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Reproductive Status and Movement of Adult Female Alligators

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ABSTRACT.— Home range size, movement, and denning behavior of 15 adult female American alligators (*Alligator mississippiensis*) of different reproductive status were compared using radio telemetry. Radio-collared adult female alligators had an annual home range of 35.8 ± 42.9 (SD) ha, and 30% of them nested in 1988. No difference was found between nesting and non-nesting adult females during the summer nesting season in home range size, daily movement, or percent of time spent at den sites. Likewise, no difference was found in any of the three variables during the fall brooding season when females with broods were compared to those without broods. Adult female alligators had larger home ranges, greater movement, and spent less time at or near their den sites during the spring breeding season than any other season of the year.

Home range and movement of adult female alligators have been studied in Louisiana and Florida (Joanen and McNease, 1970; Goodwin and Marion, 1979; Taylor, 1984). Joanen and McNease (1970) reported the home range size and movement of four nesting adult females occupying estuarine habitat. Goodwin and Marion (1979) and Taylor (1984) reported seasonal home range and movement of adult female alligators occupying lake habitats but made no reference to the animals' reproductive status.

Only 25–60% of adult female alligators nest annually in Louisiana and South Carolina; an even smaller percentage successfully hatch broods (Joanen and McNease, 1980; Taylor, 1984; Wilkinson, unpubl.; Taylor et al., 1991). The home range and movement of adult female alligators occupying freshwater marsh habitats have not been studied, nor have comparisons been made between nesting and non-nesting females or between females with broods and those without broods. The purpose of this study was to compare the seasonal home range size and movement of adult female alligators of different reproductive status in a freshwater marsh.

MATERIALS AND METHODS

The study was conducted on the 12,869-ha Lacassine National Wildlife Refuge in Cameron Parish, southwestern Louisiana. The refuge is located in the State's coastal plain, approximately 20 km inland from the Gulf of Mexico. A 6478-ha permanently flooded impoundment located within the refuge served as the principle study site. The impoundment, referred to as Lacassine Pool, consisted of floating freshwater marsh interspersed with shallow ponds, lakes, and canals. Dense emergent stands of maidencane (*Panicum hemitomon*), bulltongue (*Sagittaria lancifolia*), and spikerush (*Eleocharis* spp.) dominated the marsh. Open water areas ranged from 0.3–1.0 m deep and contained submerged and floating plants including watershield (*Brasenia schreberi*), fanwort (*Cabomba caroliniana*), coontail (*Ceratophyllum demersum*), American lotus (*Nelumbo lutea*), and fragrant waterlily (*Nymphyaea odorata*). Precipitation constituted the only source of water to the pool. Excess water was allowed to escape over three spillways located along the impoundment's perimeter levees.

Seventeen female alligators 2.05–2.54 m total length (TL) were captured from an airboat between 15 April and 12 May 1988 by harpoon and cable snare as described by Taylor (1984). TL was measured along the dorsal surface of each animal. All alligators were marked with three like-numbered monel web tags. Each alligator was fitted with a radio-transmitter (MOD-500, Telonics, Inc., Mesa, Arizona) attached to a neck collar. Two instrumented females were not included in the following discussion because of equipment failure early in the study.

To determine nesting potential of radio-collared alligators, blood samples were drawn dorsally from a branch of the internal jugular as described by Wilkinson (unpubl.). Blood was centrifuged and plasma frozen until assayed. Plasma calcium, zinc, magnesium, and iron levels were assayed as described by Lance et al. (1983). Lance et al. (1983) found that plasma calcium levels of adult (>1.82 m TL) female alligators exceeded 5 mM/L between mid-April and mid-May when the animals were developing ovarian follicles.

Transmitter signal strength was checked prior to each animal's release. All alligators were released at or near the point of capture. Two methods were used to monitor the location of each alligator. Emitted signals were followed

via airboat with a TS-1/TS-2 scanner/receiver and a RA-2A hand-held 2-element "H" type yagi antenna (Telonics, Inc., Mesa, Arizona) to the animal's exact location. To minimize the likelihood of influencing the alligators' activity pattern, a maximum of three locations per week per animal were made by this method. Additional locations were made remotely by triangulation. A minimum of three azimuths (taken within 30 min of each other) were used to fix each location. Readings were made with a twin 5-beam yagi antenna mounted on a 3-m mast with a null-combiner box (Telonics, Inc., Mesa, Arizona). Telemetric error was determined by reference transmitters at three known locations prior to each remote sensing session. Maximum error was ±4 degrees.

