

Use of alligator hole abundance and occupancy rate as indicators for restoration of a human-altered wetland

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ABSTRACT

Use of indicator species as a measure of ecosystem conditions is an established science application in environmental management. Because of its role in shaping wetland systems, the American alligator (*Alligator mississippiensis*) is one of the ecological indicators for wetland restoration in south Florida, USA. We conducted landscape-level aerial surveys of alligator holes in two different habitats in a wetland where anthropogenic modification of surface hydrology has altered the natural system. Alligator holes were scarcer in an area where modified hydrology caused draining and frequent dry-downs compared to another area that maintains a functional wetland system. Lower abundance of alligator holes indicates lack of alligator activities, lower overall species diversity, and lack of dry-season aquatic refugia for other organisms. The occupancy rate of alligator holes was lower than the current restoration target for the Everglades, and was variable by size class with large size-class alligators predominantly occupying alligator holes. This may indicate unequal size-class distribution, different habitat selection by size classes, or possibly a lack of recruitment. Our study provides pre-restoration baseline information about one indicator species for the Everglades. Success of the restoration can be assessed via effective synthesis of information derived by collective research efforts on the entire suite of selected ecological indicators.

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1. Introduction

Human activities have profoundly modified the natural environment. Frequently these modifications involve abiotic controls that result in dramatic changes to biotic structure and ecosystem properties (Hopper et al., 2005). Among the interacting species in an ecosystem, some possess traits that cause broad-scale effects and are considered to be focal species (Dale et al., 2000). The functional roles of focal species in maintaining ecosystem integrity are numerous and involve direct and indirect effects on many species. For example, top predators influence density of other species by direct predation or via density- or trait-mediated indirect effects (Schmitz and Suttle, 2001). Ecological engineers are other examples of focal species (Dale et al., 2000); their activities directly or indirectly control the availability of resources to other species by altering the physical environment (Jones et al., 1994). Keystone species are ones that strongly interact with other species, and thus their removal

may significantly affect community composition (Mills et al., 1993). The population status focal species represents the environmental conditions of their habitat and the habitat suitability for other species (Landers et al., 1988). Therefore, these species are selected as indicators to assess environmental status based on criteria such as sensitivity to the habitat attributes of concern, response variability, and body size (Landers et al., 1988; Noss, 1990).

Using indicator species as a measurable surrogate to assess environmental conditions is an established approach in various disciplines of environmental science (Thomas, 1972; Noss, 1990). By explicitly linking population monitoring of indicator species to the objectives of resource management, monitoring results can provide an understanding of ecosystem changes that can be used to evaluate management efficiency and to guide future policy (Gibbs et al., 1999). Despite this potential utility, monitoring efforts often fail to provide sufficient management implications for several reasons such as lack of explicit research questions and insufficient concern for experimental design and analysis (Hinds, 1984; Gibbs et al., 1999). Population monitoring of wildlife can be expensive, involving extensive fieldwork and multiple years of observations (Witmer, 2005). Successful monitoring of indicator species requires

