

**American Alligator Distribution, Thermoregulation, and Biotic
Potential Relative to Hydroperiod in the Everglades**

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Contract Final Report

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ABSTRACT

Over the last one hundred years the hydrology of the Everglades has been greatly altered by mankind. Efforts to repair the functioning of the ecosystem are using a multicomponent model, the Across Trophic Level System Simulation (ATLSS), to predict the response of native flora and fauna to alternative water delivery scenarios. In order to provide the model with information on the natural history of the American alligator in the Everglades, we initiated a five year study on the home range, daily movement, habitat use, thermoregulation, and body temperature patterns of alligators in both Shark Slough, Everglades National Park, and in Water Conservation area 3A North.

A total of 66 alligators were captured using capture darts and cable snares and were surgically implanted with radio-transmitters. A subset 29 of these were also implanted with temperature recording data loggers. Data loggers recorded core body temperature (T_b) simultaneously at 72 minute intervals

Weekly aerial locations collected from 1 January 1997 to 1 September 1999 were used to estimate home range size. Weeklong intensive sampling efforts conducted in each fall, winter, spring, and summer from 7 November 1997 to 31 July 1998 were used to estimate daily movement and habitat use. The marsh of WCA was dominated by sawgrass with few tree islands and a shorter hydroperiod than the deeper sloughs. The Shark River Slough region of ENP was comprised of a mosaic of spike rush, sawgrass, shrub islands, and tree islands with occasional patches of low mixed marsh, cattail, water lily, and open water. "Gator" holes were more frequent throughout ENP than WCA. Canals were located in both WCA and ENP.

Alligator home range size and daily movement were most affected by gender, temperature, reproductive efforts, habitat, and water level. Home range size and daily movement for alligators located in WCA and ENP were not significantly different. Mean seasonal alligator home ranges successively decreased from spring (39.17 ha) to summer (31.77 ha) to fall (27.52 ha) to winter (14.08 ha). Mean annual home range size for male alligators (122.04 ha) was significantly greater than females (35.92 ha).

Mean seasonal daily movements successively decreased from spring (406 m/24-hr) to summer (261 m/24-hr) to fall (154 m/24-hr) to winter (100 m/24-hr). Male alligators (167.19 m/24-hr) moved significantly more than female alligators (70.05 m/24-hr).

Three distinct groups of radio-tagged alligators existed according to habitat availability. Marsh alligators located in WCA, slough alligators located in ENP, and canal alligators located in both WCA and ENP. Radio-tagged marsh alligators located in WCA used cattail, water lily, mixed marsh potholes, and holes more than their availability would suggest. Sawgrass was used less than its availability would suggest. WCA alligators were located in sawgrass 36 % of the locations, mixed marsh potholes 28 %, cattail depressions 16 %, water lily potholes 10 %, holes 7 %, and open water 1 %.

ENP slough alligators used spike rush, holes, and shrub more than their availability would suggest. Sawgrass was used less than its availability would suggest. ENP alligators were located in holes 37 % of the locations, spike rush 27 %, sawgrass 24 %, and in shrub islands 10%. The remaining time was spent in low mixed marsh and cattail habitat types.

Canal alligators used canal and hole habitats more than their availability would suggest. Canal alligators were located in canals during 83 % of the locations. On occasion, canal alligators, particularly females, moved from the canal and into the surrounding marsh. Canal alligators spent nearly 10 % of their time in marsh holes. Five percent of the locations were recorded in sawgrass with the majority of these locations recorded for nesting females.

Alligator T_b s from WCA were high and stable in summer. Fall T_b decreased corresponding to a decrease in ambient temperatures. Winter temperatures remained low, with T_b s occasionally elevated to activity levels. In spring, daily minimum T_b s increased as ambient temperatures increased. However, unlike fall, spring T_b s were elevated to activity levels on nearly a daily basis.

The percent of the total variability accounted for by seasonal, weekly, daily, and within-day components was determined by dividing the variance of each component by the combined variances of all four components. The seasonal T_b pattern was the predominant source of variability among the fall temperature trends. Seasonal variability was a much smaller component in winter. Winter variability was dominated by within-day variability. However, the weekly component was greater in winter than any other season, emphasizing the importance of cold fronts in predicting T_b . In spring the within-day component was the predominant source of variability, due to active thermoregulation which corresponds with breeding and increased feeding.

Average T_b and average daily minimum T_b s were higher in alligators from ENP than those from WCA in fall, winter, and spring seasons, but not summer. Average daily maximum T_b s were not significantly different. The variability of T_b was lower in ENP

than in WCA for fall, spring, and summer seasons, but not winter. This suggests that either; 1) the stability of ENP's environment reduced the time spent at low T_b s, raising the overall average T_b , or 2) warmer overall temperatures in ENP decreased the variability in T_b by decreasing the range in which T_b may fluctuate.

Elevated T_b in spring corresponds with both the breeding season and the peak of the dry season. Elevated T_b s likely aids sperm and egg production as well as prey digestion. Increasing the rate of digestion while prey are concentrated in pools by the decreased water levels allows greater acquisition of energy reserves. These energy reserves may be important in the summer wet season when the consistently high temperatures and reduced food availability likely represent a negative energy balance for Everglades alligators.

CHAPTER 1

INTRODUCTION

The Everglades of South Florida are characterized by complex patterns of spatial heterogeneity and temporal variability. Spatial and temporal hydrologic patterns that result from the distribution, volume, and timing of water flow are major driving forces controlling the trophic dynamics of these systems. After many decades of intense adverse water management impacts, hydrologic restoration alternatives are now being developed and proposed. Thus, there is a need to predict and to compare the future effects of alternative hydrologic restoration scenarios on the biotic components of these systems. Future projections of the effects of restoration alternatives can be realistically accomplished only by modeling.

The USGS-Biological Resources Division is employing a set of integrated models, Across Trophic Levels System Simulations (ATLSS), to simulate whole system responses across trophic levels and spatial and temporal scales of the ecosystem. This approach will enhance the South Florida Restoration Initiative Task Force's technical capability to address scientific and management questions relative to the region. Several studies are underway to verify assumptions and estimate population parameters relative to various key species at differing trophic levels.

The American alligator (Alligator mississippiensis) is not only a top consumer and a keystone species in the Everglades, but also physically influences the system through construction and maintenance of gator holes and trails (Mazzotti et al. 1994). The existence of this species is important to the faunal and floral character of the Everglades as it has evolved. Whereas the majority of extant ectotherms are of small

body size, the fossil record suggests that extremely large ectotherms were once the dominant vertebrates on Earth. Crocodilians represent all that remain of the large, ectothermic archosaurs. The American alligator has many adaptations for life in a warm temperate climate. However, their range extends into the subtropical Everglades of south Florida where consistently high temperatures are encountered.

The Everglades is believed to be a harsh environment for alligators. Everglades alligators weigh less than alligators the same length from other parts of their range (Jacobson and Kushlan, 1989; Barr, 1997). Further, maximum length is decreased, and sexual maturity is delayed (Kushlan and Jacobsen, 1990; Dalrymple, 1996). Jacobsen and Kushlan's (1989) model for growth in the Everglades of Southern Florida predicted alligators reaching a mere 1.26 meters in 10 years and requiring at least 18 years to reach sexual maturity. It is currently suspected that the reason for this poor condition is a combination of low food availability and high temperatures (Jacobson and Kushlan, 1989; Dalrymple, 1996; Barr, 1997).

The metabolic rate of alligators increases exponentially with an increase in temperature rather than doubling at each 10° C increase as in enzymatic reactions (Coulson and Hernandez, 1983). When food is available, alligators seek high temperatures and may increase their metabolic rate three fold (Coulson and Hernandez, 1979; Lang, 1987). Maintenance costs are thus very high near the upper thermal tolerance levels. This may be significant in the Everglades where the ambient water temperature is near or above alligator's reported preferred body temperature for much of the summer, and air temperature is often higher. The high heat of summer also corresponds with the wet season when high water disperses prey.

The physiological and behavioral mechanisms that allow alligators to heat rapidly and maintain high body temperatures also enable them to reduce heat inputs and dump excess heat when ambient temperatures are above activity levels. Behavioral avoidance of high temperatures by remaining low in the water column is perhaps the most effective method of thermoregulation when thermal conditions at the surface are above optimal. In areas of continuous marsh, alligators maintain depressions in the strata, “gator holes,” that function as sources of deep water and thermal buffers during the dry season (McIlhenny, 1935; Craighead, 1968; Mazzotti and Brandt, 1994).

The Everglades has a large network of canals, which play prominently in various options for restoration. An important question relates to the role canals play as a source or sink for alligator populations in the Everglades. No studies exist on movements of alligators in canals and open marsh habitats and the overlap between the two types. Further, only speculation separates an understanding of populations and habitat use among the various major sections of the Everglades. Most of the historic research data available for the species was developed from within the boundaries of the Everglades National Park.

Despite the biological and public prominence of the species, many important questions about basic behavioral and population parameters of alligators remain unanswered. Although many assumptions can be made, important gaps remain in our knowledge of Everglades alligators. We do not have empirical evidence of movements or survival of varying size classes of alligators under either stable or fluctuating water levels. The reproductive contribution by an individual animal or different size/age classes in any given year has been a principal stumbling block for attempts at modeling

any crocodilian population. Although we may postulate scenarios for thermoregulation of alligators, very little data exists on wild populations of alligators. For effective modeling of alligators, more definitive answers to these are essential.

Study Objectives

1. To determine daily and seasonal movements of varying age/size and habitat (canal, interior marsh) classes of Everglades alligators.
2. To determine the proportion of female alligators in the population that might be expected to nest in a given year.
3. To elaborate on existing hypotheses of thermoregulation in Everglades alligators.
4. To relate the above objectives to the dynamic hydroperiod of the Everglades.

Study Area

The Everglades is dominated by a large expanse of seasonally flooded sawgrass (Cladium jamaicense). Historically, a continuous sheet of water flowed from Lake Okeechobee south to Florida Bay (Light and Dineen, 1994; McIvor et al., 1994). The vegetation changes from stands of tall sawgrass in the north to a mosaic of sawgrass, spike rush (Eleocharis cellulosa) and waterlilies (Nuphar luteum, Nymphaea odorata, and Nymphoides aquatica) in the southern, deeper waters of the drainage (Gunderson, 1994). The Everglades, in most years, has distinct wet (May - September) and dry (October - April) seasons. Alligators compensate for the lack of water by maintaining "gator holes,"

depressions in the marsh that retain water in times of drought (McIlhenny, 1935; Craighead, 1968; Mazzotti and Brandt, 1994). The recent creation of canals and airboat trails has added low maintenance deepwater refuges for alligators in the Everglades.



Image 1 Sawgrass prairie interspersed with cypress trees.

Canals and levees, which were constructed to control water level and flow, (Light and Dineen, 1994) now partition the Everglades into three main subdivisions: Everglades Agricultural Area (EAA), the former headwaters of the Everglades just south of Lake Okeechobee (Snyder et al., 1994); three large water conservation areas; and Everglades National Park.

Two study sites were chosen from within the Everglades ecosystem ([Fig.1-1](#)). Water Conservation Area 3A North (WCA) represented a drier and more dynamic hydropattern while Shark Slough, Everglades National Park (ENP) typified the more stable conditions of the central drainage of the Everglades ecosystem.

The first of two study areas was in Water Conservation Area 3A North (WCA). WCA was located in the northern Everglades west of Fort Lauderdale and south of the EAA. WCA was bordered to the north by the L-5 levee, to the south by Alligator Alley (I-75), to the west by the Big Cypress Seminole Indian Reservation, and to the east by the L-38 (Hwy-27) levee. The area was open to recreational vehicles including swamp buggies,

half-tracks, and airboats with a network of airboat trails present. Recreational boaters and fishermen frequently used the area.

The marsh of WCA was dominated by sawgrass (Cladium jamaicense) that formed thick monocultures interspersed with patches of depression potholes, wet prairie, slough, cattail (Typha spp.) and tree islands. Potholes were naturally occurring depressions in the marsh that were as small as 1 m² and 10 to 40 cm deeper than the surrounding sawgrass marsh.

Three distinct pothole types were common: (1) low mixed marsh; (2) cattail; and (3) water lily. Pothole habitat types typically contained duck potato (Sagittaria lancifolia),



Image 2 Gator hole in typical everglades habitat.

arrowhead (Sagittaria latifolia), maidencane (Panicum hemitomon), pickerel weed (Pontederia cordata), cattail (Typha latifolia and Typha domingensis), white water-lily (Nymphaea odorata), swamp-lily (Crinum americanum), and

bladderwort (Utricularia foliosa). The potholes were more open than the surrounding sawgrass marsh and retained water for longer periods. Wet prairies were most often dominated by maidencane and spike rush (Eleocharis cellulosa) that formed low stature communities known as flats (Loveless, 1959). The low mixed marsh habitats and wet prairies typically had limestone near the surface with little or no organic matter present. These areas were 10 cm or more deeper than the surrounding sawgrass marsh which allowed them to pool water for longer periods of time. Slough habitats in WCA were

restricted to the southeastern section and were dominated by tall patches of sawgrass interspersed with patches of white-water lilies and bladderworts.

Radio-tagged alligators were located in two of the four canals located in WCA. The Miami Canal flowed south-southeast through WCA. Water flows were controlled by a large pump station located at the northwestern corner of WCA and a weir located approximately 7 km south of the pump station. The Miami Canal had large spoil banks on either side of the canal that were dominated by Brazilian pepper (Schinus terebinthifolius) with levee breaks approximately every 100 m. Levee breaks allowed water to flow between the canal and surrounding marsh. The I-75 canal had an east-west orientation and was bordered by Alligator Alley to the south and natural marsh to the north. Waters flowed from the marsh into the canal and under Alligator Alley through several canal underpasses.

The second study area was located in Shark River Slough within Everglades National Park ([Fig. 1-1](#)). The area was south of Tamiami Trail (Hwy-41) and included the L-67 Canal extension. Two main habitats, slough and sawgrass (*Cladium jamaicense*), were interspersed throughout the study area. The slough habitat had a longer hydroperiod than the sawgrass marshes and was dominated by spike rush (*Eleocharis cellulosa*), maidencane (*Panicum hemitomon*), white water-lily (*Nymphaea odorata*), bladderwort (*Utricularia foliosa*), sparse sawgrass and contained numerous tree islands (Lodge 1994). A thick layer of algae (periphyton) was present over most of the slough. The area was not open to recreational vehicles and the habitat was less disturbed than areas outside the park. The L-67 Canal extension had a north-south orientation and flowed approximately 14 km from the Tamiami Trail into the center of Shark River Slough. The canal was

bordered on the east by a large spoil bank that allowed travel by truck. The canal was bordered on the west by slough and sawgrass marsh. Coastal-plain willow (*Salix caroliniana*) and wax myrtle (*Myrica cerifera*) were common along the spoil bank. The willows often formed thick stands along the western edge of the canal.

Methods

Transmitters

After a series of consultations with researchers familiar with radio telemetry and the conditions under which this study was to be performed, an AVM model SB2 transmitter in the 166-170 MHz range was chosen. Three different sized radio-transmitters were utilized. The various sized radio-transmitters allowed alligators of different size to be implanted (K-16-H size with a life expectancy of 1.5 years for small animals, C-cell size with a life expectancy of 3 years for intermediate animals and D-cell



Image 3 Juvenile sized transmitter, shown beside a C- cell battery.

size with a life expectancy of 5 years for the larger animals). Radio-transmitters were equipped with a single 30 cm to 40 cm external whip antenna. Transmitters were tested under laboratory and field conditions (both from the ground and air) to determine effective ranges.

Data loggers

The disk shaped data loggers (Tidbit Stowaway Temperature Loggers manufactured by Onset Computer Corporation) had a diameter of 3.0 cm and a thickness of 1.5 cm. Each data logger was capable of recording 7944 temperature readings from a range of -5 to 37° C with an accuracy of $\pm 0.2^{\circ}$ C. Data loggers were programmed to record temperature every 72 minutes, allowing 396 days of continuous data collection. Data collection times were programmed using Logbook software (Onset Computer Corporation) and a PC computer. All data loggers were synchronized so that they recorded temperature simultaneously. Once recovered, dataloggers were recalibrated using a water bath.

Data loggers were also used to record environmental temperatures. Environmental temperatures were recorded in the marsh near the home ranges of implanted alligators. Environmental temperatures were recorded with both the -5 to 37° C range data logger and data loggers that recorded from -20 to 70° C with an accuracy of $\pm 0.5^{\circ}$ C. The air temperature data logger was shielded from direct solar radiation by a glossy white 14 l plastic bucket with slotted vents for ventilation. The bucket was attached upside down to a post and the data logger was suspended in the middle of the



Image 4 Data logger, shown beside a stack of quarters for size comparison.

bucket. The deep water temperature data logger was attached to a concrete block that

anchored it at the bottom of the water column. Shallow water temperatures were recorded using data loggers suspended from floats approximately 5 cm from the surface of the water. Black body temperature data loggers were placed in a 600 cm³ copper spheroid painted flat black and positioned to maximize solar input.

Capture

Alligators were captured at night from airboats. Suitable habitat was searched using 400,000 candlepower spotlights, and alligators were located by the reflection of the light in their eyes. Alligators were then captured using snares or toggle darts.

A Thompson 3XX steel snare was secured to the boat with a 6 m by 8 mm braided nylon rope. The loop of the snare was attached to a 2.5 m wooden pole with two metal alligator clips spaced 20 cm apart at the end of the pole. As the boat approached the alligator, the snare was slipped over the animal's head. When the snare was around the neck of the alligator, the pole and rope were jerked, simultaneously tightening the snare around the alligator's neck and detaching the snare from the pole. The pole was then placed in the boat where it was free from entanglement.

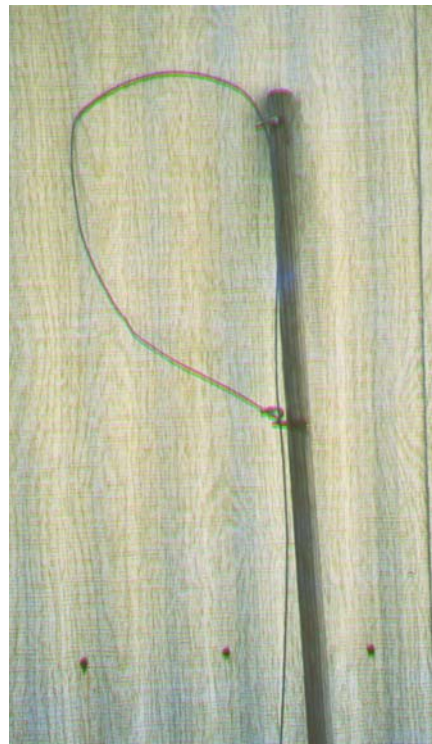


Image 5 Thompson 3XX steel snare attached to wooden pole.

The toggle dart was a stainless steel 0.5 cm x 2.5 cm detachable head, which was pointed anteriorly and flanged posteriorly. A hole

was drilled perpendicular to the long axis of the dart through which a 20 cm stainless steel wire leader was attached. The stainless steel wire leader was then secured to the boat with 6 m of 8 mm diameter braided nylon rope. The flanged end of the dart was a hollow sleeve, which fit over a post secured to a 2.5 m wooden pole. The dart fit on the post so the flange was 0.5 cm above the end of the pole. This allowed the dart to pierce the surface of the skin but prevented it from penetrating too deeply. Once under the skin, tension on the rope would pull the dart backwards, catching the flange on the under surface of the skin causing the dart to toggle. The tough skin was resistant to tearing and the alligator was attached to the line via the dart. Toggle darts provided a capture method for alligators difficult to approach or in vegetation that prohibited snaring; however, once darted, alligators were snared to prevent escape and further tissue damage at the dart site.

Once an alligator was snared it was allowed to tire and was then brought close to the boat. While still outside the boat, the alligator's mouth was closed using an additional



Image 6 Demonstrating the use of a snare to catch an adult alligator.

snare and then secured using electrical tape. The animal was then brought onto the boat where its eyes were covered and legs bound with duct tape. A temporary ID number was written on the tape over the eyes and the animal was secured with

ropes in the hull of the boat. The location was recorded using GPS along with time of capture and a description of the habitat.

Alligators were then taken to the University of Florida Fort Lauderdale Research and Education Center in Davie, Florida. The total length, snout-vent length (to the end of the vent), head length, hind foot length, tail girth, mass, and sex were recorded. Each alligator was then permanently marked with two individually numbered Monel tags, a size 6 tag on the first sagittal scute on the tail and a size 3 tag in the webbing of the right hind foot.

Surgery

Alligators were anesthetized using a combination of medetomidine and isoflurine (T.S. Gross, USGS, unpublished data). Data loggers were cold sterilized and surgically implanted intraperitoneally on the left flank between the last rib and the hind limb. This technique allowed low impact access to the center of the body, which provided accurate core body temperature readings. Two sterilized radio transmitters were then implanted between the peritoneum and the



Image 7 Preparing to surgically implant data loggers and radio transmitters into an adult alligator.

muscle layer on each side of the alligator, one accessed via the incision used to implanted the data logger, and the other through an additional incision on the right flank. After incisions were sutured, the medetomidine was reversed using atipamezole hydrochloride



Image 8 Insertion of a radio transmitter into an anesthetized alligator.

and the alligators were monitored for signs of ill health. The alligators were then released within 24 hours at the exact capture location.

After one year of temperature recording, alligators were recaptured, dataloggers were removed using the same surgical techniques, and the animals were

released at the recapture site.

Study Animals

During this study, 79 alligators were captured and surgically implanted with radio transmitters. A total of 66 alligators were subsequently radio tracked for a sufficient period of time for inclusion in home range, movement, and habitat use analyses (see Chapters 2, 3, and 4). These analyses include 31 animals from Shark Slough, Everglades National Park ([Table 1-1](#)) and 35 from Water Conservation Area 3A North ([Table 1-2](#)). A subset of 29 of these alligators were implanted with temperature recording data loggers. Of the data logger implanted alligators, 18 have been recaptured and 15 functioning data loggers recovered (see Chapters 5, 6, and 7). Finally, 15 of these animals nested at least once during the course of the study (see Chapter 8).

Data Storage

All data from this project have been stored in a database (MS Access) maintained at both the USGS-BRD, Florida Cooperative Fish and Wildlife Research Unit in Gainesville Florida and at the USGS-BRD, Florida Caribbean Science Center, Restoration Ecology Branch, Everglades National Park Field Station in Homestead Florida. The data also have been reported in the two masters theses. Stanley R. Howarter's "Thermal Ecology of the American Alligator in the Everglades" and Cory R. Morea's "Homerange, Movement, and Habitat Use of the American Alligator in the Everglades" are deposited at the University of Florida's science library and available as reprints from the Florida Cooperative Fish and Wildlife Unit (see Howarter 1999 and Morea 1999). This manuscript will be available on the web at <http://www.wec.ufl.edu/coop/>.

Table 1-1. Capture data for all radio-tagged alligators located in Everglades National Park (ENP).

Alligator ID	Sex	Habitat	Total length (cm)	Weight (kg)	Data Logger
50601	Male	canal	281	86	none
50602	Female	canal	185	25	unrecovered
50603	Male	canal	239	52	none
50604	Male	canal	269	67	unrecovered
50605	Female	canal	232	50	successful
50606	Male	canal	307	124	unrecovered
50607	Female	marsh	200	33	successful
50608	Male	marsh	243	41	successful
50609	Female	canal	213	30	none
50610	Female	slough	196	22	none
50611	Female	slough	183	22	none
50612	Male	canal	325	148	successful
50613	Female	marsh	193	19	none
50614	Male	marsh	228	35	none
50700	Female	slough	214	27	none
50732	Female	slough	187	20	failed
50733	Male	slough	227	40	unrecovered
50734	Female	slough	220	32	animal died
50735	Female	slough	200	26	none
50736	Female	slough	182	20	none
50737	Female	slough	188	21	none
50738	Male	canal	187	21	unrecovered
50739	Female	slough	191	23	none
50740	Female	slough	169	16	unrecovered
50741	Male	slough	200	26	none
50742	Female	slough	179	17	none
50743	Male	slough	246	64	none
50745	Male	slough	244	45	none
50746	Female	slough	170	17	none
50749	Male	slough	214	30	none
50750	Female	slough	198	23	none

Table 1-2. Capture data for all radio-tagged alligators located in Water Conservation Area 3A North (WCA).

Alligator ID	Sex	Habitat	Total length (cm)	Weight (kg)	Data Logger
50615	Male	marsh	224	36.4	failed
50616	Female	canal	227	40.9	successful
50617	Female	canal	175	20	successful
50618	Female	canal	189	23.6	none
50619	Female	marsh	209	29.5	successful
50620	Male	canal	282	84	failed
50621	Male	canal	184	18.2	none
50622	Female	canal	192	20.5	none
50623	Female	marsh	214	30	successful
50624	Female	marsh	201	22.7	successful
50625	Female	marsh	194	23.6	successful
50626	Female	canal	224	46.9	none
50627	Female	canal	189	22.7	none
50628	Male	marsh	265	59.4	none
50629	Male	canal	209	28.4	none
50630	Female	canal	199	21.48	none
50632	Male	canal	282	78.6	none
50633	Male	canal	192	22.7	none
50634	Female	marsh	251	49.1	none
50635	Male	canal	256	59.3	none
50636	Female	canal	198	25.5	none
50637	Male	canal	234.5	44.55	none
50638	Male	canal	248	48.2	unrecovered
50638	Male	canal	244	49	none
50639	Male	marsh	197.5	21.1	none
50640	Female	canal	222	40.5	none
50641	Male	marsh	209	24	none
50652	Male	canal	244	45.5	successful
50653	Female	marsh	214	27	successful
50726	Male	canal	282	77.2	unrecovered
50727	Male	canal	226.5	41	successful
50728	Male	canal	241	43.6	unrecovered
50729	Female	canal	195.5	21.8	unrecovered
50730	Female	canal	247	49.4	successful
50731	Female	marsh	208	25.5	successful

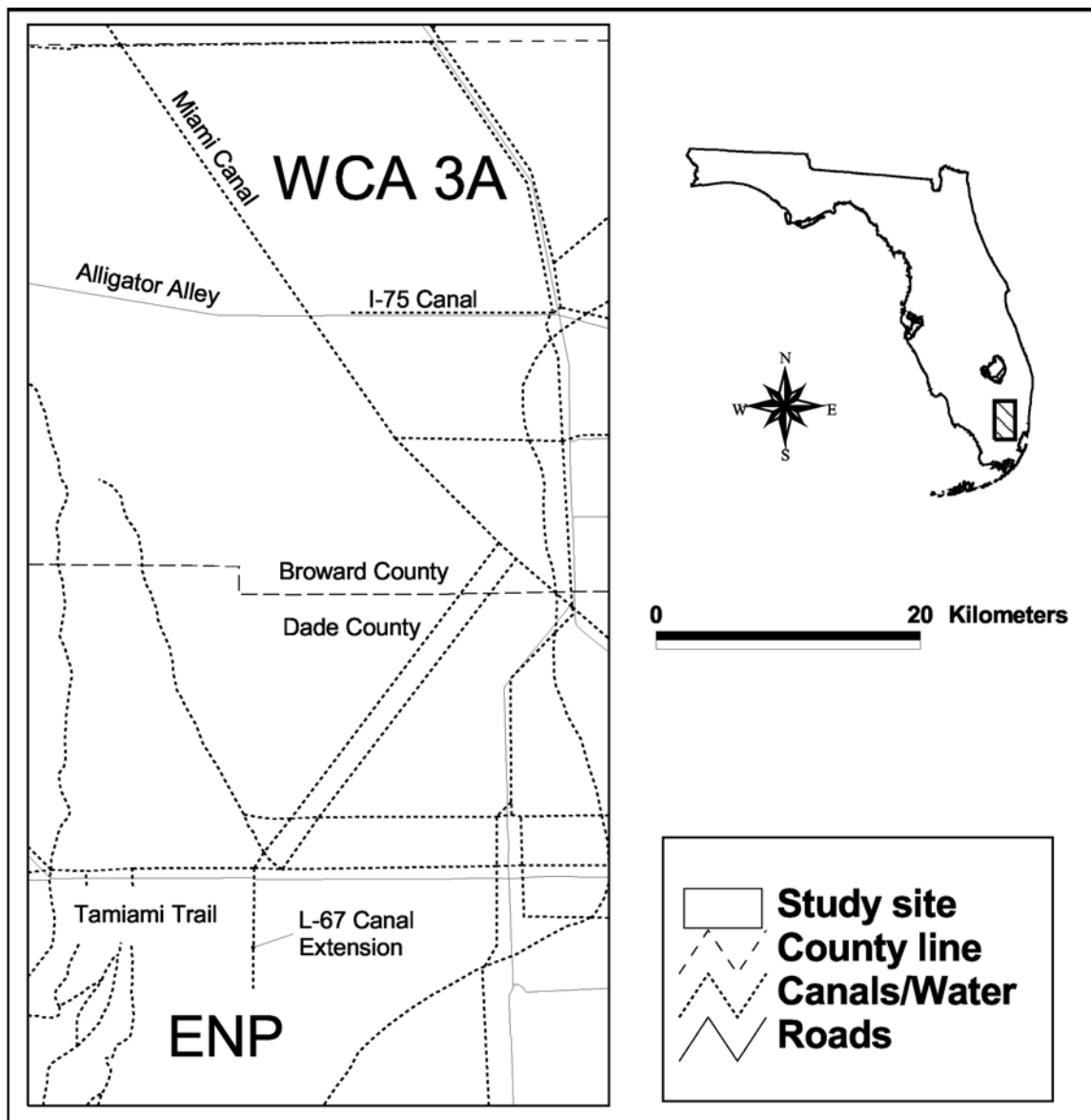


Figure 1-1. General location and detailed map of Water Conservation 3A North (WCA) and Shark River Slough region of Everglades National Park (ENP).

