



Estimating Trends in Alligator Populations from Nightlight Survey Data

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Abstract Nightlight surveys are commonly used to evaluate status and trends of crocodylian populations, but imperfect detection caused by survey- and location-specific factors makes it difficult to draw population inferences accurately from uncorrected data. We used a two-stage hierarchical model comprising population abundance and detection probability to examine recent abundance trends of American alligators (*Alligator mississippiensis*) in subareas of Everglades wetlands in Florida using nightlight survey data. During 2001–2008, there were declining trends in abundance of small and/or medium sized animals in a majority of subareas, whereas abundance of large sized animals had either demonstrated an increased or unclear trend. For small and large sized class animals, estimated detection probability declined as water depth increased. Detection probability of small animals was much lower than for larger size classes. The declining trend of smaller alligators may reflect a natural

population response to the fluctuating environment of Everglades wetlands under modified hydrology. It may have negative implications for the future of alligator populations in this region, particularly if habitat conditions do not favor recruitment of offspring in the near term. Our study provides a foundation to improve inferences made from nightlight surveys of other crocodylian populations.

Keywords *Alligator mississippiensis* · Crocodylian · Everglades · Detection probability · Hierarchical model · Monitoring

Introduction

Historically, American alligators (*Alligator mississippiensis*) in south Florida have been influenced by various anthropogenic factors. Once classified as endangered in the early 1960s due to modification of habitat, water management, and poaching, population numbers increased in the 1970s coinciding with controls on harvesting (Hines 1979; Jacobsen and Kushlan 1984; Mazzotti and Brandt 1994; Rice et al. 2005). Although current alligator population trends are uncertain, concerns exist that increasing drought frequency and dry down events could potentially affect the population (Mazzotti et al. 2009). For example, south Florida experienced a severe drought in 2001, which negatively impacted populations of fish and macroinvertebrates, common food resources for large aquatic predators (Smith et al. 2003; Trexler and Goss 2009). Lack of systematic monitoring of alligators in the Everglades has made it difficult to identify changes in population parameters.

As of the late 1990s, the only long-term monitoring of alligator population in the Everglades was standard reconnaissance flights for alligator nests (Rice et al. 2005).

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Limited nightlight surveys had been conducted by Florida Fish and Wildlife Conservation Commission in Water Conservation Areas (WCAs) to the north of Everglades National Park (ENP) (Woodward and Moore 1990). More recently, to understand population trends of alligators, nightlight surveys have been conducted along routes in subareas of Everglades wetlands as part of the Monitoring and Assessment Plan for the Comprehensive Everglades Restoration Plan (U.S. Army Corps of Engineers 1999; RECOVER 2004).

Nightlight surveys are an established, cost effective method to obtain information on abundance, distribution, and size class distribution of crocodylians (Webb and Messel 1979; Bayliss 1987; Hutton and Woolhouse 1989; Lentic and Connors 2006). Long-term monitoring data using systematic nightlight surveys are potentially useful to understand trends in these population parameters. A limitation of nightlight survey data is the effect of variation in detection probabilities caused by uncontrollable factors, such as environmental conditions and observer differences. Water depth is a particularly critical factor as it affects movement patterns of crocodylians, and thus encounter rate (Woodward and Marion 1978; Montague 1983; Wood et al. 1985). Habitat type and vegetation density, both of which affect visibility, are also known to influence the detection probability of crocodylians (Bayliss et al. 1986; Cherkiss et al. 2006). A two-stage hierarchical model has been developed to estimate both detection and changes in abundance from such data (Royle and Dorazio 2008; Kery et al. 2009). This model allows estimation of population trend by simultaneously fitting a binomial observation model and a Poisson process model to survey data. It requires count data that are replicated both in space and time.

The objective of our study was to apply the two-stage hierarchical model to examine recent trends in abundance of alligators in subareas throughout Everglades wetlands based on nightlight survey data. We provide an analytical framework to improve population inferences from alligator nightlight survey data and an overview of recent population trends in portions of the Everglades.

