included. A
backward elimination procedure, a process starting with the most complex model and
successively removing terms, was used to select a working model. At each stage, the
likelihood-ratio statistic was used to assess a model’s goodness-of-fit. An alpha of 0.05
was used for determining significance for all tests.
RESULTS

A total of 173 nests were monitored during the 1997 and 1998 nesting seasons. Ants were present in 36% of all nests, and 37% of nests producing hatchlings. Distribution of ant colonies was not significantly different from that expected randomly. Alligator attendance occurred at 68.8% of nests during the period of incubation; no strong pattern of attendance occurred across the four categories of nest fates (empty 31%, eggs 86%, pipped hatchlings 50%, and successful 80%). Adult activity was significantly higher at successful nests than at empty ($\chi^2 = 30.01, 1\ df, P = 0.001$) or pipped hatchling ($\chi^2 = 11.25, 1\ df, P = 0.001$) nests. All but two of the 117 successful nests were opened by an adult alligator; these two nests were blown open by tropical storm winds and were successful. Excluding the 29 empty nests, 95.1% of the 144 nests with eggs contained pipped eggs and nests were 81.3% successful. Mammalian nest depredation occurred at two nests; neither contained fire ants.

A logit model was used to examine the relationship that existed between year (Y), alligator attendance (A), fire ant presence (F), and nest success (N) for the 137 nests with hatched young (Table 8). The 36 nests that did not produce live young were dropped from this analysis. The simplest logit model that fit contained four 2-factor interaction terms (Y*A, Y*N, A*F, F*N) and the four main effects (Table 9). The interaction between adult attendance and nest success (A*N) was conditionally independent; nest success was not influenced by adult attendance. The relative risks of attendance and nest success varied with year (Figure 1). Attendance (60% 1997, 89%
Table 8. Summary of fates for pipped hatchling and successful nests, fire ant presence, female alligator attendance, and predicted values for logit model (YA, YN, AF, FN), Sabine National Wildlife Refuge, Louisiana, 1997-98.

<table>
<thead>
<tr>
<th>Year</th>
<th>Fate</th>
<th>Ants</th>
<th>Yes</th>
<th>No</th>
<th>n</th>
<th>Proportion</th>
<th>Sample Attendance</th>
<th>Predicted Attendance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>Pipped</td>
<td>Yes</td>
<td>4</td>
<td>8</td>
<td>12</td>
<td>0.33</td>
<td>5.5</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>0.67</td>
<td>2.0</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Successful</td>
<td>Yes</td>
<td>4</td>
<td>9</td>
<td>13</td>
<td>0.31</td>
<td>7.2</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No</td>
<td>27</td>
<td>7</td>
<td>34</td>
<td>0.79</td>
<td>22.3</td>
<td>0.72</td>
</tr>
<tr>
<td>1998</td>
<td>Pipped</td>
<td>Yes</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>1.00</td>
<td>3.1</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0.00</td>
<td>1.1</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>Successful</td>
<td>Yes</td>
<td>19</td>
<td>3</td>
<td>22</td>
<td>0.86</td>
<td>15.3</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No</td>
<td>44</td>
<td>4</td>
<td>48</td>
<td>0.92</td>
<td>47.5</td>
<td>0.93</td>
</tr>
</tbody>
</table>
Table 9. Goodness-of-fit tests for logit models relating year (Y), attendance (A), fire ant presence (F), and nest fate (N).

<table>
<thead>
<tr>
<th>Model</th>
<th>df</th>
<th>deviance</th>
<th>$\chi^2$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(AFN, YFN, YAN, YAF)</td>
<td>1</td>
<td>3.4329</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>(AFN, YAN, YAF)</td>
<td>2</td>
<td>3.5450</td>
<td>0.1121</td>
<td>0.74</td>
</tr>
<tr>
<td>(AFN, YAF, YN)</td>
<td>3</td>
<td>3.8234</td>
<td>0.2784</td>
<td>0.60</td>
</tr>
<tr>
<td>(YAF, FN, AN, YN)</td>
<td>4</td>
<td>5.9198</td>
<td>2.0964</td>
<td>0.15</td>
</tr>
<tr>
<td>(YA, YF, YN, AF, AN, FN)</td>
<td>5</td>
<td>9.5870</td>
<td>3.6672</td>
<td>0.06</td>
</tr>
<tr>
<td>(YA, YF, YN, AF, FN)</td>
<td>6</td>
<td>10.1094</td>
<td>0.4776</td>
<td>0.49</td>
</tr>
<tr>
<td>(YA, YN, AF, FN)</td>
<td>7</td>
<td>12.0168</td>
<td>1.9074</td>
<td>0.17</td>
</tr>
<tr>
<td>(YA, AF, FN)</td>
<td>8</td>
<td>18.5855</td>
<td>6.5687</td>
<td>0.01</td>
</tr>
<tr>
<td>(YA, FN)</td>
<td>9</td>
<td>28.4958</td>
<td>16.4790</td>
<td>0.001</td>
</tr>
<tr>
<td>(FN, Y, A)</td>
<td>10</td>
<td>45.2314</td>
<td>33.2146</td>
<td>0.001</td>
</tr>
<tr>
<td>(Y, A, F, N)</td>
<td>11</td>
<td>63.3238</td>
<td>51.3070</td>
<td>0.001</td>
</tr>
</tbody>
</table>
The sample proportion of attendance for the 1997 nesting season was 0.67 times that recorded for 1998.