CHAPTER 2

HOME RANGE

Cory R. Morea, Kenneth G. Rice, H. Franklin Percival, and Stanley R. Howarter

Advances in technology, particularly miniaturization of electronic components, have allowed wildlife biologists to remotely monitor free-ranging animals while they pursue their normal movements and activities (White et al., 1990). Wildlife biologists can use data collected via radio-tracking to estimate a species home range size, daily movement, habitat use, population demographics, distribution, biotic potential and other life history traits. Radio-tracking is commonly used to develop an annual or seasonal home range estimate and investigate movement patterns for the individual animals being tracked (White et al., 1990).

Home range estimates facilitate development of management strategies for populations and for varying sub-classes within a population. Topics such as resource requirements, metabolic cost associated with home range size and shape, spacing patterns within the environment, core areas of activity, and territoriality can be used to guide management decisions. Home range is defined as that area traversed by an individual in its normal activities of food gathering, mating, and caring for young and does not include occasional departures outside the area that are perhaps exploratory in nature (Burt, 1943). Home range concepts have interested biologists in two major ways: (1) like any major behavioral trait, properties of home range should have adaptive significance that can indicate among other things, habitat condition, and environmental influences; and (2)

home range characteristics can reflect variation in important population and community characteristics such as size, distribution, and territoriality (Schoener, 1981).

Radio-telemetry studies of the American alligator (*Alligator mississippiensis*) have been conducted in Louisiana (Joanen and McNease, 1970; Joanen and McNease, 1972; McNease and Joanen, 1974; Taylor, 1984; Rootes and Chabreck, 1993), South Carolina (Murphy, 1977), and Florida (Goodwin and Marion, 1979). Hines et al. (1968) studied alligator movement in the Everglades using mark and recapture techniques on juveniles. These studies have provided valuable data on the temporal and spatial variability of alligator home range attributable to differences in gender, habitat, season, reproductive class, and size. Information regarding home range size of alligators are lacking for the Everglades region of South Florida.

Factors affecting the natural movement of alligators include gender, age, temperature, breeding season, water level, food supply, and water salinity (Chabreck, 1965; Fogarty, 1984). Temperature, water level, food supply, and water salinity can vary temporally and spatially within a wetland and weakens any inferences based upon movement data collected in other wetland systems or geographic regions. Thus, in order to adequately draw in-depth conclusions concerning a species home range, the population in question must be studied.

Objectives

The objectives of the study were: (1) to estimate annual and seasonal home range size of alligators in the Everglades; and (2) to determine if differences in these parameters existed between genders, habitats, study areas, and seasons.

Methods

Alligators were located on a weekly basis with initial locations recorded within 3-5 days after release. A visual sighting was obtained during the first 3 weeks of tracking to determine the health of the animal. Study animals were located by small aircraft using a 4 MHz model R4000 ATS radio-receiver and a pair of wing mounted Telonics RA-2A 2-element yagi antennas. After an alligator's position had been



Image 9 Large alligator partially submerged.

determined, the location was recorded with a hand held Trimble Scoutmaster GPS unit equipped with a DCI (Differential Corrections Inc.) real-time differential correction (DGPS) data receiver. The DGPS receiver provided 10 m accuracy which minimized the error from the plane.

Weekly location data were used to calculate home range size. A general rule to determine if consecutive fixes are statistically independent is whether sufficient time has elapsed for the animal to move from one end of its home range to the other (White and Garrott, 1990); fixes ≥ 24 hours apart were considered independent as radio-tagged alligators were found to be able to traverse their home range within a 24-hr period. Home range size was determined by a 95% adaptive kernel (AK) model using Ranges V

(Institute of Terrestrial Ecology, Wareham, United Kingdom). The adaptive kernel model is a density estimator uninfluenced by grid size and placement, and is nonparametric which allows it to accurately estimate densities of any shape (Seaman and Powell, 1996). Decreasing the home range estimate by 5% made up for the varying number of locations on each alligator and excluded any extreme outliers (White and Garrott, 1990; Staus, 1998). A 0.5 smoothing parameter (H value) was used for all calculations of home range size using the AK method. The default setting for the smoothing parameter was 1.0, however, a series of visual assessments revealed that lessening the H value by 0.5 created a more realistic contour fit to fixes included in the home range analysis that more adequately reflected alligator home ranges in the Everglades. Default settings were used for contours fitted to fixes, grid cell size (40 X 40 m), and grid detection and rescaling. A 75% AK was calculated to estimate core areas of activity (Staus, 1998). A 95% and 100% minimum convex polygon (MCP) was calculated to facilitate comparison with previous studies. The MCP is a robust estimate of home range and was originally used to determine the minimum area of home range found when using a trapping grid. Using radio-tracking data the MCP method is an estimate of total area utilized and often will include areas in the home range that an animal may not use or that is unsuitable habitat. A ratio of 75% AK/ 95% MCP was calculated to quantify the proportion of the entire home range (95% MCP) that was used most frequently by each alligator (Staus, 1998). MCP estimates of home range length and width were used to determine if differences existed in home range shape between marsh and canal alligators (i.e., if longer and more narrow, then the home range would be more linearly shaped).

An analysis of variance (a series of one-way ANOVAs) was used to test for differences in home range size between genders, habitats (marsh vs. canal), study areas (WCA vs. ENP), size class (subadult 1.2 - 1.8 m, adult 1.8 - 2.7 m, and bull 2.7+ m), and seasons (fall – 22 September to 20 December; winter – 21 December to 20 March; spring – 21 March to 20 June; summer – 21 June to 21 September; wet – 1 July 1997 to 31 December 1997; dry – 1 January 1998 to 31 June 1998) using SAS (SAS Version 6.12; SAS Institute Inc.). If the ANOVA showed a significant difference ($p \leq 0.05$), a Duncan's multiple range test (DMRT) was conducted to detect differences among all possible comparisons (Ott, 1993). The 95% AK home range estimates were used for statistical analyses.

Results

Home range size was estimated for 34 radio-tagged alligators in WCA ([Table 2-1](#)) and 30 radio-tagged alligators in ENP ([Table 2-2](#)). Home range sizes for alligators located in WCA and ENP were not significantly different ($F_{1,51} = 0.34$; $p = 0.561$). Therefore, the data were pooled for tests of seasonal differences in home range size for gender and habitat.

Annual home range size for male alligators was significantly greater than females ($F_{1,49} = 23.90$; $p < 0.0001$; [Table 2-3](#)). Male home ranges were approximately 4 times larger in the spring, nearly 3 times larger in the summer, 3 times larger in the fall, and 3 times larger in the winter than those of females ([Fig. 2-1](#)). Female alligators exhibited high site fidelity for a particular area of the natural marsh or section of a canal and had

nearly identical home range sizes among seasons. Home range size for male alligators successively decreased from spring to summer to fall to winter ([Fig. 2-1](#)). Mean home range size for female alligators decreased from summer to spring to fall to winter ([Fig. 2-1](#)).

Male alligators had significantly longer ($F_{1,29} = 5.32$; $p = 0.029$) and wider home ranges ($F_{1,29} = 3.07$; $p = 0.090$) than females ([Table 2-4](#)). Male alligators had significantly larger 95 % MCP home ranges than female alligators ($F_{1,49} = 23.44$; $p < 0.0001$). Mean number of core areas ($F_{1,29} = 4.67$; $p = 0.039$) and core area size ($F_{1,29} = 8.34$; $p = 0.007$) for female alligators were significantly less than for male alligators. Male and female alligators used similar amounts of their home range in core areas ([Table 2-4](#)).

Annual home range size for alligators occurring in marsh and canal habitats did not differ ($F_{1,49} = 0.41$; $p = 0.525$; [Table 2-3](#)). Home range size for marsh alligators successively decreased from spring to summer to fall to winter ([Fig. 2-2](#)). Mean home range size for canal alligators decreased from summer to spring to fall to winter ([Fig. 2-2](#)). Alligators located in canals had more linearly shaped home ranges than marsh alligators ($F_{1,29} = 3.66$; $p = 0.065$; [Table 2-4](#)). Canal and marsh alligators had similar numbers of core areas and used similar amounts of their home range in core areas ([Table 2-4](#)).

No difference was found in annual



Image 10 Typical canal habitat.

home range size between wet and dry seasons (paired t-test; $t = 0.29$; $df = 36$; $p = 0.776$; [Table 2-3](#); [Figs. 2-1 and 2-2](#)).

Female ($F_{1,28} = 8.28$; $p = 0.008$, $R^2 = 0.23$) and male ($F_{1,26} = 5.68$; $p = 0.025$, $R^2 = 0.18$) alligator home range size tended to decrease with an increase in total body length ([Figs. 2-3 and 2-4](#)). Other commonly used methods of determining home range size were included to facilitate home range comparisons with previous studies ([Table 2-5](#)).

Discussion

Radio-tagged alligators in the Everglades exhibited a high affinity for a particular portion of the natural marsh or section of a canal; however, males were likely to have 2 or more preferred core areas within their home ranges. Male core areas were larger than those of females.

Both male and female alligator home range size tended to decrease with increasing size (total length; [Fig. 2-3 and 2-4](#)). Larger sized animals would be better equipped to defend their preferred core areas and would less likely be forced into marginal habitats. Mature adults also would have learned how to best use their natural environment to obtain the needed resources resulting in a smaller home range.

Alligator home range size varies according to seasonal and daily temperature variation. In the Everglades, increased home range sizes were observed with increasing temperatures. Home range sizes were greatest during periods of elevated temperatures that existed from late spring to early fall ([Fig. 2-5](#)). Alligator home range also was positively correlated with environmental temperatures in other studies (Chabreck, 1965;

Joanen and McNease, 1970; Joanen and McNease, 1972; McNease and Joanen, 1974; Goodwin and Marion, 1979; Taylor, 1984; Rootes and Chabreck, 1993; Table 2-12 and 2-13)

Alligators were found to use the same holes, depression potholes, and shrub complexes throughout the year as thermal refugia from extreme hot or cold temperatures. Alligators used more of these habitat types during warmer temperatures, particularly during the spring breeding season (personal observation). Alligators had a larger home range during the spring due to increasing temperatures and to the onset of the breeding season. Once the breeding season ended and temperatures peaked during the summer months, alligator movements were confined to more restricted core areas and activity areas as thermoregulatory needs seemed to restrict alligator movement. However, total home range size did not differ in spring and summer.

Movements of Everglades alligators were greater in the winter than in more northern areas. Alligators in Louisiana remained in holes or dens during the winter in a semi-torpor state (McIlhenny, 1935). Alligators in the Everglades face warmer fall and winter temperatures than those in more northern areas ([Table 2-6](#)). This resulted in greater home range size for the fall and winter months. Everglades alligators were found to be quite active during the fall. Temperatures in the fall were comparable to spring temperatures and thus favored regular movements.

Summer female movements were affected more by reproductive efforts than temperature. Nesting females had smaller home ranges than non-nesting females (personal observation). Spring activity ranges for male alligators were 13 times larger than their winter ranges suggesting that increasing temperatures promote greater

movements. However, with spring coinciding with the breeding season, increased movements were probably attributed to increasing temperature and, further, by males searching for mates.

Increased home range size can be attributed to increased reproductive activity as alligators expend tremendous amounts of energy in the pursuit of reproductive opportunities. Adult alligators, particularly males, had larger home ranges, activity ranges, and moved more on a daily basis during the spring breeding season.

Male alligators were found to maintain large home range sizes during each season of the year (excluding winter) suggesting that some level of territory maintenance exists throughout the year. The larger home range size of male alligators encompassed several female home ranges allowing males to maximize their breeding opportunities. Neither male nor female alligators moved to deep open water for breeding purposes. It was presumed that breeding took place within female alligators preferred core area habitats (i.e., holes, potholes or canals).

Structural differences between canal and marsh habitat types were presumed to affect alligator home range size and movement in the Everglades. Canal alligators had a slightly larger home range than marsh alligators. McNease and Joanen (1974) hypothesized that differences in habitat utilization of alligators in the Rockefeller Refuge, Louisiana was partially responsible for different movement patterns and home range sizes. Alligators located in the natural marsh, where extended travel was relatively difficult due to thick vegetation, probably tended to restrict movement and home range size, where as, alligators located in deep-water areas (i.e., canals), which offered

convenient, unimpeded travel lanes, tended to elevate home range sizes (McNease and Joanen, 1974).

Everglades alligators located in canals had unrestricted open water travel lanes that allowed them to traverse long distances over a short time period (i.e., 24 hrs). Long distance movements of short duration, particularly by males, attributed to the greater seasonal home range size of canal alligators. Canal alligators tended to have longer, more linear home ranges than marsh alligators, which were related to these movements.

Canals offered alligators large prey populations of small and large fish (Loftus and Kushlan, 1987) and spoil banks often had small mammals and birds. Marsh habitats appeared to have fewer fish that were more dispersed (an exception to this was in the dry season when water levels dropped and greater concentrations of fish were observed within holes and depressions in the marsh that retained water). Canal alligators also had easy access to large spoil banks and levee breaks that offered prime basking sites and helped shield them during unfavorable weather conditions.

During the dry season, canal alligators had a much larger average home range size than did alligators located in the natural marsh. Canal water levels varied little as the deep, open waters of the canals allowed alligators to move freely throughout the year. The presence of water in canals throughout the year also allowed alligators in these environments to avoid any adverse conditions that marsh alligators would endure during prolonged droughts.

Conclusions

Alligator home range size was affected by gender, temperature, reproductive efforts, habitat, and water level. Male home ranges were considerably larger than for female alligators except during the winter. Alligator home range size generally increased with increasing temperatures. Excessively hot temperatures in summer appeared to limit movements and resulted in smaller core areas than in the spring. Increased spring home ranges for male alligators were probably due to the onset of the breeding season and increasing temperatures. Female alligators remained within their preferred core areas throughout the year and female marsh alligators did not seek deep open water for breeding purposes. Females with a recently hatched pod remained at the nest site and eventually sought preferred habitats (i.e., potholes, holes, low mixed marsh, etc.), which were usually near the nest site.

Linear movements of canal alligators were unimpeded by vegetation and other physical barriers. Marsh alligators had to travel through thick vegetation and, during periods of low rainfall, were required to traverse portions of the marsh with little or no water. Lower water levels forced alligators to walk through the marsh instead of swimming and would have increased energy expenditures. Movements during these low water conditions would also have increased exposure to extreme temperatures and direct sunlight, as alligators would not have had deep water to buffer their body temperatures. Smaller home ranges for marsh alligators in certain seasons (annual home range size was not different) were thus probably attributed to thick vegetation that impeded movements and limited movements due to extreme temperatures. Home range sizes of marsh

alligators decreased with decreasing water levels; canal alligators were unaffected (Morea 1999).

The Everglades are dependent upon a fluctuating hydrology for its structure and function. Current restoration efforts may result in the restoration of some canal habitats to marsh. Observed movements of alligators in canals suggest that they would either move into the surrounding marsh or disperse to other near-by canals. Alligators were found to have well-defined home ranges, however, long-distance movements did occur. Two alligators captured in the Miami Canal moved several kilometers into the marsh and established home ranges from which they did not depart. Therefore, canal alligators can disperse from canals into the marsh, establish a home range, and survive. If conditions in peripheral marshes improve, then alligators could eventually occupy that habitat.

Table 2-1. Annual and seasonal home range size for radio-tagged American alligators located in Water Conservation Area 3A North. Home range size (ha) was calculated with a 95% adaptive kernel model using locations collected from November 1996 to August 1999.

Alligator	Gender	Habitat	Annual (ha)	Fall (ha)	Winter (ha)	Spring (ha)	Summer (ha)	Wet (ha)	Dry (ha)
54751	Female	Canal	27.42	9.88	3.55	8.47	2.74	12.62	13.00
54763	Female	Canal	35.76	11.30	7.98	5.82	25.61	22.67	13.58
54935	Female	Canal	32.75	1.95	26.69	3.73	6.09	7.92	24.96
54735	Female	Marsh	45.30	6.02	8.96	19.65	24.60	16.41	23.40
54915	Female	Marsh	24.43	10.24	1.44	13.95	5.99	15.67	16.99
55037	Female	Marsh	39.68	11.37	5.48	4.89	3.27	22.66	15.32
54752	Male	Canal	25.27	11.10	4.43	1.67	1.88	19.37	11.29
54767	Male	Canal	47.92	23.37	1.97	23.62	2.93	53.72	18.68
54919	Male	Canal	91.77	20.73	42.79	36.77	24.90	47.84	67.53
54924	Male	Canal	73.80	31.29	1.02	43.76	9.20	57.75	42.39
54955	Male	Canal	446.49	132.68	9.02	428.30	366.43	137.96	801.88
54996	Male	Canal	275.54	32.42	1.50	221.69	94.70	167.76	165.08
55029	Male	Canal	68.08	74.87	6.29	2.27	5.79	94.29	12.90
54742	Male	Marsh	27.06	3.74	5.81	1.46	15.56	15.28	7.81
55004	Male	Marsh	44.57	12.77	9.37	10.24	17.38	30.59	31.86
54746	Male	Marsh	139.95	37.33	9.18	12.01	64.94	99.02	33.84
Mean			90.36	26.94	9.09	52.39	42.00	51.35	81.28
SD			114.22	33.46	10.84	113.57	90.14	48.65	195.93

Table 2-2. Annual and seasonal home range size for radio-tagged alligators located in the Shark River Slough region of Everglades National Park. Home range size (ha) was calculated with a 95% adaptive kernel model using locations collected from November 1996 to August 1999.

Alligator	Gender	Habitat	Annual (ha)	Fall (ha)	Winter (ha)	Spring (ha)	Summer (ha)	Wet (ha)	Dry (ha)
54936	Female	Canal	56.87	14.10	23.20	6.13	24.56	42.12	18.17
55016	Female	Canal	34.56	8.02	10.72	16.49	2.47	28.93	23.46
54770	Female	Marsh	.	10.90	.	.	.	12.66	.
54942	Female	Marsh	34.50	10.62	9.64	6.99	14.77	18.37	15.49
55000	Female	Marsh	27.91	4.53	3.09	14.46	8.00	5.72	19.00
54744	Male	Canal	122.28	17.87	8.75	93.23	11.47	20.11	105.38
54750	Male	Canal	34.75	4.04	1.35	19.37	2.33	24.00	27.44
54983	Male	Canal	26.14	4.48	5.67	2.22	11.53	19.51	8.91
54991	Male	Canal	254.55	30.04	5.21	19.77	43.10	51.12	32.70
55011	Male	Canal	151.52	26.66	28.21	13.42	66.10	49.90	93.47
55544	Male	Canal	195.53	85.90	11.68	30.84	25.78	107.17	86.75
54768	Male	Marsh	187.34	60.27	92.27	41.97	17.65	59.56	94.56
54772	Male	Marsh	53.14	33.65	10.63	7.44	1.31	43.16	16.73
54917	Male	Marsh	57.05	8.98	38.89	16.66	28.25	14.03	50.56
55022	Male	Marsh	118.11	101.90	27.63	47.77	23.86	105.91	53.43
Mean			96.73	28.13	19.78	24.05	20.08	40.15	46.15
SD			75.11	30.73	23.61	23.92	17.73	31.32	34.61

Table 2-3. Mean annual and seasonal home range size for radio-tagged alligators located in Water Conservation Area 3A North and Everglades National Park. Home range size was calculated with a 95% adaptive kernel model using locations collected from November 1996 to August 1999.

Comparison		Season	<u>Home Range Size (ha)</u>				Season	<u>Home Range Size (ha)</u>		
			Pooled	Marsh	Canal			Pooled	Marsh	Canal
Gender	Male	Study	144.34 ^a	153.58 ^a	138.17 ^a	Female	Study	57.04 ^b	60.17 ^b	49.96 ^b
		Fall	68.41 ^a				Fall	24.99 ^b		
		Winter	46.07 ^a				Winter	17.11 ^b		
		Spring	75.02 ^a				Spring	27.21 ^b		
		Summer	72.97 ^a				Summer	30.23 ^b		
		Wet	46.19 ^a				Wet	20.86 ^b		
		Dry	48.29 ^a				Dry	22.95 ^b		
Habitat	Marsh	Study	93.54			Canal	Study	107.49		
		Fall	39.98				Fall	53.29		
		Winter	24.85				Winter	42.94		
		Spring	43.06				Spring	57.81		
		Summer	41.37				Summer	64.36		
		Wet	36.09				Wet	31.71		
		Dry	36.78				Dry	32.81		

Means with different lower case letters were significantly different ($p < 0.05$).

Table 2-4. Annual minimum convex polygon (95%) and adaptive kernel (75%) home range size for radio-tagged marsh alligators in Water Conservation Area 3A North and Everglades National Park located from November 1996 to August 1999. Range length and width were estimated from 95% minimum convex polygons and number of core areas were from 75% adaptive kernel polygons.

Comparison	<u>Gender</u>		<u>Habitat</u>	
	Male	Female	Marsh	Canal
No. of locations	2027	1767	1986	1808
Range length (m)	3174.15	1603.95	2073.70	2620.51
Range width (m)	772.34	571.21	704.14	615.67
Linearity	4.43	2.89	4.43	2.89
95% MCP (ha)	144.73	55.72	103.77	93.97
75% AK (ha)	54.24	25.65	40.38	38.80
Core areas	1.80 ^a	1.18 ^b	1.62	1.56
AK/MCP	0.41	0.47	0.44	0.44

Table 2-5. Mean annual and seasonal home range size for radio-tagged alligators located in Water Conservation Area 3A North (WCA) and Everglades National Park (ENP) located from November 1996 to August 1999. Home range size was calculated by adaptive kernel (AK) model and minimum convex polygon (MCP).

Comparison		95% AK (ha)	75% AK (ha)	100% MCP (ha)	95% MCP (ha)
Area	ENP	107.26	44.41	167.82	109.83
	WCA	91.07	34.33	195.36	87.57
Gender	Male	144.34	54.24	286.52	144.73
	Female	35.91	17.31	58.77	36.13
Habitat	Marsh	93.54	40.38	151.28	103.77
	Canal	107.49	38.80	216.70	93.97
Season	Overall	99.83	39.67	180.78	99.35
	Fall	27.52	16.64	45.64	37.53
	Winter	14.08	8.37	26.06	26.06
	Spring	39.17	17.52	48.83	44.94
	Summer	31.77	16.96	44.92	41.60
	Wet	45.93	23.13	68.87	51.17
	Dry	64.89	28.11	78.33	65.24

Table 2-6. Mean seasonal home range size (ha) for adult (>183 cm) radio-tagged alligators located in Rockefeller Refuge, Louisiana; Newnans Lake, Florida; and the Everglades calculated with a 100% minimum convex polygon model.

Season	Male Rockefeller Refuge ¹	Male Newnans Lake ²	Female Newnans Lake ²	Male Everglades ³	Female Everglades ³
Spring	224	257	16	75	27
Summer	679	95	13	73	30
Fall	393	38	10	68	25
Winter	0	9	6	46	17

¹Joanen and McNease, 1972.

²Goodwin and Marion, 1979.

³This study.

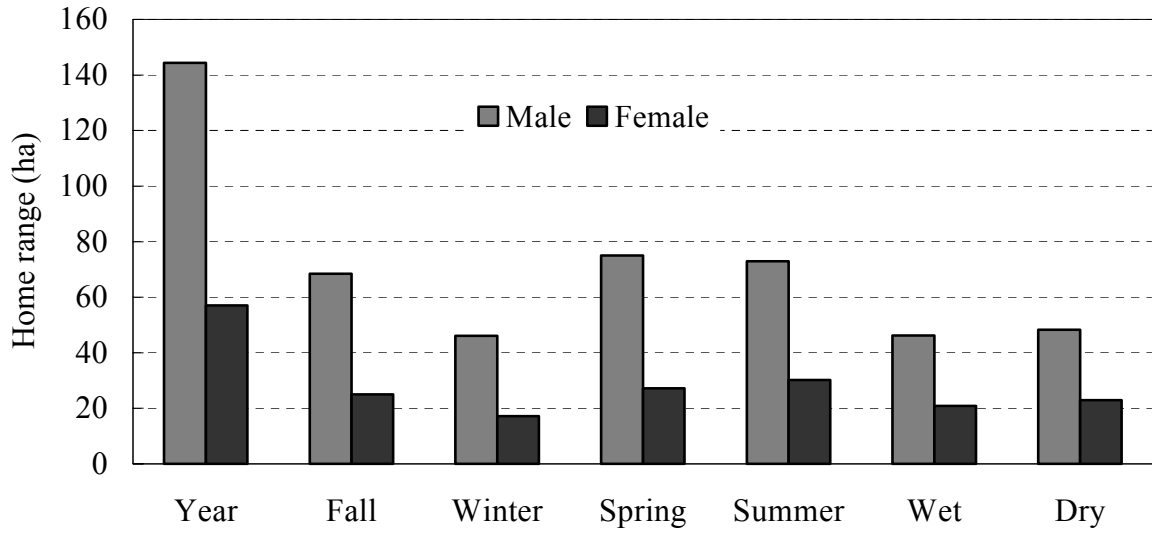


Figure 2-1. Mean annual and seasonal home range size (95% adaptive kernel) of radio-tagged male and female alligators located in Water Conservation Area 3A North and Everglades National Park from November 1996 to August 1999.

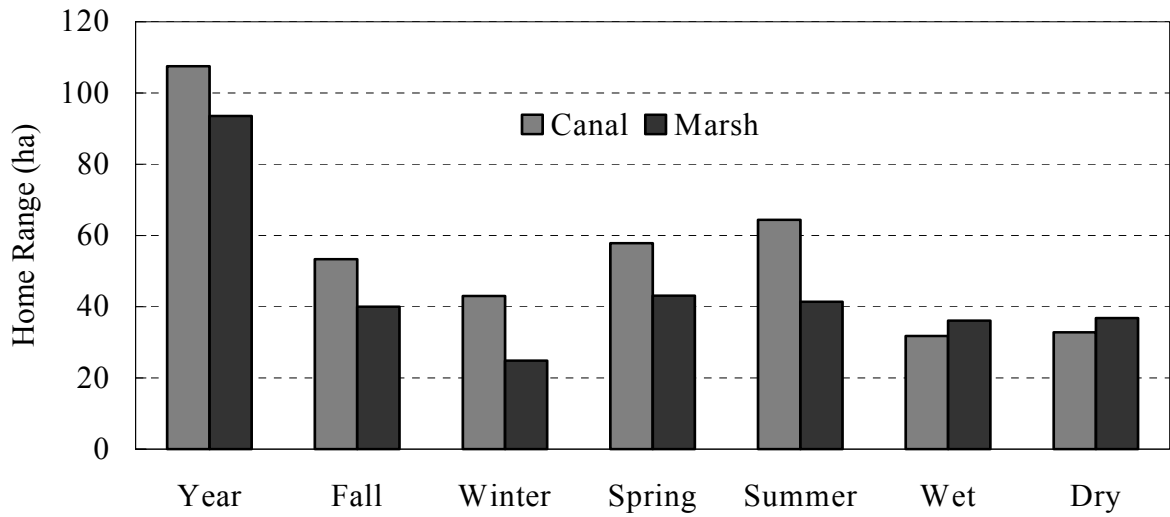


Figure 2-2. Mean annual and seasonal home range size (95% adaptive kernel) of radio-tagged canal and marsh alligators located in Water Conservation Area 3A North and Everglades National Park from November 1996 to August 1999.

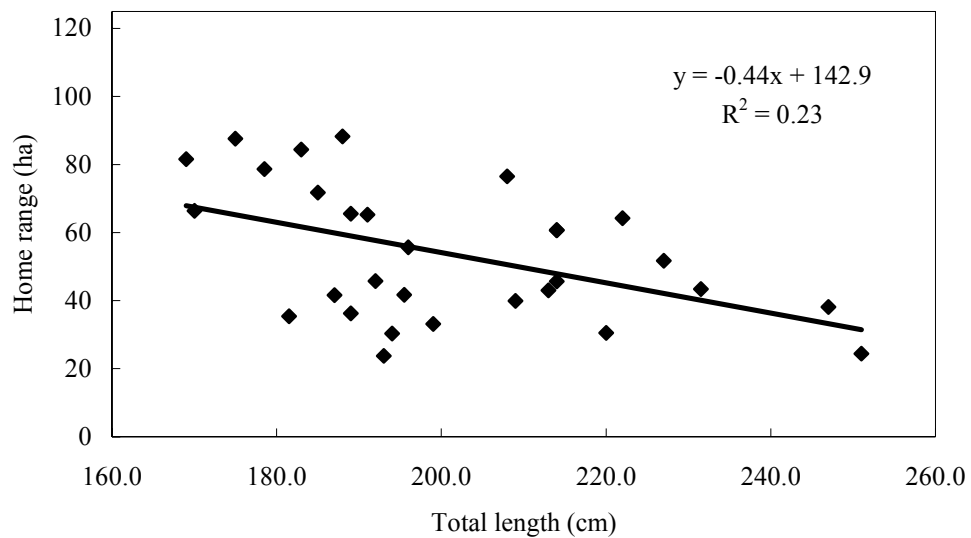


Figure 2-3. Home range size (95% adaptive kernel) plotted against total length for radio-tagged female alligators located in Water Conservation Area 3A North and Everglades National Park from November 1996 to 21 August 1999.

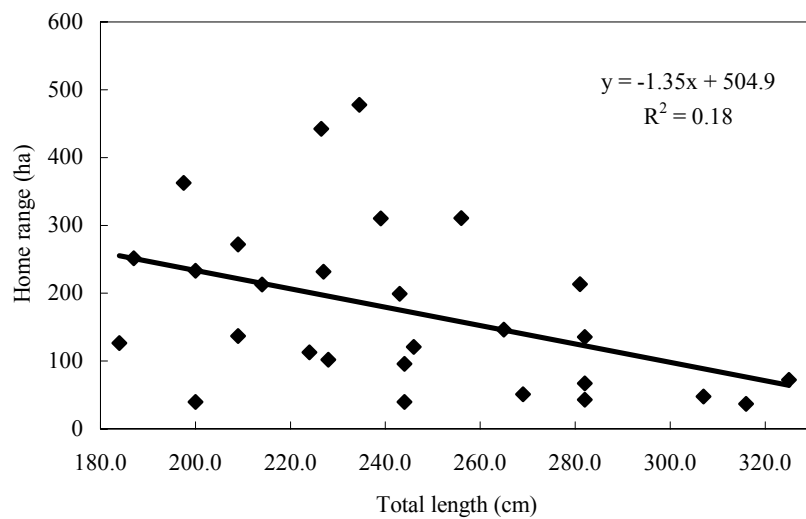


Figure 2-4. Home range size (95% adaptive kernel) plotted against total length for radio-tagged male alligators located in Water Conservation Area 3A North and Everglades National Park from November 1996 to August 1999.