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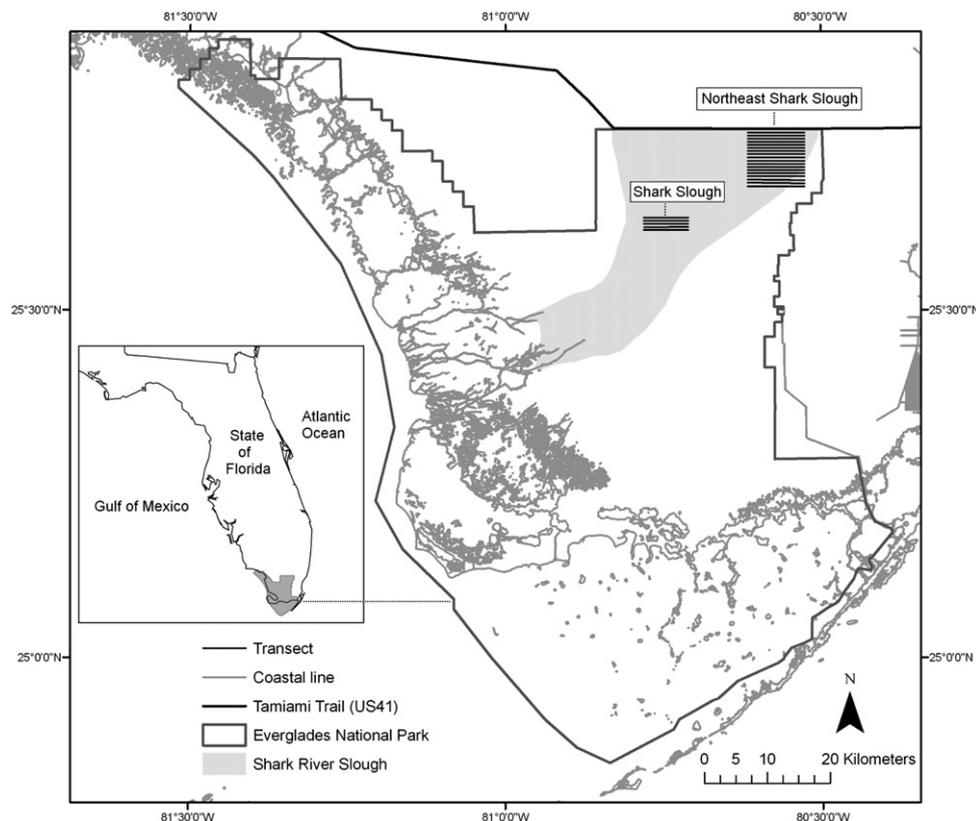


Fig. 1. Map of Everglades National Park and its location in the state of Florida. Flight transects in two study areas are indicated with solid lines within the park map.

selection of appropriate species combined with a well-designed study plan that includes effective hypothesis testing (Hinds, 1984; Noss, 1990).

In close proximity to areas of expanding urban and agricultural development, the Everglades wetlands in southern Florida have experienced significant hydrological modifications that resulted in dramatic changes in the ecosystem (Gunderson et al., 1995). Extensive efforts to restore the natural wetland system are underway (U.S. Army Corps of Engineers, 1999). Among a variety of resident species, the American alligator (*Alligator mississippiensis*) is one of the selected ecological indicators for the restoration because of its unique functional roles that shape the ecosystem (Mazzotti et al., 2009). In addition to being top predators, they are a keystone species and ecological engineers that alter landscape structure and vegetation composition of the wetland; they create and maintain small ponds called alligator holes by removing vegetation from the basin and pushing soil sediments into the banks (Loveless, 1959; Kushlan, 1974; Campbell and Mazzotti, 2004; Palmer and Mazzotti, 2004). In the southern part of the Greater Everglades wetlands, alligators take advantage of depressions in the bedrocks, and therefore the alligator holes are comparably long-lasting landscape features, whereas in the central Everglades ridge-and-slough matrix some of the peat ponds are not fixed features but rather are created when animals need access to water (Campbell and Mazzotti, 2004; Mazzotti et al., 2009). Alligator holes contribute to increase habitat diversity and maintain species richness in the wetland (Kushlan, 1974; Campbell and Mazzotti, 2004; Palmer and Mazzotti, 2004). Micro-topographic gradients around the banks of alligator holes support vegetation with specific requirements for germination and survival, including woody plants, which might lead to different nutrient levels in alligator holes (Craighead, 1968; Campbell and Mazzotti, 2004; Palmer and Mazzotti, 2004). Alligator holes serve as dry-season aquatic refugia for alligators and

other aquatic organisms including fish, amphibians, and invertebrates; and as foraging sites for wading birds which prey upon these species (Kushlan and Kushlan, 1980; Hoffman et al., 1994; Loftus and Eklund, 1994). The slightly higher elevation around holes supports nest sites for other aquatic reptiles (Kushlan, 1974; Diez and Jackson, 1979; Kushlan and Kushlan, 1980). Historically, alligator holes occur throughout the Everglades wetlands, however they are scarcer in some parts of the landscape as a result of altered hydrology and lack of animal activities to maintain them. Because of their numerous ecological implications, alligator holes are used as a performance measure for success of Everglades restoration (Mazzotti et al., 2009).