Methods

Study Area

The study area comprised freshwater marshes in the greater Everglades including ENP and WCAs 1 (a.k.a. Arthur R. Marshall Loxahatchee National Wildlife Refuge), 2A, 3A, and 3B (Fig. 1). Within ENP, our surveys focused on Shark River Slough, a major slough and primary flow path in the Everglades ecosystem that moves southwest through the

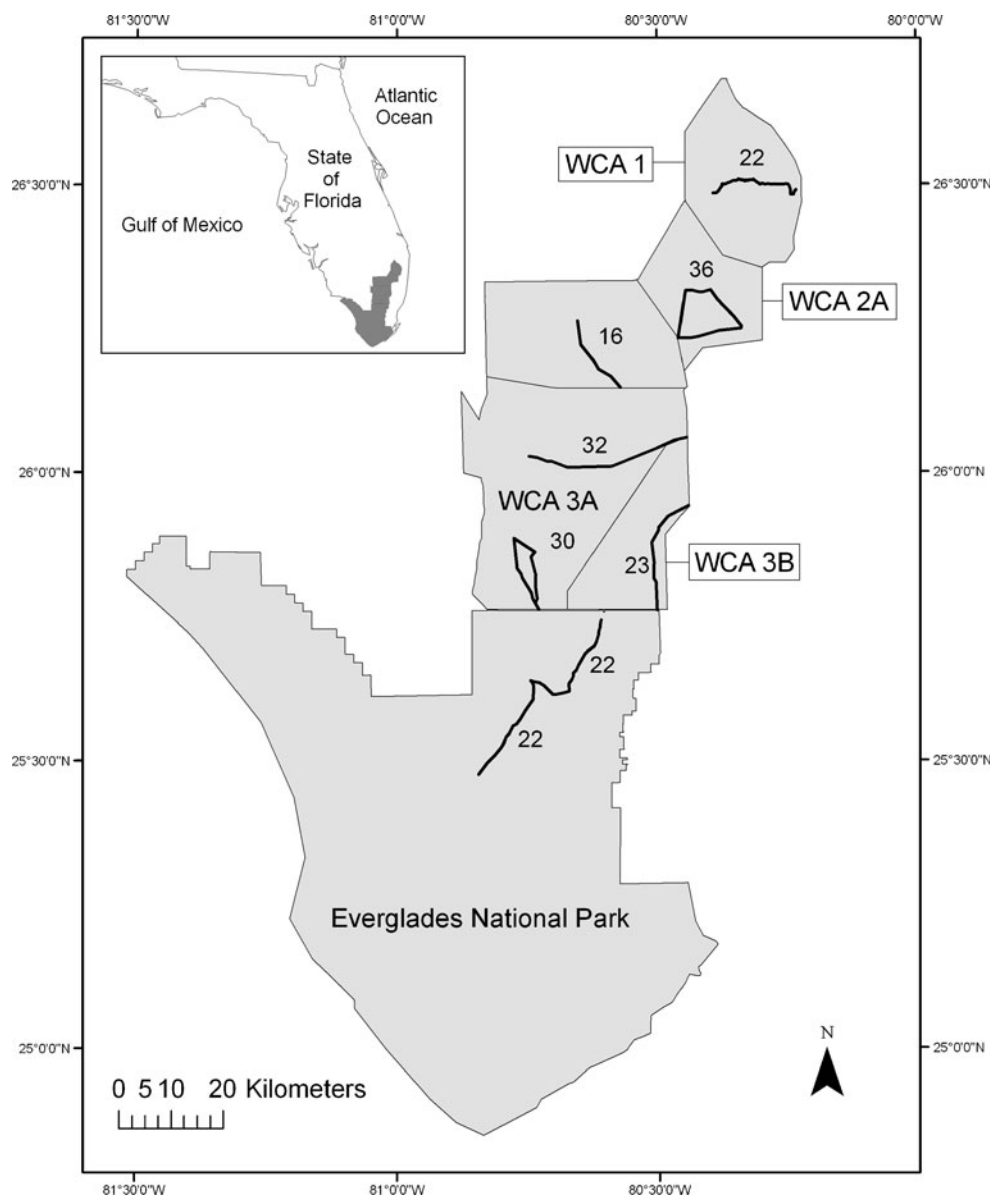
central portion of ENP. The area is dominated by tree islands, wet prairies, and tall sawgrass (*Cladium jamaicense*) marshes, with muck soils, and nearly year-round surface water (Loftus and Kushlan 1987).

