



# Effects of hydrology on the movements of a large-bodied predator in a managed freshwater marsh

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**Abstract** Wetlands are dynamic environments where aquatic organisms are affected by both predictable and unpredictable changes in hydrology. Understanding how abundant large-bodied predators respond to these changes is especially important in context of wetland restoration. We used satellite telemetry to investigate how individual (e.g., sex, size, body condition) and environmental factors influenced movement behaviors of American Alligators [*Alligator mississippiensis* (Daudin, 1801)] in a managed freshwater marsh ecosystem of the Florida Everglades. We quantified space use, movement activity, and habitat selection of animals ( $n = 18$ ) across hydrological seasons and the breeding period and performed stable isotope analyses to infer seasonal dietary changes. Though individual animals did not change space use across seasons, movement activity was lower for some individuals and  $\delta^{15}$

Nitrogen isotopic values were higher in the dry season possibly reflecting greater foraging opportunities when marsh dry down concentrates prey. Alligators may be using canals as foraging sites which have abundant prey year-round and shallow sawgrass habitats as spots for basking. Based on our findings, ongoing restoration of water inflow will likely change the distribution and movement behavior of alligators.

**Keywords** Movement · Habitat selection · Wetlands · Predator · Hydrology · Alligator

## Introduction

Wetlands are often dynamic habitats exhibiting both predictable and unpredictable changes in hydrology. In fact, many wetlands rely on seasonal pulses of rainfall and many depend on water management practices to maintain community structure and ecosystem function (Trexler et al., 2005; Mitsch & Gosselink, 2015). Wetland ecosystems support a wide range of valued functions including water storage, flood protection, and water purification (Beerens et al., 2017). Wetlands also serve as sources of habitat and food, supporting high biodiversity and biomass relative to their global coverage (Mitsch & Gosselink, 2015). On a global scale and over the last century, these important habitats have been drained and hydrologic regimes have been modified leading to a

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loss of ecological functions, economic value, and renewable ecosystem services (Zedler, 2000; Mitsch & Gosselink, 2015). Wetland services are also under threat from changes in global climate, invasive species pressures, and non-point source pollution (Erwin, 2009). Restoration of shallow water ecosystems remains an important goal for many regions and success relies on not only the redistribution of water, but also on aspects of water quality, water timing, and management of fish and wildlife populations (Zedler, 2000). Biogeochemical, hydrological, and biodiversity responses to restoration have been well-documented in some aquatic systems; however, expected shifts in animal behavior after restoration efforts are rarely studied despite their potential to have important feedbacks on ecosystem function (Brusati et al., 2001; Armitage et al., 2007; Lindell, 2008).

Seasonal, natural, and managed disturbances such as fire, drought, and flood characterize many wetlands. Effects of these disturbances on the environmental conditions faced by aquatic animals lead to behavioral changes both directly (i.e., responses to physical environmental changes) and indirectly (i.e., responses to changes in the distribution or abundance of food or predators). For instance, increased rainfall in the Mississippi River floodplain led to decreased foraging patch quality for marsh rice rats [*Oryzomys palustris* (Harlan, 1837)] and indirectly decreased site-specific patterns of colonization and ultimately increased extinction rates (van der Merwe et al., 2016). Within highly altered habitats, populations may face scarcity and fluctuations in resources which may drive plasticity in foraging and movement decisions. For example, in natural sloughs and artificial canals of managed wetlands, Florida Gar (*Lepisosteus platyrhincus* DeKay, 1842) move more frequently and across greater distances during seasonal flooding and dry down than in timeframes of stable water depths (Parkos et al., 2015). The complexity and importance of behavioral responses of animals suggests that models to inform wetland management practices and to evaluate restoration efforts should include species-specific components that integrate environmental drivers such as hydrology with biological drivers such as demographics (Gawlik, 2006).

Predators can exert considerable effects on the structure and function of aquatic ecosystems (Estes et al., 2016; Atkinson et al., 2017). Understanding drivers of the movements and distribution of species

that have disproportionate ecological effects relative to their density facilitates better predictions of the effects of disturbances and environmental change on community and ecosystem dynamics. Crocodylians are dominant predators in numerous tropical and subtropical aquatic ecosystems. American Alligators [*Alligator mississippiensis* (Daudin, 1801)] are the most abundant large-bodied predator in wetlands of the southeastern United States (Mazzotti & Brandt, 1994). The alligator is widely regarded as a dietary generalist and has the potential to generate top-down effects (Nifong & Silliman, 2013; Rosenblatt et al., 2015). Alligators have also been studied as physical ecosystem engineers (Kushlan, 1974) and may be important mobile vectors of nutrients between terrestrial and aquatic systems or between different aquatic systems (Subalusky et al., 2009; Rosenblatt & Heithaus, 2011). Despite being a primarily freshwater species, drivers of movement for alligators in freshwater wetlands (Subalusky et al., 2009; Strickland et al., 2016) have not been well-studied compared to coastal systems including estuaries (Rosenblatt & Heithaus, 2011; Fujisaki et al., 2014, 2016) and coastal marshes (Joanen & McNease, 1970, 1972).

The Florida Everglades is a large wetland that has experienced major changes in freshwater inflow, hydroperiods, and nutrient enrichment as a result of anthropogenic land use changes since the late 1800s (Sklar et al., 2005; Gawlik, 2006). Historically, the Everglades was a contiguous wetland with southward-oriented sheetflow towards the coast (Sklar et al., 2005). However, the system has been largely compartmentalized into marsh reservoirs separated by canals and levees, each section with a different water management plan. Water levels of Everglades freshwater marshes fluctuate from seasonal differences in rainfall in defined wet and dry periods and annually with high and low rainfall years (Trexler et al., 2005). Current efforts to restore the Everglades have focused on recreating natural hydrological patterns by decompartmentalizing areas blocked by canals and levees (NASEM, 2016). These actions are enacted within the Comprehensive Everglades Restoration Plan (CERP) to restore the natural hydrology of the Everglades. The Decompartmentalization and Sheet Flow Enhancement Physical Model (DPM), installed in October 2013, is a scientific field-scale test of specific plans within CERP (NASEM, 2016). One important piece of DPM involved

controlled water deliveries released early in the dry season of 2014. These DPM water deliveries were a large-scale experimental manipulation to investigate impacts of restoration and restore flowing water to an area impounded for more than 60 years (NASEM, 2016). The ecological impacts of major restoration efforts such as these are relatively unstudied. Overall, historic changes in hydrology are thought to have caused declines in some species' abundances and distributions (Sklar et al., 2005), but several restoration scenarios predict increases in many aquatic fauna including in the abundance of small fish and occurrence of wading birds in the Everglades (Beerens et al., 2017).

Because of their important roles as predators and ecosystem engineers and their relationship to local hydrological patterns, alligators may serve as useful indicators of the effects of restoration efforts on the Everglades (Mazzotti et al., 2009). Therefore, understanding aspects of their movement behaviors could be significant in determining the impact of environmental change on wetland ecosystems. Our current knowledge of how large-scale changes impact alligator movements and distribution across the landscape is inadequate to develop effective restoration plans. Important questions remain such as what factors drive alligator movement decisions, at what scales are decisions made, and what are the behavioral impacts of hydrology and wetland restoration? To address these questions, we used satellite telemetry and an individual-based movement modeling framework to quantify the movements of alligators across a range of environmental conditions in space and time in the oligotrophic freshwater marshes of the central Florida Everglades. We tracked both sexes over a range of adult size classes. Our main objective was to investigate behavioral drivers and assess the impact of hydrological changes on the movement behavior of alligators in a freshwater marsh.