Our objectives were to understand the current abundance and occupancy rates of alligator holes in two distinctly different alligator habitats in the southern Everglades, both of which have experienced severe hydrological modifications, and to infer ecological and management implications from our findings. We designed aerial surveys to collect necessary data to quantify abundance and occupancy rate. To correct the problem of imperfect detection in hole abundance (count) and hole occupancy rate (presence/absence), likely caused by various uncontrollable factors such as water depth variation and observer change, surveys were spatially and temporally replicated to analyze the data using two-stage hierarchical models (Royle and Dorazio, 2008). This resulted in simultaneous estimates of detection probability and unbiased population parameters.

2. Methods

2.1. Study site

The study area is Shark River Slough within Everglades National Park (a designated International Biosphere Reserve), a large

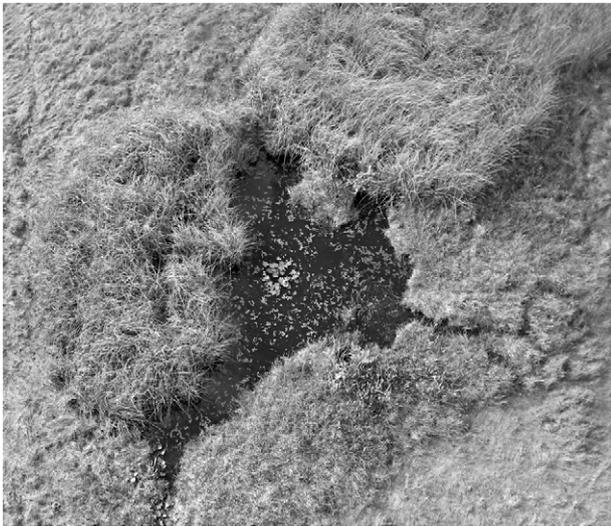


Fig. 2. An alligator hole in Shark Slough (photograph taken by Mat Denton, University of Florida).

subtropical wetland system characterized by oligotrophic waters and carbonaceous sediments (Ross et al., 2003). Located close to Miami-Dade County where human population has been growing for several decades, the natural water flow in the wetland system was greatly modified by canal and levee construction and water management practices. We selected two sites which are important but distinctly different alligator habitats in the area: central Shark Slough (SS) and northeast Shark Slough (NESS) (Fig. 1). Shark Slough is one of the remaining extensive long-hydroperiod freshwater sloughs in the Everglades, characterized by sawgrass and spike rush marsh (South Florida Natural Resources Center, 2005). The slough is a broad bedrock depression extending from the northern park boundary near Tamiami Trail (U.S. Highway 41) toward the southwest where it flows into mangrove communities along the coast. Located to the east of a levee, NESS is characterized primarily by water-deprived marshes (Ross et al., 2003). Major marsh vegetation in NESS is the same as in SS, but this historically deepest portion of the system became shallower as a result of water diversion to the west (Light and Dineen, 1994; Ross et al., 2003). Compared to SS, which maintains a functional wetland ecosystem more similar to natural (pre-drainage) conditions, historical slough structure in NESS disappeared as a result of drainage after canal and levee construction.