Water Conservation Areas are managed by South Florida Water Management District in cooperation with U.S. Fish and Wildlife Service (WCA 1) and Florida Fish and Wildlife Conservation Commission (WCAs 2A, 3A, and 3B). Surface hydrology in the WCAs is managed primarily for flood control, water supply, and wildlife conservation. Water Conservation Area 1 (596 km²) is a northern remnant of the Everglades ridge and slough wetland located in Palm Beach County, Florida (Brandt et al. 2002). A landscape mosaic composed of sawgrass marshes, wet prairies, sloughs, and tree islands provides alligators various habitat options and maintains high density of prey items such as invertebrates, fish, amphibians, and turtles (Brandt and Mazzotti 2000). Water Conservation Area 2A (448 km²) is a traditional sawgrass-dominated landscape replaced by cattail (*Typha* spp.) stands and cattail/sawgrass slough vegetation due to phosphorous enrichment caused by water management (DeBusk et al. 2001). The landscape varies from cattails to sawgrass along the north to south gradient. WCA 3A (1,995 km²) and 3B (398 km²), are partitioned by a levee and 3A is further divided into north and south by a road. The area is the center of a ridge and slough landscape composed of sawgrass, tree islands, and slough. In WCA 3A, hydrologic modification caused over-drainage in the north while prolonged flooding occurred in the south; however, due to a relatively short route with a small number of surveys in the north area, we examined the overall trend in 3A area for this study. Water Conservation Area 3B is natural ridge and slough vegetation replaced by dense sawgrass and cattail stands due to loss of flow and high nutrient waters introduced from the Miami Canal.

Nightlight Survey

Survey routes were initially established in subareas within study areas between 2000 and 2001 and additional routes were established in subsequent years. Routes were of variable length due to limitations of accessibility produced by typical dry season water levels. We conducted nightlight surveys from 2001–2008 along routes by airboat twice in each of spring (dry season) and fall (wet season) at least 14 days apart to achieve independent counts (Woodward and Moore 1990). We did not conduct marsh surveys when water depth was ≤ 15 cm, the day of, before, or after a full moon, or when heavy rain or high winds (> 24 km/h) were occurring. By controlling for these conditions, which were found to affect counts in other studies (Woodward and Moore 1990), we did not need to account for their effects

Fig. 1 Location of survey routes in each subarea within the study area (the Everglades marsh) and their location within the state of Florida. Numbers indicate survey route length in km



on detection probability. A trained primary observer (boat driver) traveling at ≈ 25 km/h, used a 200,000 candlepower spotlight to spot animals within 50 m on either side of the designated route. When an eyeshine was observed, the boat approached the animal, paused long enough to make a size estimate, record a waypoint and returned to the route. A headlamp was used at times to reestablish close proximity eye shines or to count hatchlings. The primary observer placed animals into quarter-meter size classes using total length (TL), and a second person recorded alligator locations using GPS and size class, habitat, and vegetation type using a personal digital assistant. For this study, we classified animals in one of four size classes based on TL, hatchlings (< 0.5 m), small ($0.5 \text{ m} \leq \text{TL} < 1.25$ m), medium ($1.25 \text{ m} \leq \text{TL} < 1.75$ m), and large ($1.75 \text{ m} \leq \text{TL}$) representing hatchlings, juvenile, subadults, and adults.

Animals for which we were not able to estimate size were not included in the analysis. In this study, we used data collected along eight survey routes (Fig. 1).

Water Depth

We used 400 m resolution raster data of model-predicted daily surface water depths in the Everglades from 2000 to 2008 that are available from the U.S. Geological Survey at the Everglades Depth Estimation Network website (<http://sofia.usgs.gov/eden>). For each survey route and date, we calculated mean water depth of raster grids that intersect with each survey route, weighting for the length of the survey route falling within each grid cell using Line Raster Intersection Statistics function with Hawth's Analysis Tool (Beyer 2004) in ArcGIS 9.3.

Model

We used a binomial-Poisson hierarchical model, which has been used previously to estimate population size or trend from replicated data (Royle 2004; Royle and Dorazio 2008; Kery et al. 2009) to estimate changes in alligator population abundance and detection probability. Let N_{it} and y_{ijt} denote the unobserved local abundance and observed count of individuals at route i , within-route replicate j , and year t , respectively. Assuming that individuals at route i are sampled independently and that there is no change in unobserved population size between replicated surveys, y_{ijt} has binomial distribution,

$$y_{ijt} \sim \text{Binomial}(N_{it}, p_{ijt})$$

where p_{ijt} is the probability of detection of each individual present during the j th survey of route i in year t . We model p_{ijt} on the logit scale as a function of route- and survey-specific covariates, such as route-specific vegetation type and density (route), water depth (W), season, and observer (obs):