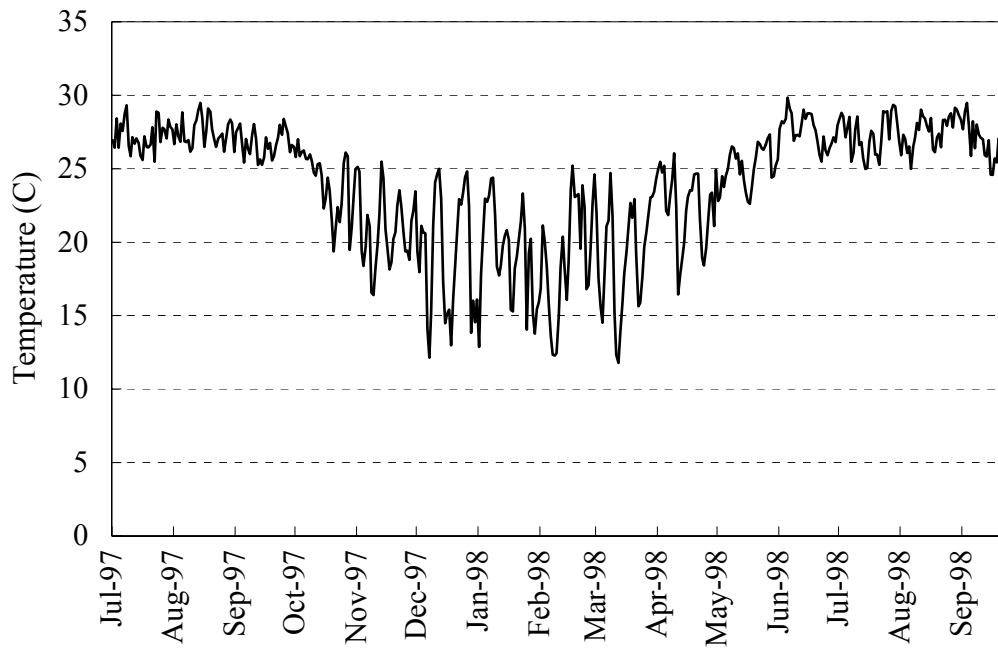


Figure 2-5. Mean daily air temperature (°C) for the Everglades region of southern Florida from 1 July 1997 to 21 September 1998
(Source: South Florida Water Management District).

CHAPTER 3

DAILY MOVEMENTS

Cory R. Morea, , Kenneth G. Rice, H. Franklin Percival, and Stanley R. Howarter

Alligators in the Everglades are subjected to limited food availability, high metabolic costs, habitat degradation and destruction, altered hydrologic conditions, high levels of nest flooding, and high levels of mercury. Everglades restoration has been initiated and comprehensive modeling of biotic and abiotic attributes have been undertaken to determine suitable restoration alternatives (USACE, 1999). A modeling effort, Across Trophic Levels System Simulation (ATLSS), is being developed to compare the future effects of alternative hydrologic scenarios on the biotic components of the systems (ATLSS, 1999). The alligator's role in the trophic dynamics of the Everglades is significant. Information concerning alligator daily movement and habitat use in the Everglades are needed for modeling efforts and to improve management strategies for this keystone species.

Daily movement estimates facilitate development of management strategies for populations and for varying sub-classes within a population. Topics such as resource requirements, metabolic cost associated with spacing patterns within the environment, core areas of activity, and territoriality can be used to guide management decisions. Much is known concerning fundamental movement patterns, basic home range size, and habitat use of adult alligators, however, detailed information concerning alligator daily movements, core areas of activity, and habitat use in the Everglades is not known. In

order to properly model these parameters for Everglades alligators and to determine possible responses to different hydrologic scenarios being explored for Everglades restoration more detailed information is needed.

Objectives

The objectives of the study were: (1) to estimate daily movement patterns of alligators in the Everglades; and (2) to determine if differences in these parameters existed between genders, habitats, study areas, and seasons.

Methods

Daily movement was estimated from 4 weeklong intensive tracking samples conducted once during each fall, winter, spring, and summer from 7 November 1997 to 31 July 1998 in WCA and ENP. A series of tests revealed that the aerial method of collecting radio-locations was not precise enough to accurately estimate the daily movements of alligators (accuracy ≤ 500 m). Further testing revealed that radio-locations estimated from 3 or more bearings taken from known locations using the airboat-mounted null-combiner antenna system were precise enough to accurately estimate daily movements (accuracy ≤ 10 m). The hand held yagi antenna was used when field conditions warranted (accuracy ≤ 20 m). An unplanned blind test of the accuracy of the null-combiner antenna system occurred when a radio-tagged alligator died in a gator

hole. Upon analysis, all radio-locations estimated during a 1-week period were within a 6 m radius of the radio-transmitter's actual location.

A roving "tower" method was used to estimate daily movements. At least three towers were established to triangulate on each study animal located in marsh habitats. Triangulation is the process of estimating the location of a transmitter by using two or more directional bearings obtained from known locations remote from the transmitter's position (White and Garrott, 1990). Towers consisted of a 2 m PVC pipe marked with orange flagging and reflective tape to increase visibility in both light and dark conditions respectively. The PVC pipes were hammered vertically into the marsh substrate within 100 m of an animal's initial location in such a pattern that visually connecting the towers within the landscape formed a polygon in the center of which the radio-tagged alligator was located. Towers had unique identification numbers and a DGPS position was recorded at each tower. Additional towers were erected when a radio-tagged alligator moved beyond the range of the original set of towers such that each radio-tagged alligator being tracked was always located within a polygonal area encompassed by a set of towers.

Travel routes were established from tower-to-tower and alligator-to-alligator in an effort to minimize the disturbance to study animals and the surrounding ecosystem. Routes were marked with orange flagging and recorded using a DGPS receiver. To ensure repeated precision, the airboat was maneuvered to a stop such that the bow of the boat was pointed towards magnetic north and the starboard gunwale adjacent to the captain's seat was within 0.5 m of the tower. Upon arrival at a specified tower, the tower's identification was recorded, along with air temperature, water temperature, wind

speed and direction, relative humidity, water depth, habitat description, and general weather conditions. The bearing of the boat was taken from the center of the boat to the front-center of the bow using a Silva hand-held compass. A bearing was taken to the alligator's location with the airboat-mounted null-combiner antenna system and later corrected with the boat bearing to obtain a true bearing.

Animals tracked in the L-67 Canal extension (ENP) were located from the levee that borders the canal to the east. An animal's location was determined from three or more bearings taken from a hand held yagi antenna with a hand held compass. A DGPS position and environmental measurements were recorded at each bearing location.

Animals tracked in the Miami canal were located from an airboat using a continuous tracking method. Once a signal was detected, a bearing to the alligator was determined. The bearing to the animal was tracked as the airboat continued its movement within the canal until the animal's exact position could be determined. Environmental measurements were recorded and a position was taken using a DGPS unit.

These procedures were repeated until three or more bearings were recorded for each study animal (excluding alligators located in the Miami Canal). Locations were obtained approximately twice during a 24-hour period for each weeklong intensive sample.

Locations were presumed to be auto-correlated, which was deemed unimportant for estimating the minimum linear distance an alligator moved in a 24-hr period. Ranges V was used to estimate the minimum linear daily movement (m/24-hr) and activity areas (ha). Activity area is the area encompassed within the outward boundaries of an animal's locations collected during a relatively short period of time and deemed as being highly accurate. In fact, activity area is a detailed, extremely focused, measure of

an animal's core area of movement over a 2-dimensional plane. Activity ranges only included fixes collected during the weeklong intensive samples and was used to estimate seasonal averages and year-long averages for animals that were tracked intensively during all four seasons of the year. Activity areas were determined for radio-tagged alligator's by estimating the 95% MCP area (see Chapter 2 for discussion of home range size estimation) for each animal for each weeklong intensive sample (seasonal activity area) and from all the fixes collected on an animal during weeklong intensive samples collected during the fall, winter, spring, and summer (annual activity area). For example, if an animal was only tracked intensively for a week during the spring, this animal's activity area for that week would be included in the spring activity area average and not the annual. However, if an animal was tracked for a week during the fall, winter, spring, and summer, then all of the fixes were included in the 95% MCP estimate to get an annual activity area. An analysis of variance (a series of one-way ANOVAs) was used to test for differences in daily movements and activity ranges between genders, habitats, study areas, and seasons using SAS. If the ANOVA showed a significant difference ($p \leq 0.10$), a Duncan's multiple range test was conducted to detect differences among all possible comparisons. Fix dispersion was determined from the kernel home range model and is a measure of spatial variability among all fixes for a given animal. Greater fix dispersion meant that an animal was found to frequent a larger area within its home range on a regular basis.

Results

Movement

Mean daily movement (m/24-hr) was estimated for 16 radio-tagged alligators in WCA ([Table 3-1](#)) and 15 radio-tagged alligators in ENP ([Table 3-2](#)). Movement for alligators located in WCA and ENP were not significantly different ($F_{1,84} = 1.07$; $p = 0.305$). Therefore, the data were pooled for tests of seasonal differences in home range size for gender and habitat.

Daily Movement

Male alligators moved significantly more in a 24-hour period than female alligators ($F_{1,11} = 25.60$; $p = 0.0004$; [Table 3-3](#)). Males moved significantly more than females in the fall ($F_{1,18} = 10.18$; $p = 0.005$), winter ($F_{1,22} = 5.20$; $p = 0.033$), and spring ($F_{1,10} = 6.91$; $p = 0.016$). Movements for male alligators decreased from spring to summer to fall to winter ([Fig. 3-1](#)). Movements for female alligators decreased from spring to fall to winter to summer ([Fig. 3-1](#)).

No significant differences were found in the mean daily movements of marsh and canal alligators ($F_{1,86} = 1.94$; $p = 0.167$). Both marsh and canal alligator (male and female) mean daily movement decreased from spring to summer to fall to winter ([Fig. 3-2](#)).

Activity Range

Female alligators exhibited high site fidelity for a very small area of preferred habitat within the natural marsh or canal contained within their home ranges. Female seasonal activity ranges successively decreased from fall to spring to winter to summer ([Table 3-4](#)). Male alligators exhibited high site fidelity for a larger area within the natural marsh or canal than females. Male seasonal activity ranges successively decreased from spring to summer to fall to winter. Male alligators had a significantly larger activity range in fall than females ($F_{1,18} = 7.53$; $p = 0.013$). Males had significantly greater activity range lengths than females for fall ($F_{1,18} = 10.03$; $p = 0.005$), winter ($F_{1,22} = 3.46$; $p = 0.076$), spring ($F_{1,20} = 2.99$; $p = 0.099$), and summer ($F_{1,18} = 4.04$; $p = 0.059$). Male activity range widths were significantly greater than for females in the fall ($F_{1,18} = 5.64$; $p = 0.028$). Male alligators had significantly greater fix dispersion within activity ranges than females during fall ($F_{1,18} = 8.80$; $p = 0.008$), winter ($F_{1,22} = 3.16$; $p = 0.089$), spring ($F_{1,20} = 3.44$; $p = 0.078$), and summer ($F_{1,18} = 5.00$; $p = 0.038$).

Marsh alligators had significantly greater activity range sizes than canal alligators during fall ($F_{1,18} = 3.04$; $p = 0.093$), and winter ($F_{1,22} = 3.60$; $p = 0.071$; [Table 3-4](#)). Marsh alligators had significantly wider activity ranges than canal alligators during fall ($F_{1,18} = 3.87$; $p = 0.064$), winter ($F_{1,22} = 6.35$; $p = 0.019$), and spring ($F_{1,20} = 4.83$; $p = 0.039$).

Male alligators had > 3 times annual activity ranges than females with greater range length, width, and mean fix dispersion within their ranges ([Table 3-5](#)). Marsh alligators had >2.5 times mean activity range than canal alligators. Canal alligators had longer more narrow ranges. The mean estimated annual activity range for all radio-

tagged alligators was 4.81 ha, of which nearly all was used by male alligators during the spring breeding season. Activity range size for all radio-tagged alligators successively decreased from spring to fall to summer to winter.

Discussion

Daily movement of adult alligators varied according to gender, temperature, reproductive efforts, habitat, and water level. Other factors such as food availability, competition, anthropogenic disturbances, and major weather events may have influenced alligator movements, but were less likely to have lasting effects during normal years.

Male alligators had larger home ranges and moved more on a daily basis than females. Males used more of their home range during regular daily movements. Males tended to regularly traverse their home range, particularly alligators located in marsh habitats. Male movements within core areas were more dispersed and movements between core areas expanded their home range. Females tended to limit their movements within small activity ranges and core areas whereas males tended to cover larger areas.

Alligator movement in general appeared to be nonrandom, that is, alligators seemed to determine their destination prior to moving. Male and female alligators that were located in a hole during the evening were often found in another hole at dawn. Regular and repetitive movements throughout an alligator's home range were observed. Alligators may have moved about in search of food or for territory maintenance. Regular movements were often within preferred core areas or activity areas and no other alligators were usually observed in holes that a radio-tagged adult alligator occupied. For females,

movements were short in distance and covered little area. However, male alligators would travel several hundred meters between stops at preferred potholes or holes, or sections of a canal. Movements between preferred habitats were methodical and repeated. For example, male alligator 54746, located in the marsh of WCA, had a home range oriented in a northeast direction and consistently moved from one end to the other throughout the study period.

Body size was similar for radio-tagged male and female alligators. Therefore, energy needs based on body size probably did not result in the differences of movements between genders. Greater movements of males were probably attributable to territory maintenance. While maintaining large home ranges males would have experienced increased energy expenditures. Restricted home range size and daily movements observed for females would have minimized energy expenditures and allowed potential breeders to maximize their body condition while maintaining a potential nest site. These differences between males and females were consistent throughout both study areas.

Alligator daily movement varied according to seasonal and daily temperature variation. In the Everglades, increased daily movements were observed with increasing temperatures. Daily movements were greatest during periods of elevated temperatures that existed from late spring to early fall ([Fig. 3-3](#)). Alligator daily movement also was positively correlated with environmental temperatures in other studies (Chabreck, 1965; Joanen and McNease, 1970; Joanen and McNease, 1972; McNease and Joanen, 1974; Goodwin and Marion, 1979; Taylor, 1984; Rootes and Chabreck, 1993; [Table 3-6](#)). In the Rockefeller Wildlife Refuge, Sabine National Wildlife Refuge and various marsh areas in Cameron Parish in Southwest Louisiana, the seasonal daily movement of

alligators was largely in response to temperature changes (Chabreck, 1965). Temperature was found to effect movements similarly for alligators in Louisiana (Chabreck, 1965; Joanen and McNease, 1970; Joanen and McNease, 1972; McNease and Joanen, 1974; Taylor, 1984; Rootes and Chabreck, 1993), South Carolina (Murphy, 1977), and Florida (Goodwin and Marion, 1979) with warmer temperatures promoting greater movements. In a thermally altered reservoir in South Carolina, Murphy (1977) found that alligators located in the section of the reservoir that received heated water had a mean daily movement of 707 m while animals using the rest of the reservoir averaged 178 m. This suggested that increased movement was associated with thermal loading (Murphy, 1977).

Movements of radio-tagged Everglades alligators tended to follow a defined path either linear in nature or along the outside contours of tree islands and sawgrass clumps. Edge habitats along tree islands and thick sawgrass clumps offered an ecotone that provided thick cover on one side and open habitats on the other. Trails along the ecotone may have been used for their temperature gradient, as the temperature within these trails was often several degrees cooler (personal observation) than the more open habitats (i.e., slough).

Alligators were found to use the same holes, depression potholes, and shrub complexes throughout the year as thermal refugia from extreme hot or cold temperatures. Alligators used more of these habitat types during warmer temperatures, particularly during the spring breeding season (personal observation). Alligators had a larger home range, activity range, and greater daily movement during the spring due to increasing temperatures and to the onset of the breeding season. Once the breeding season ended and temperatures peaked during the summer months, alligator movements were confined

to more restricted core areas and activity areas as thermoregulatory needs seemed to restrict alligator movement.

Daylight locations for canal alligators were most often located in the shade of shrubs that lined canal edges during periods of high temperature or basking during cooler periods with movements into the open water area of the canal at night being observed. For example, male 54924 located in the Miami Canal (WCA) was most often found along a 100 m section basking on a large levee that bordered the canal or in the shallow marsh-like levee break during daylight and would move into the open waters of the canal at night. On occasion, this animal was found to move > 1 km south in the canal but would quickly return (i.e., within 24 hrs) to his preferred core area associated with the levee break. Long distance movements of short duration were more frequent in the spring for male alligators and were probably a function of increased temperatures and the ongoing breeding season.

Movements of Everglades alligators were greater in the winter than in more northern areas. Alligators in Louisiana remained in holes or dens during the winter in a state of semi-torpor (McIlhenny, 1935). Alligators in the Everglades face warmer fall and winter temperatures than those in more northern areas. This resulted in greater daily movement for the fall and winter months. Everglades alligators were found to be quite active during the fall. Temperatures in the fall were comparable to spring temperatures and thus favored regular movements.

Increased movements and home range size can be attributed to increased reproductive activity as alligators expend tremendous amounts of energy in the pursuit of

reproductive opportunities. Adult alligators, particularly males, had larger home ranges, activity ranges, and moved more on a daily basis during the spring breeding season.

Both male and female alligators had the greatest mean daily movement during the breeding season. Male alligators moved throughout their home ranges during the breeding season visiting 7 or more hole habitat types, presumably in the search for females. Females moved more on a daily basis during the breeding season, but remained within their preferred core areas. Therefore, mating opportunities were more dependent on male movements.

The breeding season for alligators takes place in April and May and adults of both sexes move much more during that period (Chabreck, 1965). Increased home range sizes have been found to coincide with the alligator's spring breeding season in other studies (Joanen and McNease, 1970; Joanen and McNease, 1972; Goodwin and Marion, 1979; [Table 3-6](#)). Adult females were found to move the most during the breeding season in the Rockefeller Refuge, Louisiana (Joanen and McNease, 1970) and Lacassine National Wildlife Refuge, Louisiana (Rootes and Chabreck, 1993). Adult female alligators located in Clear-Smithport Lake, Louisiana and male alligators located in Rockefeller Refuge, Louisiana moved more during the spring breeding season than during the fall or winter, however, the movements were less than those observed during the summer ([Table 3-6](#)). Male alligator spring activity areas were longer than in any other season. This long linear activity area was evidence of the wandering nature of males during their search for breeding opportunities. For example, male 54917 (ENP) moved from hole to hole in the slough during the breeding season and occupied more than 7 holes within a week. This male was found to use only 3 of the 7 holes during the summer. Females apparently

utilized several of the holes as 2 of the holes were found to have nests and hatchling alligators were heard vocalizing from another.

In the Lacassine National Wildlife Refuge in Cameron Parish, southwestern Louisiana, no differences were found between nesting and non-nesting females in either mean home range size or daily movement during the summer nesting season suggesting that nesting status and the presence of a previous year's brood did not restrict the movement of adult female alligators (Rootes and Chabreck, 1993). However, in the Everglades, adult female alligators were affected by reproductive efforts more so during the nesting season than the breeding season. Nesting females were found to have smaller home ranges and decreased daily movements as compared to non-nesting females (Morea 1999). Once females constructed a nest, they were found to remain at or near the nest site in small guard pools, caves, and holes or in the marsh near their nests. For example, female 54942 (ENP) had a large hole at the south end of a small tree island located in the slough and a smaller secondary hole located in thick sawgrass approximately 100 m northwest of the larger hole. This female repeatedly moved from her large primary hole to her smaller secondary hole during the fall, winter, and spring seasons. She then nested on a small tree island located approximately 60 m west-southwest of her large primary hole and spent the majority of her time in the spike rush slough within 15 m of the nest. Her regular movements were altered and constricted by her nesting effort.

Excluding long distance bursts of movement; canal alligators moved less and had smaller activity areas than marsh alligators. Marsh alligators had 3 times larger activity areas than canal alligators. This exemplifies the problems with home range calculations. At a coarse scale, canal alligators had a larger home range, but at a finer scale, marsh

alligators had a larger activity area. This suggests that on a daily basis canal alligators were able to meet their needs in a smaller area than marsh alligators.

In the marsh, prime habitat types were often separated by less desirable alligator habitats. This forced alligators to traverse several hundred meters or more of less desirable habitat to reach preferred areas of the marsh. Movements between preferred habitats, food availability, and lack of basking sites could explain the larger activity areas for marsh alligators.

Alligator movement increases with increased water level (Chabreck, 1965). Oliver (1935) stated that alligators sometimes exhibited seasonal movement associated with changes in water levels and would move from drying holes to deep water. In the Everglades, water levels fluctuate between the wet season (summer/fall) and the dry season (winter/spring). Water levels in the Everglades marshes and sloughs begin to lower during the winter and reach their lowest levels during the spring and early summer (Fig. 3-4). Fish and other aquatic prey species were observed in greater concentrations in holes and depression potholes throughout the marsh during the dry season (Loftus and Kushlan, 1987; Kushlan, 1974). The naturally occurring drydowns and the resultant congregation of aquatic prey provided a plentiful energy source for both male and female alligators just prior to the rigorous spring breeding season. However, prolonged drought periods stress alligators and can result in alligator die-offs.

In WCA during the 1997-1998 dry season, standing water was only found in alligator holes, deep depression potholes, and airboat trails. During this time, marsh alligator movement was restricted to a hole or from hole to hole. When marshes are flooded as a result of rainfall, alligator movement increases (Chabreck, 1965). Although

alligators can survive on dry ground, they prefer to be in deep water and travel considerable distances to find it during exceptionally dry periods (Chabreck, 1965). Alligator daily movement in canals was not heavily impacted during the dry season as canals were always at or near their water holding capacity. During the dry season an influx of alligators from the surrounding marsh became apparent as 30 to 40 alligators could be found basking on a single levee break. Hines et al. (1968) found that water level fluctuation affected the movement of alligators in WCA and that during dry periods juveniles and adult males moved into canals from the bordering marsh. During times of high water levels, canal alligators were more likely to travel into the marsh. Alligator movements between canal and surrounding marsh habitats were most often limited to a few hundred meters and rarely exceeded a kilometer. Therefore, it is unlikely that canals attract alligators from interior marshes during periods of normal rainfall. However, movements between marsh and canal habitats may vary during periods of abnormal rainfall.

Conclusions

Alligator daily movement was affected by gender, temperature, reproductive efforts, habitat, and water level. Alligator daily movements generally increased with increasing temperatures. Excessively hot temperatures in summer appeared to limit movements and resulted in smaller home ranges than in the spring. Female alligators remained within their preferred core areas throughout the year and female marsh alligators did not seek deep open water for breeding purposes. Females with a recently

hatched pod remained at the nest site and eventually sought preferred habitats (i.e., potholes, holes, low mixed marsh, etc.), which were usually near the nest site.

Everglades alligators are adapted to a naturally fluctuating hydrology. Decreasing water levels pool aquatic prey allowing alligators to have a more abundant food supply available to them during the dry season. This increased food supply probably allows alligators to build up energy reserves and prepare for increased movements and energy requirements needed during the spring breeding season and would provide valuable nutrients for potential nesting females. The spring breeding season and the summer nesting season were the most critical for adult male and female alligators respectively. Male alligators had greater movements and larger activity areas during the breeding season and females moved least and had smaller activity ranges during the nesting season.

Temperature greatly affected alligator movements in the Everglades. Mean daily movement was least in winter for adult males and second least for females (the least movement for females occurred during the summer nesting season). Cool temperatures restricted most movements to the warmer daylight hours or to dawn and dusk periods. As temperatures increase so do alligator movements. However, extreme hot conditions forced alligators to move less and confined most movements to the cooler evening hours.

The breeding season acted as a catalyst by increasing daily movements and activity areas in the spring. After the breeding season, alligator movement decreased as nesting efforts and thermoregulation appeared to dominate summer movements of female and male alligators respectively.

Table 3-1. Annual and seasonal 24-hour linear movement for radio-tagged American alligators located in Water Conservation Area 3A North estimated from week-long intensive samples conducted during each season from 7 November 1997 to 31 July 1998.

Alligator	Gender	Habitat	Annual (m/24hr)	Fall (m/24hr)	Winter (m/24hr)	Spring (m/24hr)	Summer (m/24hr)
54751	Female	Canal	.	.	23.52	.	.
54763	Female	Canal	87.26	108.48	66.96	133.44	28.32
54935	Female	Canal	.	81.12	32.88	124.08	.
54735	Female	Marsh	75.86	132.96	61.92	85.68	19.44
54915	Female	Marsh	47.38	51.60	46.08	82.32	16.08
55037	Female	Marsh	61.30	131.76	71.76	58.32	12.00
54752	Male	Canal	.	.	130.56	.	.
54767	Male	Canal	.	.	.	.	23.04
54919	Male	Canal	.	210.72	14.64	.	.
54924	Male	Canal	.	.	.	474.96	38.64
54955	Male	Canal	.	.	.	455.04	.
54996	Male	Canal	.	.	.	693.60	.
55029	Male	Canal	.	42.00	120.24	.	52.80
54742	Male	Marsh	111.62	186.72	11.76	145.20	91.44
55004	Male	Marsh	164.62	138.00	117.60	168.24	230.88
54746	Male	Marsh	.	.	126.72	435.12	408.96
Mean			91.34	120.37	68.72	259.64	92.16
SD			42.12	56.70	45.02	214.86	129.26
SE			17.20	18.90	13.00	64.78	10.86

Table 3-2. Annual and seasonal 24-hour linear movement for radio-tagged American alligators located in Everglades National Park estimated from week-long intensive samples conducted during each season from 7 November 1997 to 31 July 1998.

Alligator	Gender	Habitat	Annual (m/24hr)	Fall (m/24hr)	Winter (m/24hr)	Spring (m/24hr)	Summer (m/24hr)
54936	Female	Canal	.	61.68	14.40	12.48	.
55016	Female	Canal	36.21	73.44	40.56	28.08	7.20
54770	Female	Marsh	.	57.60	48.72	.	.
54942	Female	Marsh	112.77	84.00	122.40	155.04	82.80
55000	Female	Marsh	69.56	73.44	32.40	143.04	21.60
54744	Male	Canal	.	.	.	1410.24 ^a	83.28
54750	Male	Canal	216.31	89.52	82.08	427.92	238.08
54983	Male	Canal	164.80	141.12	259.68	55.44	205.20
54991	Male	Canal	.	.	58.80	120.96	1474.56 ^a
55011	Male	Canal	.	110.64	136.32	.	.
55544	Male	Canal	.	189.12	.	.	.
54768	Male	Marsh	130.30	188.88	59.76	145.44	132.24
54772	Male	Marsh	215.50	241.92	135.84	322.80	164.40
54917	Male	Marsh	.	.	.	424.56	252.00
55022	Male	Marsh	.	.	47.76	.	.
Mean			121.88	119.21	86.56	183.58	131.87
SD			73.94	62.26	68.00	154.51	89.87
SE			26.14	18.77	19.63	48.86	29.96

^a Daily movement estimate was excluded from the mean.

Table 3-3. Mean annual and seasonal linear movement for radio-tagged alligators located in Water Conservation Area 3A North and Everglades National Park combined. Linear movements were estimated from weeklong intensive samples conducted during each season from 7 November 1997 to 31 July 1998.

Comparison		<u>Linear Movement (m/24-hr)</u>						<u>Linear Movement (m/24-hr)</u>			
		Season	Pooled	Marsh	Canal			Season	Pooled	Marsh	Canal
Gender	Male	Year	167.19 ^a	155.51 ^a	190.56 ^A	Female	Year	70.05 ^b	73.37 ^b	61.74 ^B	
		Fall	153.86 ^a	188.88 ^a	130.52		Fall	85.61 ^b	88.56 ^b	81.18	
		Winter	100.14 ^a	83.24	114.62 ^a		Winter	51.05 ^b	63.88	35.66 ^b	
		Spring	406.12 ^a	273.56 ^a	519.74 ^A		Spring	91.39 ^b	104.88 ^b	74.52 ^B	
		Summer	261.19	213.32 ^a	302.23		Summer	26.78	30.38 ^b	17.76	
Habitat	Marsh	Year	109.88			Canal	Year	126.15			
		Fall	128.69				Fall	110.78			
		Winter	73.56				Winter	81.72			
		Spring	196.89				Spring	357.84			
		Summer	130.17				Summer	239.01			

¹ Means with different lower case letters were significantly different ($p < 0.05$).

² Means with different upper case letters were significantly different ($p < 0.10$).

Table 3-4. Mean seasonal activity area estimates for radio-tagged American alligators located in Water Conservation Area 3A North and Everglades National Park estimated from 4 seasonal intensive weeklong samples conducted from 7 November 1997 to 31 July 1998. Activity ranges were determined by a 95% minimum convex polygon model.