The sample proportion of attendance for nests without fire ants was 1.40 times that of nests with fire ants.

The sample proportion of successful nests for the 1997 nesting season was 0.81 times that recorded for 1998.

The sample proportion of successful nests without fire ants was 1.39 times that of nests with fire ants.

Figure 1. Model (YA, YN, AF, FN) association graph with estimated relative risks and 95% confidence intervals.
1998) and nest success (76% 1997, 93% 1998) were higher in 1998. Attendance and
nest success also varied with fire ant presence. Attendance (61% ants, 85% no ants) and
nest success (69% ants, 95% no ants) were lower for nests with fire ants.

All grunts from hatchlings within the nests had ceased by 30 October; researchers
then opened all unopened nests. Fire ants were observed to be actively consuming
hatchlings in 16 of 20 nests; hatchlings of the four remaining nests were dead but not due
to ants. An average of 1.8 (SD = 1.3) unreleased hatchlings remained alive within six of
the abandoned nests. The live hatchlings were always located at the side farthest away
from the ant colony. These individual hatchlings were each observed to have obvious
ant stings, to the point of deformity. Deformities observed included exposed flesh, and
swollen heads and bodies. Two of the hatchlings died within an hour of being removed
from the nest. The remaining hatchlings were released in water near the nest. It was
assumed these hatchlings would have died without intervention. Four nests with peeping
young within the nest cavity were monitored until the time of failure. Two of these nests
had sign of active attendance throughout the period, the remaining two had no sign of
active attendance. Hatchlings within these 4 nests survived an average of 26.8 days (SD
= 8.8). Average clutch size, through direct count of eggs or egg membranes for 33
intact nests examined, was 29.1 (SD = 9.9).

DISCUSSION

The statistical model developed using 137 nests observed during two consecutive
nesting seasons re-enforces conclusions by Allen et al. (1997); fire ants are capable of
affecting alligator nest success. The model did not show that attendance by female
alligators during incubation enhanced the probability of success. Observations of no hatchlings escaping the nest without assistance, however, suggest that assisted release by the female alligator opening the nest is necessary for nest success. It is believed the lower levels of attendance and nest success by year are due to monthly differences in amounts of rain which directly effect marsh levels. Joanen and McNease (1989) have reported low marsh levels have a negative effect on nest success. The 1997 nesting season average rainfall was half that recorded for the 1998 season.

In summary, fire ants affect alligator nest success by killing hatchlings in the nest, and possibly by deterring the opening of nests by the maternal alligator. Nests with fire ants and hatchlings were significantly less successful. Ants were associated with unsuccessful nests and some nests were not opened even when pipped hatchlings were within the nest. Fire ants are hypothesized as colonizing alligator nests because they provide suitable habitat, some protection from water in a wet environment, and on-site food supplies (i.e., hatchlings). Fire ants may be affecting the willingness of the adult alligators to open the nest. These opportunistic generalists depredate cracked eggs and hatchlings left within the nests. Inclusion of losses associated with fire ants increase nest loss rates to 14.6%. This overall rate is similar to yearly predation rates others reported within Louisiana (Joanen 1969, Ruckel and Steele 1984, Platt et al. 1995). Nest depredation by fire ants is suspected has going unobserved because of overlapping predation with mammalian predators and researcher effects. These researcher effects may include researchers releasing hatchlings (Platt et al. 1995), or loosening nest material while making internal nest measurements, thus facilitating hatchling escape.
For the alligators occupying the fresh and intermediate marshes of Sabine National Wildlife Refuge, fire ants colonized nests to the detriment of alligators. Attendance by the female alligator did not have an effect on nest success until it was time for the nest to be opened. Two hypotheses needing further investigation: 1) alligator attendance does not effect nest success until incubation is complete; and, 2) fire ants interfere with female alligators’ ability or willingness to release hatchlings.
Chapter 5. Testing David and Goliath: an Experimental Approach