Annual alligator activity was divided into four biological seasons: nesting (7 June–18 August 1988), brooding (19 August–31 October 1988), wintering (1 November 1988–28 February 1989), and breeding (1 March–7 June 1989). These seasons were based on the observed initiation of nest construction and egg hatching along with the inactive period of winter reported by Chabreck and Joanen (1979).

Reproductive status of each female was classified within seasons and based on observations made when alligators were tracked repeatedly to one location. During the nesting season, the reproductive status was classified as non-nesting with a previous year's brood (two or more young) present at the den, non-nesting without a previous year's brood, or nesting. No nesting females were observed with a previous year's brood. During the brooding season alligators were classified as either with broods or without broods. Initially, females were to be classified during the breeding season as breeding or non-breeding based on their nesting effort in June 1989. Only two females eventually nested. Because of sample sizes, statistical comparisons within the breeding season were not possible.

Approximately 50% of the locations made during the nesting, brooding, and breeding seasons were made at night. Less than 10% of the winter locations were made at night.

Home range size was estimated by the minimum convex polygon method (Mohr, 1947) because of its robustness with autocorrelated data (Swihart and Slade, 1985) and to facilitate comparisons with other studies. Adequate sample size for home range analysis was determined from area observations curves (Odum and Kueknzler, 1955). Alligator activity was assessed by two variables: 1) Minimum daily movement—the distance between successive locations divided by the time elapsed between these locations; and 2) percent of times the female was located <25 m from her den.

Three habitat types were available to alligators in Lacassine Pool: freshwater marsh, shallow ponds, and canals. These habitat types were well-interspersed in small blocks. Because of homogeneity and interspersion, analysis of habitat use was not practical.

Analysis of variance (ANOVA) was used to test for differences in home range size and alligator movement among seasons and reproductive status. If ANOVA showed a significant difference ($P \leq 0.05$), a Duncan's multiple range test was conducted to detect differences among all possible paired comparisons (Steel and Torrie, 1980).

Results

Six of the 15 radio-collared females were found to have calcium levels above 5 mM/L. Of these, five constructed nests and deposited eggs in June 1988. One of four females between 1.83–2.13 m TL nested; three of nine females between 2.14–2.44 m TL nested, and one of two females >2.44 m TL nested. Of the 15 adult female alligators monitored in 1988, 30% nested (Table 1).

Pods of young alligators that hatched the previous year were present at dens or in the vicinity of five of the ten radio-collared non-nesting females. However, no broods from previous years were observed at dens of the five radio-collared nesting females (Table 2).

The home range of adult female, radio-collared alligators during the nesting season ranged from 5.9–47.1 ha ($\bar{x}$ = 10.2 ha; Table 3). Movement for all females averaged 25.1 ± 17.4 (SD) m/d and ranged from 5.9–73.1 m/d. Home range size of nesting females, non-nesting females with broods, and non-nesting females without broods did not differ during the nesting season ($F = 0.65$, df = 2,12, $P = 0.54$) (Table 3). Likewise, movement did not differ ($F = 0.17$, df = 2,12, $P = 0.85$) among the three groups.

Of the fifteen radio-collared females, only one (a nesting female) occupied what could be classified as lake habitat (>80% open water). The other 14 occupied marsh habitat (<40% open water). The alligator in lake habitat occupied a consistently larger home range throughout the study, moving considerable distances in and around the edge of the lake. When this alligator was dropped from analysis, the mean home range of the remaining nesting alligators was 10.5 ± 4.8 ha.

Dens (Joanen and McNease, 1970) were used consistently by all classes of females during the nesting season. Because of the error inherent in triangulation, only observations obtained by tracking signals to their exact location were used to determine the percent of time females were at or near (within 25 m) their dens. Females

TABLE 1. Percentage of all adult female alligators in Lacassine Pool that nested during the summer 1988.