	Season	<u>Gender</u>		<u>Habitat</u>	
		Female	Male	Marsh	Canal
Activity Range (ha)	Fall	0.57 ^a	3.03 ^b	2.67 ^A	0.93 ^B
	Winter	0.25	0.60	0.65 ^A	0.22 ^B
	Spring	0.48	7.90	5.38	4.35
	Summer	0.06	4.87	1.68	0.62
Range Length (m)	Fall	170.69 ^a	383.74 ^b	306.53	247.90
	Winter	121.06 ^A	209.33 ^B	193.10	144.65
	Spring	200.02 ^A	1407.47 ^B	567.26	1259.77
	Summer	53.94 ^a	574.13 ^b	403.73	377.81
Range Width (m)	Fall	28.37 ^a	69.81 ^b	66.94 ^A	31.24 ^B
	Winter	17.62	21.14	26.38 ^a	12.68 ^b
	Spring	21.81	51.66	62.24 ^a	16.65 ^b
	Summer	9.46	48.82	31.50	16.46
Fix Dispersion (m)	Fall	44.89 ^a	107.65 ^b	91.38	61.17
	Winter	33.64 ^A	55.24 ^B	50.10	40.59
	Spring	48.62 ^A	309.42 ^B	164.92	240.54
	Summer	13.81 ^a	128.31 ^b	88.66	87.72

Table 3-5. Mean annual and seasonal activity range estimates for radio-tagged American alligators located in Water Conservation Area 3A North and Everglades National Park estimated from 4 seasonal intensive weeklong samples conducted from 7 November 1997 to 31 July 1998.

Comparison		95% Ak (ha)	95% MCP (ha)	Range length (m)	Range width (m)	Fix Dispersion (m)
Area	ENP	2.89 ^a	4.57 ^a	504.98	80.67	117.23
	WCA	6.74	8.83	616.66	126.32	145.30
Gender	Male	7.87 ^a	12.06 ^a	787.01	150.77	166.48
	Female	2.63	2.88	399.25	69.73	106.10
Habitat	Marsh	5.98 ^a	8.99 ^a	546.79	135.68	139.98
	Canal	2.47	2.13	588.87	39.12	113.83
Season	Year	4.81 ^a	6.70 ^a	560.82	103.50	131.26
	Fall	1.96	1.80	277.22	49.09	76.27
	Winter	0.41	0.44	168.87	19.53	45.34
	Spring	4.45	4.86	874.30	37.99	194.08
	Summer	1.68	1.20	374.37	23.65	84.40

^a Alligator 54768 was excluded due to its large home range size.

Table 3-6. Mean daily movements (m/24-hr) for radio-tagged adult (> 183 cm) radio-tagged alligators located in the Rockefeller Refuge, Louisiana, a cypress lake in Louisiana, and the Everglades (this study).

Season	Immature (< 183 cm) Rockefeller Refuge ¹	Female Clear- Smithport Lake ²	Male Rockefeller Refuge ³	Female Everglades ⁴	Male Everglades ⁴
Fall	205	3	587	86	154
Winter	139	1	0	51	100
Spring	303	27	763	91	406
Summer	281	46	855	27	261

¹McNease and Joanen, 1974.

²Taylor, 1984.

³Joanen and McNease 1972.

⁴This study.

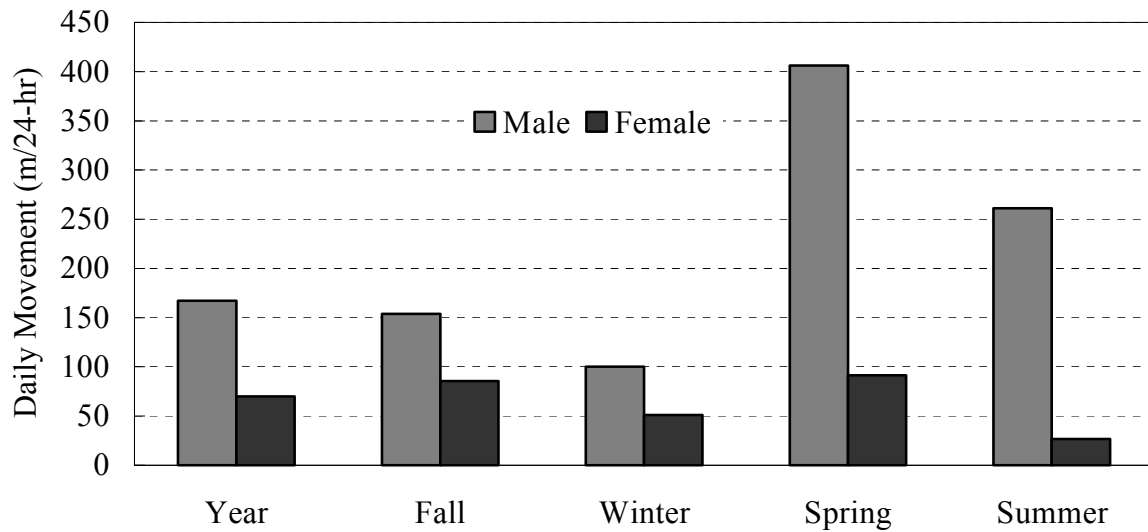


Figure 3-1. Mean annual and seasonal daily movement of radio-tagged male and female alligators located in Water Conservation Area 3A North and Everglades National Park estimated from 4 seasonal intensive weeklong samples conducted from 7 November 1997 to 31 July 1998.

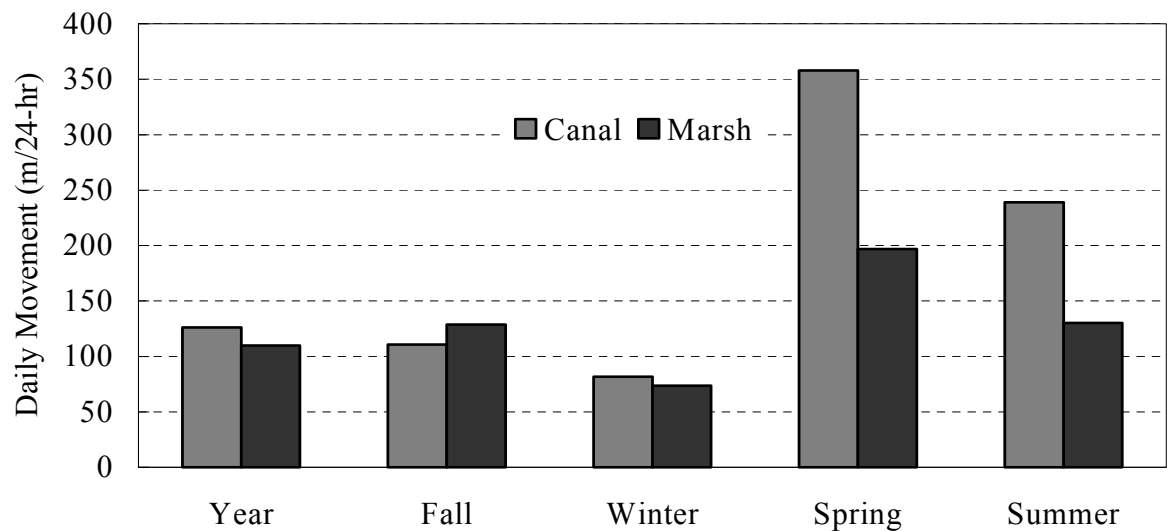


Figure 3-2. Mean annual and seasonal daily movement of radio-tagged canal and marsh alligators located in Water Conservation Area 3A North and Everglades National Park estimated from 4 seasonal intensive weeklong samples conducted from 7 November 1997 to 31 July 1998.

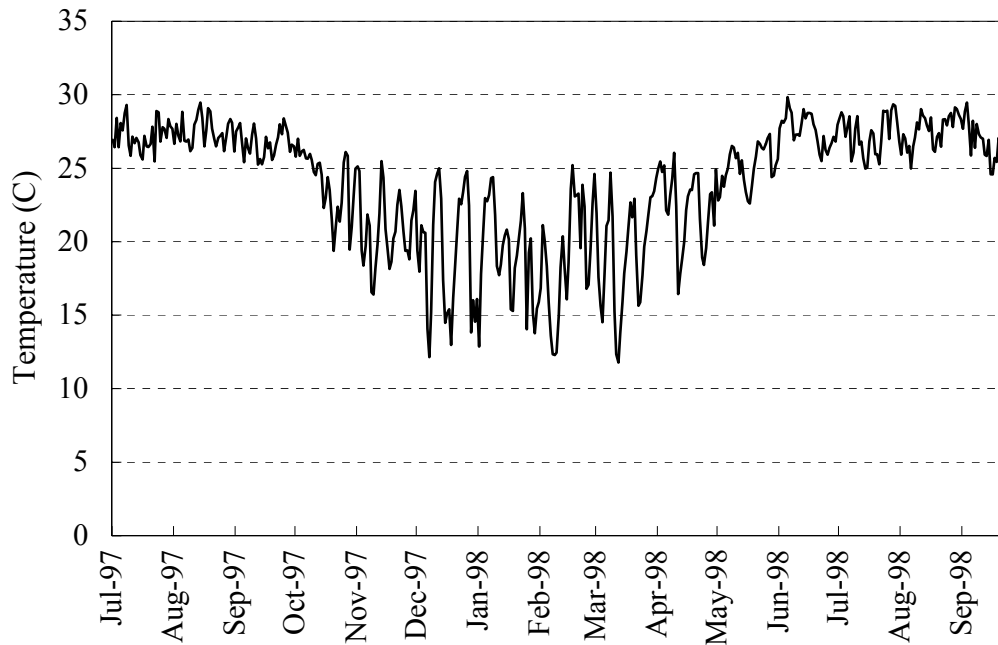


Figure 3-3. Mean daily air temperature (°C) for the Everglades region of southern Florida from 1 July 1997 to 21 September 1998. (Source: South Florida Water Management District).

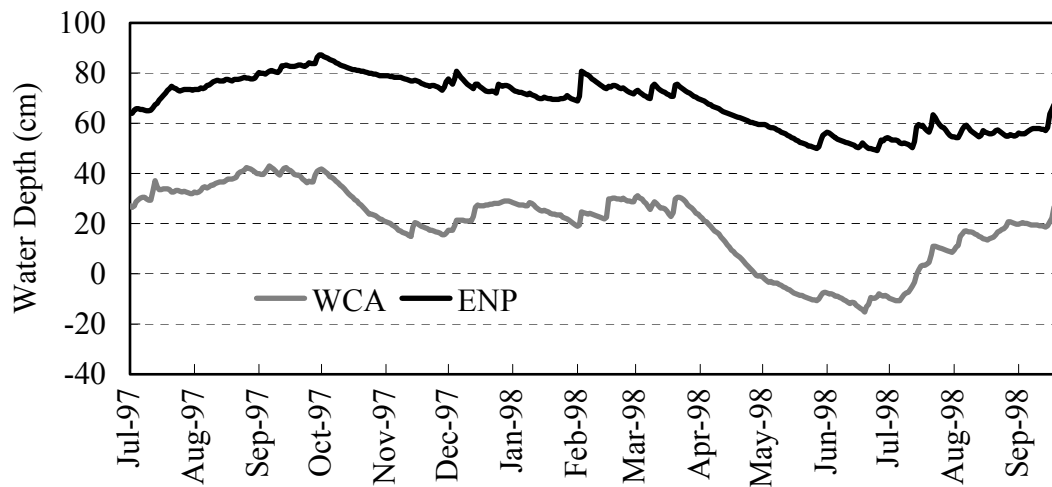


Figure 3-4. Daily water depth (cm) for Water Conservation Area 3A North (WCA) and Everglades National Park (ENP) from 1 July 1997 to 21 September 1998. (Source: South Florida Water Management District and Everglades National Park).

CHAPTER 4

HABITAT USE

Cory R. Morea, H. Franklin Percival, Kenneth G. Rice, Stanley R. Howarter,
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The Everglades, covering an area of about 6,300 square km, is the lower segment of a huge, naturally integrated drainage system of about 15,000 square km (Parker, 1974). Water flow is the major factor controlling the trophic dynamics of the Everglades (ATLSS, 1999). The natural hydrology of the area was altered beginning in 1882 with the construction of levees and canals (Douglas, 1994). These structures allowed the northern portions of the Everglades to be drained and converted to agriculture (primarily sugarcane) and the eastern portions for urban development. Remaining marsh and slough habitats are heavily influenced by the presence of levees and canals. Everglades restoration has been mandated by Congress and comprehensive modeling of biotic and abiotic attributes have been undertaken to compare restoration alternatives (USACE, 1999). A multi-component modeling effort of the Everglades, Across Trophic Levels System Simulation (ATLSS), is being developed to predict the future effects of alternative hydrologic scenarios on the biotic components of the systems (ATLSS, 1999). Due to the varying scales at which trophic interactions occur, and the importance of population structure and individual behavior for population prediction in higher trophic level organisms, use of a single modeling approach is not appropriate (ATLSS, 1999). The alligator's role in the trophic dynamics of the Everglades is significant and will be an integral component of the ATLSS models.

Habitat use of alligators has been studied in Louisiana (Joanen and McNease, 1970; Joanen and McNease, 1972; McNease and Joanen, 1974; Taylor, 1984; Rootes and Chabreck, 1993), South Carolina (Murphy, 1977), and Florida (Goodwin and Marion, 1979). Male alligators have been shown to use open water habitats more than females (Joanen and McNease, 1970; Joanen and McNease, 1972; Goodwin and Marion, 1979). Male and female alligators often have a centrally located hole or den, which pool water and provide thermal refugia (McIlhenny, 1935; Hines et al., 1968; Chabreck, 1965; Joanen and McNease, 1970; Joanen and McNease, 1972). Murphy (1977) found that alligators tended to use the vegetated portions of a lake in South Carolina more than the open water portions.

Beyond the fact that alligators are known to show a high affinity for holes and other open water patches in the Everglades, little is known of how alligators use marsh and canal habitats. Site-specific habitat use information is needed for Everglades alligators to be incorporated into the ATLSS modeling effort and to help guide management decisions and restoration alternatives.

Objectives

The objectives of this study were: (1) to determine habitat use for Everglades alligators in Water Conservation Area 3A North (WCA), and Everglades National Park (ENP); and (2) to test for habitat preferences.

Methods

Habitat Categories

Ten habitat types were identified as potentially available for alligators located in WCA and ENP. The habitats were: (1) open water with little or no floating or emergent vegetation (“open water”); (2) tropical hardwood hammocks, South Florida bayheads, and dwarf cypress prairies (*Taxodium* sp.) (“forested wetlands”); (3) flooded cold-deciduous shrublands and shrub islands (“shrub”), usually dominated by buttonbush (*Cephalanthus occidentalis*); (4) graminoid emergent marsh compositional group, muhly grass (*Muhlenbergia capillaris*), and forb emergents (“low mixed marsh”); (5) sawgrass; (6) spike rush (*Eleocharis cellulosa*); (7) cattail (*Typha* spp.) marsh compositional group (“cattail”); (8) water lily and floating leafed vegetation (“water lily”); (9) canal; (10) alligator holes (“hole”).

Habitat Use

Habitat use was estimated from 4 weeklong intensive tracking samples conducted once during the fall, winter, spring, and summer from 7 November 1997 to 31 July 1998 in WCA and ENP (See Chapter 2 methods for Daily Movement). Three distinct groups of alligators were identified according to habitat availability: (1) canal animals located in WCA and ENP (alligators that were captured and spent the majority of their time associated with canals); (2) marsh animals located in WCA (alligators captured within the shallow sawgrass marshes of WCA); and (3) slough animals located in ENP (alligators captured within Shark River Slough, ENP).

Habitat selection was considered from observed habitat use within the home range (detailed view of resource use; Johnson's third-order selection; Aebischer, 1993), wherein each animal's movements determined habitats available to them (Staus, 1998). To include all habitats available to each alligator, 100% minimum convex polygon (MCP; Mohr, 1947) home ranges were constructed using Ranges V (See Chapter 2 methods for Home Range; Institute of Terrestrial Ecology, Wareham, United Kingdom). Any of the previously described 10 habitat types were considered available habitats to each individual alligator.

Area coverage estimates of each habitat type located within an alligator's home range were determined using a geographic information system (GIS; ERDAS Imagine Version 8.3.1, ERDAS Inc.). An annotation layer was created from a comprehensive habitat coverage of South Florida using an alligator's 100% MCP. The comprehensive coverage of South Florida was created using the GAP coverage (National Gap Analysis Project; USGS/BRD) of South Florida and integrating canal coverages developed by the South Florida Water Management District and Everglades National Park. Areas of each habitat type (habitats 1 to 10) located in MCPs were summed for each alligator group and divided by the total area encompassed in those group home ranges to give the proportion of habitat (habitats 1 to 10) available for that group of alligators. Alligator holes were not included in the integrated habitat coverage of South Florida. For analysis, the proportion of holes available to each animal was set to 0.0004. This estimate was determined by overlaying an alligator home range coverage (See Chapter 2) onto an alligator hole coverage of WCA (Campbell, 1999). Holes were buffered 5 m to represent the average area of a hole (Campbell, personal communication), and the total area of hole habitat

located within individual alligator home ranges were averaged. A habitat type (1 to 10) was assigned to each radio-location obtained during the weeklong intensive field missions (See Chapter 2 methods) to determine proportional habitat use for each alligator. Habitat use was tested for each group of alligators to determine habitat preferences using a compositional analysis (Aebischer et al., 1993).

Results

All Alligators

Habitats used more than their availability would suggest were low mixed marsh, spike rush, cattail, canal, and hole ([Fig.4-1](#)). Third-order selection of habitat for all radio-tagged alligators ranked: canal > spike rush > cattail > hole > sawgrass > water lily > mixed marsh > open water > shrub ([Table 4-1](#)). There was no difference in preference of canal, spike rush, cattail, and holes ($n = 31$; $P = 0.074$ to 0.629), but canal was significantly preferred to sawgrass, water lily, mixed marsh, open water, and shrub ($P = 0.001$ to 0.012). Spike rush was preferred to sawgrass, mixed marsh, open water, and shrub ($P = 0.001$ to 0.020). Cattail habitats were preferred to sawgrass, open water, and shrub ($P = 0.001$ to 0.037). Hole and sawgrass habitats were preferred to shrub ($P = 0.001$ to 0.005). No alligator radio-locations were recorded in forested wetlands.

WCA Marsh Alligators

Radio-tagged marsh alligators located in WCA used cattail, water lily, mixed marsh potholes, and holes more than their availability would suggest ([Fig.4-2](#)). Sawgrass was used less than its availability would suggest. WCA alligators were located in sawgrass 36 % of the locations, mixed marsh potholes 28 %, cattail depressions 16 %, water lily potholes 10 %, holes 7 %, and open water 1 %. Third-order selection of habitat for radio-tagged alligators located in the marsh of WCA ranked: cattail > water lily > sawgrass > open water > mixed marsh > hole. Cattail habitats were preferred to mixed marsh ($n = 7$; $P = 0.033$; [Table 4-1](#)). Forested wetlands, shrub, spike rush, and canal habitats were not utilized. These habitat types were not abundant within the home ranges of this group of radio-tagged alligators.

ENP Slough Alligators

ENP slough alligators used spike rush, holes, and shrub more than their availability would suggest ([Fig.4-3](#)). Sawgrass was used less than its availability would suggest. ENP alligators were located in holes 37 % of the locations, spike rush 27 %, sawgrass 24 %, and in shrub 10%. The remaining time was spent in low mixed marsh and cattail habitat types. Third-order selection of habitat for radio-tagged alligators located in the slough of ENP ranked: spike rush > hole > shrub > sawgrass > cattail > mixed marsh. Spike rush was significantly preferred to all other available habitats ($n = 7$; $p = 0.011$ to 0.033 ; [Table 4-1](#)). Hole and shrub habitats were preferred to mixed marsh habitats ($p = 0.018$ and $p = 0.016$ respectively). Forested wetlands, open water, water

lily, and canal habitats were not utilized. Alligators were often located near forested wetlands in holes or in vegetation; however, no alligators were located within the interior portions of forested wetlands. Open water and water lily habitat types were not abundant within the home ranges of this group of radio-tagged alligators. The canal habitat type was absent from the home ranges of all radio-tagged alligators located in Shark River Slough.

Canal Alligators

For canal alligators located in WCA and ENP, habitats used more than their availability would suggest were canal and hole ([Fig.4-4](#)). This group of alligators was located in canals during 83 % of the locations. On occasion, canal alligators, particularly females, moved from the canal and into the surrounding marsh. Canal alligators spent nearly 10 % of their time in marsh holes. Five percent of the locations were recorded in sawgrass with the majority of these locations recorded for nesting females. Third-order selection of habitat for radio-tagged canal alligators ranked: canal > spike rush > hole > cattail > mixed marsh > sawgrass > shrub ([Table 4-1](#)). Canals were preferred to all other available habitats ($n = 17$; $p = 0.001$). Spike rush was preferred to sawgrass and shrub ($p = 0.001$ to 0.021). Holes were preferred to shrub ($p = 0.001$). Cattail habitats were preferred to sawgrass and shrub ($p = 0.001$ to 0.050). Mixed marsh and sawgrass habitats were preferred to shrub ($p = 0.005$ and $p = 0.038$ respectively).

Discussion

Three distinct groups of alligators were studied: marsh alligators in WCA; slough alligators in ENP; and canal alligators located in WCA and ENP. Habitat use and preferences varied among these groups.

Marsh Alligators

The marsh of WCA was dominated by sawgrass with few tree islands and a shorter hydroperiod than the deeper sloughs. Potholes were used more by radio-tagged alligators in WCA than would be expected from their availability. Potholes were naturally occurring depressions in the marsh that were as small as 1 m² and 10 to 40 cm deeper than the surrounding sawgrass marsh. Three distinct pothole types were common: low mixed marsh; cattail; and water lily. Pothole habitat types typically contained duck potato (*Sagittaria lancifolia*), arrowhead (*Sagittaria latifolia*), maidencane (*Panicum hemitomon*), pickerel weed (*Pontederia cordata*), cattail (*Typha latifolia* and *Typha domingensis*), white water-lily (*Nymphaea odorata*), swamp-lily (*Crinum americanum*), and bladderwort (*Utricularia foliosa*). The potholes were more open than the surrounding sawgrass marsh and retained water for longer periods. Classic gator holes were deeper and more open (often clear of vegetation). These holes usually had 1 or more caves that extended laterally in the peat layer. When holes were used in WCA, they tended to be smaller in size than the larger gator holes that were more frequent in ENP (personal observation). Radio-tagged marsh alligators in WCA had several favored potholes in which they were located in often. For example, male alligator 55004 (WCA) was regularly located in various potholes within his home range. This male often

traversed several hundred meters along an airboat trail or through the marsh during an evening and would settle in a pothole before dawn. The majority of these movements between potholes were initiated just after dusk. This male had a single classic gator hole that he used on occasion. Classic gator holes were used when available; however, potholes and wet prairies were more abundant in WCA.

Alligators in WCA were located in sawgrass more than any other habitat type. However, sawgrass was used less than its availability would suggest by radio-tagged alligators throughout the year except by nesting females suggesting that alligators avoided thick sawgrass habitats. Sawgrass tended to form thick monocultures that impeded alligator movements, however, thick sawgrass habitats offered cover and nest material and appeared to be the preferred nesting habitat available.

Slough Alligators

The Shark River Slough region of ENP was comprised of a mosaic of spike rush, sawgrass, shrub islands, and tree islands with occasional patches of low mixed marsh, cattail, water lily, and open water. Gator holes were frequent throughout the slough. Radio-tagged alligators located in the slough of ENP were located most often in classic gator holes and these holes were the preferred habitat type within Shark River Slough. Holes were more abundant, and overall more critical, to radio-tagged alligators in ENP than WCA. Holes provided a deep, open water habitat in the slough that provided thermal refugia (Howarter, 1999) and pooled aquatic prey during drydowns (Loftus and Kushlan, 1987). Alligators used several holes regularly and 50 m or more of spike rush or sawgrass habitat typically separated these holes. Radio-tagged alligators were often

located in spike rush habitats near their hole at night and would then be located within a hole the next morning. For example, female 54942 (ENP) had a large hole at the south end of a small tree island located in the slough and a smaller secondary hole located in thick sawgrass approximately 100 m northwest of the larger hole. This female repeatedly moved from her large primary hole to her smaller secondary hole and was often located in the spike rush habitat between the holes at night.

Shrub islands were preferred after spike rush and holes by radio-tagged alligators in ENP. Shrub islands were more abundant in ENP than WCA. Radio-tagged alligators in ENP were regularly located in shrub islands and appeared to seek refuge in these habitats to avoid extreme temperatures. Caves and or small holes were commonly associated with shrub islands.

Canal Alligators

Canals appeared structurally as long, deep alligator holes and offered prime habitat for adult alligators. The canal habitat type was the most preferred habitat available ([Table 4-1](#)). Canal alligators were most often associated with canal levee breaks in the Miami Canal (WCA), canal edges with cattail in the I-75 Canal (WCA), and canal edges with shrubs in the L-67 Canal extension (ENP). Levee breaks offered good basking sites and ambush zones for prey. Shrubs along the L-67 Canal extension offered shade and also offered prime ambush zones. Alligators tended to remain at or near the edges of the canals amongst emergent vegetation and shrubs or basking during the day and would move into the open waters of the canal at night. For example, male 54924 located in the Miami Canal (WCA) was most often found along a 100 m section basking

on the large levee that bordered the canal or in the same shallow marsh-like levee break during daylight and would move into the open waters of the canal at night. On occasion, this animal was found to move > 1 km south in the canal but would quickly return (i.e., within 24-hrs) to his preferred core area associated with the levee break.

During years of plentiful rainfall, canals did not act as a population sink for Everglades alligators. Alligator interactions between the canal and the surrounding marsh were limited to an area extending approximately 1 km on either side. These interactions between canal and marsh habitats may vary with extreme hydrologic conditions (i.e., severe droughts or floods).

Conclusions

Alligators located in WCA and ENP used habitats differently as available habitats varied between the two study areas. The large variation in the use of holes by alligators in ENP (40 %) and WCA (7 %) ([Figs.4-2 and 4-3](#)) was apparently due to the variation in the number of holes present within each area. As a general observation, more holes were present in ENP than in WCA, and as a result, depression potholes appeared to functionally replace classic gator holes when none were present.

Critical habitats were different for radio-tagged alligators located in marsh, slough, and canal habitats. Habitats critical for survival in the marsh of WCA were depression potholes dominated by mixed broad-leafed emergent vegetation, water lily, and cattail ([Fig.4-2](#)). Holes were critical but were less represented. Critical habitats for ENP slough alligators were: gator holes; shrub islands; and spike rush ([Fig.4-3](#)). Critical habitats for canal alligators were the canal proper and canal edges associated with levee

breaks, emergent vegetation, and shrubs. On occasion, canal alligators, particularly females, moved from the canal into the surrounding marsh. Canal alligators spent nearly 10 % of their time in marsh holes.

Open water habitats were not abundant within the marsh and slough of WCA and ENP respectively. Open water was typically found in gator holes, canals, and artificial ponds or borrow pits. As a result, few patches of open water habitat were available to radio-tagged marsh and slough alligators.

No radio-tagged alligators were located in forested wetlands while they were specifically being monitored for habitat utilization. However, during recapture efforts, alligators were found to use flooded tree islands as barriers against recapture. Many of the holes that alligators occupied were associated with tree islands and their importance as alligator habitat was probably underrepresented.

Spike rush appeared to be underestimated in the comprehensive habitat coverage for ENP and alligator use may have closely resembled its actual availability. However, radio-tagged alligators in ENP utilized spike rush habitats regularly. Spike rush habitats were typically deeper, more open, and were more easily traversed by alligators than the thicker sawgrass habitats.

Radio-tagged alligators did not heavily use areas of the marsh or slough that were dominated by tall, dense stands of cattail. Regular use of sparse cattail habitats was common. Cattails commonly formed a ring around the outside edges of small gator holes and occasionally formed plumes downstream of a hole. Cattail presence was probably due to the disturbance created by alligators and possible nutrient accumulation near gator

holes, however, cattail can also be an indicator of deeper water (F. Mazzotti, personal communication).

The Everglades are dependent upon a fluctuating hydrology for its structures and functions. Restoration efforts call for the conversion of some canal habitats back to marsh, including the Miami Canal in WCA and the L-67 Canal extension. Habitat use of canal alligators suggest that they prefer canals; however, can utilize the surrounding marsh. Two alligators captured in the Miami Canal moved several kilometers into the marsh and established home ranges from which they did not depart. These alligators utilized depressions and holes and their habitat use was similar to animals captured in the marsh.

Alligators are adapted to a naturally fluctuating hydrology. Restoration efforts should lead to the creation of a system that mimics a more natural hydrology and increases the area of favorable alligator habitat throughout the Everglades. This will help ensure that the alligator will persist in the Everglades and to continue its role in this dynamic ecosystem.

Table 4-1. Habitat preference rankings for radio-tagged alligators located in Water Conservation Area 3A North (WCA) and Everglades National Park (ENP). Rankings were determined by a compositional analysis (Aebischer, 1993).

Alligator Group	Habitat Rankings
All 3 rd Order	CANAL > SPIKE RUSH > CATTAIL > HOLE > SAWGRASS > WATER LILLY > MIXED MARSH > OPEN WATER > SHRUB > ^a forested wetlands
WCA Marsh 3 rd Order	CATTAIL > WATER LILLY > OPEN WATER > LOW MIXED MARSH > SAWGRASS > HOLE > ^a spike rush = ^a forested wetlands = ^a canal = ^a shrub
ENP Slough 3 rd Order	SPIKE RUSH > HOLE > SHRUB > SAWGRASS > CATTAIL > MIXED MARSH > ^a canal = ^a forested wetlands = ^a open water = ^a water lilly
All-Canal 3 rd Order	CANAL > SPIKE RUSH > HOLE > CATTAIL > MIXED MARSH > SAWGRASS > SHRUB > ^a water lilly = ^a open water = ^a forested wetlands

^a Signifies a habitat type was not used.