Ants are mentioned in several papers discussing alligator (*Alligator mississippiensis*) nesting ecology, and suggest that these opportunistic generalists (Tschinkel 1988) do not affect nest success (Joanen 1969, Goodwin and Marion 1978, Taylor 1984, Platt et al. 1995). Allen et al. (1997), however, in a laboratory experiment demonstrated the ability of fire ants to cause the mortality of hatchlings, and the possible effects of ant stings on the long-term survival of hatchlings after exposure. Additionally, a model developed from the monitoring of 137 alligator nests over a two-year period depicted a negative association between fire ants and alligator nest success (Reagan et al. 2000).

The results obtained from an analysis seeking to quantify an association between two or more observed variables should be viewed cautiously. The finding of a statistically significant association among variables within a study does not establish a causal relationship. It is the goal of this study to experimentally test the effects of fire ants on alligator nest success. The experiment was conducted on naturally occurring nests at Sabine National Wildlife Refuge during the 1999 alligator nesting season, June through September.

STUDY AREA

Sabine National Wildlife Refuge is located in southwestern coastal Louisiana. The study area encompassed two impoundments on the refuge and contained vegetative types consistent with fresh (8 km²) and intermediate (21 km²) marsh (Chabreck and Linscombe 1988). The main source of water for the impoundments is rainfall. Rain
amounts averaged 13.01 cm (SD = 9.58) per month during the 1999 nesting season
(Sabine National Wildlife Refuge, unpublished data).

METHODS

Nests were assigned to treatment groups randomly. Nests containing alligator eggs
were blocked into groups of 6 nests and numbered consecutively within the group by the
order they were found. This methodology was used to control for the timing of nest
availability. Eggs located within nests were felt using a 0.3 x 30 cm metal knitting
needle. The randomization process used a random numbers table to assign the 6 nests
within the 10 groups to each treatment group. The first 3 randomly selected nests within
each group were assigned ants and the remaining 3 had ants suppressed.

Amdro (AMDRO, American Cyanamid Company, Wayne, NJ), an insecticide bait
containing Hydramethylnon, was used to suppress ants at 30 alligator nests.
Hydramethylnon was considered the most appropriate insecticide because it was readily
accepted by ants, operated well under hot conditions, and degraded within days when
exposed to sunlight (Vander Meer et al. 1982). This insecticide bait is an insect-specific
metabolic inhibitor with low toxicity to birds, mammals, and fish, and it has a half-life of
41.9 minutes in sunlight (Vander Meer et al. 1982, Mallipudi et al. 1986); toxicity to
reptiles is unknown. A strategic baiting method, scattering 30 g of bait in a radius
around alligator nests, was used to intercept ant foragers (Hooper et al. 1998). An
additional 30 g of bait was applied to ant mounds pre-existing at the alligator nests.
Bait was reapplied weekly throughout the nesting season. The alternative treatment
group had robust fire ant colonies, colonies with well domed hills and quick defense
responses, introduced from the surrounding area if not already existing at the site. Ant colonies were dug out using a shovel and transported within 18.9 L buckets with snap-on lids. These nests received no bait material. Fisher’s exact tests were used to test the effects of treatment group on the relationship between alligator attendance, hatchling release, and nest success. Estimates from Reagan et al. (2000) indicated a minimum sample size of 60 nests was needed to test nest success and have an alpha of 0.05 and 75% power.

During the period of incubation, nests were examined for adult alligator attendance, the presence of fire ants, and nest success. Adult attendance was determined by the presence of an adult female, or fresh alligator tracks or tail drag within the mud on or within 3 meters of the nest. The presence of fire ants was determined by brushing and prodding the entire surface of the nest with a pole to stimulate a defense response by ants and by examination of the entire nest after determining final nest success. Nest success was recorded after release of hatchlings by the maternal alligator, escape of hatchlings by crawling through the nest material, or when all hatchlings were believed dead within the nest. Successful nests produced at least 1 hatchling that escaped the nest alive by either female assistance or self-release. Unsuccessful nests had all hatchlings die within the nest cavity. Researchers attempted to minimize interference with the nesting process. Visits to the nest, however, included the initial location, weekly visits to determine fire ant status and maintain treatments, and a final visit when nesting was considered complete. Adult alligator attendance and presence of fire ants were recorded as present or absent at each visit.
RESULTS