Total length of female (m)	Percentage of adult female population[a]	Percentage of radio-collared females in size class that nested	Percentage of total adult female population that nested[b]
1.83–2.13	50.8	25.0	12.7
2.14–2.44	44.7	33.3	14.9
>2.44	4.5	50.0	2.3
Total	100.0	N/A	29.9

[a] Determined from 356 adult females harvested from Lacassine Pool, 1983–1988.
[b] Column B × Column C.

spent 68.6 ± 6.5% of their time at or near their dens during the nesting season (Table 1), but use of dens did not differ among classes of females ($F = 0.72$, df = 2,12, $P = 0.51$). Females were located at or near their dens on 87% of the daytime observations and 46% of the night observations.

Only two of the five nesting females successfully hatched broods (Table 2). To compare brooding and non-brooding female alligators, data from two females with 1988 broods were combined with data from five females that were accompanied by 1987 broods. No difference was found in home range size ($F = 1.48$, df = 1,13, $P = 0.25$) or movement ($F = 1.15$, df = 1,13, $P = 0.25$) between brooding ($n = 7$) and non-brooding ($n = 8$) females during the fall brooding season. Home range size of both classes of radio-collared females during the brooding season varied from 4.2–21.3 ha; movement ranged from 3.8–61.2 m/d.

Females were located at or near their dens 71.3 ± 9.8% of the time during the brooding season, and den use did not differ between brooding and non-brooding females ($F = 0.14$, df = 1,13, $P = 0.71$). The day/night pattern of den use experienced during the nesting season continued through the first part of the brooding season (18 August–mid-September 1988). After mid-September the pattern of den use began to change, and by winter (1 November) females were found away from their dens only during daylight hours. However, only 15 of 225 winter readings were made at night.

Home range size of radio-collared females during winter varied from 0.9–15.6 ha; movement ranged from 0.4–4.1 m/d. No broods were seen at den sites or with females during winter. Both females with 1988 broods were sighted with their broods the following spring. We could not determine whether 1987 broods dispersed before or immediately after the onset of winter; nevertheless, 1987 broods were not observed at the dens during the spring of 1989. Because of this uncertainty, no comparison was made between females denning with broods and those denning without broods. However, for all radio-collared females the amount of time spent at or near dens differed among seasons ($F = 19.93$, df = 3,56, $P < 0.0001$). Females spent more time at or near their den site during winter than they did during the nesting or brooding seasons ($P < 0.01$). Females were located at their dens 83.1 ± 6.2% of the time during winter.

TABLE 2. Annual home range size of radio-collared adult female alligators, Lacassine Pool, 4 June 1988 to 6 June 1989.

Radio collar number	Total length (m)	Nesting status June 1988[a]	Fall brooding status[b]	Nesting status June 1989[a]	Annual home range (ha)
1553	2.05	NNB	B	NNN	21.8
1884	2.07	NNN	NB	N	27.9
700	2.10	NNN	NB	N	12.9
1614	2.11	N	NB	NNN	45.1
1823	2.14	NNN	NB	NNN	51.8
583	2.19	N	B	NNB	6.1
1801	2.20	N	NB	NNN	10.5
649	2.20	NNB	B	NNN	19.1
610	2.21	NNB	B	NNN	24.6
593	2.30	NNB	B	NNN	165.9
782	2.34	NNN	NB	NNN	14.9
552	2.35	N	B	NNB	96.8
133	2.41	NNB	B	NNN	11.9
185	2.45	NNN	NB	NNN	9.4
204	2.54	N	NB	NNN	17.9
Mean ± SD	2.24 ± 1.5	—	—	—	35.8 ± 42.9

[a] N = nesting; NNN = non-nesting, no brood present; NNB = non-nesting, previous year's brood present.
[b] B = current year's brood present; NB = no current year's brood present.

TABLE 3. Seasonal home range size (ha), average minimum daily movement (m), and percent of locations when adult female alligators were <25 m from their den, Lacassine Pool, June 1988 to June 1989.