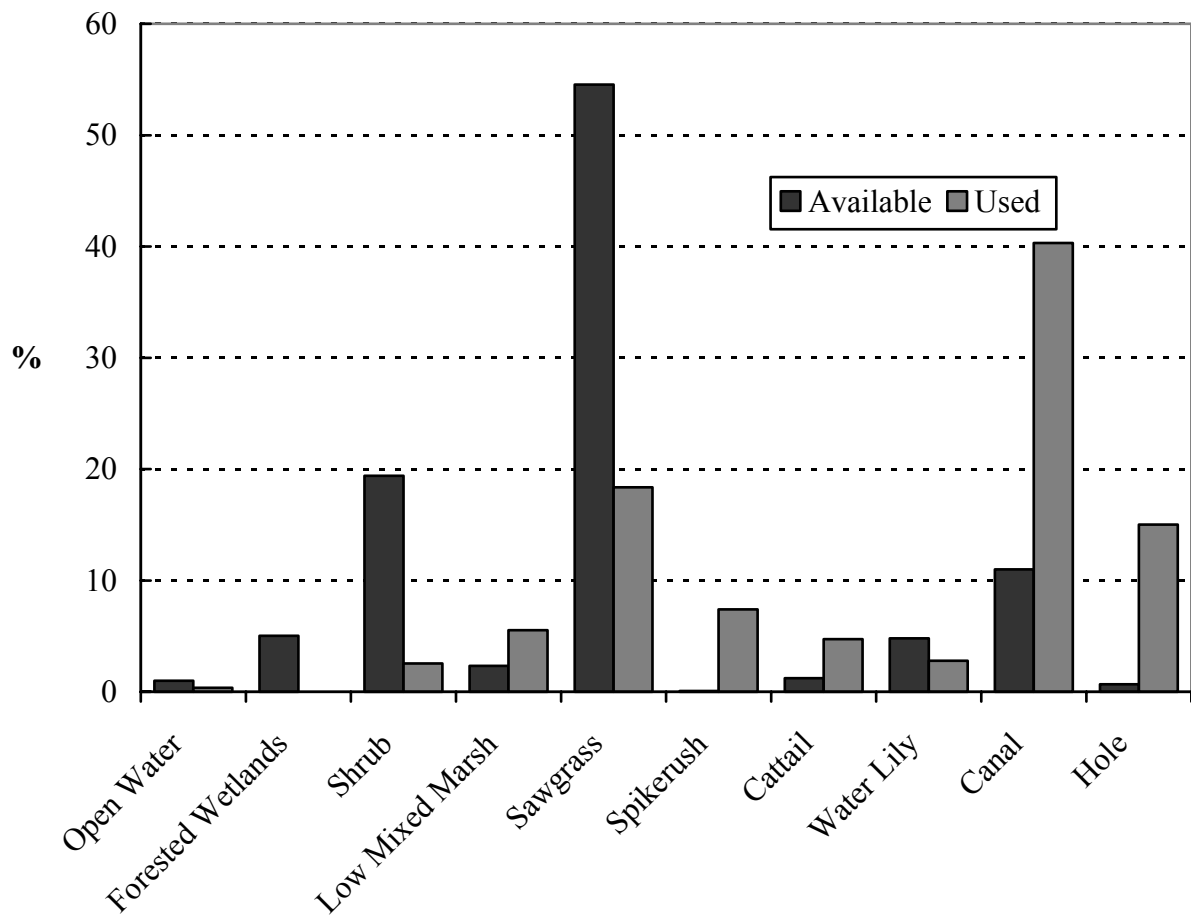


Figure 4-1. Habitat availability and use for all radio-tagged alligators located in Water Conservation Area 3A North and Everglades National Park from 1 July 1997 to 21 September 1998. Availability was determined from 100% minimum convex polygon home ranges and use was determined from radio-locations (n = 866).

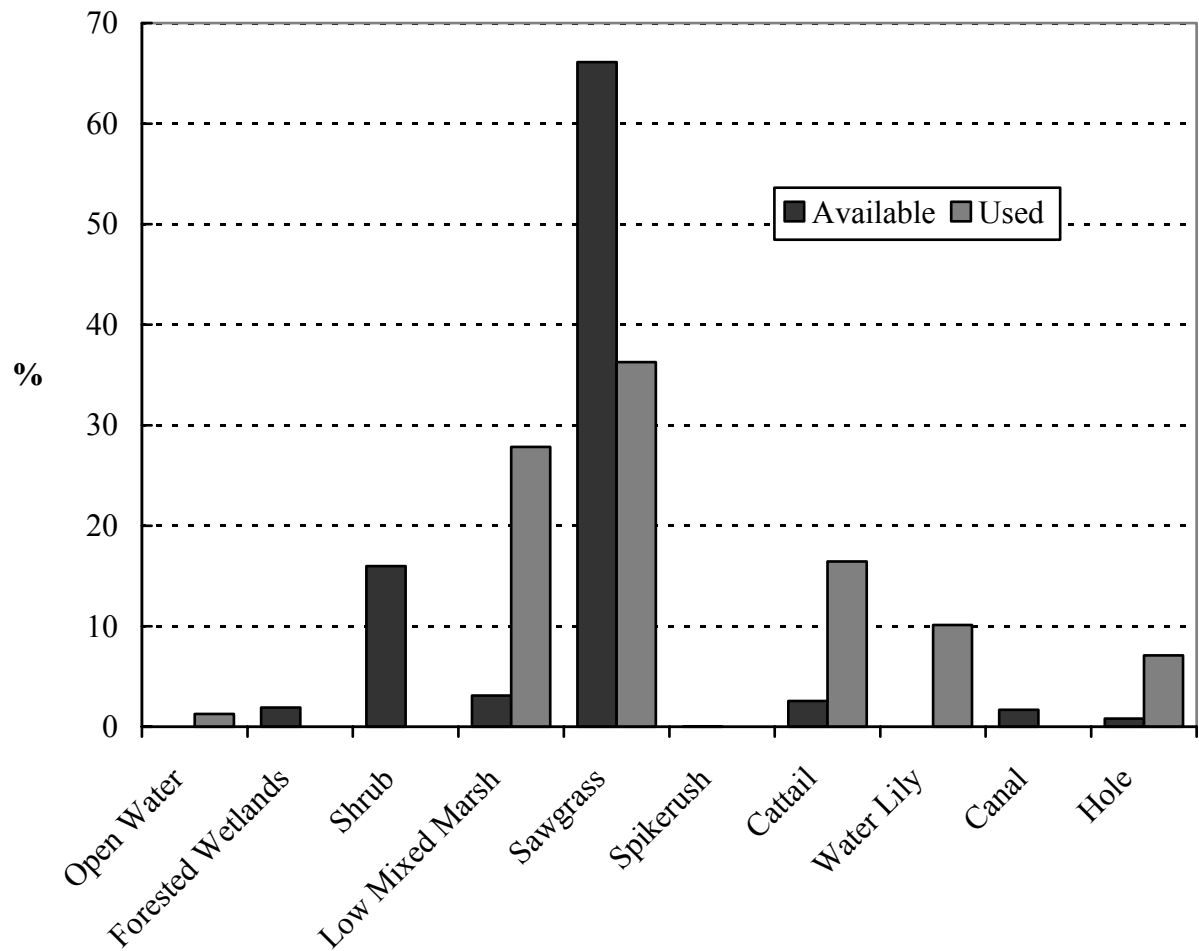


Figure 4-2. Habitat availability and use for alligators located in the marsh of Water Conservation Area 3A North from 1 July 1997 to 21 September 1998. Availability was determined from 100% minimum convex polygon home ranges and use was determined from radio-locations (n = 227).

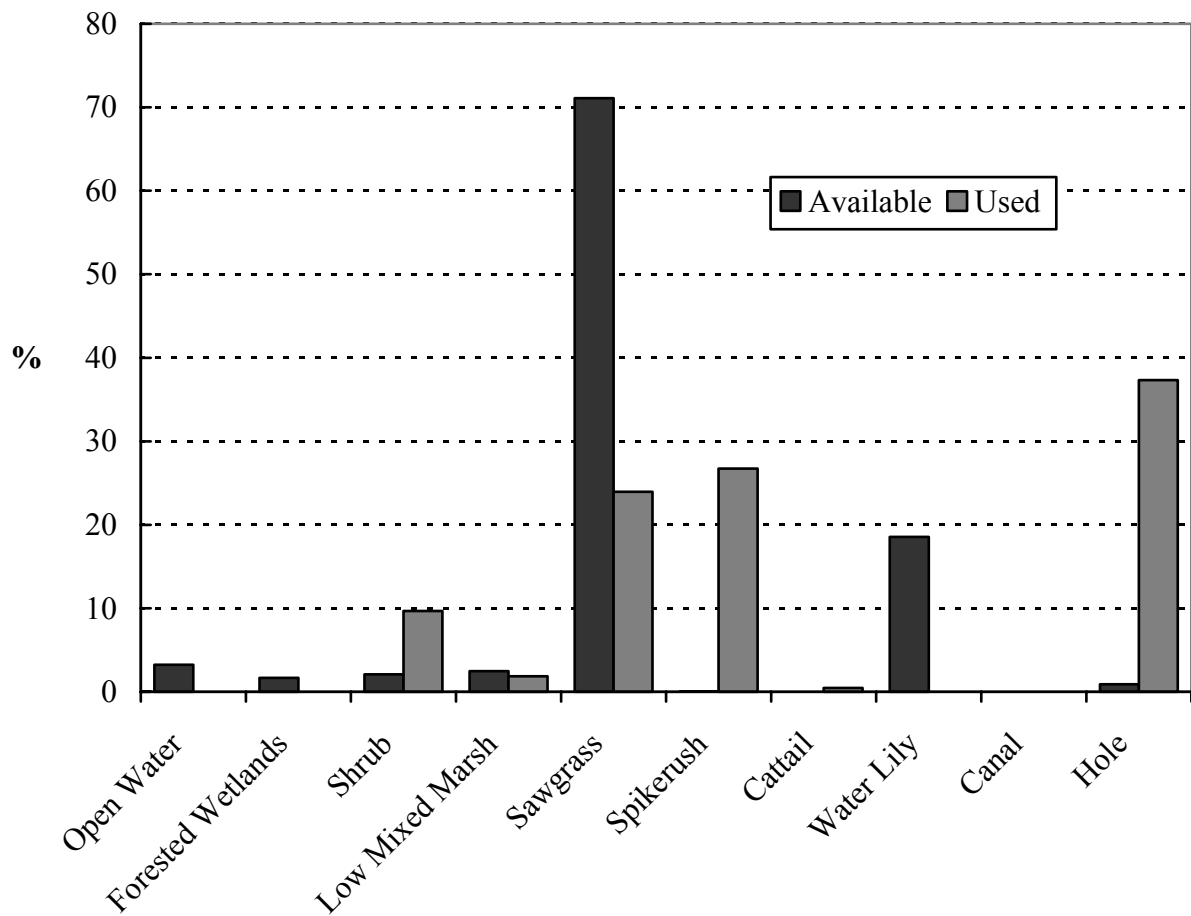


Figure 4-3. Habitat availability and use for radio-tagged alligators located in Shark River Slough of Everglades National Park from 1 July 1997 to 21 September 1998. Availability was determined from 100% minimum convex polygon home ranges and use was determined from radio-locations (n = 217).

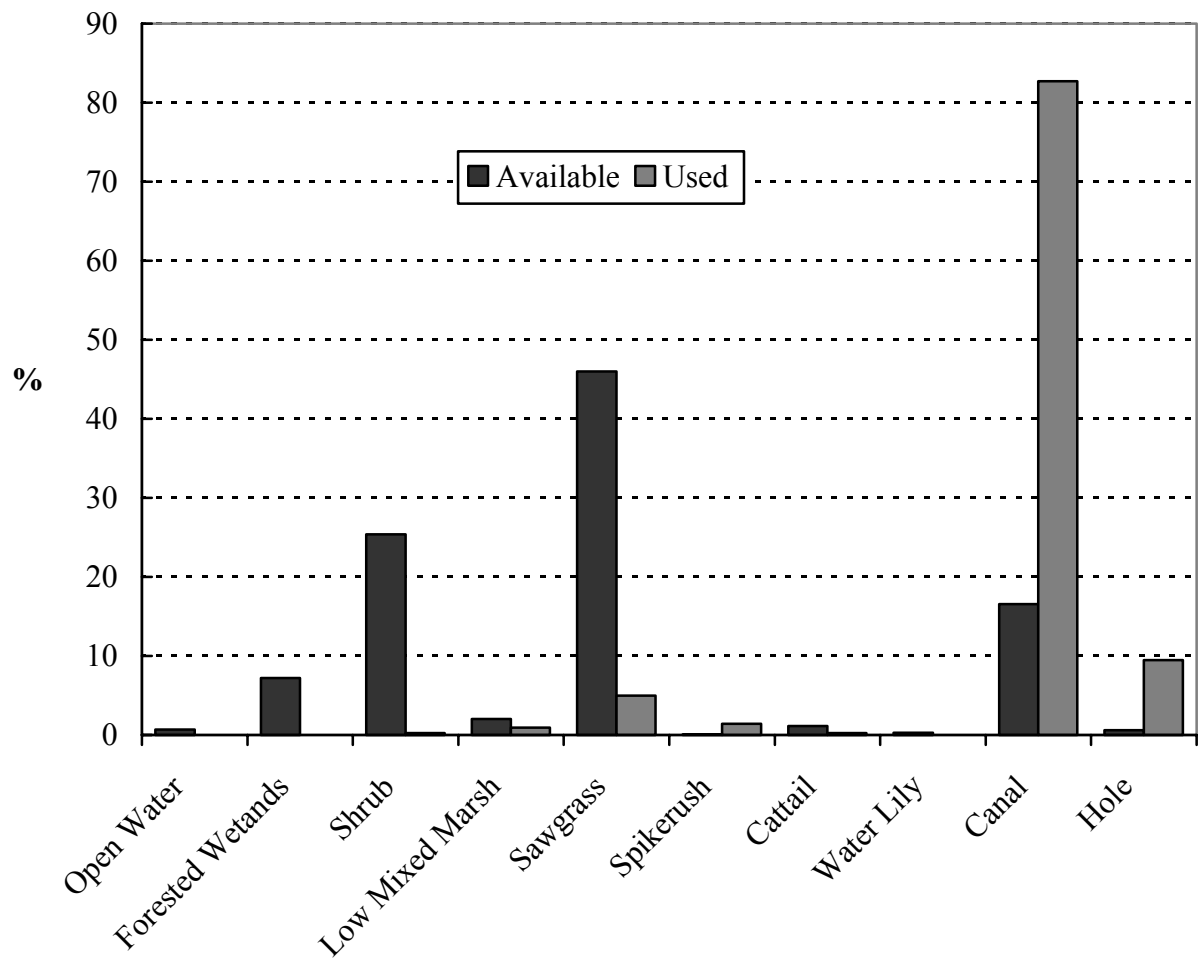


Figure 4-4. Habitat availability and use for canal alligators located in Water Conservation Area 3A North and Everglades National Park from 1 July 1997 to 21 September 1998. Availability was determined from 100% minimum convex polygon home ranges and use was determined from radio-locations (n = 422).

CHAPTER 5

ALLIGATOR THERMAL ECOLOGY IN THE EVERGLADES

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The Everglades of South Florida have been greatly altered within the last 100 years. Efforts currently are underway to restore the historic hydroperiod of the Everglades. The American alligator is a primarily temperate species whose range extends into the subtropical Everglades. In South Florida, alligators face ambient temperature patterns unlike elsewhere in their range. The consistently high temperatures lead to increased metabolic cost (Coulson and Hernandez, 1983; Lewis and Gatten, 1985). Examination of annual body temperature patterns of Everglades alligators across seasonal hydroperiods may reveal information about their physiology and ecology. By understanding the physiology and ecology of alligators and how changes in their environment may affect them, we are better able to manage the species and its habitat.

The Everglades is believed to be a harsh environment for alligators. Whereas the largest known alligators come from central Florida (Woodward et al., 1995), alligators from subtropical south Florida are much smaller and in poorer body condition indicating that they are from marginal habitat (Jacobsen and Kushlan, 1989; Dalrymple, 1996; Barr, 1997). Alligators in the Shark Slough region of the Everglades have reduced length to weight ratio (Jacobsen and Kushlan, 1989; Barr, 1997), reduced total length, and delayed onset of sexual maturity (Kushlan and Jacobsen, 1990; Dalrymple, 1996) compared with

other parts of their range. It is currently suspected that the reason for this poor condition is a combination of low food availability and very high temperatures (Jacobsen and Kushlan, 1989; Dalrymple, 1996; Barr, 1997).

When food is available, alligators seek high temperatures and may increase their metabolic rate three fold (Coulson and Hernandez, 1979; Lang, 1987). The result is a doubling of the rate of food absorption from a body temperature of 20° C to 28° C with no appreciable change in digestive efficiency (Coulson and Hernandez, 1983). Higher temperatures also promote faster protein assimilation and synthesis. By attaining higher temperatures after feeding, alligators can process their prey quickly, enabling them to acquire more food or devote attention to other behaviors (Lang, 1987).

Alligators are able to avoid the high maintenance cost of thermoregulation encountered by endotherms by allowing their body temperature to vary with their environment. Energy is conserved on both a seasonal and a daily basis. When high body temperature is desired, alligators use behavioral and physical adaptations to attain them from the environment. When they are not active, their metabolic rate is reduced, conserving energy for processes such as growth or reproduction (Lang, 1987).

Until the 1970's, data on body temperatures of wild crocodilians consisted of individual measurements of captured or killed animals (Brattstrom, 1965). With the development of radio transmitters, crocodilians could be studied unrestrained under natural conditions in captive enclosures (Smith, 1975a; Lang, 1977; Asa et al., 1998; Grigg et al., 1998) or in the wild (Smith, 1975a; Brisbin et al., 1982; Seebacher and Grigg, 1997). However, data collection was limited to times when researchers could access implanted animals or when remote recording stations could receive signals from

transmitters. Technological advances have allowed miniaturization of temperature data logging devices so that continuous data collection is now possible.

Objectives

The objectives of this study were to describe the annual pattern of body temperature in Everglades alligators and to determine how this pattern differed between seasons. If alligators' T_b patterns differ in response to differences in seasonal hydropattern, their physiological and ecological responses are also likely to differ. By understanding these patterns, we will better understand the ecology of alligators in this southern extent of its range.

Methods

Once the data loggers were downloaded using Boxcar (Onset Computer Corporation), they were imported into an Excel 97 (Microsoft Inc.) spreadsheet. All alligator and environmental temperatures were combined into a single spreadsheet and aligned with the synchronized time/date stamp. Temperatures over the course of the year were then subdivided among seasons to examine differences in means and variances among summer, fall, winter, and spring seasons. Mean $T_b \pm$ one standard deviation was used to describe the summer, fall, winter, and spring temperature regime.

Temperatures over the course of the year were then placed into biologically meaningful categories to determine the composition of their temperature profile.

Temperatures below 16 C° were considered metabolically inactive. Temperatures from

16 to 22 C° were considered metabolically restrained since alligators typically do not feed if body temperature falls below 22 C° (Coulson and Hernandez, 1983).

Temperatures from 22 to 28 C° were considered intermediate since the lower end of activity temperature has been described as 28 C° (Coulson and Hernandez, 1983; Lang, 1987). Temperatures from 28 to 31 C° were considered metabolically active. Because of their high metabolic cost, temperatures above 31 C° were considered metabolically expensive. The composition of temperatures was examined for the entire year and within seasons.

To analyze patterns, each data set was smoothed to quantify and remove seasonal, weekly, and daily components. A moving average was used to extract the temperature components. The number of data points averaged (the averaging window size) determined the pattern being quantified. For example, to determine the seasonal component, an averaging window of 1680 (84 days) data points, 839 before and 840 after a specific time point was used. The resulting time series represented the general pattern in temperature of an alligator over the year. This general pattern, or seasonal component, was then subtracted from the original data time series with the result representing the pattern of body temperatures as deviations from the seasonal pattern.

The time series of deviations from seasonal patterns was then smoothed using a window of 140 data points (seven days), 69 before and 70 after a specified time point. The resulting pattern represented the fluctuation in body temperature as it was affected by weekly weather events such as cold fronts and other weather systems. Subtracting this second weekly smooth from the time series of deviations from the seasonal pattern revealed the pattern of body temperature as deviations about a weekly component.

The time series of deviations from the weekly component was then smoothed using a window of 20 data points (one day), 9 before and 10 after each data point being smoothed. The resulting smoothed time series represented day to day variability in T_b . Subtracting this third smoothed time series from the deviations from the weekly time series revealed the within-day variability of T_b .

The smoothing process reduced the size of the data set by the number of data points being smoothed. Since only the averaged data was used, data points at the beginning and end of the data set that were used to create the average were not part of the smoothed data set. Thus seasonal, weekly and daily smoothes reduced the data set by total of 1840 observations. This limited comparison of smoothed temperatures to fall, winter, and spring seasons since data for summer was not available.

Seasonally smoothed body temperatures represented the seasonal pattern of T_b and thus were used to describe the seasonal pattern of T_b over the course of the year. The variances of the seasonal, weekly, daily, and within-day components were used to indicate the variability within each component's portion of the pattern in T_b . Means were not used to describe weekly, daily, and within-day components because they fluctuated around a baseline of zero.

The proportion of the total variability in T_b was determined for seasonal, weekly, daily, and within-day components by dividing the variance of each component by the total variance. The proportions of total variability from seasonal, weekly, daily, and within-day components were then determined for fall, winter, and spring seasons. The proportions of the components were compared among seasons using a two sample T-test

assuming unequal variances. To avoid possibility of type I errors due to multiple comparisons, only P values < 0.01 were considered significant.

For the analysis, the traditional seasons were changed to 16 September 1997 to 15 December 1997 for fall, 16 December 1997 to 16 March 1998 for winter, and 17 March 1998 to 16 June 1998 for spring. While these are eight days earlier than the traditional seasonal delineation, advancing the dates assured that equal numbers of temperature observations would be used for each season, and that all the data could be used in the analysis. This also permitted seasonal temperature patterns to represent wet (summer and fall) and dry (winter and spring) seasons. Adjusting the seasonal delineation allowed consistency in seasonal time frames when describing smoothed and non-smoothed data. Because data collection began midsummer, data from two years was combined to create the non-smoothed summer data set, which consisted of data collected from 1 August to 14 September 1997 and from 17 June to 31 July 1998.

To establish if alligator T_b s correspond to changes in fall and spring ambient temperatures, the correlation between T_b and ambient temperature was determined for all 10 alligators. Each time series was smoothed using a window of 20 data points (one day) in order to identify the pattern in temperature across the season. The time series from each alligator was then paired with the corresponding ambient temperatures and analyzed using SAS (SAS Institute). Because some ambient temperature data were missing, fall analysis was limited to 10 October 1997 to 16 December 1997.

Results

Ten functional dataloggers were recovered from alligators in WCA, seven females from the marsh habitat, one female and two males from the canal habitat. The ten recovered animals ranged in weight from 20 to 49 kg ([Table 5-1](#)). Marsh animals weighed less ($\bar{x} = 25.5$ kg, $n = 7$) than canal animals ($\bar{x} = 45.3$ kg, $n = 3$; $P = 0.006$).

All alligators followed a similar pattern of annual body temperature ([Fig. 5-1](#)). Summer temperatures were high and stable ($\bar{x} = 29.0 \pm 1.7^\circ\text{C}$; [Fig. 5-2](#)). Fall temperatures ($\bar{x} = 24.0 \pm 3.3^\circ\text{C}$; [Fig. 5-2](#)) declined corresponding to a decline in ambient temperature ($P < 0.0001$, $R^2 = 0.6397$, $n = 13910$; [Fig. 5-3](#)). Winter temperatures remained low ($\bar{x} = 20.8 \pm 3.2^\circ\text{C}$; [Fig. 5-2](#)), fluctuating with environmental temperatures ([Fig. 5-3](#)), with only occasional periods where body temperatures were raised above 28°C . During spring minimum body temperatures ($\bar{x} = 26.3 \pm 3.4^\circ\text{C}$; [Fig. 5-2](#)) increased with increasing environmental temperatures ($P < 0.0001$, $R^2 = 0.6895$, $n = 18400$; [Fig. 5-3](#)).

The distribution of the 7296 consecutive temperature observations recorded over a one-year period for alligators in the WCA fit a bell shaped curve within the five metabolically based temperature categories ([Fig. 5-4](#)). The distribution pattern of temperatures varied greatly between seasons. In the fall the bell shaped curve narrowed with most temperatures in the intermediate category ([Fig. 5-4](#)). Four alligators had no body temperatures below 16°C . Three of the four were the largest alligators in the study and inhabited a canal. In winter the majority of observations were in the colder categories ([Fig. 5-4](#)). Winter body temperatures were rarely in the warmest categories.

Spring body temperatures skewed towards the warmer categories ([Fig. 5-4](#)). No alligators had body temperatures in the inactive range. Metabolically expensive temperatures were nearly 10 times as frequent in spring as in fall. Metabolically active temperatures were more than twice as frequent in spring than in fall. In summer warm temperatures dominated the distribution ([Fig. 5-4](#)). Metabolically expensive temperatures averaged 13.8% with one individual having 27.8% of observations in this category. The lowest temperature of any alligators during summer was 23.8° C.

In fall, mean seasonally smoothed T_b s steadily decreased from 27.7° C to 20.9° C with an overall mean of 24.0° C ([Fig. 5-5](#)). In winter the seasonal body temperatures decreased to a mean of 20.0° C ([Fig. 5-5](#)), then steadily increased in the second half of the season ([Fig. 5-5](#)). All but one alligator reached its lowest seasonal smoothed body temperature on 5 or 6 January; the exception was a canal male who reached his lowest seasonal smoothed body temperature on 9 February. The ninth of February coincided with a cold front that reduced ambient temperature to 9.4° C. This was also the coldest day ($\pm$ one day) for body temperatures for all alligators. After reaching this low, seasonal smoothed body temperatures steadily increased. Overall mean winter seasonal smoothed body temperatures were 20.8° C ([Fig. 5-5](#)). In spring the mean seasonal smoothed body temperatures steadily increased from 22.4° C to 28.7° C with an overall mean of 26.1° C ([Fig. 5-5](#)).

The variance of T_b differed among temporal components and between seasons ([Fig. 5-6](#)). The average of overall variances of the alligators' seasonal T_b patterns was 7.9° C with an average variance of 4.7° C in fall, 0.4° C in winter, and 3.8° C in spring. When the deviations from the seasonal components were smoothed to identify the weekly

components, the average of the alligators' variances for the time series was 1.7° C, with an average variance of 0.8° C in fall, 3.1° C in winter, and 0.9° C in spring. The average of the alligators' variances of daily smoothed deviations from the weekly components was 0.9° C with an average variance of 0.8° C in fall, 1.3° C in winter, and 0.6° C in spring. The average of the alligators' variances from deviations from the daily component, which represented within-day variation, was 4.1°C with an average variance of 2.9° C in fall, 4.2° C in winter, and 5.2° C in spring.

When the variances from the seasonal, weekly, daily, and within-day components were combined for each alligator, the average of the total variances was 14.6° C. The average percent of total variance that was accounted for by each component was 54%, 12%, 6%, and 28% respectively ([Fig. 5-7](#)).

When the components were subdivided by season, the fall percentages were similar to the overall patterns with seasonal, weekly, daily, and within-day components accounting for 51, 9, 9, and 31 percent of the average total variance, respectively ([Fig. 5-7](#)). In winter there is a drastic shift in the composition of the total variance from fall ([Fig. 5-7](#)). The seasonal component is reduced to 5% of the total variance ($P < 0.001$), while the weekly component increased to 34% ($P < 0.001$). The daily component increased to an average of 14% ($P < 0.001$) and the within-day component increased to an average of 46% ($P = 0.014$). In spring the composition again changes with the within-day component becoming the predominant component ([Fig. 5-7](#)). The seasonal component averaged 36% of the total variance, an increase over winter ($P < 0.001$) and a decrease from fall ($P < 0.001$). The weekly component averaged 9%, a decrease from winter ($P < 0.001$) but not significantly different from fall ($P = 0.07$). The

daily component averaged 6%, a decrease from winter ($P < 0.001$) and a smaller but significant decrease from fall ($P = 0.002$). The within-day component was the dominant variance in spring. It encompassed 50% of the variance, an increase from both winter ($P = 0.004$) and fall ($P < 0.001$).

Discussion

In spring, alligators raised their body temperature well above the average ambient temperatures on a nearly daily basis. While this pattern is observed occasionally in winter and to a lesser degree in fall, it was most frequent in spring. Since spring ambient temperatures are similar to those of fall and even winter, biological factors, rather than passive fluctuations in body temperature must be driving this difference.

Elevation of T_b in spring may be a consequence of alligator's reproductive strategy. Alligators have a compressed breeding season. Females lay their eggs within a four week period beginning in mid June. To accomplish this task, they must be physiologically prepared to breed. Hormone production and efficiency are temperature dependent. Warm temperatures are necessary for proper hormone levels to induce sperm and egg production (Lance, 1987).

Spring is also the peak of the dry season in the Everglades. The Southern Everglades is a nutrient poor system and food for alligators is relatively scarce (Barr, 1997). When water levels are high, prey species are widely dispersed across the landscape. However, in the dry season the lower water levels concentrate prey in the few remaining areas of deeper water, such as gator holes (Kushlan, 1976). These areas

provide an abundant food source for alligators. To take full advantage of this feeding opportunity, alligators must be able to process as much food as possible during this time period.

Because temperatures during the dry season are relatively cool, body temperatures must be elevated to facilitate maximal assimilation of nutrients. By raising body temperatures, metabolic rate and enzymatic activity is greatly increased, allowing alligators to quickly process prey (Coulson and Hernandez, 1983). They are thus able to consume and assimilate larger amounts of nutrients in a shorter period of time.

The decrease in water level also reduces the thermal buffer that alligators use to moderate temperature fluctuations. This may account for some of the increased variability in spring T_b s, but it is unlikely that it can account for all of it. When alligator temperatures are compared with environmental temperatures, the difference between alligator and environmental patterns is distinctly greater in spring than any other season. In addition, alligators from canals, which have abundant water year round, show the same pattern of elevated spring temperatures as marsh alligators.