2.2. Alligator survey data

We conducted helicopter surveys to count alligator holes and record the presence or absence of alligators in each hole in the two study sites over a three-year study period from 2007 to 2009. We pre-defined multiple transects in each study area (5 transects in SS and 18 transects in NESS) and conducted modified Systematic Reconnaissance Flights (SRF) (Dalrymple, 2001) along transects in May and June of each year (Fig. 1). The difference in number of transects in the two areas is because of our anticipation of lower alligator hole abundance in NESS than in SS, as well as logistical constraints. Flying at an altitude of 200 m along the transect paths in an east-to-west orientation, the observers had a viewing range of approximately 250 m toward the north and south; this configuration provided full coverage of the study area. When we observed an alligator hole, we recorded the GPS location from approximately 15 m directly above the hole (Fig. 2). Two observers (one on each side of the helicopter) independently recorded presence of alligators within the hole or a short distance from the hole (e.g., in a

trail or basking next to the hole) in three size classes based on total length (TL) of animal from head to tail: small ($0.5 \leq TL < 1.25$ m), medium ($1.25 \leq TL < 1.75$ m), and large ($TL \geq 1.75$ m). To replicate the surveys spatially and temporally, each transect was flown twice in each study year. Allowing for weather conditions, the flights occurred once in the morning and once in the afternoon of the same day. Furthermore, a double observer setting was utilized for the animal detection component.

2.3. Water depth data

Surface water depths in the study areas were generally low because the survey months coincided with the end of the dry season in the Everglades. Low water depths potentially affected the hole detection rate, since dry holes are not as obvious. We used the daily water depth model from the U.S. Geological Survey's Everglades Depth Estimation Network (<http://sofia.usgs.gov/eden>) to characterize water depths in each transect on each survey date. We calculated the mean water depth within the raster grids intersecting each survey route, and weighted the values based on transect length using ArcGIS 9.3.

2.4. Alligator hole abundance model

The two-stage hierarchical model for alligator hole abundance has two components: hole abundance and detection rate. We considered the number of holes detected at each survey time (morning and afternoon) for each year as a temporal replicate. We used a binomial-Poisson hierarchical model, which has been used previously to estimate population sizes and trends from replicated data (Royle and Dorazio, 2008), to estimate area-wise abundance (i.e., density) of alligator holes.

Let $n_{i,j,k}$ denote number of holes present in i th area, which contains j th transect, and k th year, and y_{ijkl} denote number of holes detected in i th area, j th transect, k th year, l th survey, where $i \in \{1, 2\}$ (i.e., SS and NESS), $j \in \{1, \dots, 23\}$, $k \in \{1, 2, 3\}$ (i.e., 2007–2009), and $l \in \{1, 2\}$ (i.e., morning and afternoon). Hole abundance in each area in each year can be modeled in Poisson-log functions, $n_{jk} \sim \text{Poisson}(\lambda_{ijk} L_j)$ and

$$\log(\lambda_{i,j,k}) = \alpha_{0i} + \alpha_{0ik} + \alpha_{1j}$$

where $\lambda_{i,j,k}$ is Poisson mean and L_j is transect length. Hole detection rate can be modeled via Binomial-logit functions, $y_{ijkl} \sim \text{Binomial}(n_{jk}, p_{ijkl})$

and

$$\log \text{it}(p_{ijkl}) = \beta_{0i} + \beta_{1i} \text{time} + \beta_2 \frac{W - \bar{W}}{SD(W)} + b_{ijkl} + b_{\text{obs}_{ijkl}}$$

where time is the survey time (morning or afternoon), W and \bar{W} are water depth at each survey and mean water depth, and b_{ijkl} and $b_{\text{obs}_{ijkl}}$ are random effects associated with each survey (area-transect-year-survey) and observer combinations.

2.5. Alligator hole occupancy rate model

Using a two-stage hierarchical model, we modeled hole occupancy and animal detection rate separately for each size class (three size classes and total) because of potential differences in hole usage and detection rate. Let ns_{ikl} denote the true number of holes occupied by small animals, ys_{ijkl} be observed number of holes occupied by small animals, rs_{ijkl} be hole occupancy rate by small animals, and ps_{ijkl} be probability of small animal detection in i th area, j th transect, k th year, l th survey. Both hole occupancy and animal detection rates can be modeled as Binomial-logit functions. The models for hole occupancy rate are

Table 1

Summary of posterior mean, standard deviation (SD), median, and lower and upper 95% credible interval (CI) of parameters of the alligator hole abundance, i.e., intercept (α_{0i}), and detection rate, i.e., intercept (β_{0i}), and effects of water depth (β_1) and time (β_2).