A total of 30 nests were treated with Amdro, however, ants were successfully eliminated only from 27 nests. Ant colonies were introduced to 17 of the 30 nests treated with ants; ants occurred naturally at 13 nests. Ant colonies, however, were successfully maintained only at 21 nests. Artificial applications of ants accounted for eight of the nine treatment failures. Analysis only included those nests where treatment applications were successful. Nest success was 20% less for nests with ants present (Fisher’s exact test: \( P = 0.049 \)), and pre-hatch adult activity did not differ between the treatments (Fisher’s exact test: \( P = 0.151 \), Power \( = 0.61 \)) (Table 10). Five occurrences of self-release were observed during the course of the experiment with no difference being detected between nests with and without ants present (Fisher’s exact test: \( P = 0.262 \), Power \( = 0.41 \)) (Table 11). Excluding nests with self-released hatchlings, nest success was not different between nests with and without ants present (Fisher’s exact test: \( P = 0.065 \), Power \( = 0.51 \)).

DISCUSSION

Too often associations are made without trying to demonstrate a cause and effect relationship. Fire ants can cause the death of alligator hatchlings under laboratory conditions (Allen et al. 1997), but fire ants have been associated only with decreased alligator productivity (Reagan et al. 2000). This study demonstrated experimentally that fire ants do cause a decrease in alligator productivity, but can not demonstrate why the reduction occurs.
Table 10. Nest success and adult alligator activity for treatment groups, ants and no ants, Sabine National Wildlife Refuge, Louisiana, 1999. An asterisk indicates significance at the 0.05 level.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Nest Success*</th>
<th>Adult Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ants (n=21)</td>
<td>16 (76%)</td>
<td>10 (48%)</td>
</tr>
<tr>
<td>No Ants (n=27)</td>
<td>26 (96%)</td>
<td>18 (67%)</td>
</tr>
</tbody>
</table>

Table 11. Self-releases and release rates within treatment groups, ants and no ants, Sabine National Wildlife Refuge, Louisiana, 1999. An asterisk indicates significance at the 0.05 level.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Adult Assisted Release</th>
<th>Self-release</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ants (n=21)</td>
<td>15 (71%)</td>
<td>1 (5%)</td>
</tr>
<tr>
<td>No Ants (n=27)</td>
<td>22 (81%)</td>
<td>4 (15%)</td>
</tr>
</tbody>
</table>

Reagan et al. (2000) suggests that declines in productivity were related to decreases in nest openings by females. However, no differences were detected in levels of female release, number of self-releases, and adult activity during incubation between nests with and without ants present. Differences were only detected for the number of nests with unreleased hatchlings. It is still not known how ants are negatively affecting nest success. Due to low statistical power, it could not be distinguished if lowered nest success at nests with ants was caused by fewer nests being opened by the maternal alligator or by inability of hatchlings to self-release. Fire ants reduce alligator nest success, and adult activity prior to hatch appears unaffected by fire ant presence. Fire ants do not have a one-to-one relationship with nest failure. The reduce level of success may be caused by interactions of several factors and may include hatchling health, nest
structure, and nest environmental conditions. Fire ants are hypothesized, however, as causing lowered nest success because of one or more of the following reasons: ants cause the mortality of hatchlings prior to the time of release, ants block hatchling escape routes, ants are reducing the levels of calls produced by hatchlings and are therefore not stimulating the female to open the nest, or ants aversively condition the female during her repeated trips to the nest throughout the incubation period or during previous nest openings.
Chapter 6. Post-hatching Movements of Alligator Hatchlings

Nest attendance is part of a complex relationship between a female alligator (Alligator mississippiensis) and her offspring, which may include maternal defense of the nest and hatchlings (McIlhenny 1935, Deitz and Hines 1980, Hunt and Watanabe 1982, Delany 1990). Hatchlings have been documented to remain near the nest from the time of hatching through winter and until the next breeding season (Deitz 1979, Woodward et al. 1987). Large scale movements have been documented only when permanent water is lacking near the nest (Woodward et al. 1987). Hatchlings remain in a cohesive group throughout their first year of life (Deitz 1979, Woodward et al. 1987). Internal food supplies, the egg yolk, and invertebrates are believed to provide abundant foods up to the first winter and make large scale movement unnecessary (Delany 1990, Fischer et al. 1991). Group integrity is less conspicuous by the second summer (Woodward et al. 1987) and prey for 1- and 2-year-old alligators may require more extensive movements (Chabreck 1972, Delany 1990). Knowledge of hatchling alligators is intertwined with assumptions. One assumption is that hatchling alligators associated with an adult female or nest represent one clutch (Metzen 1977). Another assumption is that pods, which are hatchlings clustered within a few meters, consist only of siblings (Delany 1990). Still another supposition is that hatchlings remain near a nest or female den for some period of time after hatching (Chabreck 1965, Deitz and Hines 1980, Ferguson and Joanen 1983). Hypotheses of hatchlings readily dispersing and females not brooding young have been made within the literature (Joanen and McNease 1970, Neill 1971, Joanen and McNease 1989, Rootes and Chabreck 1993), but there is no supporting data.
objectives of this study were to observe and describe post-hatching movements of marked hatchling alligators between September 1997 and October 1999 on Sabine National Wildlife Refuge in southwestern coastal Louisiana.