## Methods

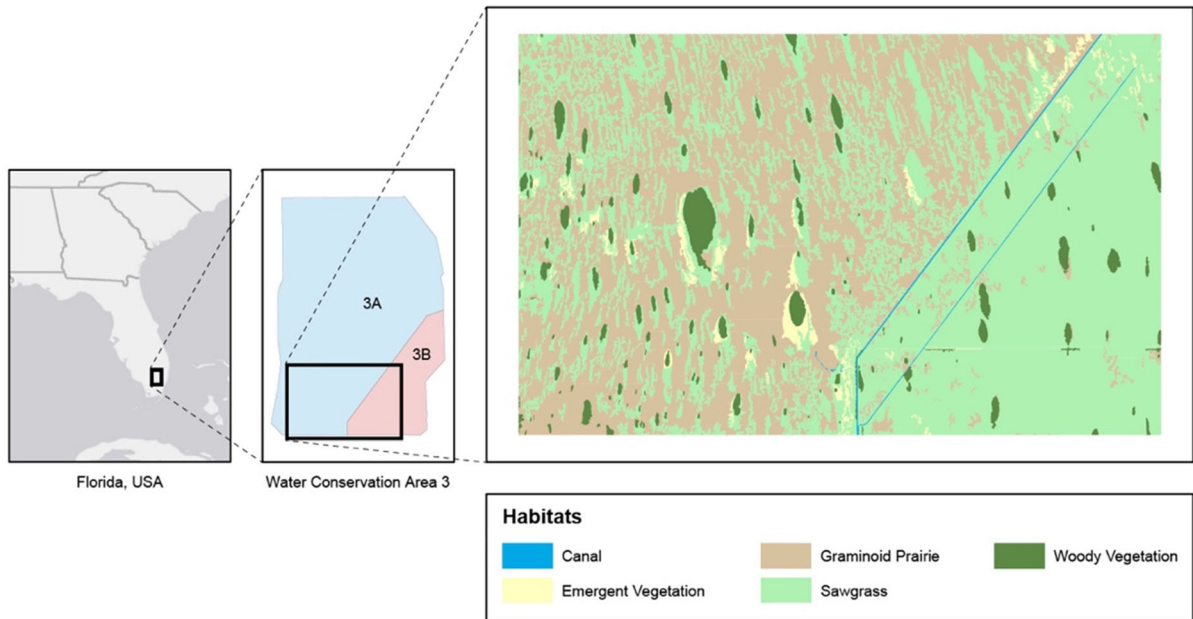
### Study area

Animals were tracked within Water Conservation Area 3 (WCA 3) in the central Everglades in two areas: 3A and 3B (Fig. 1) in 2014 and 2015. The WCA 3 is a 2442 km<sup>2</sup> area used for wildlife management, flood

protection, recreation, and water supply with surrounding man-made levees and canals. Organic peat soils overlay limestone bedrock and marsh water levels fluctuate seasonally, but the southern portion of 3A is excessively flooded (Bruland et al., 2006). Macrophytes, periphyton, and floating plants are abundant primary producers. WCA 3 and other Everglades marshes are often mosaics of spikerush-dominated wet prairies (e.g., *Eleocharis cellulosa* Torr.) and shallower (– 20 cm less) sawgrass (*Cladium jamaicense* Crantz) stands (Jordan et al., 1997). Water levels throughout WCA 3 are primarily controlled by rainfall (Julian, 2013), but 3A exhibits a longer hydroperiod with higher average water levels than 3B, which is more prone to drying. The area exhibits strong seasonal pulses of rainfall in the wet season (May through October) (Duever et al., 1994). Controlled water deliveries from the S-152 culverts affected water levels and flow in the area between the L67-A and L67-C canals (known as “the gap”) and WCA 3B (NASEM, 2016; USGS, 2019). These experimental releases were expected to have little to no impact on WCA 3A, but water levels did rise after the release in 3A along with 3B and the gap (USGS, 2019; see Appendix Fig. 6). Specifically, the water release lasted 86 days from 4 November 2014 to 29 January 2015 (USGS, 2019). Over this time period, discharge averaged  $7.7 \pm 0.4$  m<sup>3</sup>/s ranging from 6.2 to 8.5 m<sup>3</sup>/s (USGS, 2019).

### Alligator capture and sampling

Alligators were located using high-powered spotlights and captured using a pole and snare technique from an airboat. For each captured alligator, we determined sex by cloaca examination of the genitalia (Chabreck, 1963) and measured total length, tail girth, head length, snout-vent length, and weight using a spring scale. After collection of tissues for stable isotope analysis (see below), animals were released at their capture locations. We calculated Fulton's body condition factor ( $K$ ) using weight ( $M$ ) and snout-vent length (SVL) as  $K = M/SVL^3 \times 10^5$  (Brandt et al., 2016). Alligators were considered as being in poor ( $K \leq 1.95$ ), fair ( $1.95 < K \leq 2.10$ ), good ( $2.10 < K \leq 2.27$ ), or excellent condition ( $K > 2.27$ ) (Mazzotti et al., 2009; Brandt et al., 2016). When assessing correlations between body size and body condition metrics, we used Spearman's rank coefficient. We



**Fig. 1** Map of water conservation area 3, Florida, USA

used exact Wilcoxon rank sum tests when comparing total length and body condition between males and females and between alligators captured in WCA 3A and WCA 3B as a result of low sample sizes in each group.

### Telemetry

A satellite transmitter (Spot 5; Wildlife Computers; Redmond, Washington, USA) was attached to the nuchal scutes of each sexually mature alligator. Two stainless steel needles were forced through the skin on the posterior side of the rosette, and ran subcutaneously under the osteoderms of the rosette to the anterior side. We drew two strands of ethanol-soaked stainless steel wire (each approx. 50 cm in length) until they protruded through the skin near the rosette. We constructed a mold of marine epoxy the width of the transmitter along the top of the rosette. The transmitter was positioned on this bed and the subcutaneous wires were threaded back through the attachment loops on both sides of the transmitter, tightened and crimped with aluminum sleeves that locked the wires together. We used additional epoxy to complete the mold of the rosette shaped into a dome encasing the transmitter (Brien et al., 2010).

These tags transmit signals to the Argos satellite array when the animal surfaces and the sensor detects that it is dry. We programmed the tags to transmit a maximum of 250 locations per day checking for a dry sensor every 0.25 s with a fast repetition rate of 44.5 s and a slow repetition rate of 89.5 s, switched on after 10 successive dry transmissions. At these settings, the estimated battery life range was between 400 and 540 days. The tags were scheduled to transmit every hour of every deployment day. We used the Argos Low Earth Orbit global satellite-based location and data collection system for satellite tracking. Argos position estimates are grouped into six classes assigned by location accuracy: class 3 (accurate within 250 m), 2 (250–500 m), 1 (500–1,500 m), 0 (more than 1,500 m), A and B (unbounded accuracy estimation), and Z (invalid location). Using the Douglas filtering method for Argos satellite data, we filtered locations using possible animal speed and accuracy retaining only class 3 and 2 locations, the two most accurate categories, for analyses and discarded other locations. Within the filtered dataset, duplicate timestamps within one minute were removed with the best class location retained. Animals with fewer than 40 total filtered relocations were omitted. Nearly all locations (> 98%) were obtained between sunset and sunrise. We removed daytime locations from future

analyses to avoid bias. Average daily fix rate (calculated as number of days with a successful relocation divided by total number of days within the tracking period) for all tagged animals used in subsequent analyses including only filtered locations was  $30 \pm 15\%$ .