Parameter	Mean	SD	2.5% CI	Median	97.5% CI
$\alpha_{0, SS}$	1.587	0.216	1.143	1.579	2.068
$\alpha_{0, NESS}$	0.400	0.401	-0.240	0.327	1.340
$\beta_{0, SS}$	14.230	10.450	2.039	10.73	41.320
$\beta_{0, NESS}$	0.136	1.086	-1.709	0.089	2.428
β_1	0.095	0.345	-0.453	0.041	0.897
β_2	-0.916	0.637	-2.507	-0.822	0.015

$$ns_{i,j,kl} \sim \text{Binomial}(n_{jk}, rs_{ikl}) \text{ and}$$

$$\log \text{it}(rs_{ikl}) = \gamma_{0i} + \gamma_1 * \text{time} + c_{ik},$$

where time is the survey time and c_{ik} is random effect associated with area by year. The models for animal detection rate are

$$ys_{ijkl} \sim \text{Binomial}(ns_{i,j,kl}, ps_{ijkl})$$

and

$$\log \text{it}(ps_{ijkl}) = \delta_0 + d_{ijk} + d_{obs_{ijkl}},$$

where d_{ijk} and $d_{obs_{ijkl}}$ are random effects associated with area-year-transect and observers. We should note that water depth is a factor that may affect alligator hole occupancy rate, since animals are dispersed when water level is high, but we did not include it in the model because of consistently low water depth during our survey time. Hole occupancy and animal detection rates for medium and large size classes can be modeled in the same manner.

We followed Royle and Dorazio (2008) and estimated model parameters in a Bayesian framework via Markov Chain Monte Carlo (MCMC). We used non-informative priors, Normal (0, 1000) for fixed effect parameters ($\alpha_0, \alpha_1, \beta_0, \beta_1, \gamma_0, \gamma_1, \gamma_2, \delta_0, \delta_1$, and δ_2) and Normal (0, σ^2) for random effects (a_{kj}, b_{kj} , and $b_{obs_{ijkl}}$) with Uniform (0, 10) for variance components. We estimated model parameters using Gibbs sampling with 20,000 draws obtained by sampling five independent Markov chains using WinBUGS 1.4. Each chain ran for 40,000 iterations after 10,000 burn-ins and was thinned by 10 samples. Potential scale reduction factors (PSRF) from Gelman-Rubin diagnostics, a diagnostics indicator of iterative simulations that suggests approximate convergence when the upper limit is close to one, were computed using the CODA package of R to confirm convergence (Brooks and Gelman, 1998).

3. Results

3.1. Alligator hole abundance

The point estimate of PSRF for all fixed effects in the alligator hole abundance model was close to 1 (1.01–1.61), which suggests approximate convergence and allows us to make inferences from the estimated parameters. Estimated hole density was distinctly higher in SS than in NESS; the 95% credible intervals (CIs) of the area effect (α_0) was larger in SS (Table 1). This resulted in larger estimates of hole density in SS than in NESS (Fig. 3). On average, the estimated hole density (number of holes/km) was 4.9 in SS and 1.5 in NESS. Estimated variance parameters of random effects on alligator hole abundance were 0.27 for year ($\hat{\sigma}_{a_1}$) and 0.14 for transect ($\hat{\sigma}_{a_2}$). The 95% CIs of coefficients for both flight time (morning or afternoon) (-0.45–0.9) and water depth (-2.51–0.02) contained zero, implying that effects of flight time and water depth are neither clearly positive nor negative (Table 1). Hole detection rates were also distinctly different by area (i.e., 95% CIs of intercepts for