STUDY AREA

The study area encompassed two impoundments on the refuge and contained vegetative types consistent with fresh (8 km²) and intermediate (21 km²) marsh (Chabreck and Linscombe 1988). The main source of water for the impoundments was rainfall. Water levels within the 2 impoundments varied among years; the 1999 study year had significantly less water during the period of May through August (Sabine National Wildlife Refuge, unpublished data). Dense marshhay cordgrass (*Spartina patens*) dominated the habitat. A marsh lake and canals bordered the dense marsh. The border levees of the impoundments were vegetated with Chinese tallow-tree (*Sapium sebiferum*), sea-myrtle (*Baccharis halimifolia*), and clumps of roseau cane (*Phragmites communis*). The marsh was interspersed with shallow, open water pools many of which were being colonized by bullwhip (*Scirpus californicus*) and cattail (*Typha spp.*).

METHODS

Nests were systematically located during daylight hours using only an airboat during the 1997 and 1998 nesting seasons, and by helicopter and airboat during the 1999 nesting season. Alligator nests were uniquely marked with poles and numbered tags. Universal Transverse Mercator (UTM) coordinates were obtained using a Global Positioning System (GPS) with real time correction.
Nests were monitored for success and visited within a week after the successful escape of the hatchlings from the nest. Adult females captured during systematic searches throughout the marsh, as well as at nests, and hatchlings captured at nest sites were each marked with a non-unique tail notch and an uniquely coded Passive Integrated Transponder (PIT) tag. Hatchlings originally captured together at nest sites were assumed to be siblings. The adult females captured at those nest sites were assumed to be the respective maternal parent. Adults were injected with 12 mm x 2 mm (American Veterinary Identification Devices [AVID], Norco, CA) or 11 mm x 2 mm (Destron-Fearing Corp, St. Paul, MN) PIT tags subcutaneously within the right earflap. Hatchlings were injected with 11 mm x 2 mm PIT tags with BioBond (Destron-Fearing Corp, St. Paul, MN) into the right side of the neck with the tag resting subcutaneously above the sternomandibularis muscle. Adult females and hatchlings were recaptured opportunistically within the study area over the course of the 3-year project. Searches did not extend beyond the study area borders. Recapture sites were assigned UTM coordinates using GPS. All movements were calculated as straight line distances between natal and relocation sites. Movements were grouped within annual time periods; prior to first spring (September through February), first spring to nesting (March through May), nesting (June through August). The percent of pods and hatchlings marked yearly were estimated using estimated total numbers of nests present, average clutch size, and nest success rates.
RESULTS

A total of 314 nests with eggs were monitored and 2,674 hatchlings were marked from 219 clutches. The estimated percentage of hatchlings marked were 20%, 21%, and 32% for 1997, 1998, and 1999, respectively. These estimates were derived from estimated number of successful nests and average clutch size. Nest success averaged 82% (78%, 90%, and 81% for 1997, 1998, and 1999, respectively). Successful nests totaled 79, 71, and 108 for the 1997, 1998, and 1999 seasons, respectively. An estimated 71% of alligator nests were found with an airboat. Helicopter and airboat searches combined to find an estimated 98% of nests. Average clutch size ($x = 32.7, SD = 8.65$) was estimated from 68 nests left unopened by the maternal alligator. One hundred twenty-two females were associated with nests of marked clutches. Dens with permanent water, assumed to be created by the female, were found at 179 nests with eggs. For nests that successfully produced young and had dens present, hatchlings were initially captured at those dens 79% of the time. At least one hatchling was marked from 64%, 60%, and 71% of the estimated total number of nests present during 1997, 1998, and 1999, respectively. An average of 12.2 ($SD = 9.3$) hatchlings were marked within each original pod of hatchlings. Recaptures of 204 hatchlings from 52 of the original pods (26, 21, and 5 pods from 1997, 1998, and 1999, respectively) were made during the course of the study. Females were originally associated with 27 of these 52 nests. Eight of the 27 associated females were recaptured during the same time periods that the nest’s hatchlings were relocated. Two of the 8 females were associated with marked hatchlings when recaptured, but only 1 of these females appeared associated with her
own pod. Average female movement was 458 m (SE = 158) over an average period of 221 days (SE = 64) after exodus of hatchlings from the nest.