During the summer wet season in the Everglades, prey items are dispersed and difficult to acquire (Kushlan, 1976). Because summer is also a time of consistently high temperatures, metabolic rates are very high, increasing the demand for food resources. Since energy resources are most difficult to acquire when they are needed most, summer is likely a time of negative energy balance for Everglades alligators.

In summer T_b frequently rises above the normal activity temperature of 31°C and may attain temperatures as high as 36°C . While gator holes and caves provide some refuge from the heat, alligators that are attending nests or otherwise exposed must endure

temperatures above the normal activity level. While alligators will raise their body temperature above 31° C at other times of the year, this usually occurs during periods when nighttime ambient temperatures are low. At such times, raising daytime body temperature above 31° C may well be an attempt to use thermal inertia to maintain an overall higher temperature into the cool night. In contrast, high summer temperatures represent an increased metabolic burden resulting from high ambient temperatures.

In the fall T_b follows a pattern of thermoconformity similar to summer in that temperatures fluctuate little around the daily mean. However, unlike summer, when ambient temperatures are stable around an alligator's activity temperature, fall ambient temperatures decline steadily. Fall T_b s decline along with declining ambient temperatures. Only occasionally are T_b s raised to activity temperatures in the cooler portions of fall. Because water levels are very high this time of year, the limited availability of food probably drives alligators to minimize T_b in order to minimize metabolic costs.

Although Everglades alligators maintain low T_b s during the winter months, T_b s are occasionally raised to activity levels. These heating events are not synchronized as would be expected if environmental factors alone were inducing basking behavior. Rarely did more than one alligator elevate T_b on the same day. While high T_b s are associated with feeding, winter T_b s are elevated only for short periods, usually one day. Digestion of prey could not be accomplished in such a short time (Barr, 1997). Perhaps elevated T_b s in winter are necessary for excretion of metabolic wastes (Coulson and Hernandez, 1983).

No alligators had T_{bs} below 11°C and rarely were they below 15°C . Since alligators are adapted to temperate climates, they have evolved an annual cycle that includes winter hibernation. While throughout most of the alligator's range cold winter temperatures promote a deep hibernation in which metabolism is greatly reduced, winter temperatures in the Everglades are not low enough for effective hibernation. Thus, while winter temperatures average 22°C , the approximate temperature at which alligators refrain from eating (Coulson and Hernandez, 1983), their metabolic rates are sufficiently high to create waste that must be excreted. Occasional high body temperatures may be necessary to accomplish this task. A more thorough study of the physiological ecology of these animals is necessary in order to understand the biological forces driving these temperature patterns.

Conclusion

Summer represents a difficult period in the annual cycle of the Everglades alligator. To acquire sufficient resources to survive this metabolically expensive time of year, alligators rely on the spring reduction of free standing water in the marsh to concentrate prey. Without natural fluctuation of hydropattern to concentrate food, alligator populations would be negatively impacted. Since many species in the Everglades depend on the maintenance of gator holes for refugia during time of drought, factors negatively affecting alligator populations would impact the entire ecosystem.

While a complete drawdown would make the majority of the prey items in the marsh available for consumption, this would increase the recovery period needed for prey to repopulate the marsh. A more natural balance must be struck where prey becomes available to alligators but enough standing water remains so that breeding sized adult prey survive. By restoring the historic hydrologic patterns of the Everglades, fringe marshes could dry out while the deeper sloughs and drainages would retain water. This would insure that food would become available in the short term yet not be eliminated in the long term.

Table 5-1. The weight, gender, and habitat of 10 alligators in Water Conservation Area 3A North implanted with temperature recording data loggers.

Alligator #	Weight (Kg)	Gender	Habitat
870	20	Female	Marsh
914	23	Female	Marsh
987	24	Female	Marsh
875	26	Female	Marsh
916	27	Female	Marsh
882	30	Female	Marsh
878	30	Female	Marsh
867	41	Male	Canal
915	46	Male	Canal
866	49	Female	Canal

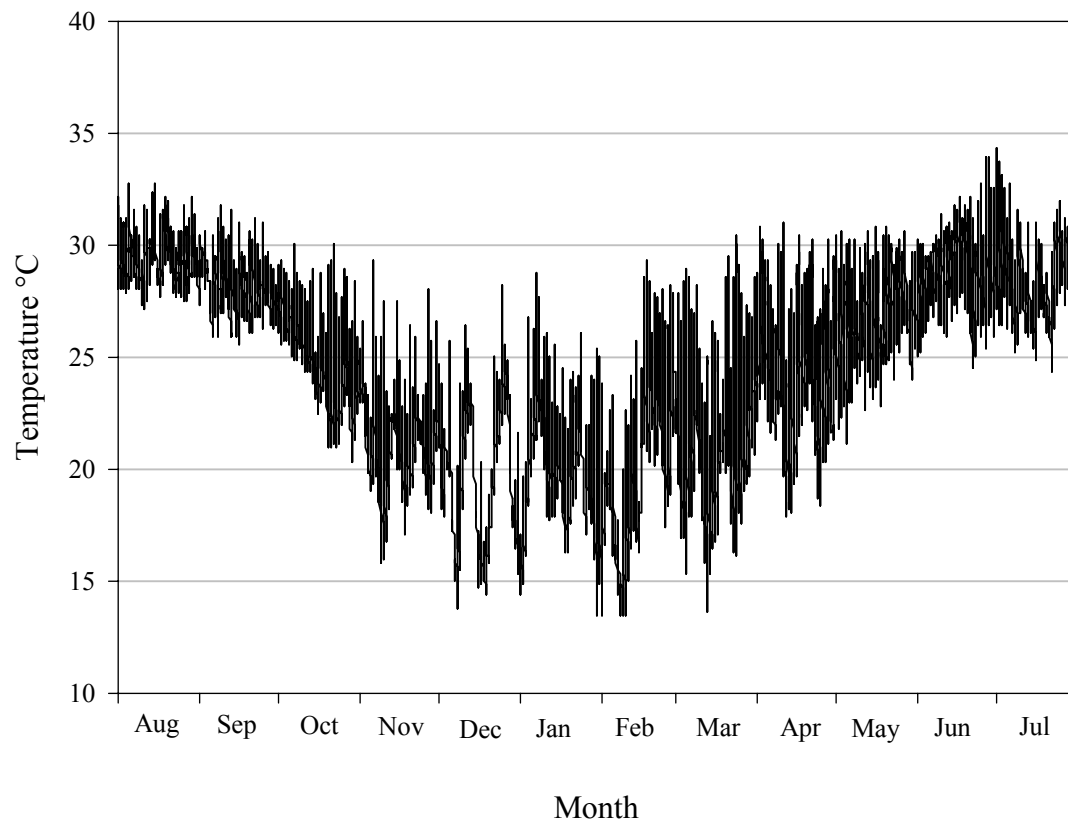


Figure 5-1. The typical pattern of body temperature of an alligator from Water Conservation Area 3A North (from alligator # 878, a 30 Kg female). Temperature was recorded at 72 minute intervals from 1 August 1997 to 31 July 1998.

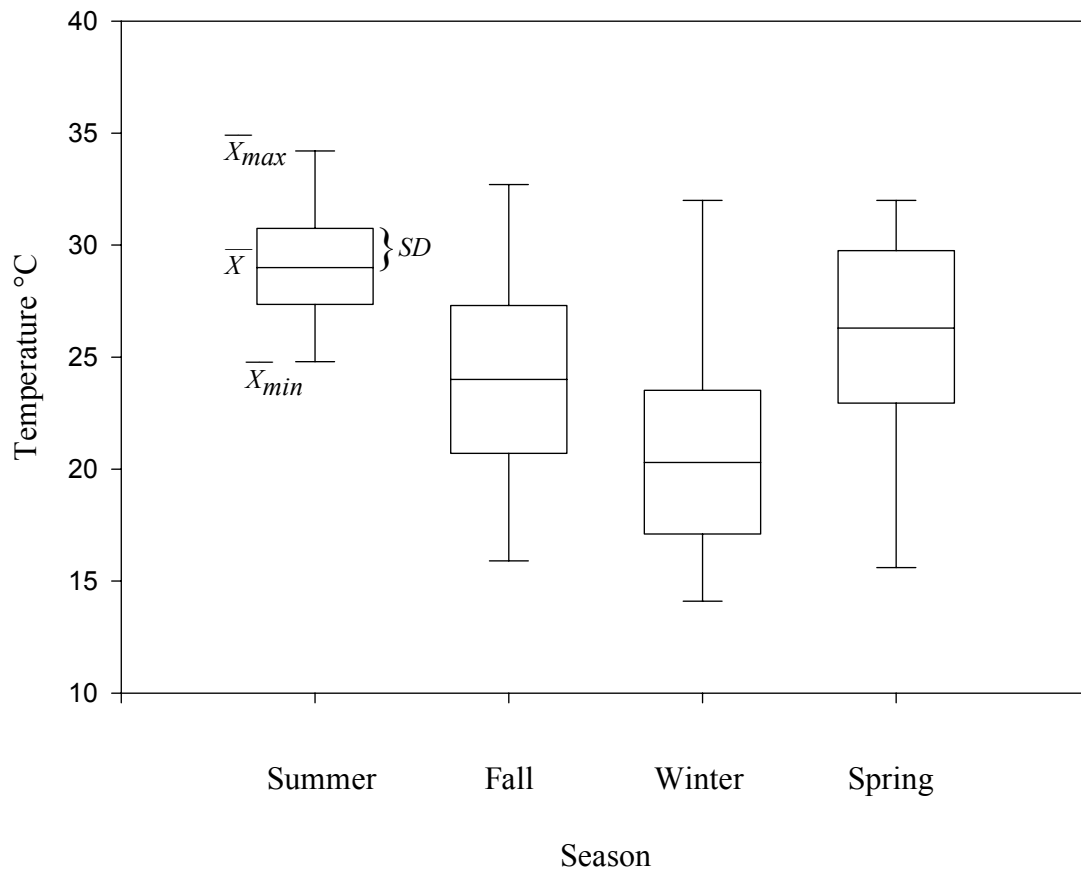


Figure 5-2. Mean of ten alligator's mean seasonal body temperature ($\bar{x}$), +/- one mean standard deviation (SD), mean maximum body temperature ($\bar{x}_{max}$), and mean minimum body temperature ($\bar{x}_{min}$) were recorded from free ranging adult alligators in Water Conservation Area 3A North for summer (1 August to 14 September 1997 and 17 June to 31 July 1998), fall (16 September to 15 December 1997), winter (16 December 1997 to 16 March 1998), and spring (17 March to 16 June 1998).

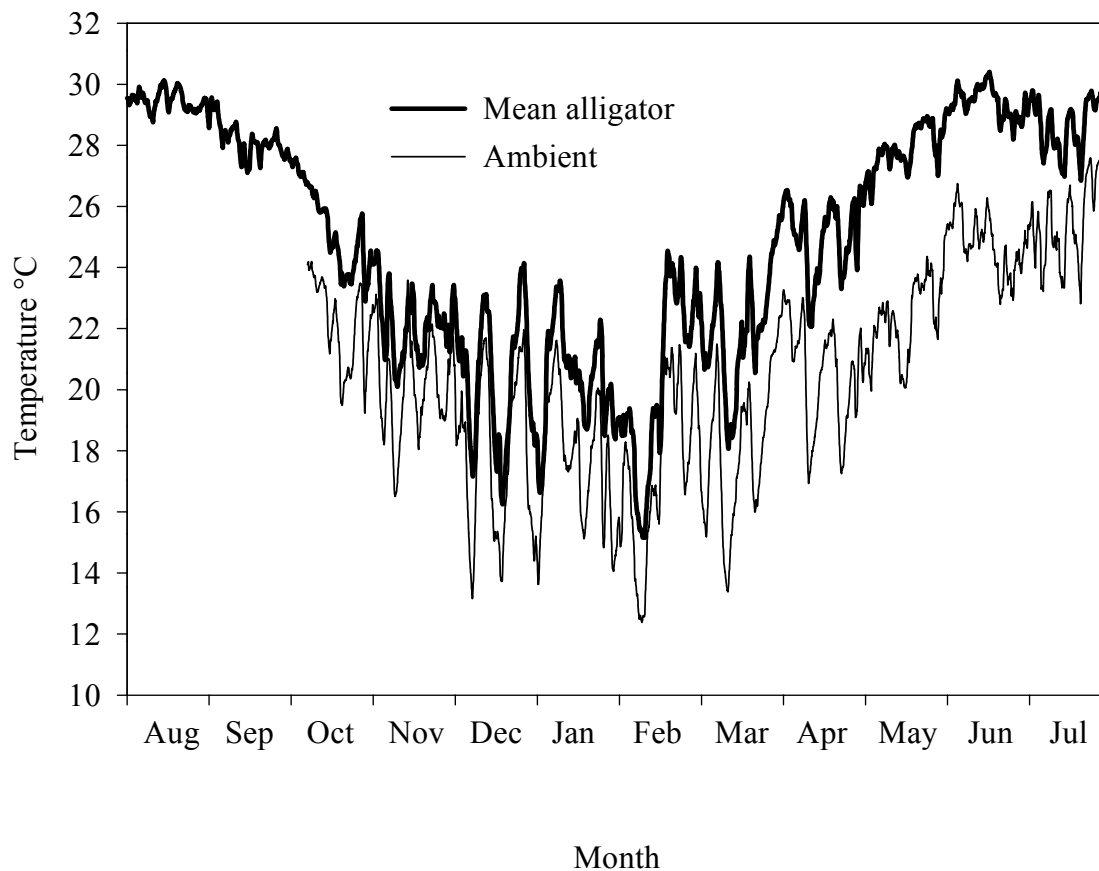


Figure 5-3. Mean smoothed body temperature of ten alligators from WCA 3A North (1 August 1997 to 31 July 1998) plotted with ambient temperature (7 October 1997 to 31 July 1998). All temperatures were recorded simultaneously at 72 minute intervals and then smoothed using a moving average of 20 observations (one day). Ambient temperature was the average of air and marsh water temperature.

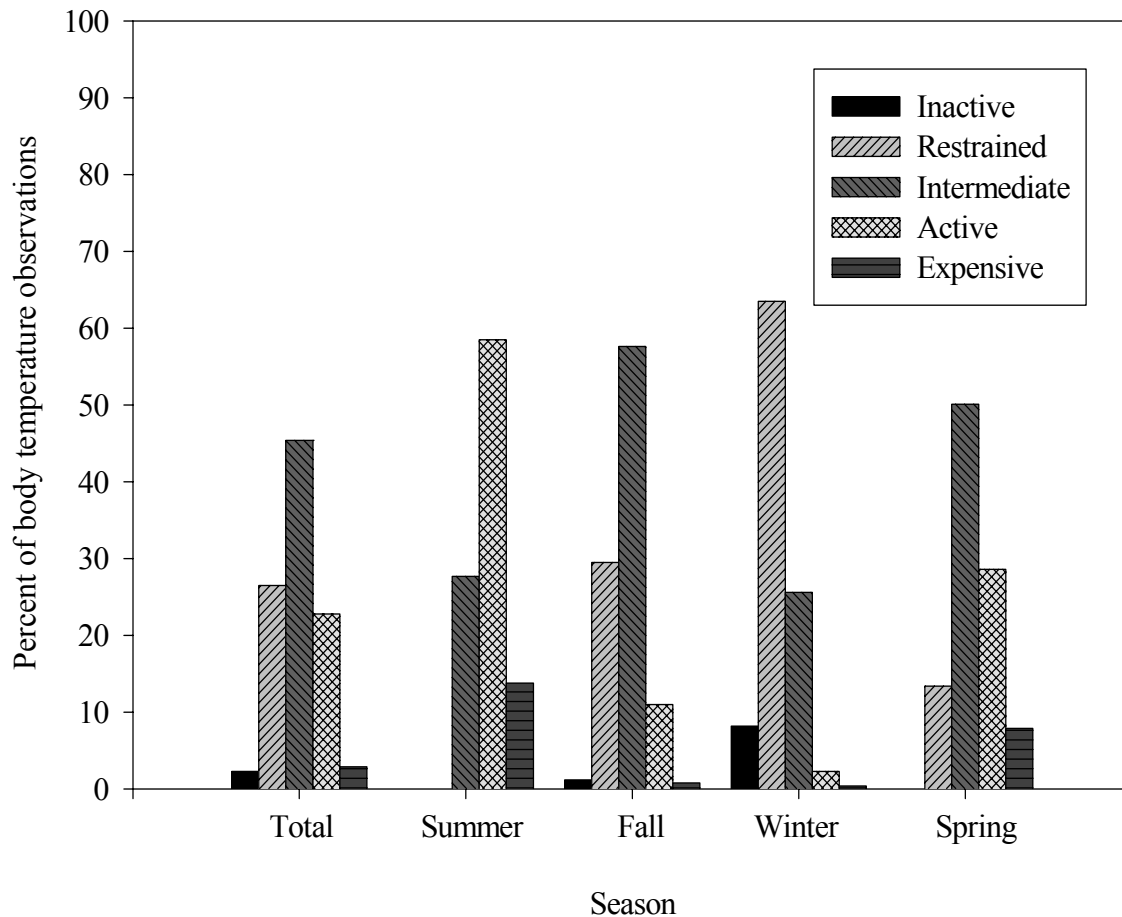


Figure 5-4. Percent of body temperature observations distributed within inactive (11.01 - 16.00° C), restrained (16.01 - 22.00° C), intermediate (22.01 - 28.00° C), active (28.01 - 31.00° C), and expensive (>31.01° C) metabolic temperature categories. A total of 7296 observations were recorded for each of ten alligators in Water Conservation Area 3A North. Temperatures were recorded simultaneously at 72 minute intervals from 1 August 1997 to 31 July 1998. Seasons consisted of 1820 observations each for summer (1 August to 14 September 1997 and 17 June to 31 July 1998), fall (16 September to 15 December 1997), winter (16 December 1998 to 16 March 1998), and spring (17 March to 16 June 1998).

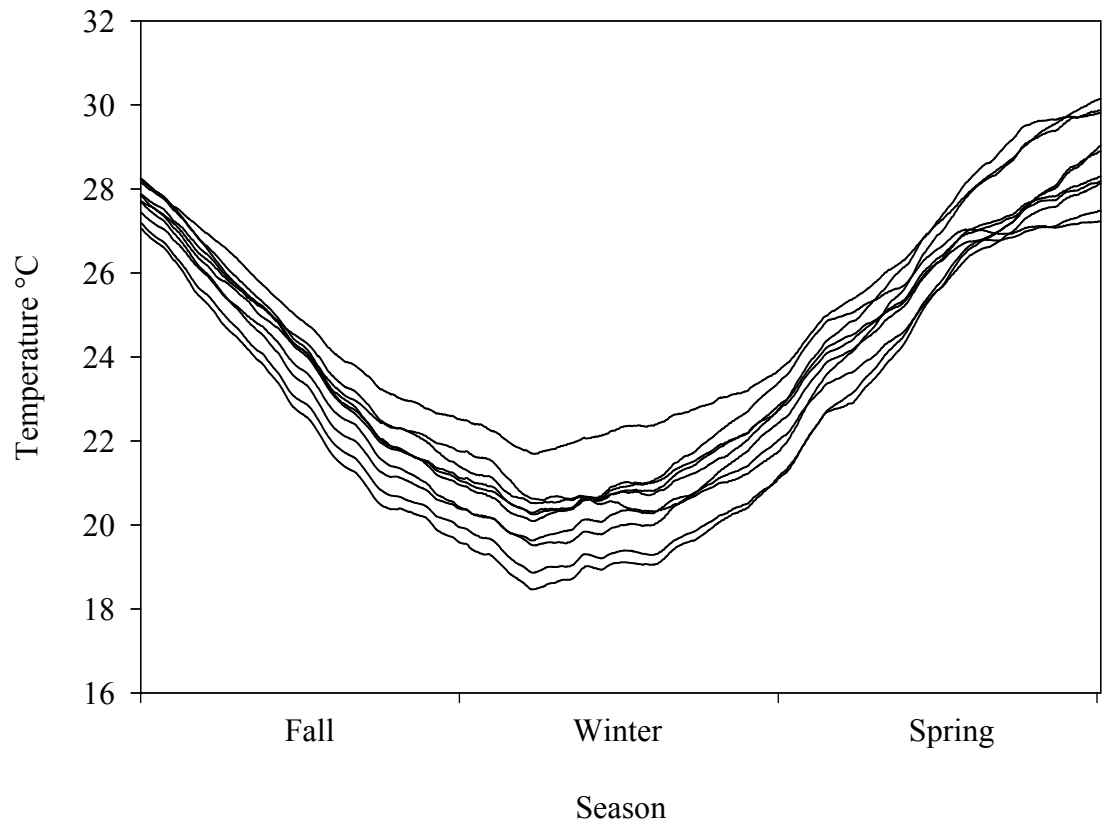


Figure 5-5. Seasonally smoothed body temperatures of ten alligators from Water Conservation Area 3A North. Body temperatures were recorded simultaneously at 72 minute intervals from 1 August 1997 to 31 July 1998 and then smoothed using a moving average of 1680 data points (84 days).

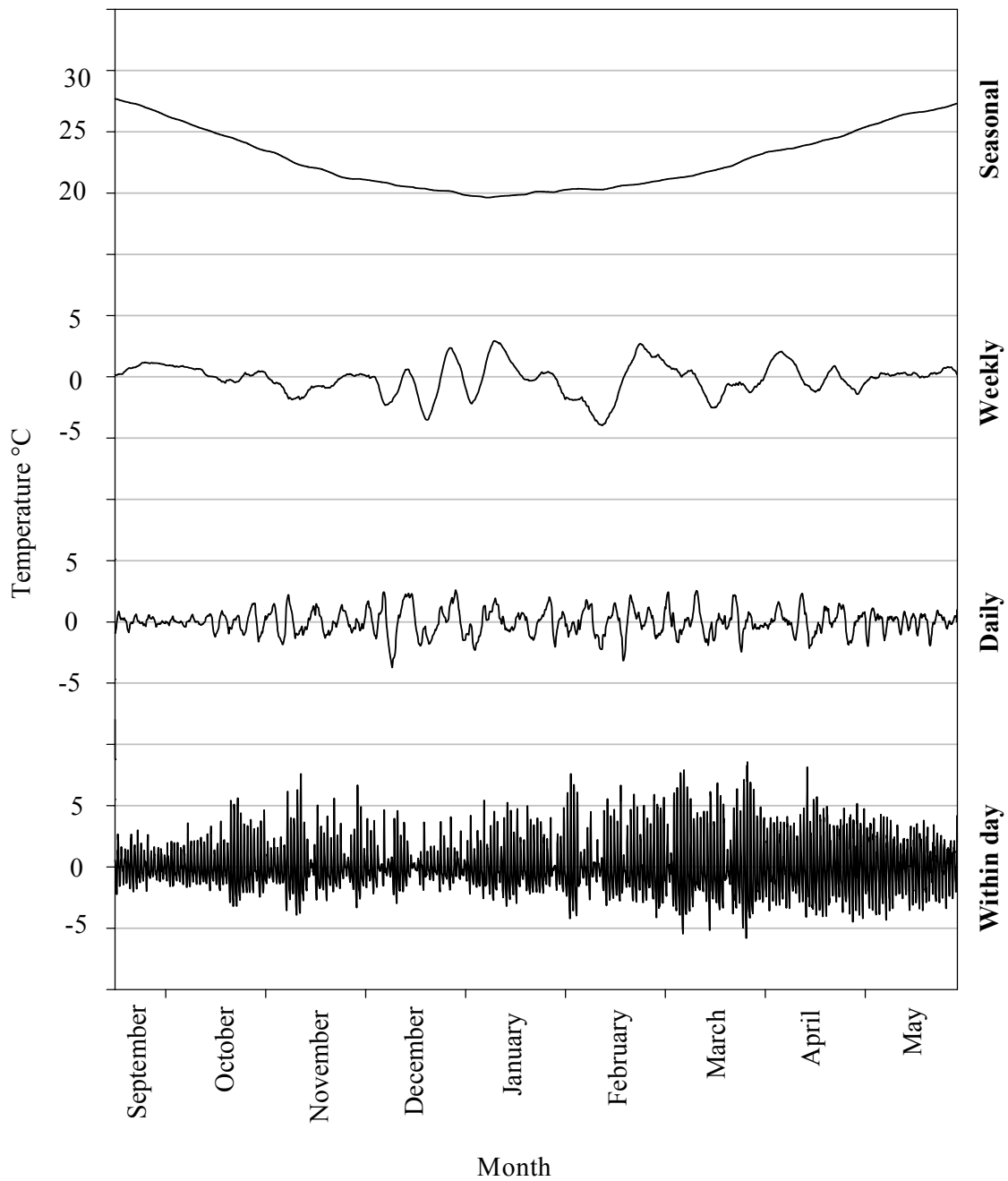


Figure 5-6. Seasonal, weekly, daily, and within-day components of body temperature of a typical alligator (alligator# 878, a 30 Kg female) from Water Conservation Area 3A North.

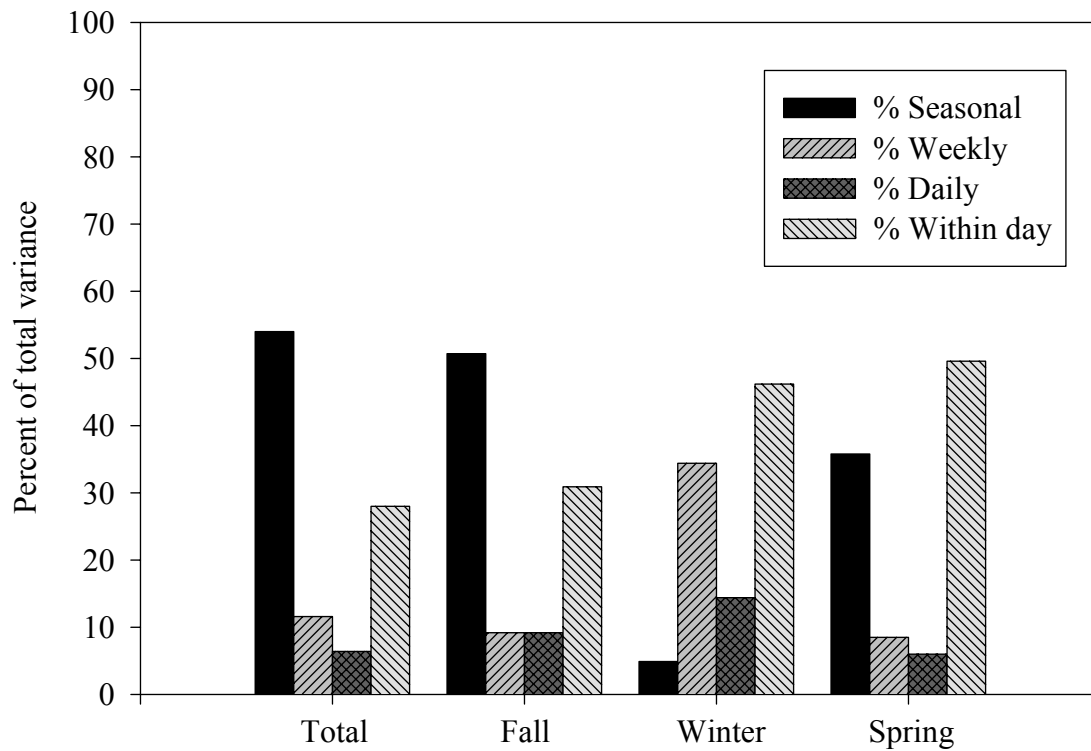


Figure 5-7. Percent of total variance accounted by seasonal, weekly, daily, and within-day components in body temperature from 10 alligators from Water Conservation Area 3A North. The total smoothed time series consisted of observations from 16 September 1997 to 16 June 1998. The time series was then subdivided into fall (16 September to 15 December 1997), winter (16 December 1998 to 16 March 1998), and spring (17 March to 16 June 1998) seasons for inter-seasonal comparisons.

CHAPTER 6

COMPARATIVE THERMAL ECOLOGY OF EVERGLADES ALLIGATORS

Stanley R. Howarter, H. Franklin Percival, Kenneth G. Rice, and Cory R. Morea

The American alligator is primarily a temperate species whose range extends into the southern tip of the Florida peninsula. While the largest known alligators are from central Florida (Woodward et al., 1995), alligators in the southern Everglades of Florida are much smaller and appear to be in poor condition (Jacobsen and Kushlan, 1989; Dalrymple, 1996; Barr, 1997). This apparent poor body condition is thought to result from low food availability combined with high ambient temperatures. Much of the evidence supporting this theory comes from the Shark Slough drainage in Everglades National Park (Jacobsen and Kushlan, 1989; Dalrymple, 1996; Barr, 1997).

Body temperature patterns of animals provide insight into their physiology and ecology. Examining differences in body temperature patterns between alligator populations may reveal how differences within habitat affect individuals' physiology and ecology. Because most of the biological data on Everglades alligators come from Shark Slough, determining whether or not this population represents the entire Everglades is critical in understanding the ecosystem as a whole.

Restoration efforts are currently underway to reverse human alterations of Everglades hydrology. The Across Trophic Level System Simulation (ATLSS) is a computer based model being developed by the United States Geological Survey which

uses biological data to predict the impact of these restoration efforts on wildlife species (DeAngelis et al., 1998). Since the model is intended to predict wildlife response to alternative hydropatterns, knowing how alligators respond to differences in hydropattern within the annual cycle and between habitats allows us to understand how alternate hydropatterns might affect alligator ecology.

Objectives

The objective of this study was to identify differences in the annual T_b pattern of two populations of Everglades alligators. If the two population's T_b patterns differ in habitats with different hydropatterns, their physiological and ecological responses to the hydropatterns of the two habitats are also likely to differ. Knowing if and how ENP alligators differ from alligators in other parts of the Everglades will increase our understanding of the ecosystem and prevents information about subpopulations from being overgeneralized to represent the entire population.