### Stable isotope analysis

We collected 5 mL of blood from the dorsal sinus cavity of each alligator using a syringe and 21-gauge needle. Blood samples were immediately centrifuged at 3,000 rpm for 30 s to separate red blood cells and plasma. We also clipped one tail scute from the single caudal whorl. Samples were immediately placed on ice in the field and later frozen at  $-20\text{ }^{\circ}\text{C}$  until they were homogenized and dried. Lipids were not extracted because removal does not significantly affect alligator isotope values (Rosenblatt & Heithaus, 2013). Samples were analyzed at the Stable Isotope Laboratory at Florida International University where variation among standards was  $0.04$  and  $0.09\text{ }‰ \pm \text{SD}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. Isotope samples were collected from five animals in late April and early May 2014 representing the dry season and 12 animals (eight with sufficient relocations for further spatial analyses) in late October and early November 2014 representing the wet season. Blood plasma and scutes of juvenile alligators have  $\delta^{13}\text{C}$  half-lives of *ca.* 60 and 150 days and  $\delta^{15}\text{N}$  half-lives of *ca.* 60 and 100 days, respectively (Rosenblatt & Heithaus, 2013). We compared carbon and nitrogen values of both tissues across sexes and seasons using exact Wilcoxon rank sum tests.

### Environmental data

We obtained daily weather data including precipitation and air temperature through National Oceanic and Atmospheric Administration's National Centers for Environmental Information data access web portal for the closest weather station, Miami International Airport (NOAA, 2019). We then used the *suncalc* and *maptools* R packages to obtain solar position by hour (Bivand & Lewin-Koh, 2019; Thierurnmel & Elmarhraoui, 2019). Hydrological data were obtained from the United States Geological Survey/National Park Service Everglades Depth Estimation Network database using Site EDEN 8 for relocations in WCA 3A,

Site 71 for relocations in WCA 3B, and Site 69E for relocations in the gap (USGS, 2019).

### Movement model and space use estimator

We used dynamic Brownian bridge movement models in the *move* R package (Kranstauber et al., 2019) to study the movement patterns and space use of individual animals (Kranstauber et al., 2012). These models use the time, angle, and distance between two locations to interpolate intermediate points, calculate motion variances along a path, and estimate density surfaces. We incorporated the estimated maximum error of each location corresponding to its assigned location class [i.e., class 3 (250 m) and class 2 (500 m)]. In addition, we used a margin of 11 locations and 31 as a window size (Kranstauber et al., 2012). The model results produce a UD, or utilization distribution, which is a probability distribution that is useful in predicting the relative intensity of use of cells (i.e., patches) within an animal's home range (Fieberg & Kochanny, 2005). The 95% UD contour area is expected to approximate the overall home range of the animal and the 50% UD contour area describes its area of core use (Said & Servanty, 2005; Kie et al., 2010). Multi-annual, seasonal, and breeding period dynamic Brownian bridge movement models and UD estimations were only performed for animals with 40 or more locations within the time-frame. We defined the breeding period as courtship and mating only which occurs April 1–June 1 each year (Mazzotti & Brandt, 1994). To evaluate the correlation between total length and range sizes as well as body condition and range sizes, we used Spearman's rank coefficient test. We also used exact Wilcoxon rank sum tests to compare overall, seasonal, and breeding range sizes between males and females. We used a paired two-sample Wilcoxon test to compare seasonal and breeding period range sizes across animals.

The movement model also estimates motion variance along the pathway using step length, turning angle, and speed between two relocations (Byrne et al., 2014). Changes in motion variance indicate changes in an animal's activity and behavioral state where higher values imply increased activity and/or irregular movement paths and lower values are coupled with decreased activity and/or regular paths (Kranstauber et al., 2012; Byrne et al., 2014). We



performed loess smoothed conditional means and used t-based approximation of standard error bounds to visualize how movement activity changed over seasons and the breeding period for each animal. To compare individual movement activity across seasons, we used an asymptotic Wilcoxon rank sum test. For some animals, we also compared the 60 days before and the 60 days during the experimental water release. Using short 60-day timeframes mitigates some of the potentially confounding effects of seasonal changes in movement patterns. We used a linear mixed model to determine animal movement activity (i.e., Brownian motion variance) as a function of individual animal state and external environmental variables. Alligator identification number was a random effect in all models. Fixed effects included sex, total length, body condition, breeding period (normal or during breeding period), water release (normal or during release), average daily temperature, daily rainfall, site-standardized gage height (i.e., water level), and an interaction of breeding period with sex. We tested correlation among explanatory variables to avoid issues with multicollinearity (Zuur et al., 2009). All covariates were scaled due to orders of magnitude differences in means (mean = 0, standard deviation (SD) = 1). Movement activity was  $\log(x + 1)$  transformed. We also included a continuous time autocorrelation structure of order of one in each model to account for the temporal autocorrelation in successive motion variance estimates within the random effect, animal. We included a null model and global model as well as all combinations of variables. We used Akaike's Information Criterion corrected for small sample sizes ( $AIC_C$ ) to rank models and selected competing model(s) where  $AIC_C$  was less than two units from the most supported model (Burnham & Anderson, 2002). In addition, Akaike weights ( $w_i$ ) allowed us to perform model averaging and we reported full model averaged coefficients and 95% confidence intervals with shrinkage (Burnham & Anderson, 2002).

### Habitat selection

We obtained 2014–2016 land cover and land use data from the South Florida Water Management District (SFWMD, 2019). The dataset was prepared by photo interpretation from aerial photography, classified using an internal cover and use classification system,

and verified with ground truthing (SFWMD, 2019). We used a minimum bounding polygon of all relocations plus a 5 km buffer to define the study site. We combined and collapsed several land cover and use categories to yield five habitat classes: (1) canal, (2) sawgrass marsh, (3) spikerush marsh, (4) woody vegetation (shrubs and trees), and (5) mixed emergent aquatic vegetation including broadleaf and floating plants. We performed geospatial analyses and created a 30 m resolution habitat map using ArcMap 10.6.1 (Environmental Systems Research Institute; Redlands, California, USA). We determined the habitat class for each relocation and calculated the proportion of each habitat within each animal's range. We used Manly selection ratios to evaluate habitat selection within a use-availability design at two spatial scales: second order, or the selection of home range (used) within our study area (available), and third order, or the selection of patches (used) within an animal's home range (available) (Thomas & Taylor, 1990; Manly et al., 2002). Selection ratios  $< 1$  indicate avoidance and  $> 1$  signify preference with the deviance from one explaining the strength of selection (Manly et al., 2002). We used 95% confidence intervals to designate preference and avoidance if the interval did not overlap one; if the interval overlapped one, then the habitat was neither preferred nor avoided. We used a Chi-squared test to compare habitat use between pre- and during experimental water releases using only the 60 days before and the first 60 days of release, wet and dry seasons, and breeding and non-breeding periods. We also used a Chi-squared test to compare mean habitat use between males and females. A relationship between the calculated motion variance and habitat class can reveal an association between animal behaviors in specific habitats (Kranstauber et al., 2012). We used a Kruskal–Wallis test, to determine if such a relationship existed. We performed all statistical analyses using R (Mac version 3.6.1; R Foundation for Statistical Computing; Vienna, Austria), and report means with  $\pm 1$  standard deviation (SD).

### Results

We deployed 18 satellite tags on alligators in WCA 3, with six tags in WCA 3A and 12 tags in WCA 3B. The first group of animals were tagged in April 2014 and

the last transmission occurred in November 2015 (Appendix Table 5). The final filtered dataset for movement analyses included 1,886 locations of 14 animals (Tables 1 and 2) with a mean of  $135 \pm 92$  locations per animal (range = 42–280; Appendix Table 5).