Hatchlings of all ages moved away from the nest sites where they were originally captured (Figure 2). Hatchling pods marked and recaptured prior to their first spring moved an average 68 m (SD = 73). One of 7 sampled hatchling pods mixed with marked non-siblings prior to their first spring. Seventeen of 25 marked hatchlings had moved 85 m from their nest site and mixed with another pod of hatchlings within 5 days of hatching, while at least 1 individual remained at the natal den. These hatchlings were marked the day of their release. Hatchling movement and mixing with non-siblings was also seen within the period from the hatchlings' first spring to initiation of nesting by adult females. Hatchling pods (n = 44) recaptured during this period moved an average 317 m (SD = 739). Twenty of these 44 pods contained marked non-siblings.

Movements observed for hatchlings under one-year of age, however, appears to become less variable after adult begin building nests. Twelve pods were recaptured during this period and average movement away from the original nest site was 230 m (SD = 178). Four of the 12 pods contained marked non-siblings. For hatchlings from 20 pods recaptured after a one year period, movement from the original nest site appeared similar to that of hatchlings under one year of age. These older hatchlings moved an average 250 m (SD = 310) from the original nest site. Over half (55%) of these 20 pods contained marked non-siblings. The amount of mixing with non-siblings did not differ among these time periods ($\chi^2 = 4.96, 3 \text{ df}, P = 0.175$). Water levels did not differ among the periods covering hatchlings' first 365 days of life ($F_{2,38} = 0.95, P = 0.394$).
The distance hatchlings moved varied greatly; some remained at the nest, while others traveled several kilometers (Figure 3). No general patterns were seen in hatchling movements and movement also varied greatly within clutches. Siblings were observed having traveled similar distances in opposite directions, in multiple directions, and in similar directions but of varying distances. Siblings were also recaptured on opposite sides of levees and in different impoundments. The number of siblings moving together varied with time, but not with distance moved. An average of 3.0 (SE = 2.9) and 2.6 (SE = 4.3) siblings, less than 1 year old, were captured at ≤ 15 m and > 200 m, respectively, from the natal nest site.

The distance hatchlings moved did not appear to affect the amount of mixing among pods. When hatchlings had stayed within 15 m of their natal nests, 45.5% of pods (n = 11) were found to contain non-siblings. Approximately 55% of hatchlings that moved over 200 m from the natal nest site (n = 22) were within pods containing non-siblings. Overall, 43% of pods examined that contained previously marked hatchlings also contained marked non-siblings.

A total of 24.5% of previously marked hatchlings were relocated at the same site as originally marked and released. Seventeen of 27 pods relocated at nest sites had hatchlings of only one clutch; however, 37% of these pods contained none of the original inhabitants of the nest. Adult females found with non-mixed pods moved an average of 423 m (SE = 320), while females of mixed pods moved an average of 474 m (SE = 178).
Figure 2. Ages and distances moved for alligators marked as young at nests within 2 marsh impoundments, Sabine National Wildlife Refuge, Louisiana, 1997-99.
Figure 3. Movements of alligators marked as young at nests within 2 marsh impoundments, Sabine National Wildlife Refuge, Louisiana, 1997-99.
DISCUSSION

Hatchling alligators clearly demonstrated movement following release from the nest. These observations support the hypotheses made previously of hatchlings readily dispersing and females not brooding young (Joanen and McNease 1970, Neill 1971, Joanen and McNease 1989, Rootes and Chabreck 1993). Previous information on mixing of hatchlings with non-siblings suggests mixing of pods generally does not occur (Chabreck 1965, Kushlan 1973, Metzen 1977), or only occurs infrequently during hatchlings’ first year of life (Woodward et al. 1987). However, this study established that 39% of pods contained non-siblings during the first year. Mixing of pods with non-siblings needs further evaluation. The assumption that hatchlings remain near the nest site has possibly led to erroneous calculations of hatching success (Metzen 1977) and survival rates (Deitz 1979) and explanations of the advantage of temperature-dependent sex determination (Nichols and Chabreck 1980, Ferguson and Joanen 1983).