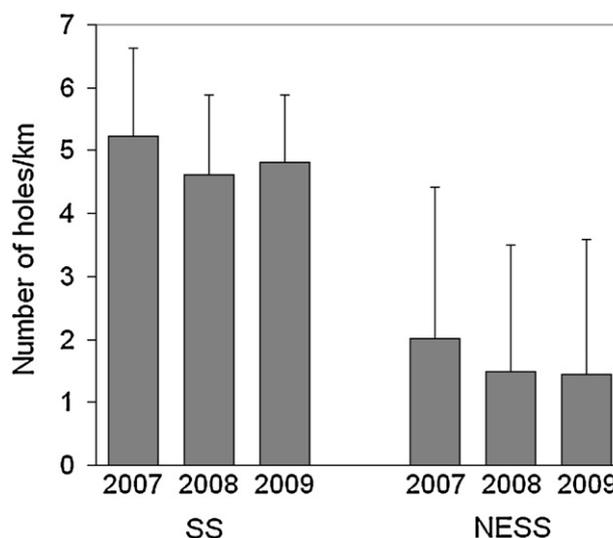


Fig. 3. Estimated alligator hole abundance (number of holes/km) from 2007 to 2009 in Shark Slough (SS) and northeast Shark Slough (NESS), Everglades National Park in south Florida. Vertical lines indicate upper 95% credible intervals.

each area did not overlap). The estimated detection rate was ≈ 1.0 for SS and 0.53 for NESS.

3.2. Alligator hole occupancy rate

The point estimate of PSRF for all fixed effects in the alligator hole occupancy model was ≤ 1.02 for all size classes, confirming approximate convergence. The effect of flight time (morning or afternoon) was not clear (i.e., 95% CI contained zero) for all size classes (Table 2). In contrast, there was a common pattern in hole occupancy rate by size class in the two study areas: the large size-class animals had a higher hole occupancy rate than the small and medium size classes (Fig. 4). The small and large size classes' occupancy rates were both similar across the study areas, but medium size-class animals had higher occupancy rates in NESS than in SS. In SS, estimated mean hole occupancy rates by small and medium size classes were both less than 6% (1–2% for small and 2–5% for medium), whereas the rate for the large size class was 22–41% (Table 1, Fig. 4). This did not agree with the previously observed greater abundance of medium size class than smaller and larger size classes in SS (Fujisaki et al., 2011). In NESS, the occupancy rates ranged from 3–4%, 10–17%, and 21–32% for small, medium, and large size classes respectively. The estimated total hole occupancy rates were 25–46% in SS and 32–47% in NESS during the study period; however, large 95% CIs indicate uncertainty of these estimates.

4. Discussion

The American alligator is an excellent indicator species for the wetland systems it inhabits because it exhibits high sensitivity to hydrologic conditions; its life history traits such as survival, reproduction (mating and nesting effort and success), and condition, are closely related to hydrology (Kushlan and Jacobsen, 1990). Furthermore, alligators' activities influence the physical environment and biotic communities by direct and indirect interactions (Campbell and Mazzotti, 2004; Mazzotti et al., 2009). Whereas altered hydrology and landscape changes in the Everglades wetlands have been recognized for a long time (Gunderson et al., 1995), our study provided additional information to understand the biotic community, using alligator hole abundance and occupancy rate as measures in two distinctly different areas. Obtaining reliable measures of

Table 2

Summary of posterior mean, standard deviation (SD), median, and lower and upper 95% credible interval (CI) of parameters of the alligator hole occupancy coefficient, i.e., intercept (γ_{0i}), for time (γ_1), and animal detection rate (δ_0).