Season	Sample size	Number of locations	Home range size[a]	Average minimum daily movement[a]	Percentage of locations when females were <25 m from den[a]
Nesting season	15	543	13.7 ± 10.2	25.1 ± 17.4	68.6 ± 6.5
Nesting females	5	195	17.8 ± 16.9	27.3 ± 14.1	68.8 ± 5.8
Non-nesting females without previous year's brood	5	181	10.5 ± 21.2	26.7 ± 27.4	66.2 ± 6.7
Non-nesting females with previous year's brood	5	167	12.9 ± 6.1	21.2 ± 8.7	71.0 ± 7.3
Brooding season	15	327	10.9 ± 4.6	18.6 ± 13.9	71.3 ± 9.8
Females with broods	7	156	12.5 ± 5.4	14.0 ± 8.5	70.3 ± 11.7
Females wihtout broods	8	171	9.6 ± 3.6	22.6 ± 16.9	72.3 ± 8.6
Winter season	15	225	4.6 ± 4.3	1.7 ± 1.1	83.1 ± 6.2
Breeding season	15	360	27.6 ± 30.9	57.9 ± 40.6	56.1 ± 13.8
Females that nested-June 1989	2	44	17.6 ± 6.9	52.1 ± 3.5	50.0 ± 19.8
Females that did not nest-June 1989	13	316	29.2 ± 33.3	58.9 ± 43.8	57.1 ± 13.6

[a] Values are mean ± SD.

Home range size of radio-collared females ranged from 4.1–109.4 ha during the breeding season and included parts or all of their nesting, brooding, and winter home ranges; movement ranged from 9.7–145.2 m/d. Females were located at or near their den less frequently during the breeding season than during the other three seasons of the year ($P < 0.01$; Table 3). Based on successive locations, females appeared to use their dens on a daily basis during the nesting, brooding, and winter seasons. However, as the breeding season progressed, females were frequently located away from their dens as long as 50 h during 72-h periods.

Only two of the 15 radio-collared females nested in June 1989. The mean home range size during the breeding season of females that later nested was 17.6 ± 6.9 ha versus 29.2 ± 33.3 ha for those that did not nest. Because of low sample size, statistical comparisons of home range between breeding and non-breeding females were not possible.

Mean home range size differed among seasons of the year ($F = 5.16$, df = 3,56, $P = 0.003$). Female home range was larger during the breeding season than during the other three seasons of the year ($P < 0.05$). Movement also differed among seasons ($F = 15.50$, df = 3,56, $P = 0.0001$) and was greatest during the breeding season ($P < 0.01$).

The annual home range size of radio-collared females in Lacassine pool varied from 6.1–165.9 ha (Table 2). Two instances of excessive movement greatly affected mean home range size. When these two females were dropped from analysis, the mean annual home range declined to 25.5 ± 24.3 ha.

DISCUSSION

Seasonal home range size of adult female radio-collared alligators in Lacassine Pool was similar to home range sizes reported by other authors. Goodwin and Marion (1979) reported that the home ranges of four adult females in a north-central Florida lake were largest during spring, intermediate during summer and fall, and smallest during winter. Joanen and McNease (1970) reported that the home ranges of three adult females in a Louisiana coastal marsh were larger in spring than in summer and fall. Although alligators followed the same seasonal patterns during the three studies, mean seasonal home ranges of females in Lacassine Pool appeared to be larger in most cases than those from other areas. Goodwin and Marion (1979) reported that mean seasonal home ranges varied from 5.7–15.6 ha. Joanen and McNease (1970) reported mean seasonal home ranges of 0.81–3.5 ha. The mean seasonal home range of adult females in Lacassine Pool varied from 4.6–27.6 ha.

Taylor (1984) monitored adult female alligators in a northern Louisiana lake surrounded by forested wetlands and reported a mean annual home range of 56.0 ha, which was 35% greater than the mean annual home range size of adult females in Lacassine Pool. However, the difference in home range between the two areas was not significant ($t = 0.81$, df = 22, $P = 0.43$). In all studies, considerable variation was found among individual alligators. Habitat conditions, prey availability, and sample size could have accounted for differences among studies.