Newly released hatchlings were found moving longer distances than what has been previously expected for 1-year-old alligators (Chabreck 1965) or hatchlings in search of permanent water (Woodward et al. 1987). Hatchlings appear to be able to disperse over the surface of the marsh with time, and clump together with other hatchlings when they are available. Hatchlings moved in all directions and crossed apparent barriers such as levees. Without PIT tags, it would have been difficult to discriminate between original and colonizing hatchlings; nest sites had hatchlings from other nests yet none of the original hatchlings were detected. Since only 20% of hatchlings were marked during each of the study’s first 2 years, actual amounts of mixing and splitting probably are
greater than that observed and reported. Additionally, movements of several kilometers were observed for hatchlings. It is possible that hatchlings were censored due to no collection effort being made outside of the study area borders. If this censoring occurred, the estimates of mixing and distances moved may not fully represent reality.

The appearance of a peak in movements near 200 days post-hatch may represent where censoring, due to movement beyond study area borders, begins to affect sampling of hatchlings, and not where dispersal reverses.

Some hatchlings clearly dispersed immediately following hatch and did not stay associated with the maternal female, den, or the nest. Conversely, hatchlings of the same age were also observed making relatively small movements from the nest. Not only did hatchling alligators readily disperse, but the female was not always present and attending her own offspring following release. This suggests hatchlings do not require parental attendance. Adult alligators modify marsh habitat during the process of building pools, dens, and nests. These modified habitats appear suitable and attractive to hatchlings, whether or not they are directly related to the adult or each other. Adults apparently share sites with hatchlings.

MANAGEMENT IMPLICATIONS

Prior to this study, it was assumed that female reproductive effort and hatchling survival could be reliably estimated through hatchlings seen near the female or the nest. However, early hatchling dispersal from the natal nest should now be considered when assessing alligator reproductive ecology. Early dispersal of hatchlings may provide additional opportunity to reduce impacts of management programs that incorporate
alligator egg collection. Interspersion of nests with and without eggs collected over an area on a scale within the range of hatchling movements would make hatchlings available for recruitment into areas impacted by egg collection. However, further study on hatchling dispersal and survival rates of dispersing hatchling alligators is needed prior to the implementation of such a plan.
Discussion

Female alligators are expected to spend significant amounts of time at nest sites. McIlhenny (1935) implies alligators maintain the internal nest environment and affect nest success. Additionally, alligators are routinely characterized as guarding nests (McIlhenny 1935, Joanen 1969, Herzog 1975, Deitz and Hines 1980, Hunt and Watanabe 1982) and guarded nests have been associated with higher nest success (Metzen 1977, Deitz and Hines 1980, Hunt and Ogden 1991). Adults are further implied as having a role in the raising of hatchling alligators. Observations describe alligators assisting hatchlings both in escaping the nest (McIlhenny 1935, Joanen 1969, Joanen and McNease 1970, Herzog 1975, Kushlan and Simon 1981, Hunt and Watanabe 1982, Platt et al. 1995) and later while present in nursery areas (Hunt and Watanabe 1982).

The antitheses of these statements, however, have also been presented. LeBuff (1957) states that alligators do not care or protect their eggs or young, and that young are self-powered at getting out of nests. He further hypothesizes that nests are protected not for their reproductive value but instead as valuable habitat. Joanen (1969) provides the only quantitative view of alligator nest attendance and also concludes that alligators have little to do with their nest after deposition of eggs. Hatchlings can escape from nests without adult assistance (Kushlan and Simon 1981, Platt et al. 1995). Although there have been hypotheses made that hatchlings readily disperse and females do not brood young (Joanen and McNease 1970, Neill 1971, Joanen and McNease 1989, Rootes and Chabreck 1993), there has been little supporting data. McIlhenny (1935) documents hatchlings spending the winter with a large animal known to be male and
observed the young basking on the male’s body within the shared pool; behavior usually attributed to only maternal female alligators.

This dissertation, although designed to estimate annual nesting rates, provides additional meaningful knowledge into methods of capture, tag retention rates, nest spacing patterns, segregation of size classes, nest site fidelity, the relationship between attendance and nest success, the effects of fire ants on alligator nest success, the relationship between hatchling alligators and their mother, and hatchling dispersal. The following three hypotheses, of several presented within this dissertation, demand further evaluation: annual nesting rates are inversely related to population density, nest spacing and segregation of size classes are determined by agonistic behavior that occurs during courtship, and females fill an optional role in reproductive success following the deposition of eggs within the nest.