Alligator size class	Parameter	Mean	SD	2.5% CI	Median	97.5% CI
Small	$\gamma_{0, SS}$	-3.440	0.551	-4.525	-3.457	-2.365
	$\gamma_{0, NESS}$	-3.430	0.628	-4.590	-3.471	-2.132
	γ_1	0.119	0.376	-0.620	0.115	0.867
	δ_0	0.532	99.600	-193.900	0.409	194.300
Medium	$\gamma_{0, SS}$	-3.635	0.7184	5.119	-3.629	-2.265
	$\gamma_{0, NESS}$	-1.928	0.699	-3.273	-1.963	-0.508
	γ_1	-0.099	0.233	-0.571	-0.098	0.347
	δ_0	-0.449	99.570	-195.600	0.135	194.600
Large	$\gamma_{0, SS}$	-0.990	0.647	-2.383	-0.967	0.207
	$\gamma_{0, NESS}$	-0.972	0.669	-2.174	-1.034	0.503
	γ_1	-0.378	0.309	-0.966	-0.382	0.252
	δ_0	-1.679	99.92	-197.100	-2.434	195.800
Total	$\gamma_{0, SS}$	-0.898	0.709	-2.528	-0.844	0.343
	$\gamma_{0, NESS}$	-0.552	0.712	-1.917	-0.582	0.925
	γ_1	-0.273	0.292	-0.791	-0.294	0.372
	δ_0	-0.869	99.910	-195.700	-2.070	199.200

population parameters from observational studies, such as wildlife population surveys, is challenging because of uncontrollable factors and logistical difficulties; however, advances in quantitative methods provided us opportunities to obtain robust estimates of parameters of interest by accounting for spatial variability within an area (Royle and Dorazio, 2008). By applying these quantitative methods of analysis, our study based on aerial surveys fills an information gap on the condition of important alligator habitats in the southern part of the Greater Everglades wetland, particularly in NESS which has limited accessibility from the ground. Further, since alligator holes are also present in other geographic areas (Joanen, 1969; Joanen and McNease, 1970), our methodological and analytical approach could be applied in alligator population monitoring in other areas.

Alligator hole abundance was consistent over the course of the three-year study period in both areas and was greater in SS than in NESS. On average, more than three times as many alligator holes across the landscape were observed in SS compared to NESS. Although alligator holes in the northern Everglades are relatively long-lasting features, lack of alligator activities to maintain holes can lead to loss of signatures due to overgrowth of vegetation and filling of holes with sediment. Our results may imply different habitat suitability for habitats between the two sites. The less disturbed and longer-hydroperiod wetlands of SS are considered more conducive to alligator activity (Mazzotti and Brandt, 1994) than the drained wetlands of NESS (Sklar et al., 2002). The generally low water depth in NESS leads to periodic dry-downs and

reduced aquatic prey populations, making this area less suitable habitat for alligators (Loftus et al., 1990). The results imply that the functionality of the two study sites to support the wetland system could be very different despite the close proximity because alligator holes contribute to mosaic patterns in the typical wetland marsh landscape.

Site occupancy represents habitat selection and/or suitability, and therefore occupancy rate has been used for habitat assessments for variety of organisms (Wiens et al., 1987; MacKenzie et al., 2005). Because of a lack of hard data using consistent survey methods, we are not able to make a direct comparison between historical and current alligator hole abundances and occupancy rates. However, reports by early explorers prior to drainage indicated that alligator holes were present throughout and to the east and west of the main sloughs (Simmons and Ogden, 1998). Further, based on Craighead (1968) who reported that in the early years of hydrologic development of the Everglades, when an animal was removed from a hole another would soon replace it and sometimes multiple animals occupied a hole, it is believed that the historical hole occupancy rate in these areas was very high. Our estimates of hole occupancy rate were lower than the current restoration goal (75–100% occupancy rate) for the Everglades wetland (RECOVER, 2004) which was set based on earlier observations. The comparably low alligator hole occupancy rates we estimated may represent an adverse impact of increased drought frequency in recent years and reduced habitat suitability in the areas for alligators (Mazzotti et al., 2009). However, we also should note limitations of our study. First, our surveys