Body size measurements were highly correlated (all Spearman's rho ( $P$ ) > 0.73); thus, we used only total length as a proxy for body size in subsequent analyses. Alligator total length averaged 2.0 m and ranged from 1.7 to 2.6 m (Appendix Table 5). Males ( $n = 4$ ) had a mean total length of  $2.4 \pm 0.2$  m whereas females ( $n = 14$ ) had a smaller average length of  $1.9 \pm 0.1$  m ( $W = 54$ ,  $p < 0.01$ ). Animals had intact (non-amputated) tails. All tagged animals were likely sexually mature. Alligators in the Everglades sexually mature at smaller body sizes than elsewhere in their range; for instance, female alligators reach maturity at 1.5 m in total length compared to 1.8 m for both sexes elsewhere (Dalrymple 1996). Fulton's condition factor ranged from 1.08 to 2.23 with a mean of 1.92. Half (50%) of the tagged animals were in poor condition, 29% in fair, 21% in good, and none exhibited excellent body condition (Appendix Table 5). Fulton's condition factor was not correlated with total length ( $P = -0.23$ ,  $S = 1190.5$ ,  $p = 0.36$ ). In addition, we found no difference in the body conditions of alligators caught in 3A versus 3B and the gap ( $W = 36$ ,  $p = 1$ ) or between males and females ( $W = 27$ ,  $p = 0.9$ ).

Mean home range size was  $7.0 \pm 3.8$  km<sup>2</sup> (range = 1.1–14.4 km<sup>2</sup>) and mean core use area was  $1.0 \pm 0.5$  km<sup>2</sup> (range = 0.2–1.7 km<sup>2</sup>) (Table 1). All animals had one centralized area of activity within their home

range except animal  $\times 142,358$  who had two centers of activity. We detected no differences in home range sizes between alligators in 3A and 3B ( $W = 17$ ,  $p = 0.70$ ) or core use area sizes ( $W = 14$ ,  $p = 0.45$ ). Male alligators had larger 95% UD areas (mean =  $11.3 \pm 2.4$  km<sup>2</sup>) ( $W = 39$ ,  $p < 0.01$ ) than females (mean =  $5.3 \pm 2.7$  km<sup>2</sup>), but we did not detect a sex-specific difference in 50% UD areas ( $W = 34$ ,  $p = 0.05$ ). Males had larger wet season 95% UD areas ( $W = 23$ ,  $p = 0.01$ ) and 50% UD areas ( $W = 24$ ,  $p = 0.01$ ) than females (Fig. 2A). In addition, males had larger dry season 95% UD areas ( $W = 16$ ,  $p = 0.01$ ) and 50% UD areas ( $W = 15$ ,  $p = 0.03$ ) than females. Though there was a trend towards males having larger breeding period home ranges than females, this difference was not significant ( $W = 18$ ,  $p = 0.06$ ). Total length was positively correlated with home range size ( $P = 0.63$ ,  $S = 166.7$ ,  $p = 0.02$ ), but not core use area ( $P = 0.33$ ,  $S = 303.3$ ,  $p = 0.24$ ) (Fig. 3). Total length was also positively correlated with breeding period home range size ( $P = 0.90$ ,  $S = 11.5$ ,  $p < 0.001$ ), breeding period core use area, wet season home range size ( $P = 0.79$ ,  $S = 34.4$ ,  $p = 0.01$ ), wet season core use area, and dry season home range size ( $P = 0.76$ ,  $S = 20.6$ ,  $p = 0.03$ ), but not dry season core use area ( $P = 0.57$ ,  $S = 35.7$ ,  $p = 0.14$ ). Body condition was negatively correlated with home range size ( $P = -0.57$ ,  $S = 714$ ,  $p = 0.04$ ) and core use area ( $P = -0.58$ ,  $S = 720$ ,  $p = 0.03$ ). Body condition was not correlated with breeding period home range size ( $P = -0.63$ ,  $S = 196$ ,  $p = 0.08$ ) or core use area. Even though body condition was not correlated with dry season home range size ( $P = 0.07$ ,  $S = 78$ ,  $p = 0.88$ ), dry

**Table 1** Median and range of home range and core use area size, defined by the area in km<sup>2</sup> of the 95% and 50% utilization distributions, respectively, and mean and standard deviation (SD) of Brownian motion variance, an indicator of movement

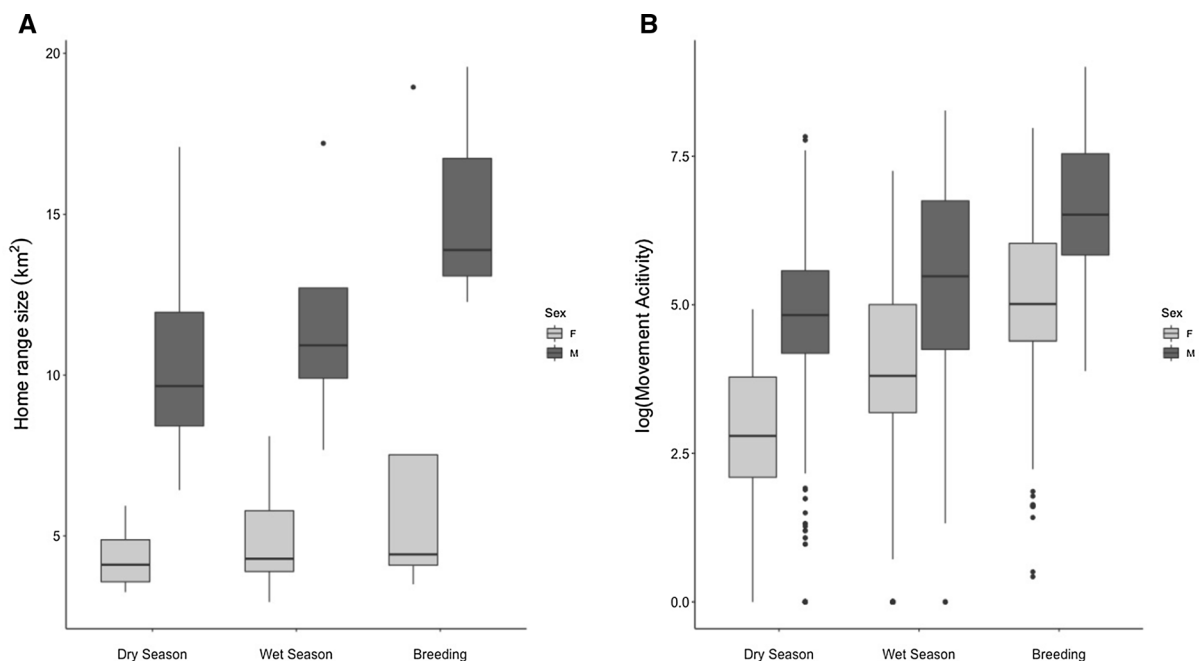
Timeframe	n (animals)	Home range	Core use area	Motion variance	
		Median (range) (km <sup>2</sup> )	Median (range) (km <sup>2</sup> )	n (relocations)	Mean $\pm$ SD
Study period	14	6.5 (1.0, 14.4)	1.1 (0.2, 1.7)	1,886	481 $\pm$ 806
Wet season	10	6.9 (3.0, 17.2)	1.1 (0.4, 1.7)	1,211	559 $\pm$ 843
Dry season	8	6.2 (3.2, 17.1)	1.0 (0.5, 2.1)	675	339 $\pm$ 712
Breeding period	9	12.3 (3.5, 62.3)	1.6 (0.7, 5.3)	493	912 $\pm$ 1226
Non-breeding period	9	6.1 (2.6, 8.0)	1.0 (0.4, 1.6)	1,393	336 $\pm$ 529

activity, across seasons and breeding period for American alligators (*Alligator mississippiensis*) in Water Conservation Area 3, Florida, USA tracked using satellite telemetry (2014–2015) for which there were sufficient relocations

**Table 2** Percent composition of the study area, percent mean and standard deviation (SD) of home range, defined by the area of the 95% utilization distribution, and relocations, and mean and SD of Brownian motion variance, an indicator of

movement activity, by habitat type for American alligators (*Alligator mississippiensis*) in Water Conservation Area 3, Florida, USA tracked using satellite telemetry (2014–2015) for which there were sufficient relocations