Based on published information, results from this study, personal observations, and hypotheses generated during the course of this study, the author has come to believe the reproductive ecology of the alligator is not best described by four distinct components but by three. The three components include courtship, nesting, and hatchling release.

During the period of courtship male alligators select for deep water habitats (Joanen and McNease 1972) and females select for habitats within the marsh interior (Joanen and McNease 1970, Taylor 1984). The majority of females are located within interior marsh and may only access quality males within interior pools and ponds (Taylor 1984). These pools and ponds may be unique to each year. Within secluded territories males display and females move among the males and select mates (Garrick and Lang 1975, Rootes
Reproductive females may compete for quality males (Joanen and McNease 1971). The dominate reproductive females may form clusters of nests around these habitats (Platt et al. 1995). Within the core use area and often near the site of a den the female builds the mound-like nest (Joanen 1969, Kushlan 1973, Hunt and Ogden 1991, Rootes and Chabreck 1993) using the vegetation and material found immediately adjacent to the site (Joanen 1969, Metzen 1977, Goodwin and Marion 1978, Ruckel and Steele 1984, Taylor 1984, Platt et al. 1995). The female deposits eggs within the top center of the mound (Joanen 1969). Over the next 30 days the female may continue to add material to the nest, but after this period little more is done to the nest (Deitz and Hines 1980, Hunt and Ogden 1991). The female maintains a presence at the site, not for the purpose of attending to the needs or defense of the eggs, but because this area represents valuable habitat (LeBuff 1957, Rootes and Chabreck 1993). While the eggs incubate during the 60-65 day incubation period, the female will have little to do with the nest, although she may continue to cross or rest on the top of the nest (Joanen 1969). If fire ants are present, the female will receive stings and retreat from the nest (personal observation). With repeated aversive conditioning the female may return with less frequency (Deitz and Hines 1980, Kushlan and Kushlan 1980). If the female hears calling from within the nest during one of her visits she will wedge her snout into the nest and instinctively help release the hatchling alligators found within the egg cavity (Joanen 1969, Hunt 1987, personal observation). Adults respond to young calling during late incubation and hatched young respond to nest vibrations. Both females and hatchlings may be less responsive if previously subjected to aversive conditioning from
ants. If the female den is not immediately adjacent to the site, the female will transport some and possibly all young to the nearest water by mouth (Kushlan and Simon 1981, Hunt 1987). Any remaining hatchling alligators will follow trails to water left behind by the female (personal observation).

The relationship between the mother and the offspring ends at this point in time. The female will tolerate and share her den habitat with the young, and hatchlings will form small sub-tunnels off of the females main den tunnel (personal observation). Some hatchlings from nearby nests will move into the site and some native hatchlings will leave. Over time hatchlings will be dispersed throughout the marsh habitat. The adult alligator may also move to new or existing den sites prior to winter (Joanen 1969).


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October 7, 1999

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Dear Dr. Seigel:

I would like to request permission to use my manuscript “David and Goliath retold: fire ants and alligators” (MS #76-99N) as a chapter within my Ph.D. dissertation. If so, please send me written permission for inclusion of it and this letter within the appendix of the dissertation.

Sincerely,

Steven R. Reagan
School of Forestry, Wildlife and Fisheries
Louisiana State University Agricultural Center
Baton Rouge, LA 70803-6202
Dear Mr. Reagan:

You are hereby granted permission to duplicate your article from the Journal of Herpetology (MS #76-99N) in your dissertation.

Sincerely,

R. A. Seigel
Editor
Vita

Steven Richard Reagan was born in Massachusetts during the year 1964. He graduated from Ware High School in 1982. He belonged to the Air National Guard from 1982 to 1988. He received a degree of Associate of Science in 1985 from Holyoke Community College, Massachusetts, a degree of Bachelor of Science with a major in wildlife and fisheries biology in 1987 from the University of Massachusetts, Amherst, and a degree of Master of Science in 1991 from The University of Tennessee, Knoxville, with a major in wildlife and fisheries science. He has worked for the National Park Service, the Massachusetts and Louisiana Fish and Wildlife Cooperative Study Units, the U.S. Forest Service, and the Wyoming Game and Fish Department. He was granted the designation of Certified Wildlife Biologist from The Wildlife Society in January 1999. Steven Reagan is currently a candidate for the degree of Doctor of Philosophy with a major in wildlife and fisheries science, which will be conferred in May, 2000.
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Steven Richard Reagan

Major Field: Wildlife and Fisheries Science

Title of Dissertation: American Alligator Nesting Ecology in Impounded Marsh Habitat, Louisiana

Approved:

[Signatures]

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination: April 03, 2000