Methods

Alligator body temperatures were analyzed both as a raw time series and as seasonal, weekly, daily, and within-day components decomposed using smoothing techniques developed in Chapter 5. For the analysis, the traditional seasons were changed 16 September 1997 to 9 December 1997 for fall, 9 December 1997 to 3 March

1998 for winter, and 3 March 1998 to 26 May 1998 for spring. Advancing the dates assured that equal numbers of temperature observations would be used for each season, and that all the data could be used in the analysis. Adjusting the seasonal delineation allowed consistency in seasonal time frames when describing smoothed and non-smoothed data. Because data collection began midsummer, data from two years was combined to create the non-smoothed summer data set, which consisted of data collected 1 August 1997 to 16 September 1997 and 27 May 1998 to 10 July 1998.

In order to identify differences between study sites, mean T_b , standard deviation of T_b , mean daily minimum T_b , and mean daily maximum T_b were calculated from the sample time series for each alligator and compared using a two sample T-test assuming unequal variances. This test was used to compare differences in means and standard deviations of total, fall, winter, and spring components of seasonally smoothed body temperature patterns of alligators from the two study sites. Further, the standard deviations of weekly, daily and within-day components were compared using two sample T-tests assuming unequal variances for total, fall, winter, and spring components of temperature patterns of alligators from the two study sites.

Two sample T-tests assuming unequal variances were used instead of ANOVA because the variability between seasons violated ANOVA's assumption of independence. To avoid type I errors that may have resulted from analyzing multiple patterns, and because of the large sample size of temperatures, only P-values less than 0.01 were considered significant.

Results

Average body temperatures were higher in alligators from ENP than those from WCA in fall ($P = 0.001$), winter, ($P = 0.001$), and spring ($P < 0.001$), but no difference was detected in summer ($P = 0.232$; [Fig. 6-1](#)). The average daily minimum T_b was higher in ENP than WCA for fall, winter and spring ($P < 0.001$) but not summer ($P = 0.042$), while average daily maximum T_b s were not significantly different in any season (fall $P = 0.751$, winter $P = 0.055$, spring $P = 0.023$, and summer $P = 0.768$).

The standard deviation of T_b was smaller in ENP alligators than in alligators from WCA in fall ($P = 0.003$), spring ($P < 0.001$), and summer ($P < 0.001$), but not in winter ($P = 0.691$; [Fig. 6-1](#)). When the standard deviations of seasonal, weekly, daily, and within-day components of body temperatures of ENP and WCA alligators are compared, only the within-day components are significantly different among the two groups and only for fall and spring seasons ($P < 0.001$). The average seasonal smoothed temperature of ENP alligators was higher in fall, winter and spring ($P < 0.001$, $P = 0.001$, and $P < 0.001$ respectively; [Fig. 6-2](#)) than that of WCA alligators.

Discussion and Conclusion

The Everglades lies on the northern boundary of the subtropical zone. The transition to a temperate climate north of Lake Okeechobee limits the northern distribution of many native and introduced species in South Florida. This small zone of subtropical habitat represents the southern extent of the alligator's range and is unique

among the habitats in which they occur. Within this subtropical landscape, alligators from the two study areas examined appear to differ in their pattern of T_b . This difference may result from differences in the hydropattern of the two areas.

Average daily minimum T_b s for ENP alligators were higher in fall, winter, and spring than those of WCA alligators. Despite warmer overall T_b in ENP, average daily maximum temperatures were similar in both areas. Because maximum T_b s are often the result of behavioral and physiological thermoregulation, differences between study sites would not be expected. On the other hand, minimum daily temperatures occur at night when the ability to elevate T_b is limited, so differences in temperature regimes would not be biased by behavior.

The deeper water in the marsh of ENP (Morea, 1999) may act as a buffer to limit extreme fluctuations in T_b . A buffer limiting exposure to extremely cold temperatures could raise both average daily minimum T_b and overall average T_b . It could also allow greater activity when surface temperatures were above comfort levels. In summer, average T_b s are similar in ENP and WCA but the variation is lower in ENP, suggesting that ENP alligators are able to more precisely regulate their body temperatures. While it is possible that deeper water levels in ENP are responsible for differences in T_b patterns, it can not be forgotten that three of the ten alligators from WCA were from canal habitat and thus had access to deep, thermally stable water.

On the other hand, average winter T_b s are higher in ENP than in WCA while the variability is equal. This suggests that the winter pattern of T_b fluctuation is similar in the two locations, but the average T_b of alligators in ENP is consistently higher than those in

WCA. A more thorough examination of the differences in ambient temperatures between the two areas is necessary.

Although the mean seasonal T_b was higher in ENP than WCA, the variability within seasonal, weekly and daily components was approximately equivalent. The effect of climate and major weather systems on patterns of body temperature within the two study sites would likely be similar due to their close proximity to each other. The within-day variability of ENP alligators, however, was less in fall and spring, and presumably in summer than WCA alligators. Stable T_b s increase the efficiency of metabolic reactions. Stability of T_b reflects the stability of the habitat and when temperatures are within the activity range, reduces the need for thermoregulation.

Higher marsh water levels in ENP may have allowed fall and spring mean T_b to be higher than WCA by stabilizing temperature fluctuations and reducing the time spent at lower temperatures. Conversely, variability in T_b may be less in ENP as a result of a higher overall body temperature that would decrease the range in which T_b may fluctuate and thus limit variability.

Lower temperatures in WCA may be beneficial to alligators in a nutrient poor environment. Decreased T_b results in a decreased metabolic rate and thus decreases the maintenance cost of alligators. Because metabolic rate increases exponentially with increase in body temperature, small increases in T_b at the upper temperature range may have substantial effects on energy requirements (Coulson and Hernandez, 1983). This would be especially beneficial in the times of high water when food is limited.

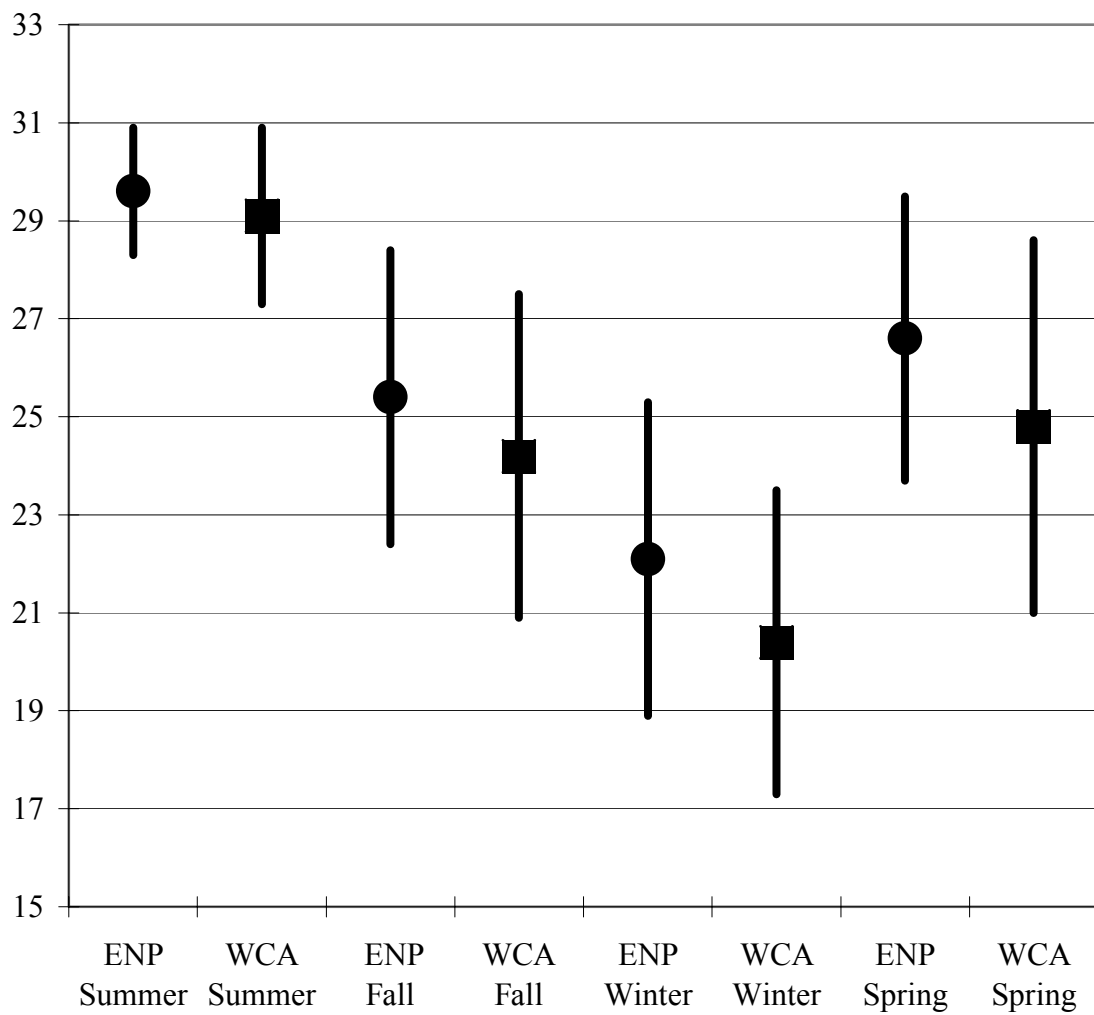


Figure 6-1. Mean of mean body temperatures $\pm$ one mean standard deviation from ten alligators from Water Conservation Area 3A North (WCA) and four alligators from Shark Slough, Everglades National Park (ENP).

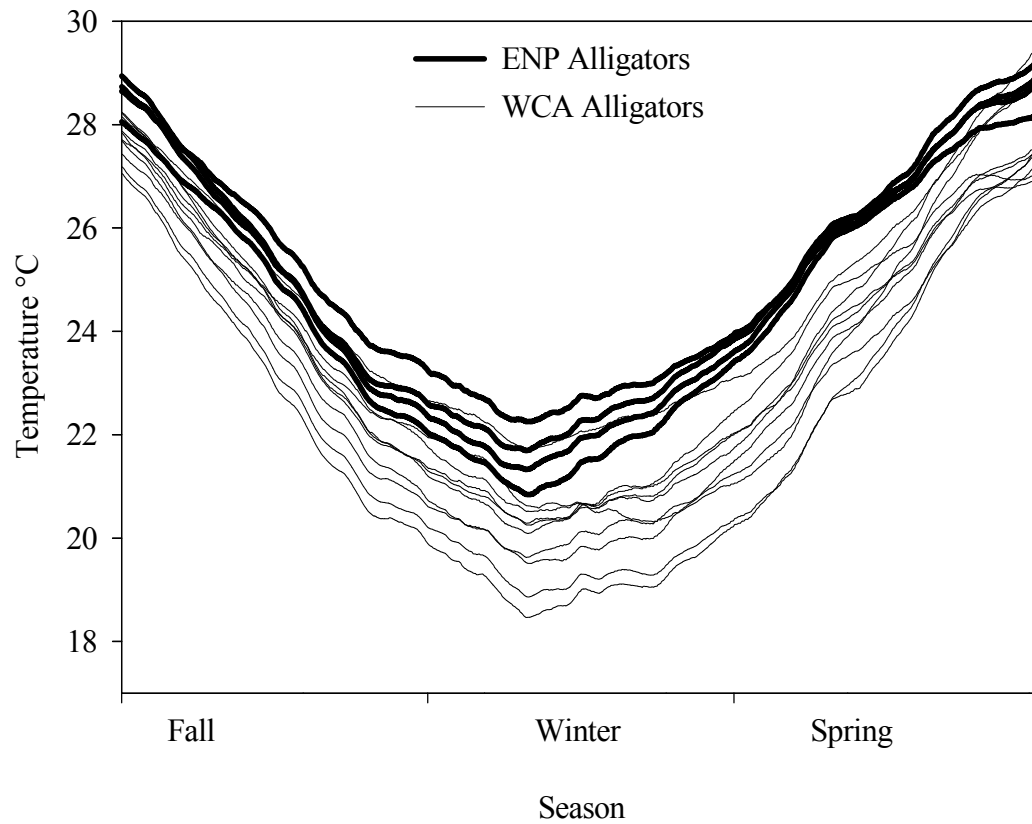


Figure 6-2. Seasonally smoothed body temperatures of ten alligators from Water Conservation Area 3A North (WCA) and four alligators from Shark Slough, Everglades National Park (ENP). Body temperatures were recorded simultaneously at 72 minute intervals from 1 August 1997 to 11 July 1998 and then smoothed using a moving average of 1680 data points (84 days).

CHAPTER 7

THERMOREGULATION OF EVERGLADES ALLIGATORS

Clarence L. Abercrombie, Stanley R. Howarter, H. Franklin Percival,
Kenneth G. Rice, and Cory R. Morea

Whereas the majority of extant ectotherms are of small body size, the fossil record suggests that extremely large ectotherms were once the dominant vertebrates on Earth. Crocodilians represent all that remain of the large, ectothermic archosaurs. The American alligator (Alligator mississippiensis) has many adaptations for life in a warm temperate climate. However, their range extends into subtropical south Florida where consistently high temperatures are encountered. Temperature affects all aspects of an alligator's life, with the effects becoming most acute at the upper tolerance levels. Understanding alligator's thermal ecology is important in order to conserve and manage this species at the southern extent of its range.

Until the 1970's, the data on body temperatures of wild crocodilians consisted of individual measurements on captured or fresh-killed animals (Brattstrom, 1965). The development of appropriate radio transmitters allowed crocodilians to be studied unrestrained in captive enclosures (Lang, 1987; Asa et al. 1998; Grigg et al., 1998) or in the wild (Seebacher and Grigg, 1997), and such studies have become even more feasible with the advent of small, accurate, and reliable data loggers.

While data loggers eliminate the problem of gaps within observational data sets, they provide new challenges to scientists who must make ecological interpretations of the large accumulations of data. In this paper, we employ existing statistical techniques to

address questions relative to seasonal trends in body temperature and comparisons of body temperatures with environmental temperatures.

Methods

The data analyzed in this paper included 4860 timed observations (20 observations per day from 1 October 1997 through 31 May 1998), each, on 13 alligators, deep water (WCA), shallow water (ENP), black body (ENP), and air (ENP). Data from alligator and environmental temperature data loggers were exported to SYSTAT 7.0 (SPSS Corporation) for analysis.

In order to analyze the relationship between alligator body temperature and environmental temperature, an environmental temperature index (E) and an average alligator temperature (G_{ave}) were defined as:

$$E = [2(\text{deep water temperature}) + \text{shallow water temperature} + \text{air temperature}]/4;$$

$$G_{ave} = \text{mean temperature of 12 alligators (9 WCA and 3 ENP)}.$$

Incorporating the three distinct environmental temperature profiles into an index of "operative environmental temperature" allowed us to easily examine multiple co-factors that affect alligator body temperature patterns. Environmental data from both study sites were combined to avoid problems with gaps in certain temperature profiles. All analyses were duplicated using fragmented series of data and other measures of overall environmental temperatures and no results were qualitatively different. Because of their extreme daily cycles black-body temperatures were excluded from this general environmental measure and we briefly analyzed them separately.

For each of the 4860 timed observations, E , G_{ave} , and the difference (D) between E and G_{ave} were calculated, as well as monthly averages of D . The difference was then smoothed by a running weekly median and we plotted the variable (D_{smooth}) against date (Fig. 7-1).

Fourier decomposition was used to analyze G_{ave} and E (Wilkinson, 1996). The magnitude of the largest Fourier component provided an index for the intensity of the daily thermal cycle. Cycle-intensity of environmental and alligator indices were compared by month.

Taking January as an example of winter, time-series plots of each alligator's T_b were compared against time-series plots of all environmental temperature measures. Pairs of alligator time-series T_b plots were compared, and the number of days when individual alligator $T_b > 30^{\circ}\text{C}$ was noted (Colbert et al., 1946; Avery, 1982; Coulson and Hernandez, 1983).

For each month and each sequential pair of months a joining-cluster analysis was performed to determine which alligators exhibited similar thermal patterns. Three clustering variables were defined: (1) mean daily maximum, (2) mean daily minimum, and (3) magnitude of largest (daily) Fourier component. The distance metric was Euclidean. Only clusters that replicated under both Ward's and median linkage methods were considered significant (Milligan, 1980; Milligan and Cooper, 1985; Wilkinson, 1996; Wilkinson et al., 1996). Several values were calculated from one specific cluster and the following statistic was used to determine the appropriate number of clusters to analyze:

$$“F” = (\text{mean-square-model})/(\text{mean-square-error}), \text{ or}$$

$$“F” = [(SSED_{c-1} - SSED_c)/(c-1)] / [(SSED_c)/(n-(c-1)-1)],$$

where n is number of observations;

c represents the number of clusters under consideration, and

SSED_c and SSED_{c-1} represent sums of squared Euclidean distances around cluster centroids.

If, for instance, one wishes to investigate whether a 2-cluster structure provides considerably more explanatory power than a 1-cluster (one big group) structure, then one calculates “F” for c = 2. Because the data did not comply with the probability model underlying conventional F-statistics, the statistic was denoted by quotation marks. Monte Carlo simulations (Beale, 1969) suggest that if one reads standard F-tables at “P”(“F”, c-1, n-c), then “probabilities” ≤ 0.005 provide an appropriate cut-off for accepting additional clusters. Because the analyses indicated that body mass was important in the thermal clustering of alligators, least-squares regression was used to test this relationship.

Results

[Fig. 7-1](#) plots D_{smooth} as a function of date for 1 October 1997 – 31 May 1998.

(Recall that the alligator-minus-environment difference-variable has been smoothed by a running median of 140 points; this was a weekly smooth.) Note that the plot is very noisy, with the value of D_{smooth} fluctuating roughly around 0°C difference until late February, after which the alligators become substantially warmer than most of their environment.

Monthly averages of D , the mean difference between average alligator temperature (G_{ave}) and environmental index (E), averaged 0.15°C in winter/fall while averaging 1.75°C in spring ([Table 7-1](#)). [Table 7-2](#) shows magnitudes of largest Fourier components for G_{ave} ($G_{Fourier}$) and for E ($E_{Fourier}$) by month. These magnitudes are indices of the intensity of daily thermal cycles, and their ratio ($G_{Fourier}/E_{Fourier}$) indicates the intensity of the alligator daily cycle relative to that of the environment. The column labeled $G_{Fourier}/BB_{Fourier}$ indicates the ratio of alligator daily magnitude to the daily magnitude of black-body temperatures. Note that both ratios are highest in spring, and particularly in March.

All the analyses reported thus far indicate that throughout most of the study period the alligators conformed at least roughly to general environmental thermal conditions. In the spring the animals averaged substantially warmer than their environment; their daily thermal cycle was more intense than that of their general environment although it never approached the cycle-intensity of black-body temperatures.

As indicated by [Fig. 7-1](#) and [Table 7-1](#), average alligator temperatures were usually close to an overall thermal index except during spring. However, the general term, “thermal conformity,” is inadequate for describing alligator temperatures in winter. For any timed observation E_{max} was defined as the maximum temperature of air, shallow-water, and deep-water temperatures. During January each of 13 study alligators exceeded E_{max} at least once by at least 6.4°C . It appeared that animals used radiant energy occasionally to achieve relatively high winter temperatures. The pattern is illustrated by [Fig. 7-2](#), which plots black-body temperature and temperature of a representative

alligator against date. To facilitate visual interpretation, only 10-20 January was plotted. As expected, each spike in alligator T_b inevitably co-occurred with a black-body high. However, not every black-body extreme was accompanied by a proportionally extreme T_b for the example alligator (or for any of the other study animals). Furthermore, different alligators, even in similar, proximate habitats did not always share thermal-high spikes. This is illustrated in [Fig. 7-3](#), which overlays January thermal plots for two female animals from ENP. Similarly, among 9 WCA alligators, T_b s of 7 animals (labeled A-G in [Table 7-3](#)) exceeded 30°C at least once during January. One animal warmed 13 times, but of the other 6, there was only one day on which more than one achieved $\geq$ 30°C. In other words, most animals broke 30°C occasionally during January, but they tended to warm up on different days ([Table 7-3](#)).

Cluster patterns and memberships varied in detail throughout the year, but usually two-cluster solutions divided the alligators roughly by size. One example is [Fig. 7-4](#). The two-cluster solution is “significant” (by the modified “F”-analysis as defined above; “F”[1,11] = 61.4); others are not (e.g., for the next higher order, or three-cluster, solution, “F”[2,10]=2.084; the associated “P”-value would be 0.175).

Like the cluster diagrams, linear least-squares regression also suggested the importance of size, particularly in relation to daily lows and diurnal cycle intensities ([Table 7-4](#)).

Discussion

Everglades alligators were found to be approximate thermal conformers throughout much of the year. In the spring, however, alligators warmed appreciably compared to their surroundings. This relative increase in alligator temperature is probably associated with increases in both breeding and feeding activities (McIlhenny, 1935; Neill, 1971). Alligator daily thermal cycles increase in intensity (relative to the environmental index, E) in spring ([Table 7-2](#)). During this season, “black-body” radiant energy was the likely source of heat for raising alligator T_b s higher than temperatures of water or air. The ratios of alligator daily cycle-intensities relative to black-body-temperature cycle intensities are also highest in spring ([Table 7-2](#)), as are correlations between black-body and alligator temperatures. In other words the data suggest, as most authorities have believed for many years (McIlhenny, 1935; Neill, 1971; Brandt, 1989), that in spring alligators increase body temperatures by basking.

In winter alligator temperatures tend to approximate those of their surroundings, but T_b s occasionally spike to higher levels. These spikes are associated with black-body highs ([Fig. 7-2](#)), but black-body highs do not inevitably translate to T_b spikes. Furthermore, the T_b spikes are not simultaneous across individual alligators ([Fig. 7-3](#) and [Table 7-3](#)). These factors suggest that T_b spikes result from alligator thermal “choices.” Since it is likely that alligators are not eating when average temperatures are below 22C°, the temperature-spiking behavior would be energetically inefficient since raising T_b would raise metabolic costs without apparent benefit (Colson and Hernandez, 1983; Lewis and Gatten, 1985; Peterson et al., 1993). Interestingly, monotremes and perhaps

other mammals show similar winter T_B spikes (Grigg, unpubl. data), and one of us has observed them in Crotalus horridus as well (Hope and Abercrombie, unpubl. data).

If alligators were warming up in order to digest food, one might expect them to warm up for several days. The fact that most temperature spikes were much briefer suggests that food was either digested quickly or that the alligators were warming up for other reasons. The excretion of metabolic wastes is one alternative explanation. Because Everglades alligators are unable to lower body temperatures to the levels of more northern alligators during winter, metabolic costs are higher; perhaps, as a result, metabolic wastes must be dumped more frequently. Warming the body to facilitate kidney function may be the most efficient way to deal with ionic and osmotic regulation (Minnich, 1982).

When alligator clusters were established by means of thermal variables, animals were found associated by size ([Fig. 7-4](#)). In many months larger alligators had relatively high minimum temperatures and less intense daily thermal cycles ([Table 7-4](#)). Numerous authors have commented on such relationships between size and thermoregulation (Spotila et al., 1973; Smith, 1975, 1976; Grigg, 1977; Johnson et al., 1978; Smith and Adams, 1978; Bartholomew, 1982; Grigg et al., 1998; Seebacher et al., 1999). Also, this relationship is what one would predict upon consideration of surface-to-volume ratios. However, social ranking has also been found to influence crocodilian thermal ecology (Seebacher and Grigg, 1997). It is likely that larger (dominant) alligators have relatively more choice of thermal macrohabitats (canals versus marsh) and microhabitats (placement, size/shape, and water depth of hole within marsh), than smaller alligators.

Conclusions

In recent years data logger technology has increased exponentially leading to smaller, less expensive loggers with greater memory capacities. Data loggers provide a useful and important tool in investigating thermoregulation in large reptiles. They allow us to remotely monitor body temperatures of free ranging animals without disturbing their behavior. Because data loggers provide continuous core body temperatures, it is possible to use analysis techniques not appropriate for fragmented data sets. While data loggers provide new opportunities for data acquisition, they also create new challenges for data analysis. A varied and comprehensive set of statistical techniques were needed to effectively analyze the large amount of data accumulated by these devices.

While we now know a great deal about the thermal patterns of alligators in the sloughs, marshes and canals of the Everglades, future studies should be conducted to examine the thermal patterns of alligators in drier regions of the Everglades. This would provide great insight into the physiologic response of alligators to drought conditions and aid in predicting the effect of changes in hydropattern on alligators.

In addition it is recommended that studies be conducted in northern parts of the alligators range in order to compare their winter ecology with Everglades alligators. The effect of the mild winters on the body condition of Everglades alligators is still unclear. The erratic spikes in T_b were especially interesting and unexplainable with current data. We suggest an examination of winter feeding habits also is warranted.

Finally, since this technique has proven successful in American alligators, we recommend its use in other species. Comparative studies to examine tropical crocodilians would be of great interest, especial when sympatric species are involved. To

examine the effect of the subtropical climate on Everglades alligators, a comparative study examining the northern alligators, Everglades alligators, and a tropical species would be especially valuable.

TABLE 7-1. Monthly and seasonal averages of D, the mean difference between average alligator temperature (G_{ave}) and environmental index (E). “Fall-Winter” includes January, February, and October-December, and “Spring” includes March-May.

Month	D (or, $G_{ave} - E$)	Month	D (or, $G_{ave} - E$)
January	0.19°C	October	0.34°C
February	0.10°C	November	-0.32°C
March	1.16°C	December	0.39°C
April	1.55°C	Fall-Winter	0.15°C
May	2.57°C	Spring	1.75°C

TABLE 7-2. Magnitudes of Fourier (daily) components for G_{ave} ($G_{Fourier}$) and for environmental index ($E_{Fourier}$); ratio of $G_{Fourier}/E_{Fourier}$; ratio of alligator circadian magnitude to circadian magnitude of black-body temperatures ($G_{Fourier}/BB_{Fourier}$); all by month.

Month	$G_{Fourier}$	$E_{Fourier}$	Ratio: $G_{Fourier}/E_{Fourier}$	Ratio: $G_{Fourier}/BB_{Fourier}$
January	4.83	3.61	1.34	0.043
February	10.70	6.73	1.59	0.098
March	19.18	6.18	3.11	0.133
April	19.00	10.60	1.79	0.099
May	10.91	25.50	0.43	0.034
October	4.41	5.24	0.84	0.024
November	7.15	6.67	1.07	0.048
December	5.25	5.67	0.93	0.044

TABLE 7-3. January dates on which T_B 's of 7 CA alligators (labeled A-G) exceeded 30°C .

Date	Animals warming to $\geq 30^{\circ}\text{C}$				Date	Animals warming to $\geq 30^{\circ}\text{C}$			
4 Jan.	A				13 Jan.	A		E	
5 Jan.	A				17 Jan.	A		F	
6 Jan.	A				21 Jan.				G
7 Jan.	A				22 Jan.	A			
9 Jan.		B	C	D	24 Jan.			F	
10 Jan.	A				28 Jan.	A		F	
11 Jan.	A				29 Jan.	A			
12 Jan.	A			E	31 Jan.	A		F	

TABLE 7-4. Linear regression of thermal variables on alligator size. Mass is in kg; “mean low” is mean, for month indicated, of daily minimum T_B ; “mean high” is mean, for month indicated, of daily maximum T_B ; “day-cycle intensity” is magnitude of largest (daily) Fourier component; “N/S” indicates $P > 0.05$; N is all 13 alligators.

Month	Slope / P-value for mean low = $f(\text{mass})$	Slope / P-value for mean high = $f(\text{mass})$	Slope / P-value for day-cycle intensity = $f(\text{mass})$
Nov.	0.07 / $P = 0.011$	N/S	N/S
Dec.	0.08 / $P = 0.001$	N/S	N/S
Jan.	0.07 / $P = 0.005$	N/S	N/S
Feb.	0.06 / $P = 0.014$	N/S	N/S
Mar.	0.06 / $P = 0.024$	N/S	N/S
Apr.	0.05 / $P = 0.050$	N/S	N/S
May	0.08 / $P = 0.001$	N/S	-0.06 / $P = 0.026$
Jun.	0.07 / $P = 0.003$	N/S	-0.08 / $P < 0.001$
Aug.	N/S	N/S	-0.07 / $P = 0.004$
Sep.	N/S	N/S	-0.07 / $P = 0.007$
Oct.	N/S	N/S	N/S

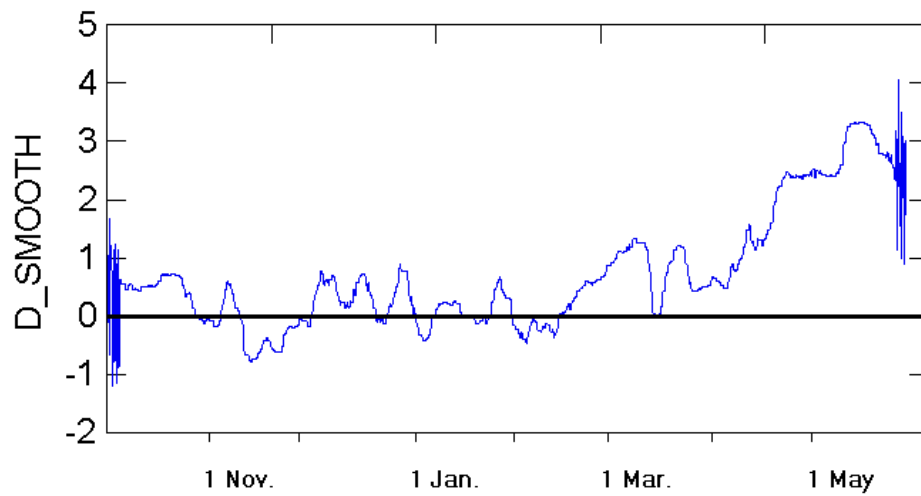


Figure 7-1. Plot of the difference between alligator ($n = 12$ animals) and environmental temperature average, D_{smooth} , as a function of time for 1 October 1997 to 31 May 1998. D_{smooth} is the running median of 140 points; this is a weekly smooth.