Habitat	Study area % Composition	Home range % Mean $\pm$ SD	Relocations % Mean $\pm$ SD	Motion variance Mean $\pm$ SD
Sawgrass marsh	50.7	28.3 $\pm$ 17.0	59.8 $\pm$ 31.2	443 $\pm$ 742
Spikerush marsh	43.6	30.6 $\pm$ 18.2	33.2 $\pm$ 30.2	491 $\pm$ 842
Woody vegetation	3.5	21.0 $\pm$ 10.8	3.2 $\pm$ 4.2	703 $\pm$ 1113
Mixed emergent vegetation	1.9	5.8 $\pm$ 2.7	3.4 $\pm$ 5.8	747 $\pm$ 1010
Canal	0.3	14.3 $\pm$ 8.3	0.4 $\pm$ 0.6	941 $\pm$ 1255



**Fig. 2** Home range size (A), defined by the area of the 95% utilization distribution, and Brownian motion variance (B), or movement activity, across the wet season, dry season, and breeding period for both male and female satellite-tracked

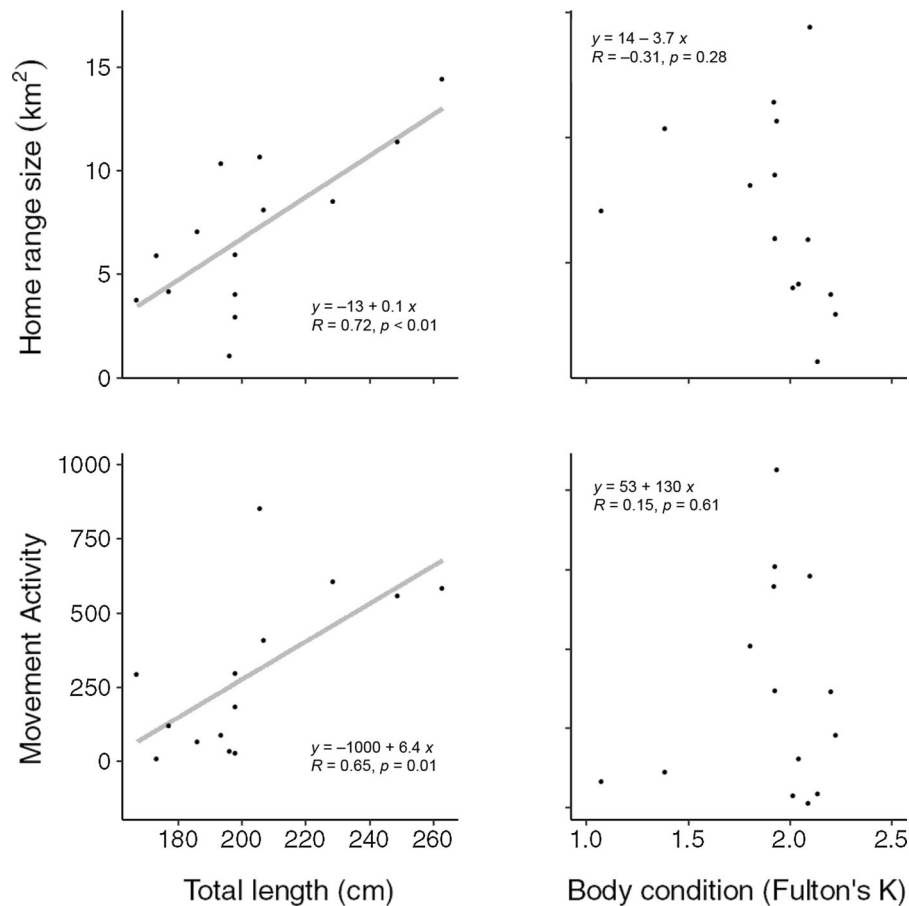
American alligators (*Alligator mississippiensis*) in Water Conservation Area 3, Florida, USA (2014–2015). One male alligator with a breeding period range size of 62 sq km was removed for plotting in A

season core use area, or wet season core use area, it was negatively correlated with wet season home range size ( $P = -0.65$ ,  $S = 272$ ,  $p = 0.05$ ). Individual animals did not differ in seasonal space use for 95% UD areas ( $V = 18$ ,  $p = 0.58$ ) or 50% UD areas ( $V = 15$ ,  $p = 0.94$ ) across the wet and dry seasons. However, individual animals did have larger 95% UD areas ( $V = 44$ ,  $p < 0.01$ ) and 50% UD areas ( $V = 45$ ,

$p < 0.01$ ) during the breeding period compared to the non-breeding period.

Five animals had greater activity in the wet season and exhibited a more sedentary tactic in the dry season (Appendix Table 6). Two animals had the opposite relationship with more activity in the dry season. Three animals showed no difference in activity across seasons. Other animals did not have enough locations to compare across seasons. The loess curve for the





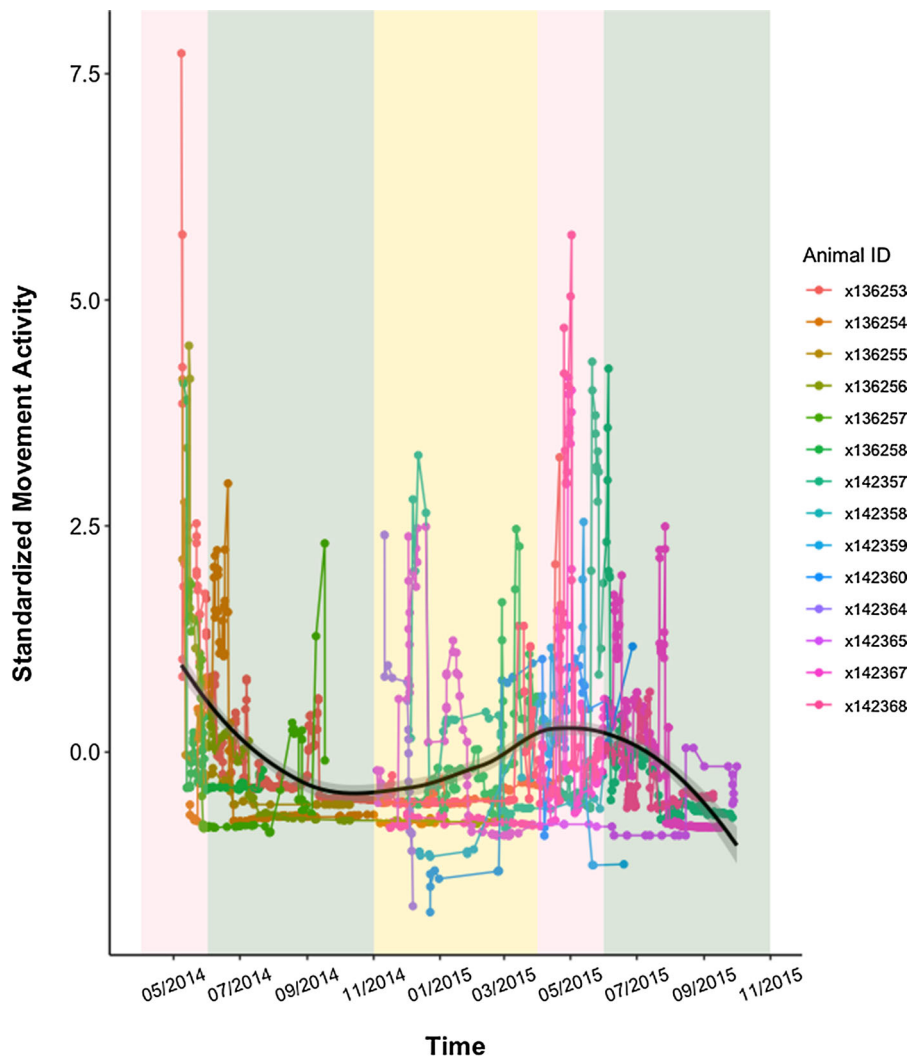
**Fig. 3** Multi-season home range size, defined by the area of the 95% utilization distribution, and mean movement activity (Brownian motion variance) compared across satellite-tracked American alligators (*Alligator mississippiensis*) of different total lengths and body conditions in Water Conservation Area 3, Florida, USA (2014–2015). The trend lines (dark gray) and