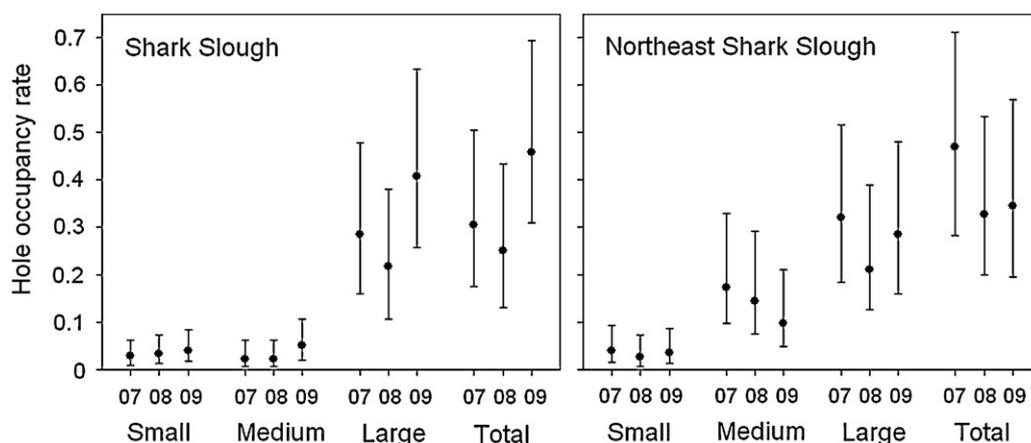


Fig. 4. Estimated alligator hole occupancy rate by size class from 2007 to 2009 in Shark Slough and northeast Shark Slough, Everglades National Park in south Florida. Vertical lines indicate 95% credible intervals.

were conducted in spring when the area is generally dry, and thus we did not account for seasonal variability and possibly underestimate the total annual alligator hole occupancy rate. Second, we did not consider the effect of water quality on alligator hole occupancy. While a previous study (Yanochko et al., 1997) found elevated metal concentrations in alligator tissue, no studies have yet examined how metal content in the water may affect alligator hole occupancy. Furthermore, this study did not address the question of how animal presence/absence in alligator holes affects wetland functions and community condition. Such an investigation, perhaps through observation of individual alligator holes, would provide a clearer picture of the process by which alligator activities in holes shapes the ecosystem.

Our results also indicated size-mediated alligator hole use. We found that the majority of observed occupied holes (84%) contained a single animal and co-occurrence of different size classes was rare (5%). Large size-class alligators dominantly occupied holes in both study sites, which suggests either different habitat selection by size class or different size-class distributions. The lower hole occupancy rates by smaller size-class alligators may be due to attempts to avoid predation by larger alligators (Rice et al., 2005). Because alligator holes serve as aquatic refugia for alligators in drought and high-temperature conditions (Craighead, 1968; Kushlan, 1974), such size-mediated habitat selection may imply a greater vulnerability of small animals during extreme weather events. Our previous study via airboat surveys indicated decreasing abundance of small- and medium size-class alligators in SS, and we suspected that a severe drought in 2001 and subsequent prolonged dry conditions in the area might be a cause (Fujisaki et al., 2011). The lack of dry-season aquatic refugia and decreasing abundance of smaller size-class alligators together suggest a reduction in current recruitment rates and concern for the future population status of alligators.

A continually growing human population and associated conversion of natural areas in south Florida are major causes of loss of natural landscape features. Wetland ecosystems are disappearing throughout the world at an alarming rate and are the subject of restoration projects in various locations (Henry and Amoros, 1995; Klötzli and Grootjans, 2001). Current environmental conditions and restoration efforts in the Everglades epitomize this global trend. The Comprehensive Everglades Restoration Plan (CERP) is a multi-billion dollar restoration program coordinated by multiple agencies including federal, state, local, and tribal governments (www.evergladesplan.org). Planned restoration activities, such as partial backfilling of canals and removal of some levees, are expected to improve sheet flow and return the wetland ecosystem to more natural conditions. As reliable measures of health and ecological integrity of the Everglades ecosystem as restoration proceeds, 11 system-wide indicators including alligators were selected based on various criteria and lessons learned from other indicator programs (Doren et al., 2009). Extensive research efforts have been undertaken to seek linkages between science and management, using ecological indicators as tools to communicate between scientists and managers (Doren et al., 2009). While our study provides necessary baseline information for a performance measure for one indicator species, the American alligator, effective synthesis of information derived from collective research efforts is necessary for success of adaptive ecosystem management and restoration.

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