One instance of excessive movement greatly influenced the mean annual home range size in our study. Shortly after emerging from winter dormancy, one radio-collared female, which had occupied the territory in and around a 14-ha pond, moved to another pond 700 m away, established a den, and remained in and around the second pond for the remainder of the study. Her home range was estimated by the minimum convex polygon method to be 165.9 ha. However, only 39.7 ha of this area was apparently used.

No difference was found among reproductive status classes of females in either mean home range size or daily movement during the summer nesting season. This suggests that nesting status and the presence of a previous year's brood do not restrict the activity pattern of adult female alligators. Unquestionably, nest construction and the deposition of eggs would limit a female's activity during the onset of the season. However, nesting females appear to be as active during the remainder of the season as non-nesting females.

Nesting and non-nesting females were found to spend a similar amount of time at or near their dens during the nesting season. This suggests that what has been interpreted as nest attendance by productive female alligators (McIlhenny, 1935; Joanen, 1969) may be simply a general tendency for all adult females to use dens heavily during the heat of summer daylight hours.

No difference was found in the home range, daily movement, or time spent at or near a den between females with broods and those without broods during fall. This suggests that the presence of a brood neither restricts or enhances a female alligator's activity pattern. When the female moved to another den, the young did not accompany her.

All females used dens as activity centers throughout the year. Thirteen of the fifteen radio-collared females changed den sites during the study. Although the timing of these changes generally coincided with a change in reproductive status or biological season, they did not follow a clear pattern. Four of the five females that nested in 1988 changed den sites immediately after the nesting cycle. The remaining nesting female changed den locations the following spring. One nesting female that occupied a new den after the 1988 nesting cycle relocated to a third site the following spring. Three of the eight females that did not nest in 1988 or 1989 changed den sites immediately before the onset of winter, and four changed den locations shortly after emerging from winter dormancy. One of the two females that nested in 1989 changed den-sites prior to nest construction and one maintained the same den location throughout the study. Excluding one female that relocated to a new area in the spring of 1989, the mean distance between successive den locations was 48.6 ± 40.6 m and ranged from 9–131 m.

The reason for den relocations could not be determined. The distances involved were apparently too short to provide better access to mates or prey. Likewise the moves did not involve apparent changes in elevation, habitat type, or provide more or less access to open water. Disturbance by other alligators may have caused some females to relocate their dens.

Radio-collared females in Lacassine Pool did not occupy exclusive territories. Ten of the radio-collared females were captured in the same area of the refuge. Considerable overlap in the annual home ranges of alligators within the group occurred. Parts of the annual home ranges of as many as four radio-collared females overlapped. The home ranges of several radio-collared females overlapped with non-instrumented females as well. During summer 1988, nests attended by uncollared females were located within the activity ranges of several radio-collared females. Two females, one instrumented and one non-instrumented, constructed nests and deposited eggs within 30 m of each other.

Plasma calcium essays indicated that six of the radio-collared females in this study were developing ovarian follicles in spring 1988. Of these, five eventually laid eggs. Wilkinson (unpubl.) reported similar results in South Carolina and of 10 radio-collared females with elevated plasma calcium levels in spring, eight eventually laid eggs. Wilkinson assumed that the failure of some of the females to lay was the result of stress associated with capture and instrumentation. However, Taylor et al. (1991) reported that 45% of 502 adult females examined in May 1986 at Marsh Island, Louisiana, were vitellogenic, but only 26% of 298 adult females examined in July 1986 had laid. This indicated that 19% of the adult females had developed follicles and would have had elevated plasma calcium levels the preceding spring. They did not ovulate or had ovulated and were reabsorbing the resulting ovum but could not have laid eggs. This suggests that plasma calcium assays may overestimate the number of females that will eventually lay eggs.

An estimated 29.9% of the radio-collared adult female alligators in Lacassine Pool nested in 1988. This rate is comparable to those reported in other studies. Taylor (1984) reported an annual nesting rate of 28% based on a telemetric study of nine adult female alligators monitored in a northern Louisiana lake over a three-year period. Wilkinson (unpubl.) reported an aver-