shaded areas (light gray) depict linear model regression lines and the 95% confidence region, respectively. Regression equations, Pearson's correlation coefficient, and  $p$  value is presented. Fulton's K was not a good predictor of home range size or movement activity thus regressions are not presented

population shows activity peaked in the breeding period, then declined in the wet season (Fig. 4). At the beginning of the dry season, activity reached a low point but began to rise before peaking again in the breeding period. Model selection shows that many of our hypothesized drivers may play roles in predicting movement activity (Table 3). However, our strongest predictors were water level and animal sex. Higher water levels resulted in lower movement activity, even though the relationship appears somewhat non-linear. Males were more active than female alligators, averaging  $653 \pm 934$  compared to  $178 \pm 338$ , respectively (Fig. 2B). Other variables including body size, body condition, breeding period, the experimental water release, and rainfall were important in top

models, but ultimately may not be good predictors of alligator movement activity since their confidence intervals overlap zero in the averaged model (Table 4). At the population level, we may not have had enough data to determine the effect of the water release on movement activity. Three animals had sufficient estimates of movement activity rates ( $n > 5$  estimates per group) to compare the first 60 days of the water release to the 60 days immediately before. All three animals exhibited decreased activity associated with the release (x136253:  $W = 1306$ ,  $p < 0.001$ ; x136254:  $W = 117$ ,  $p < 0.001$ ; x136256:  $W = 46$ ,  $p = 0.001$ ) (Fig. 5).

Males and females did not differ in plasma  $\delta^{13}\text{C}$  ( $W = 35$ ,  $p = 0.50$ ) or  $\delta^{15}\text{N}$  values ( $W = 28$ ,  $p = 1$ )



**Fig. 4** Movement activity (Brownian motion variance) of satellite-tracked American alligators (*Alligator mississippiensis*) compared across wet (green-shaded area), dry (yellow-shaded area) seasons, and breeding period (pink-shaded area) in Water Conservation Area 3, Florida, USA (2014–2015).

(FAppendix Fig. 7). Similarly, males and females did not differ in scute  $\delta^{13}\text{C}$  ( $W = 32$ ,  $p = 0.55$ ) or  $\delta^{15}\text{N}$  values ( $W = 1.5$ ,  $p = 0.11$ ), but only one female was grouped with males with low  $\delta^{15}\text{N}$  values (Appendix Fig. 7). For blood plasma tissue,  $\delta^{13}\text{C}$  values averaged  $-27.5 \pm 0.9\text{‰}$  in the wet season and  $-27.7 \pm 1.0\text{‰}$  in the dry season and were not different across seasons ( $W = 38$ ,  $p = 0.89$ ). For plasma,  $\delta^{15}\text{N}$  values were lower in the wet season ( $7.3 \pm 0.8\text{‰}$ ) than the dry season ( $8.3 \pm 0.6\text{‰}$ ;  $W = 10$ ,  $p = 0.01$ ). For scute tissue,  $\delta^{13}\text{C}$  values averaged  $-25.5 \pm 1.0\text{‰}$

Movement activity was scaled over the time series for each animal. The line (black) represents loess smoothed conditional means and the t-based approximation of standard error bound (light gray)

in the wet season and  $-25.8 \pm 0.9\text{‰}$  in the dry season ( $W = 36$ ,  $p = 0.57$ ). However,  $\delta^{15}\text{N}$  scute values in the wet season ( $8.2 \pm 0.8\text{‰}$ ) were lower than those of the dry season ( $9.1 \pm 0.5\text{‰}$ ;  $W = 9$ ,  $p = 0.01$ ).

Sawgrass marsh covered 50.7% of the study area, followed by spikerush marsh (43.6%), woody vegetation (3.5%), mixed emergent vegetation (1.9%), and canal (0.3%). Animals were relocated most often in sawgrass marsh (59.8%), then spikerush marsh (33.2%), trailed by emergent vegetation (3.4%), woody vegetation (3.2%), and canal (0.4%). However,

**Table 3** Results from linear mixed models from candidate set with  $\Delta AIC_c \leq 2$  and the null and global models to describe American alligator (*Alligator mississippiensis*) Brownian motion variance, an indicator of movement activity

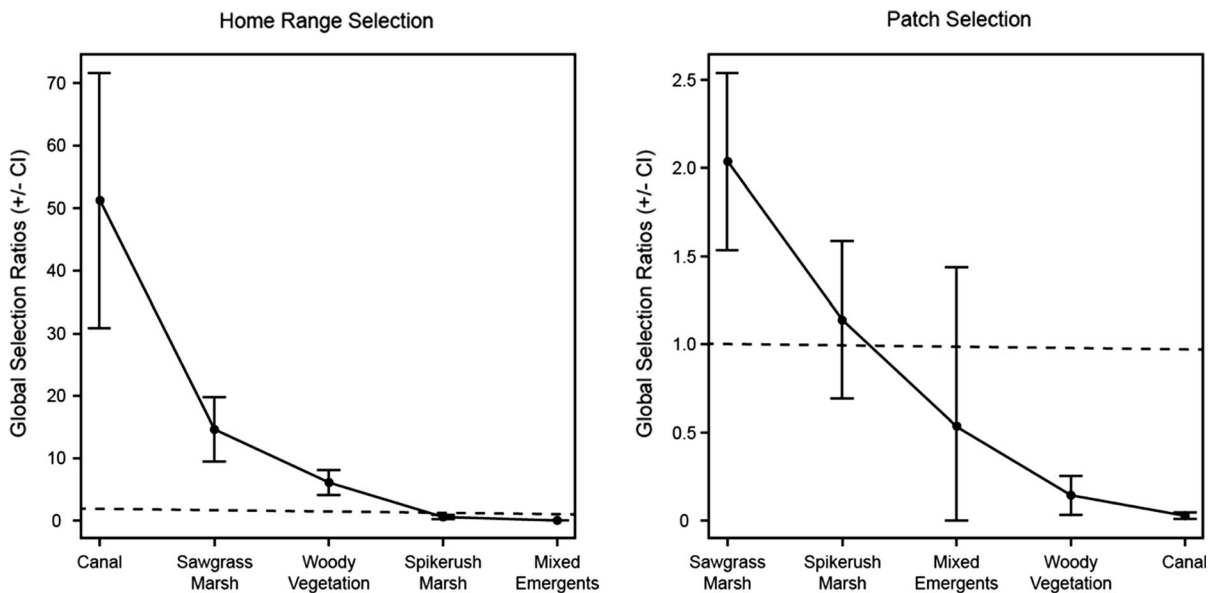
Model	Df	Log L	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
WaterLevel + sex	6	− 1401.1	2814.2	0.00	0.71
WaterLevel + sex + release	7	− 1400.3	2814.6	0.38	0.14
WaterLevel + breeding + sex	7	− 1400.4	2814.9	0.73	0.12
WaterLevel + sex + rainfall	7	− 1400.5	2815.1	0.86	0.11
WaterLevel + breeding + sex + release	8	− 1399.6	2815.3	1.12	0.10
WaterLevel + sex + release + rainfall	8	− 1399.7	2815.5	1.28	0.09
WaterLevel + breeding + sex + rainfall	8	− 1399.8	2815.8	1.57	0.08
WaterLevel + sex + BodyCondition	7	− 1401.0	2816.1	1.89	0.07
WaterLevel + sex + BodySize	7	− 1401.1	2816.2	1.99	0.06
WaterLevel + breeding + sex + release + rainfall	9	− 1399.0	2816.2	2.00	0.06
Global (also includes temp and sex*breeding)	13	− 1398.9	2823.7	9.50	0.00
Intercept only	4	− 1409.9	2827.7	13.52	0.00