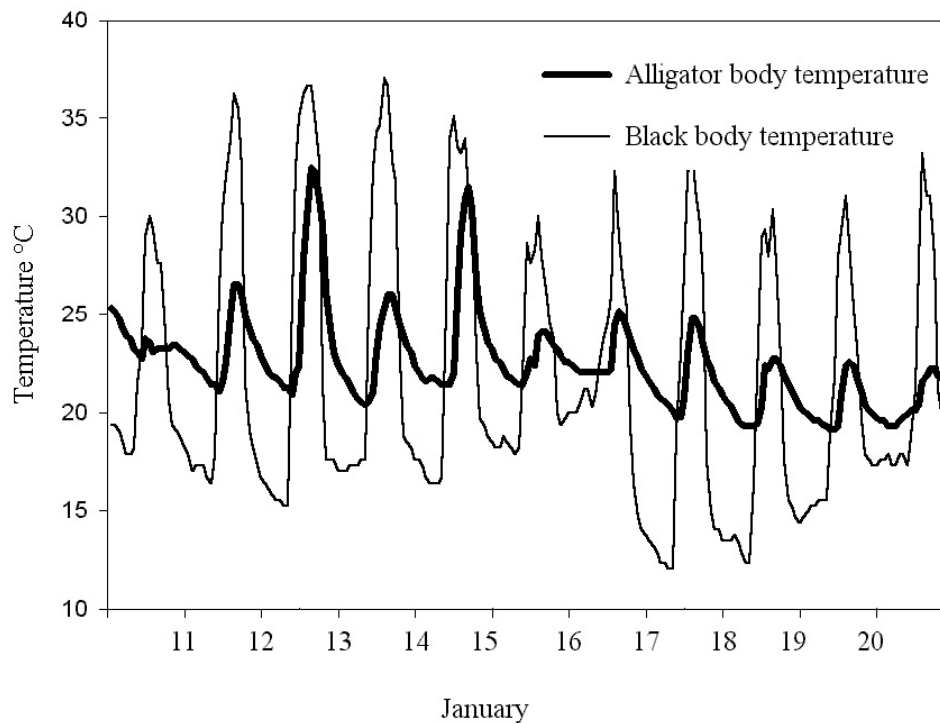


Figure 7-2. Overlay plot of black-body temperature and temperature of a representative alligator (alligator 50608) as a function of time for 10 - 20 January 1998.

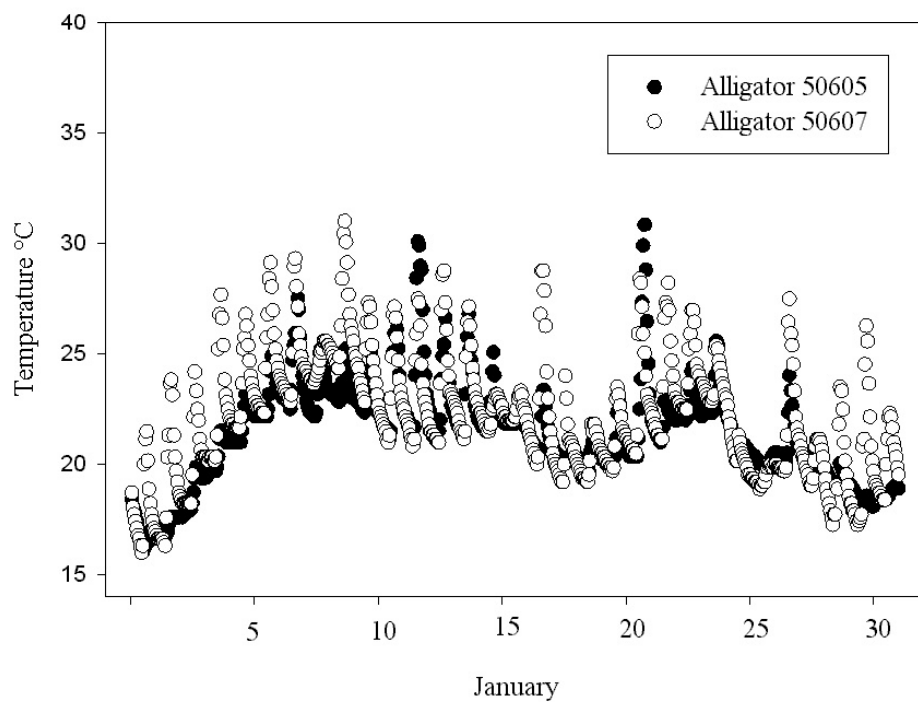


Figure 7-3. Overlay plot of body temperature for two alligators in Shark Slough, Everglades National Park for January 1998.

Cluster Tree

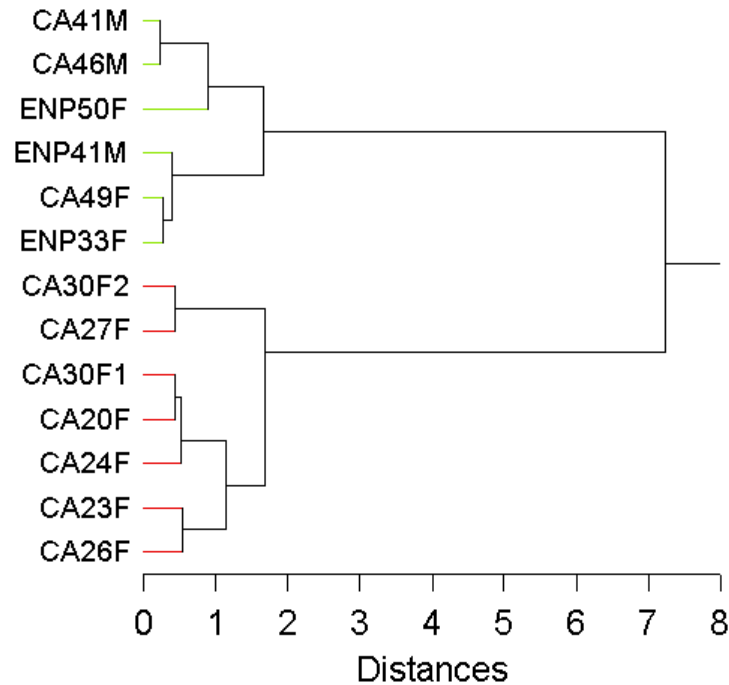


Figure 7-4. Cluster tree of all 13 study alligators. Clustering variables were May mean daily minimum body temperature, May Fourier (daily) magnitude, June daily minimum body temperature, and June Fourier magnitude. Initial letters on the branch tips designate study areas, central numbers show alligator mass (kg); the last letter indicates gender (M/F); a terminal digit distinguishes two 30 kg females. "Distances" shows proportional distances at which individuals or clusters were joined. Distance metric was Euclidean; linkage was Ward's method.

CHAPTER 8

REPRODUCTIVE STATUS AND MOVEMENT OF NESTING ALLIGATORS

Cory R. Morea and Stanley R. Howarter

The American alligator (*Alligator mississippiensis*) inhabits wetland environments throughout the southeast coastal plain from North Carolina to southern Florida and westward to eastern Texas and subsequently alligators must endure a broad distribution of environmental variability. Alligators utilize naturally occurring and man-made environments such as lakes, rivers, canals, marshes, sloughs, wet prairies, ephemeral ponds, and tidal salt marshes. The alligators northern environment is classified as temperate while its southern range in parts of Florida are considered warm-temperate and sub-tropical. With such a vast spectrum of habitat and environmental variability compounded by the dynamic nature of its wetland environments, the alligators' demographic characteristics vary both temporally and spatially.

The American alligator is not only a top consumer and a keystone species in the Everglades, but also physically influences the system through construction and maintenance of gator holes and trails (Kushlan 1974). The existence of this species is important to the faunal and floral character of the Everglades as it has evolved. Despite its prominence biologically and publicly in the system, many important questions about basic behavioral and population parameters of alligators remain unanswered. Although many assumptions can be made, we are not certain of movements or survival of varying size classes of alligators under either stable or fluctuating water levels. The reproductive

contribution of an individual animal or different size/age classes in any given year has been a principal stumbling block for attempts at modeling any crocodilian population. For effective modeling of alligators, more definitive answers to those latter two questions are essential.

Alligator nesting ecology has been investigated throughout parts of its range (Joanen 1969, Deitz and Hines 1980, Fogarty 1984, Ruckel and Steele 1984, Kushlan and Jacobsen 1990). Alligators initiate courtship and breeding from March-May (Joanen and McNease 1980) and female alligators construct nests and lay eggs from late May-July with peak nesting taking place from mid-June through mid-July (Deitz and Hines 1980, Fogarty 1984, Kushlan and Jacobsen 1990).

Fogarty (1984) and Kushlan and Jacobsen (1990) have studied the nesting ecology and related population parameters of alligators in the Everglades ecosystem; however, as restoration efforts increase within the region more information is needed to determine population demographics, especially reproductive characteristics as they relate to hydrology, to best manage this keystone species.

Objectives

The objectives of this study were: (1) to determine seasonal home range for nesting female alligators; (2) to observe the proportion of nesting female alligators in the population; (3) to determine nest characteristics of alligators in the Everglades ecosystem.

Methods

All telemetered female alligators in WCA 3A North and ENP were located on a weekly basis from 1 November 1997 to 31 October 1998. Positions were determined using methods discussed in Chapter 2. Home range was determined using a 95% Minimum Convex Polygon (MCP) method estimation model (Mohr 1947). The 95% MCP was used to facilitate comparisons to other studies.

Radio-tagged females were located in July-August, 1998 to determine the presence or absence of a nest. Upon discovery of a nest air temperature, water temperature, water depth, nest height, nest length and nest width were measured. The nests were then opened and depth to the top of the clutch and egg cavity temperature was measured. The top of each egg was marked and the eggs were removed and placed on the side of the nest. The eggs were counted and recorded as being viable (banded), partially flooded, flooded or badly damaged. Primary and secondary nest material, moisture content and percent shade at high noon was then recorded. Nests status was classified as high, dry, and intact; partially flooded; completely flooded; depredated; false; or under construction. Clutches of turtle eggs and the presence of fire ants were noted. A DGPS position was taken at the nest site and the habitat surrounding the nest was recorded. Any behaviors exhibited by the nesting female were also noted.

Home range for nesting females was calculated according to the biological seasons stated by Rootes and Chabreck (1993): annual (1 November 1997- 31 October 1998); winter (1 November 1997-28 February 1998); breeding (1 March 1998- 7 June

1998); nesting (7 June 1998-18 August 1998); and brooding (19 August 1998-31 October 1998).

Results

Six of the 15 radio-tagged female alligators located in ENP (Shark Slough) were found to have nested during the 1998 nesting season ([Table 8-1](#)). The annual home range of the nesting females ranged from 30.76 ha to 72.23 ha and averaged 54.08 ± 17.1 ha ([Table 8-2](#)). The seasonal home range sizes were: 54.8 ± 27.2 ha during winter; 24.4 ± 7.9 ha during the breeding season; 14.7 ± 6.7 ha during the nesting season; and 19.2 ± 11.2 ha for the brooding season ([Table 8-2](#)). Mean nest dimensions for ENP were: 61.5 cm height; 165.5 cm length; and 160.2 cm width ([Table 8-3](#)). Mean depth to the uppermost egg was 20.8 cm and mean clutch size was 24.2 eggs ([Table 8-3](#)).

Eight of 13 radio-tagged female alligators located in Water Conservation Area 3A North were found to have nested during the summer of 1998 ([Table 8-1](#)). The annual home range of the nesting females ranged from 26.1 ha to 53.3 ha and averaged 38.0 ± 8.6 ha ([Table 8-2](#)). The seasonal home range sizes were: 16.3 ± 5.2 ha during winter; 13.7 ± 11.2 ha during the breeding season; 22.4 ± 9.1 ha during the nesting season; and 13.2 ± 5.7 ha for the brooding season ([Table 8-2](#)). Two of 3 females that nested in 1997 nested during the 1998 nesting season.

Nest data for the 8 nesting females located in Water Conservation Area 3A North in 1998 were pooled with the 3 females that nested during the summer of 1997 for analysis. The nest dimensions were: 38.2 cm height; 121.7 cm length; and 115.1 cm

width ([Table 8-3](#)). Mean depth to the uppermost egg was 20.9 cm and mean clutch size was 26.6 eggs ([Table 8-3](#)).

Females 50653 and 50619 nested in 1997 and re-nested during the 1998 nesting season. Clutch size in 1997 and 1998 for female 50653 was 32 eggs and 30 eggs respectively. Clutch size in 1997 and 1998 for female 50619 was 27 eggs and 28 eggs respectively. Nesting efforts of both females failed due to nest flooding in both 1997 and 1998.

Pooled annual home range of the nesting females ranged from 26.1 ha to 72.2 ha and averaged 44.9 ± 14.9 ha ([Table 8-2](#)). Pooled nest data also were reported ([Table 8-3](#)).

Discussion

Annual home range size of radio-tagged nesting females determined by this study was similar to those reported by other authors. However, home range sizes were smaller during the breeding, nesting, and brooding seasons than those reported by Rootes and Chabreck (1993). This in part may be explained by the limited number of radio-locations gathered during these time periods for this study. The Minimum Convex Polygon (MCP) method of home range determination is a robust estimate and home range sizes calculated with this method usually increase with an increasing number of radio-locations as it estimates the total area utilized, not the area utilized in normal movements (White and Garrott 1990).

Nest characteristics varied between Shark Slough and Water Conservation Area 3A North for nest height (61.5 to 38.2 cm), nest length (165.5 to 121.7 cm), and nest width (160.2 to 115.1 cm). No significant difference existed between Shark Slough and WCA 3A for clutch depth (20.8 to 21.9 cm), viable eggs (24.0 to 20.2) or for clutch size (24.2 to 26.6). Kushlan and Jacobsen (1990) found that nest height averaged 65.0 cm and average clutch depth was 19.3 cm. They also found a average clutch size of 30 eggs per nest.

The depth and duration of marsh flooding for Shark Slough during this study was deeper and longer then Water Conservation Area 3A North. The larger nests found in Shark Slough might be an adaptation to higher water levels. Also during this study, fewer nests were flooded in Shark Slough. Water depths at the location of the nests were similar for Shark Slough and WCA 3A.

Water levels in June 1998 were very low as water was only observed in depressions, holes, canals, airboat trails and the deeper southeast slough within Water Conservation Area 3A North. The rainy season arrived in mid-July 1998 (after nest construction) and water levels quickly rose 30 cm or more in WCA 3A North. This rise in marsh water levels resulted in the majority of the nests being flooded or partially flooded.

Nest predation was not noted for any of the 17 nests observed in this study and Kushlan and Jacobsen (1990) observed similar low predation rates. They hypothesized that low predation rates were due to the isolated nest locations within the marsh proper.

The number of females that nested in Shark Slough and Water Conservation Area 3A North was 40% (6 of 15 females nested) and 62% (8 of 13 females nested)

respectively. Kushlan and Jacobsen (1990) stated that 29% of the females nested. The true proportion of females that nested within each area might have been higher. Thick vegetation and movement of females away from the nest after the first few weeks of nesting may have resulted in some of the nests being overlooked. More emphasis needs to be placed on nest searches early in the nesting season to avoid overlooking nests of radio-tagged female alligators.

Flooding losses are caused naturally by heavy rainfall and its concurrent increase in water flow, but can be exaggerated by management manipulations that result in higher flows and increased water levels, especially when these are postponed into the incubation period (Kushlan and Jacobsen 1990). The conservation of Everglades alligators, in addition to specific management measures, requires the re-establishment of the natural predictability of seasonal water level fluctuation.

Table 8-1. Annual home range size and clutch size of radio-tagged female alligators located in Everglades National Park (ENP) and Water Conservation Area 3A North from 1 November 1997 to 31 October 1998.

Area	Female	Total Length (cm)	Weight (Kg)	Clutch Size	Annual Home range (ha)
ENP	50602	185	24.5	22	64.41
	50605	232	50	33	67.37
	50607	200	32.7	32	36.54
	50732	187	20	18	53.17
	50737	188	20.5	21	72.23
	50739	191	22.7	19	30.76
WCA 3A	50616	227	40.9	28	28.95
	50617	175	20	29	26.06
	50618	189	23.6	21	32.6
	50653	214	30	30 ^a	41.8
	50619	209	29.5	28 ^b	42.35
	50640	222	40.5	31	52.99
	50653	214	27	24	39.71

^a Female nested in 1997 and had a clutch size of 32 eggs.

^b Female nested in 1997 and had a clutch size of 27 eggs.

Table 8-2. Mean home range size of radio-tagged females that nested in 1998 located in Everglades National Park and Water Conservation Area 3A North. Home range was calculated by the 95% Minimum Convex Polygon method.

Area	Sample Size	Year (ha)	Winter (ha)	Breeding (ha)	Nesting (ha)	Brooding (ha)
ENP	6	54.1	54.8	24.4	14.7	19.2 ^a
Range		30.8 – 72.2	23.8 – 92.6	14.7 – 35.8	3.4 – 23.3	13.1 – 36.1
WCA 3A	11	38.0	16.3	13.7	22.4	13.2
Range		26.1 – 53.3	5.2 – 22.0	2.7 – 39.1	7.5 – 38.5	3.7 – 21.5
Pooled Data	17	44.9	32.8	18.3	19.1	15.2
Range		26.1 – 72.2	5.2 – 92.6	2.7 – 39.1	3.4 – 38.5	3.7 – 36.1

^a Sample size was reduced to four females as one transmitter failed after the nesting season and a second had to be removed from the female due to infection.

Table 8-3. Mean nest characteristics for radio-tagged female alligators located in Everglades National Park (Shark Slough) and Water Conservation Area 3A North for the 1998 nesting season.

Area	Sample Size	Nest Height (cm)	Nest Length (cm)	Nest Width (cm)	Clutch Depth (cm)	Live Eggs	Total Eggs
ENP	6	61.5	165.5	160.2	20.8	24	24.2
WCA 3A	11 ^a	38.2	121.7	115.1	21.9	20.2	26.6
Pooled Data	17	46.4	137.2	131.0	21.5	21.5	25.8

^a Nest data for 3 females captured during the summer of 1997 were pooled with nest data collected during the summer of 1998.

CHAPTER 9

Conclusions

Everglades alligators live in a unique wetland system located in the southern most portion of their natural range. The Everglades is an oligotrophic system that provides a limited prey base for alligators. Further, South Florida has a distinctive wet and dry season with most of the rainfall coming from May through October and thus alligators must adapt continually to changing hydrologic conditions. In addition, periods of drought or excessive rainfall can envelop the region for years at a time drastically changing food availability, cover, and reproductive opportunities.

Alligators in the Everglades must endure high temperatures throughout the year with only occasional cool fronts during the mild winter. Alligators are ectothermic and as such extreme temperatures can stress alligators and adversely affect both their physical and reproductive condition. In the Everglades, high ambient temperatures coupled with a sprawling shallow-water wetland result in high water temperatures that offer little temperature relief for alligators. Therefore, Everglades alligators live in a highly dynamic system that requires constant behavioral adjustments for survival. Alligators in the Everglades have adjusted or adapted to their environment in two major ways: (1) by altering the landscape; and (2) by maximizing their efficiency in using both engineered and natural landscape patches to access their basic requirements for survival and reproduction.

It is well known that alligators clear vegetation and create marsh depressions called gator holes (McIlhenny, 1935; Craighead, 1968). Gator holes offer protection from extreme temperatures and human predators, provide a dry season refugia for both

alligators and other wetland species (Loftus et al., 1987), and act as breeding and nursery areas (Hines et al., 1969). Therefore, gator holes are extremely valuable habitats that provide alligators with the basics of food, water, shelter, and reproductive opportunities. Alligators uproot vegetation and move soil and organic matter to the hole's edge allowing woody vegetation to become established (McIlhenny, 1935). However, many areas of the Everglades marsh are not conducive to the construction of gator holes, and as a result, naturally occurring depressions often functionally replace gator holes. In the Shark River Slough of ENP, alligators were found to be heavily dependent upon traditional gator holes, whereas, alligators located in the marsh of WCA were more likely to use naturally occurring depression potholes. In all, the habitats that were used the most included gator holes, depression potholes (with any combination of graminoid emergent vegetation, floating vegetation, cattails, and open water), shrub islands (which often had a small hole or cave), spike rush sloughs, wet prairies, and sawgrass. Canal alligators mostly used levee breaks, edges with emergent or shrub vegetation, the canal proper, and near-by gator holes in the marsh. All of these are important habitats to alligators in the Everglades. How alligators used these created and naturally occurring habitats in the landscape are absolutely critical to their survival.

Home range size and shape and daily movement varied according to gender, temperature, reproductive efforts, habitat and water level. Male alligators had much larger home ranges and moved more on a daily basis than did females. Home range size and daily movement were positively correlated with temperature. However, the spring breeding season promoted greater home range sizes and daily movements than were observed during the summer. Limited summer movements were probably due to the

passing of the breeding season, high temperatures, and for females, the onset of the nesting season. Increased movements in the spring may also have been a result of increased feeding opportunities as air temperatures increased and water levels decreased pooling aquatic prey.

An alligator's location in the landscape of the Everglades affected their movements. Canal alligators had larger home range length and area in certain seasons than alligators located in marsh habitats. However, marsh alligators regularly used a higher proportion of their home range on a regular basis. Canal habitats were considered to be prime habitats for adult animals due to the consistently deep water and apparent abundance of prey. Canals offered open water travel corridors than tended to increase home range size by promoting long-distance movements of short duration, whereas, marsh habitats tended to limit these movements. However, it must be noted that while adult animals did prefer canal habitats for thermal refugia and feeding, these animals did not occupy and maintain alligator holes in the marsh. These holes are extremely important to other species (wading birds, fish species, etc..) as well as juvenile alligators. Further, canals offer little or no brood habitat for hatchling alligators and, as such, little production presumably results from nesting of canal animals. Cannibalism and predation certainly accounts for a high proportion of alligator production in canal habitats. An extension of this study will examine the relative reproductive contribution of alligators by marsh and canal habitats in 2000 and 2001.

Water level effected home range sizes and daily movements. Alligators moved less and had smaller home ranges in portions of the marsh that experienced near-dry conditions. Alligators located in canals and sloughs, where water was more abundant,

were less affected. Alligators in the marsh where water levels were lowest spent the majority of their time in holes, depression potholes, and airboat trails where pools of water remained. Travels through the marsh were of short duration as alligators were forced to walk over the near-dry peat soils while maneuvering through thick vegetation. As a result, during low water conditions, alligators were found to use well-used gator trails and airboat trails as travel corridors more exclusively than during high water conditions. Lowering water levels forced aquatic prey into remaining pools of water and probably favored alligator feeding for short periods of time. However, longer drought conditions resulted in loss of both water and prey in hole habitats, and therefore stress alligators. Water level tends to be lower during late spring and early summer, and extended drought conditions could adversely affect alligator reproduction in the Everglades.

Alligators were found to have 1 or more preferred gator holes or depression potholes within their home range. Regular movements were observed for alligators within their respective home ranges and daily movements were often from one preferred hole to another. These movements were most often initiated at dusk and commenced prior to dawn. However, similar movements were observed during daylight conditions. Everglades alligators in the marsh are dependent upon hole habitats. Alligators can survive during high water conditions without holes, however, the regular use of hole habitats throughout the year suggests that these are prime alligator habitats regardless of season, temperature or water level variation.

Everglades alligators may live in an adverse environment, but have adapted accordingly. Adult alligators establish a home range that encompasses several habitat

types that allow them to access the basic requirements of food, water, shelter, and reproductive opportunities. Of these natural habitats, traditional gator holes and depression potholes are the most critical.

Alligators in the Everglades exhibit distinct patterns of T_b within the annual temperature cycle. Alligator T_b is more variable in spring than in any other season. Alligators are elevating their T_b s on nearly a daily basis, which increases the time spent at warmer temperatures. Warm temperatures not only aid sperm and egg production for the coming reproductive season (Lance, 1987), but they also facilitate prey digestion (Lang, 1987). This is important to Everglades alligators since the normally limited prey base becomes concentrated in pools during the dry season, which peaks in spring. The increased activity of spring reflects the importance of this season in the ecology of alligators in the Everglades.

The high temperatures of summer increase the metabolic cost to alligators in the Everglades. When combined with low food availability resulting from the high water levels of the renewed wet season, summer appears to be a time of negative energy balance for Everglades alligators. Without the energy reserves gained during the spring, body condition is diminished and survivability reduced.

Fall alligator T_b s declines with the declining ambient temperatures. Alligators avoid metabolically active temperatures in fall since prey are dispersed by the high water conditions. This limits the fuel needed to maintain the metabolic rates associated with high temperatures.

Although Everglades alligators maintain low T_b s during the winter months, T_b s are occasionally raised to activity levels. These heating events are not synchronized as

would be expected if environmental factors alone were inducing basking behavior. Rarely does more than one alligator elevate T_b on the same day. While high T_b s are associated with feeding, winter T_b s were only elevated for short periods, usually one day. Since digestion of prey could not be accomplished in such a short time period (Barr, 1997), elevated T_b s in winter may be necessary for excretion of metabolic wastes.

Since winter T_b s of Everglades alligators are likely much higher than other parts of their range, it is unclear to what degree Everglades alligators are able to take advantage of hibernation to conserve resources. It is likely that in winter, Everglades alligators are caught in a limbo where they are too warm to conserve resources, yet too cool to efficiently digest prey. Food habit analysis from alligators in the coldest parts of the year, along with studies of their winter metabolic rates, would greatly improve our understanding of the winter ecology of Everglades alligators.

When alligators from the WCA and ENP were compared, differences emerged between the two study sites. It is possible that the deeper water in the marsh in ENP acted as a buffer to stabilized temperatures, preventing low minimum temperatures and allowing high temperatures gained through basking to result in higher overall mean T_b s. While there is much evidence to support this theory, there is also evidence to conclude that overall temperatures are greater in ENP because ambient temperatures are greater. Further study on the climatic differences between the two areas is needed to fully understand the dynamics of the two systems.

Because there are differences in the thermal ecology of ENP and WCA alligators, it is likely that other differences exist between Everglades alligator populations.

Managers should thus be cautious when extrapolating study findings from one area across the entire ecosystem.

Everglades alligators are adapted to fluctuating hydroperiods. While low water levels decrease their ability to thermoregulate, they also concentrate prey in an otherwise nutrient poor system. Without a food base to support the resulting high metabolic rate, a high stable T_b would be detrimental. In order to provide a sufficient food base, heterogeneity within the habitat must be maintained. By providing deep water habitat and areas where food was concentrated in times of low water, a heterogeneous environment would make food available to alligators without depleting the food base.

Management Implications

Several habitat management strategies can be utilized to promote favorable conditions for Everglades alligators. These include controlled burns, habitat manipulation, and water management. Dense monocultures of sawgrass were common in areas of the marsh where fire had not burned in recent years. Fires help to reduce fuel loads and opens up dense sawgrass, which favors alligator movement. Fires also create edge habitats that were found to be preferred travel routes of Everglades alligators. Naturally occurring fires in the Everglades often result in a mosaic of habitat types. This creates a more diverse landscape and provides alligators with travel routes, cover, and nesting habitat in close proximity to each other.

When managing habitat for alligators in the Everglades, spring is the most critical time for ensuring proper water levels. The decreased water levels at the end of the dry season concentrate prey that would otherwise be dispersed and difficult to acquire. Everglades alligators actively seek warm temperatures at this time in order to maximize their gain during this limited time of abundance. Energy reserves procured in spring are key to alligator survival during the summer wet season when the low food availability due to high water and high metabolic cost due to high environmental temperatures results in a negative energy balance.

The build up of energy reserves and elevated temperatures in spring is also correlated with the beginning of the reproductive season. Energy gained at this time is important in the reproductive success of female alligators. Warm temperatures are also necessary in sperm and egg development.

Water levels in June 1998 were very low and water was only observed in depression potholes, holes, canals, airboat trails and the deeper southeast slough within WCA. The rainy season arrived in mid-July 1998 (after nest construction) and water levels quickly rose 30 cm or more in WCA, which resulted in the majority of the nests being flooded or partially flooded. Nests located in ENP suffered fewer losses to flooding. Flooding losses are caused naturally by heavy rainfall and the resultant increase in water level, but can be exaggerated by water management practices that result in even higher water levels, especially when controlled water releases are postponed into the incubation period (Kushlan and Jacobsen, 1990). The conservation of Everglades alligators, in addition to specific management measures, requires the re-establishment of the natural predictability of seasonal water level fluctuation (Kushlan and Jacobsen,

1990). Therefore, to prevent excessive nest flooding, particularly in WCA, a more natural hydrology needs to be replicated. This would allow alligators to prepare for future water levels based on the water level at the time of nest construction (which historically indicated future water levels) and should result in fewer nests being lost to flooding.

It is important that proper water levels are maintained and alligators have opportunities to elevate body temperature. Large construction projects or other activities that would disrupt basking behavior for extended periods of time should be avoided from March until June.

While reduction in standing water in spring is necessary, reducing water levels below the rim of alligator holes is not recommended. Standing water in alligator holes is necessary for protection against temperature fluctuations. Extremely low water levels also leads to depletion of prey species, increasing the refractory period for population recovery.

Because June through September represents a time of consistently high temperatures, the increased water levels that naturally occur at this time must be maintained. Failure to elevate water levels by June may decrease alligator fitness as well as the fitness of other Everglades inhabitants.

While much of the historic research on alligators in the Everglades has been conducted in Shark Slough, this habitat does not represent the entire ecosystem. The ecology of alligators differs among the various habitats of the Everglades. Care should be taken when extrapolating data from one research site across the entire ecosystem.

Management of the Everglades needs to consider the variability that drives the system. Heterogeneity within the habitat and the hydroperiod are what makes life possible for alligators in an otherwise nutrient poor environment. Restoration efforts must strive to restore the natural sheet flow and the historic wet and dry cycle that concentrates prey, allowing alligators to survive in this unique landscape.

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