$$\text{logit}(p_{ijt}) = \alpha_0 \text{season}_{ijt} + \alpha_1 (1 - \text{season}_{ijt}) + \alpha_2 \frac{W_{ijt} - \tilde{W}}{SD(W)} + a_i + a_{obs_{ijt}}$$

where $\text{season} \in \{0, 1\}$ (0=fall, 1=spring), $a_i \sim \text{Normal}(0, \sigma_{\text{route}}^2)$, and $a_{obs} \sim \text{Normal}(0, \sigma_{\text{obs}}^2)$. Season effect was included to account for potential behavioral difference of alligators that may affect detection probability since our spring survey coincides with breeding season. We standardized mean water depths (W) using the median (\tilde{W}) and standard deviation ($SD(W)$) of water depths during the survey period.

Heterogeneity in the unknown local population abundances (N_{it}) was modeled using a Poisson distribution as follows,

$$N_{it} \sim \text{Poisson}(\lambda_{it} L_i),$$

where $l \in \{1, 2, 3, 4, 5\}$ denotes subarea, L_i is the length (km) of route i , and λ_{it} denotes the mean density of alligators (number of individuals per km) present in Everglades subarea l in year t . The trend in the mean density of alligators in subarea l is specified using a log-linear model:

$$\log(\lambda_{it}) = \beta_{0l} + \beta_{1l} \frac{t - \bar{t}}{SD(t)},$$

where the parameter β_{1l} denotes the exponential increase ($\beta_{1l} > 0$) or decrease ($\beta_{1l} < 0$) in density of alligators in subarea l . Year was standardized using mean (\bar{t}) and standard deviation ($SD(t)$). We estimated a separate set of

model parameters for each size class due to potential differences in detection probability and population trends among size classes.

Following Kery et al. (2009), we used a Bayesian approach to estimate model parameters from our spatially and temporally indexed alligator counts. Non-informative prior distributions were assumed for fixed-effect parameters α_0 , α_1 , α_2 , β_{0l} , and β_{1l} (Normal(0, 1000)) and for the variance components, σ_{route} and σ_{obs} (Uniform (0, 10)), referring to Royle and Dorazio (2008). We estimated model parameters using Gibbs sampling (20,000 draws obtained by sampling five independent Markov chains—each run for 40,000 iterations after 10,000 burn-ins and thinned by 10 samples) using WinBUGS 1.4 (Spiegelhalter et al. 2002). Convergence was assessed using potential scale reduction factors (SRF) based on the Gelman-Rubin diagnostics, which were computed using the CODA package (Brooks and Gelman 1998).

Results

Population Trend

Our estimates of detection probability assumed that local population abundance in the same season remained constant while uncontrolled factors affected detection probability (i.e., we assumed demographic closure for each route and season); therefore, counts from replicate surveys of each route within season were not expected to be extremely different. In a pure Poisson model, the correlation between two counts replicated at multiple sites is precisely a method of moments estimate of detection probability. The empirical correlation (Pearson's correlation coefficient) between untransformed alligator counts from first and second surveys of each route was relatively high for all size classes (0.87, 0.77, and 0.89 for small, medium, and large size classes) and differences between these counts were centered around zero, lending support to our closure assumption. Overall, variability in differences between counts tended to be lower for larger size classes.

The trend parameters (β_{1l}) estimated by the Gibbs sampler implemented in WinBUGS appeared to converge (SRF=1.01 for all size classes). All other fixed effect parameters had SRFs close to one (< 2.0) except for one intercept parameter (α_1 for WCA 1) of small and medium size classes that had a relatively large SRF (> 2.0). There were significant decreasing trends, i.e. $\hat{\beta}_{1l} < 0$ and 95% credible intervals (CI) do not contain zero, for small size class in ENP and WCAs 1 and 2A and for medium size class in ENP and WCA 1 (Table 1, Fig. 2). In contrast, there was a significant increasing trend of alligators in the large size class in WCAs 1, 2A, and 3A.