Animals were tracked using satellite telemetry (2014–2015) for which there were sufficient relocations in Water Conservation Area 3, Florida, USA. Individual animal is the single random effect in all mixed models. All models include a continuous time auto-correlation structure of an order of one. Models are ranked from most to least supported with all including an intercept. Number of parameters is described by “df” with all models containing an intercept term, random term, and an error term. “Log L” denotes the log likelihood of each model. Akaike information criterion were corrected for small sample sizes (“AIC<sub>c</sub>”) and number of units from the top model is denoted by “ $\Delta AIC_c$ .” Weight of support for each model within the entire model set is given by “ $w_i$ ” in a total of 1. All covariates are scaled (mean = 0, SD = 1). “WaterLevel” relates to standardized site-specific gage height, “Sex” is the animal’s sex, “Release” describes if the estimate was calculated in within a period of experimental water release, “Breeding” means the estimate was calculated during the breeding period, “BodyCondition” is the animal’s measured body condition, “Temp” is the mean daily temperature, “Rainfall” is the total daily rainfall, and “BodySize” is the animal’s measured total length

**Table 4** Linear mixed model coefficients from an averaged model to describe American alligator (*Alligator mississippiensis*) Brownian motion variance, an indicator of movement activity

Parameter	$\beta$	SE	Pr( > Z )	95% CI
Intercept	3.83	0.33	< 0.01	3.18, 4.49
WaterLevel	− 0.25	0.10	0.01	− 0.43, − 0.06
Sex (male/female)	1.62	0.41	< 0.01	0.72, 2.51
Release (normal/experiment)	0.08	0.15	0.57	− 0.12, 0.55
Breeding (normal/breeding)	− 0.06	0.11	0.61	− 0.42, 0.11
Rainfall	0.01	0.01	0.64	− 0.01, 0.04
Body Condition	0.01	0.05	0.94	− 0.36, 0.50
Body Size	− 0.01	0.08	0.97	− 0.75, 0.64

Animals were tracked using satellite telemetry (2014–2015) for which there were sufficient relocations in Water Conservation Area 3, Florida, USA. Individual animal is the single random effect and the model includes a continuous time auto-correlation structure of an order of one.  $\beta$  denotes the beta estimates for each parameter in the averaged model reported as the full average. SE describes the standard error of the coefficient and Pr( >|Z|) is the p value of the Z statistic. 95% CI denotes the lower and upper values of the 95% confidence interval for the beta estimate of each parameter. All covariates are scaled (mean = 0, SD = 1). “WaterLevel” relates to standardized site-specific gage height, “Sex” is the animal’s sex, “Release” describes if the estimate was calculated in within a period of experimental water release, “Breeding” means the estimate was calculated during the breeding period, “BodyCondition” is the animal’s measured body condition, “Temp” is the mean daily temperature, “Rainfall” is the total daily rainfall, and “BodySize” is the animal’s measured total length



**Fig. 5** Population-level habitat selection ratios of satellite-tracked American alligators (*Alligator mississippiensis*) in Water Conservation Area 3, Florida, USA (2014–2015) at the scale of selecting home ranges within the study area (left panel)

the most abundant habitat type within home ranges across animals was spikerush marsh (30.6%), followed by sawgrass marsh (28.3%), woody vegetation (21.0%), canal (14.3%), and emergent vegetation (5.8%). We did not see a shift in population-level habitat selection within the first 60 days during water releases compared to the 60 days before water releases ( $\chi^2 = 20$ ,  $df = 16$ ,  $p = 0.22$ ). In addition, there was not a detectable relationship between motion variance and habitat type ( $\chi^2 = 8.1$ ,  $df = 4$ ,  $p = 0.09$ ). Analysis of second-order habitat selection, or selection of home range within the study area, showed that animals at the population level preferred canal habitat within their home ranges (Appendix Fig. 6). Animals also preferred home ranges composed of sawgrass marsh and woody vegetation habitats. Spikerush marshes and mixed emergent vegetation were avoided within home ranges compared to their availability in the study area. General patterns of preference and avoidance were similar in the wet and dry seasons, although there was a difference in the proportions of habitats within alligator home ranges ( $\chi^2 = 10$ ,  $df = 4$ ,  $p = 0.04$ ). In the dry season, home ranges were composed of 13% canal 10% emergent vegetation compared to 17% and 7%, respectively, during the wet season (Table 2). The selection of home ranges did not change between the

and at the scale of selecting patches within home ranges (right panel). The dotted line represents a selection ratio of 1; selection ratios < 1 indicate avoidance and > 1 signify preference with deviance from one explaining the strength of selection

breeding and non-breeding periods ( $\chi^2 = 10$ ,  $df = 6$ ,  $p = 0.13$ ). Third-order habitat selection, or the selection of patches within home ranges, revealed that at the population level, animals preferred sawgrass marshes, but avoided woody vegetation and canal habitats compared to the availability of these habitats within their home ranges (Appendix Fig. 6). Patches of spikerush marshes and emergent vegetation habitats were neither selected nor avoided in their home ranges. These habitat selection patterns applied for the wet season and outside the breeding period. In the dry season and breeding period, there was preference for sawgrass marshes and selection against mixed emergent vegetation, woody vegetation, and canal with no selection for or against spikerush marshes. We did not see a difference in habitat use between males and females at either scale (second order,  $\chi^2 = 20$ ,  $df = 16$ ,  $p = 0.22$ ; third order,  $\chi^2 = 20$ ,  $df = 16$ ,  $p = 0.22$ ).

## Discussion

Our results suggest that large-scale changes in hydrology and water management drive movement behavior of alligators. For instance, animals generally moved less in the dry season compared to the wet

season. High prey availability in habitats like canals was likely the primary factor contributing to sedentary movement behavior in the dry season. Compared to marsh habitats in the dry season, fish and invertebrates increase in density in the immediate proximity of deeper water alligator ponds and canals as they seek refuge from drydown effects (Kushlan, 1974; Rehage & Trexler, 2006; Parkos et al., 2011). Alligators may position themselves throughout the year to access deeper water areas where prey congregate. In addition, crocodylians are capable of managing their energy budgets over very long periods of time (greater than six months without eating; e.g., Lance, 2003) allowing them to potentially mitigate seasonal reductions in prey abundance. Beyond finding differences in movements with seasonal changes in hydrology, we also found that some alligators moved less after experimental water deliveries than immediately before the release. Changes in water levels resulting from these deliveries might have influenced availability, or suitability, of particular habitats based on altered prey distribution and thermal buffering capacity of water for alligators. In wetlands, fluctuating hydrological conditions can provide new access to patches, remove access to low-water habitats, alter physical parameters (e.g., oxygen availability and temperature) within patches, and impact local prey availability (DeAngelis et al., 1997; Trexler et al., 2005; Goss et al., 2014).

An individual's home range size and home range selection were consistent across seasons indicating consistency in the amount and type of habitat needed at larger spatial scales even when seasonal resource distributions differ. However, alligators did not have congruency in selection of habitats between scales. Habitat selection is a hierarchical behavioral process (e.g., Jetz et al., 2004; McMahan et al., 2017) and alligators make decisions at different scales about their most important day-to-day life functions including thermoregulation and feeding. At the finer spatial scale, animals avoided patches of mixed emergent vegetation in the dry season but showed no selection or avoidance in the wet season. During the dry season, these areas may dry out and limit structure offered to aquatic prey making these habitats less desirable. Future studies using dynamic habitat models and high temporal resolution environmental information will provide additional insight into seasonal drivers of movement.

For their home range, animals selected canal habitats in both seasons. Alligators, particularly males, prefer open water habitats because of the availability of larger prey, unobstructed courtship areas, and thermal refuges (Joanen & McNease, 1972). Other large-bodied wetland predators, such as piscivorous fish, use canals and alligator ponds disproportionate to their availability even during high water and in long hydroperiod sites indicating that these habitats may confer some advantage in prey interactions, ease of movement, or thermal properties over marsh habitats (Parkos et al., 2015; Ontkos, 2018). Alligators are hypothesized to be opportunistic, nocturnal predators that primarily use sit and wait hunting tactics (Delany & Abercrombie, 1986; Wolfe et al., 1987; Nifong et al., 2014). Thus, the most efficient movement tactic may be to remain near an alligator pond or canal where prey availability remains high compared to the shallow marsh (DeAngelis et al., 1997; Rehage & Loftus, 2007). Though alligators strongly selected canal habitats for their home range they avoided them at the patch level. Animals spend time in habitats immediately adjacent to canals and were often detected on banks and in the emergent vegetation near canals basking and resting (personal observation). The number of relocations in canal habitats should be considered conservative. Satellite transmission will not occur when the animal is completely submerged; thus, relocations in habitats like canals where alligators might be spending more time underwater were potentially missed. Across both seasons, alligators selected sawgrass marsh habitat at both scales and avoided spikerush marshes when selecting home ranges. Sawgrass habitats are typically shallower and support lower densities of fish compared to spikerush habitats (Jordan et al., 1997; Trexler et al., 2002; Chick et al., 2004). Because of the lack of prey, one biological explanation is that alligators may be using sawgrass stands for thermoregulation and/or rest. Shallow sawgrass stands may also increase the complete exposure of the dry sensor of the tags leading to more transmissions and detections compared to the other deeper water habitats. Future studies could gain insight into the bias associated with satellite tags by simultaneously co-deploying other technologies that yield underwater relocation information such as acoustic- or radio-tags (e.g., Rosenblatt & Heithaus, 2011; Strickland et al., 2016).

In our study,  $\delta^{13}\text{C}$  isotopic values were not different across seasons, but  $\delta^{15}\text{N}$  values were consistently higher in the dry season than in the wet season. Given the lack of isotopic source data, it is unclear if alligators were directly feeding on higher trophic level prey items like piscivorous fish in the dry season or if the trophic baseline shifted because higher trophic level species became concentrated in refuge habitats. Williams & Trexler (2006) in our same study system, found a similar pattern of elevated trophic positions in the dry season for two abundant small-bodied consumers, Eastern Mosquitofish (*Gambusia holbrooki* Girard, 1859) and riverine grass shrimp [*Palaemonetes paludosus* (Gibbes, 1850)]. The authors, too, were unable to determine if elevated  $\delta^{15}\text{N}$  values were related to diet shift towards higher trophic level prey, the addition of lower trophic level species, or both. In addition, high variability in  $\delta^{15}\text{N}$  discrimination values for alligators in experimental settings make assigning trophic levels in field studies difficult (Rosenblatt & Heithaus, 2013). A strong approach for future work would be to couple movement data with animal-borne cameras and/or high-resolution diet tools like fatty acid biomarkers to validate the assumption that canals and alligator holes are primary foraging habitats year-round.

Ontogenetic niche shifts and sex-specific behaviors of alligators are well-documented. In our study, male alligators had home ranges more than twice the size and had three times higher movement activity estimates than females. Male alligators generally move more often and across greater distances than females (Joanen & McNease, 1970, 1972; Goodwin & Marion, 1979). However, specific reasons for differences in movements by sex are unclear. Some differences can be attributed to the larger body size of males (Platt et al., 2011) which may correlate with higher metabolic demands and larger spaces needed to gather necessary food resources. Other disparities in movement between males and females may be related to social differences. Large males are the most dominant within dominance hierarchies and control access to resources including courtship arenas and defend larger areas (Lang, 1987). Many animals change activity and space use at the onset of the breeding period to increase encounter rates with potential mates [e.g., cottontail rabbits, *Sylvilagus floridanus* (Allen, 1890)—Trent & Rongstad, 1974; saltwater crocodiles, *Crocodylus porosus* Schneider, 1801—Kay, 2004]. To

access multiple mates in a single breeding period, animals may travel from patch to patch which increases range size and activity compared to non-breeding periods. We found that individual alligators of both sexes used more space and, as a population, movement activity was over 2.5 times higher during the breeding period than during the non-breeding season. Alligators need to access patchy and limited open water areas for courtship and mating (Joanen & McNease, 1972; Lang, 1987). In fact, every alligator selected open water cover over other habitats in the home range during the breeding period and throughout the year.

Body size and condition explained space use patterns to some degree. Larger animals are expected to require larger home range sizes because of increased metabolic demands (Said & Servanty, 2005; Ofstad et al., 2016), and our data were consistent with this pattern. Social structure may also drive this relationship. In crocodylians, social status is largely explained by body size with large males generally controlling access to both mates and food (Johnson, 1973; Lang, 1987; Strickland et al., 2016). We did not find that animal core use area size varied with body size. At small scales, adult alligators regardless of body size might have a minimum amount of space needed for basic sedentary life functions such as thermoregulation behaviors and resting which dominate their activity as ectothermic poikilotherms. Animals are predicted to shift behavior in a body condition-dependent manner to optimize trade-offs between starvation and predation (Baines et al., 2015). Everglades alligators are generally in poorer condition relative to animals across the rest of their range perhaps because of harsh environmental conditions (e.g., high temperatures and drastic changes in water levels) (Dalrymple, 1996; Fujisaki et al., 2009; Brandt et al., 2016). We anticipated that poor body condition individuals would need to move more and across larger areas to access resources compared to animals in better condition that can afford to wait. Indeed, animals in poor condition had larger home ranges, particularly in the wet season, compared to animals with better conditions; however, the relationship was not strong and body condition did not predict movement activity across our small sample size. Future studies could potentially use high numbers of individuals and recaptures to account for the plasticity of condition over time to provide insight into the



consequences of remaining in low-condition states in a dynamic wetland.

Ecological effects of restoration including regional hydrology management tools such as water releases are not always well-studied especially in the context of animal behavior. Despite on-going major restoration efforts, the Florida Everglades remains an intensively hydrologically managed system (Sklar et al., 2005). Our findings show that alligator movement behaviors are affected by changes in hydrology. However, as expected, movements are also driven by individual factors like sex, body size, and body condition as well as inter-individual interactions including breeding. Alligators are indicators for restoration of Everglades ecosystems because of their important roles as predators and ecosystem engineers (Mazzotti et al., 2009). Understanding sources of variation and identifying the relevant temporal and spatial scale of movements for alligators will allow for a thorough assessment of their ecological importance. For instance, large-bodied organisms may have increased potential to generate landscape-level nutrient heterogeneity from excretion because of their capacity for long-distance movements and consumption of considerable biomass. Hotspots such as animal resting areas may exist where the magnitude of nutrient fluxes are particularly high compared to the surrounding matrix (McClain et al., 2003). The implications of a sedentary large-bodied ectothermic apex predator like the alligator in an oligotrophic habitat like the Everglades freshwater marsh could be that local nutrient hotspots are created from concentrated excretion and sediment-resuspension from high movement activity in places like alligator ponds and canals. Empirical information about the drivers and scales of movement behavior, particularly for ecologically important large-bodied mobile predators, is important knowledge to predict community and ecosystem responses to environmental change and restoration.

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**Author Contributions** FJM, MRH, KG, and JSB: Study conception and data collection. BAS: Data analysis. BAS: First draft of manuscript. All authors commented on versions of the manuscript and read and approved the final manuscript.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** Research and animal procedures were conducted under the auspices of protocol #IACUC-15-044-CR01 from the Institutional Animal Care and Use Committee of the University of Florida and in accordance with sampling permits #EVER-2013-SCI-0020 and #EVER-2015-SCI-0036 granted by Everglades National Park.

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