Table 1 Posterior mean, standard deviation (SD), median, and lower (2.5%) and upper (97.5%) limits of credible intervals for the trend parameter (β_{11}) of each size class in area l from 2001 to 2008

Area	Size	Mean	SD	2.5%	Median	97.5%
ENP	Small	-0.360	0.117	-0.589	-0.361	-0.130
	Medium	-0.213	0.087	-0.384	-0.213	-0.042
	Large	-0.104	0.079	-0.259	-0.104	0.053
WCA 1	Small	-0.083	0.026	-0.134	-0.083	-0.033
	Medium	-0.268	0.040	-0.346	-0.268	-0.192
	Large	0.121	0.023	0.077	0.121	0.165
WCA 2A	Small	-0.312	0.097	-0.499	-0.313	-0.120
	Medium	0.166	0.106	-0.040	0.166	0.376
	Large	0.223	0.074	0.080	0.224	0.369
WCA 3A	Small	-0.093	0.060	-0.213	-0.093	0.024
	Medium	-0.023	0.063	-0.147	-0.024	0.102
	Large	0.115	0.044	0.031	0.115	0.200
WCA 3B	Small	-0.408	0.349	-1.120	-0.396	0.249
	Medium	0.123	0.246	-0.353	0.120	0.621
	Large	0.097	0.194	-0.284	0.098	0.479

Detection Probability

There was a common inverse relationship between detection probability and water depth for small and large size classes ($\hat{\alpha}_2 = -0.173$ for small and $\hat{\alpha}_2 = -0.113$ for large size classes) (Fig. 3). The 95% CI associated with α_2 for the medium size class contained zero (-0.124 – 0.134), suggesting that the effect of water depth on detection probability of this size class is neither clearly positive nor negative. While posterior of water depth effect on detection probability is greater (i.e., more negative $\hat{\alpha}_2$) for small compared to large size classes, the 95% CIs overlapped each other (-0.276 – -0.07 for small and -0.179 – -0.022 for large size classes).

Estimates of detection probability were generally higher for medium and large size classes than for the small size class (Fig. 3). In addition to the seasonal effect, seasonal differences in detection probability appear to be driven by differences in water depths. Surface water was generally deeper during our fall surveys of the Everglades than during our spring surveys. During the spring surveys, the route mean of predicted water depths ranged from -10 to 68 cm, and estimates of detection probability differed by 0.024 and 0.019 for small and large size classes, respectively, over this range of water depths (Fig. 3). During the fall surveys, the route mean of predicted water depth ranged from 10 to 139 cm, and estimates of detection probability differed by 0.033 and 0.029 for small and large size classes, respectively.

Our estimates of the variance component parameters indicate that both observer and route effects provided significant sources of heterogeneity in detection probabilities. Estimates of the variance of route effects (σ_{route}^2) were 5.81 , 2.21 , and 6.51 for small, medium, and large size

classes, respectively. Similarly, estimates of observer effects (σ_{obs}^2) were 9.82 , 2.21 , and 1.62 for small, medium, and large size classes, respectively.

Discussion

Imperfect detection is a typical problem with identifying trends in population abundance using data from animal surveys (Royle and Dorazio 2006; Royle et al. 2007). In long-term monitoring programs that cover multiple locations, differences in detection probability can be attributed to spatial and temporal heterogeneity and may cause bias in abundance estimates. This variation in detection probability limited the utility of encounter rates obtained from nightlight surveys. In the past, several correction methods were applied to use nightlight survey data as an indicator of relative abundance of crocodylians (Chabreck 1966; Woodward and Marion 1978; Bayliss et al. 1986; Hutton and Woolhouse 1989). Accounting for detection probability is essential to accurately understand population trends (Steinhorst and Samuel 1989; Thompson and Seber 1994; Cassey and McCardle 1999). A major benefit of the model used in our study is to allow probability of detection to be estimated simultaneously with trend in abundance, which is a primary target of population monitoring. Furthermore, if we want to predict future abundance of a local population based on estimated trend, the abundance component of a hierarchical model allows us to predict changes in population size simply as a function of time, taking into account confounding effects of detection errors. Such predictions could be extremely useful to managers of alligator populations.

The abundance component of the model allowed us to infer population trends between 2001 and 2008 in three

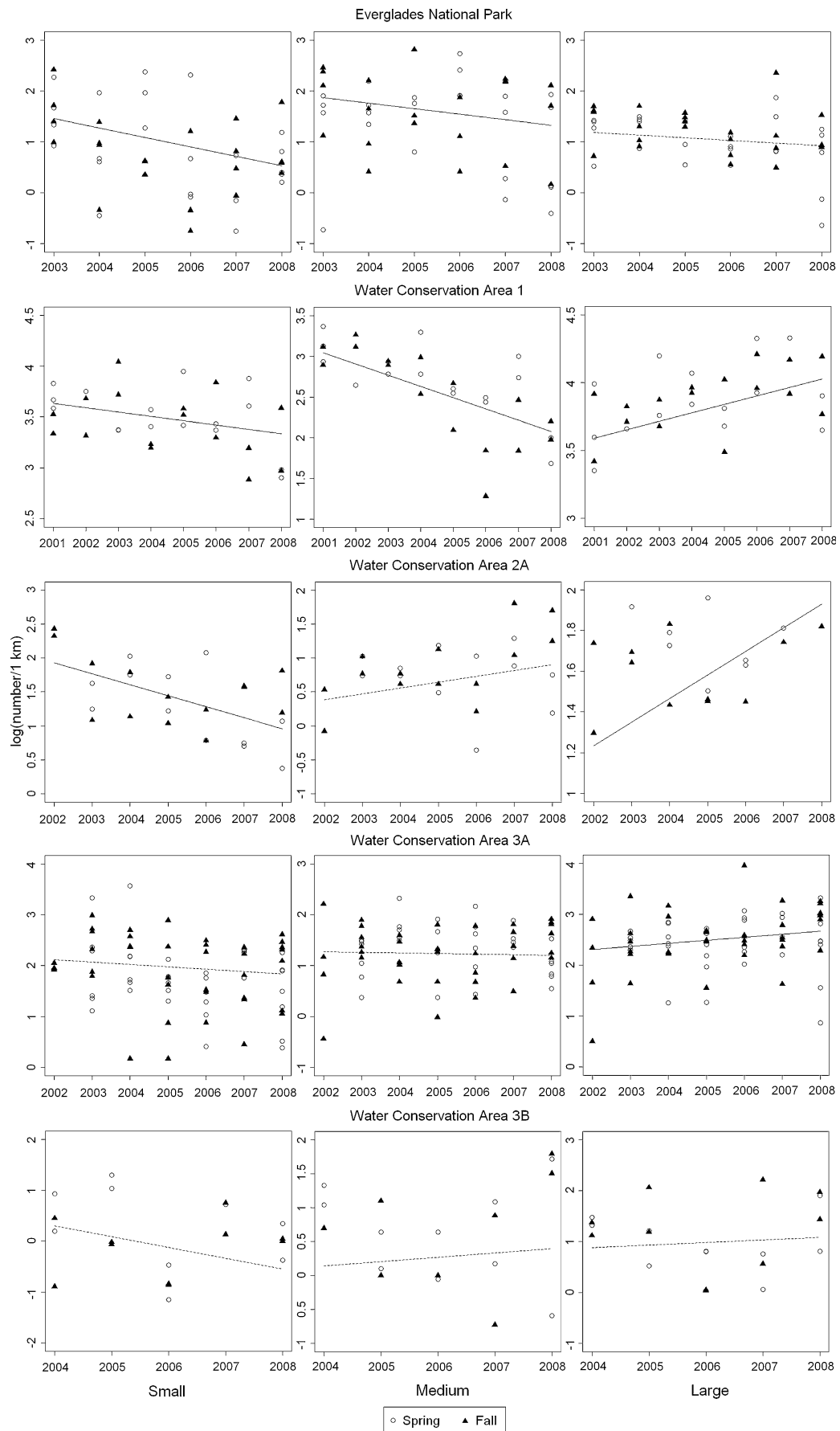


Fig. 2 Estimated slope of abundance trend by size class from American alligators in each subarea of the study area. Solid line indicates that 95% CI of the slope does not contain zero while dashed line indicates it does contain zero. Points (open circle for spring and filled triangle for fall) are mean log count/km by size class, route, and season rescaled by estimated detection probability

subareas for small and large size classes and two subareas for medium size class. Overall, decreasing population trends of small and medium size classes were indicated. In 2001, populations of various other aquatic organisms in the Everglades marsh were impacted by a severe drought (Smith et al. 2003; Trexler and Goss 2009). Reduced availability of aquatic prey likely affected feeding opportunities of small alligators to a greater extent than those of large alligators because smaller animals rely more heavily on aquatic organisms, such as macroinvertebrates, as food sources whereas large alligators consume more diverse prey, including reptiles, birds, and mammals (Barr 1997). In addition, cannibalism (i.e., large alligators eating small alligators) may occur under prolonged drought situations (Schmidt 1924; Cott 1961) as all size classes are forced into small dry season refugia such as alligator holes (depressions maintained by alligators that retain water during the dry season). For these reasons, the adult population may be less susceptible to drought, whereas decreased water depth forces smaller animals into remaining refugia and exposes them to increased cannibalism and predation (Rice et al. 2005). The declining trend of smaller animals throughout the study area may be part of a natural cycle for alligator populations in Everglades wetlands; however, historically, extremely low water depth occurred at lower frequency than today (Fennema et al. 1994), which may have caused higher rates of mortality of small animals. The decline in smaller size class may have negative implications for the future

of alligator populations in this region, particularly if habitat conditions do not favor recruitment of alligator offspring in the near term. The alligator is used as an indicator species during Everglades restoration (Mazzotti et al. 2009). Under the restoration plan, hydrologic cycles will be managed more like historical patterns which may result in more consistent population trends by size class than we see currently.

Our study showed decreasing trends in detection probability with increasing water level for small and large size classes (Fig. 3), and this result is consistent with previous studies. During periods of high water, alligators are able to disperse throughout the marsh due to an expansion of suitable habitat. Also, alligators are more likely to submerge in response to disturbance when the level is relatively higher (Bugbee 2008), and alligator movement is considered to increase in deeper water (Chabreck 1965). Large animals have greater potential for longer dives due to their mass-dependent rate of oxygen consumption (Wright 1987). These behavioral changes likely result in lower detection probability under higher water levels. Lower detection probability of small size class compared to medium and large size classes may be because smaller alligators move into cover to reduce mortality (Woodward et al. 1987). Our results also showed great variability in detection probability by observers and route. Such factors cannot be controlled over the course of long-term surveys like ours; accounting for their effect in the model solves a common inference problem in observational studies by explicitly quantifying those factors other than the ecological process of interest (Royle and Dorazio 2008).

In this study, we used a two-stage hierarchical model to estimate population abundance of alligators from nightlight surveys. Because nightlight surveys are commonly used to monitor crocodylians, our study provides a foundation for

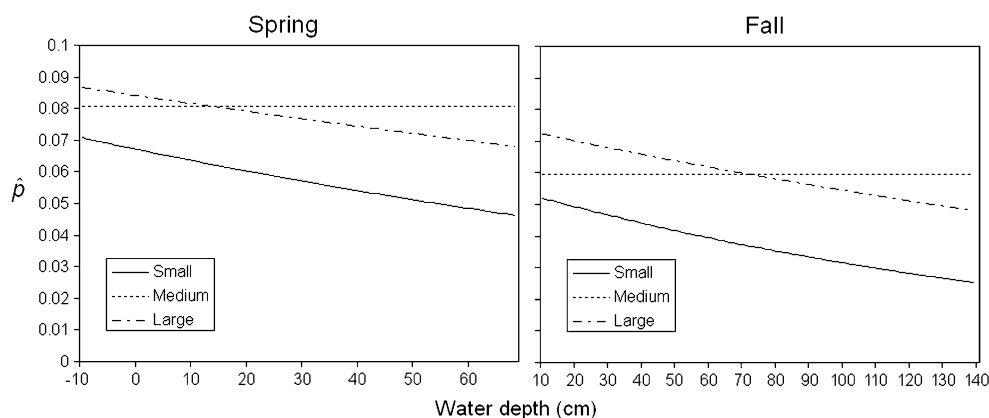


Fig. 3 Estimated response of detection probability as a function of water depth by season and size class. Detection probability of medium size class is held constant due to lack of clear trend. Water depth is based on model predicted values that were derived by water stage minus the digital elevation model of ground elevation relative to the

NAVD 88 vertical datum. Water depth is positive if predicted water stage is above ground elevation, zero if stage is at ground elevation, and negative if stage is below ground elevation. Range of water depth is minimum and maximum water depth of each season

analysis of data from other crocodylian studies. Moreover, crocodylians are only one indicator species monitored for the Comprehensive Everglades Restoration Plan (Mazzotti et al. 2009). Extensive efforts have been made to monitor various organisms as indicators of ecosystem and restoration progress in the Everglades, including aquatic fauna (fish and crustaceans), wading birds, aquatic invertebrates, and invasive plants (Doren et al. 2009). The two-stage hierarchical model may provide an effective tool for improving population inference from survey data of these other organisms as well.

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