Herpetological Conservation and Biology 13(2):331–340.
Submitted: 22 January 2018; Accepted: 8 May 2018; Published 31 August 2018.

Long-term Spotlight Surveys of American Alligators in Mississippi, USA

Bradley A. Strickland[1,4,5], Francisco J. Vilella[2], and Ricky D. Flynt[3]

[1]Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Starkville, Mississippi 39762, USA
[2]U.S. Geological Survey, Mississippi Cooperative Fish and Wildlife Research Unit, Mississippi State University, Starkville, Mississippi 39762, USA
[3]Mississippi Department of Wildlife, Fisheries, and Parks, Jackson, Mississippi 39211, USA
[4]Current affiliation, Department of Biological Sciences, Florida International University, Miami, Florida 33199, USA
[5]Corresponding author, e-mail: bstri007@fiu.edu

***Abstract*.—Accurate population estimates and assessments of trajectory are an essential part of harvest management for game species and conservation action plans for protected species. Long-term monitoring can lead to ecological understanding by identifying biotic and abiotic drivers of population dynamics. Spotlight surveys are a widely used method to monitor abundance and size-class structure of crocodilian populations. The American Alligator (*Alligator mississippiensis*) has recovered from significant population reductions in the southeastern United States. The Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) has conducted alligator spotlight surveys since 1971 to monitor populations. We analyzed this long-term alligator survey dataset to assess possible trends in counts as a proxy for potential population changes. We tested for a positive trend in count data over 46 y and evaluated covariates that could influence counts to assist future survey protocols. Alligator counts during 1971–2016 increased across survey routes in Mississippi. This observed positive response may represent an increase of the alligator population in Mississippi as a result of conservation benefits accrued from improved wetland conditions and species-specific management policies. Evaluation of survey covariates indicated recent rainfall and increasing wind velocity had negative effects on alligator counts while increasing water temperature had a positive effect. Implementing robust survey techniques will improve the reliability of alligator monitoring data and their application to the management of alligator populations. Further, these improved approaches may be useful to other conservation and management agencies as well as for other crocodilian species.**

Key Words.—crocodilians; long-term monitoring; population dynamics; survey methods; wetlands; wildlife management

Introduction

Reliable knowledge of animal abundance is necessary for the conservation and management of populations. Population monitoring is often needed to set sustainable harvest limits for game species and conservation action plans for protected species. Long-term monitoring can also lead to ecological understanding by identifying biotic and abiotic drivers of population dynamics. Secondary measures, or index counts, are commonly used in wildlife monitoring to assess population trajectories when direct measures are too costly or impractical (Anderson 2001; Garel et al. 2010). Index counts (C) are assumed to relate to population size (N), where C is a constant proportion of N across the range of survey conditions (Tracey et al. 2005). Though analysis of index counts assumes constant detectability across observers, species characteristics, environmental types, and temporal patterns, these assumptions are rarely tested (Garel et al. 2010). Approaches to deal with this failure have been validated in some instances and generally focus on standardized monitoring methodologies to maintain constant detectability and modeling potential environmental and temporal drivers (Anderson 2001; Garel et al. 2010). Analysis of index data yields important information on population fluctuations and trends (Johnson 2007). Nevertheless, future research is needed to validate the use of indices and their relationship to absolute abundance (Caughley 1977; Gerht 2002; Morellet et al. 2007).

Crocodilians serve as indicators of ecosystem health and habitat conditions given their functional roles as apex predators in aquatic ecosystems (Mazzotti et al. 2009). Thus, long-term monitoring of their populations and conservation status may be critical for effective ecosystem management. Spotlight surveys, also known as eyeshine and nightlight surveys, are a widely used method to monitor abundance and size classes of crocodilian populations (Hutton and Woolhouse 1989; Da Silveira et al. 2008; Fujisaki et al. 2011). Several studies have attempted to standardize spotlight counts and account for the influence of environmental and observer effects on detectability (Chabreck 1966; Woodward and Marion 1978; Hutton and Woolhouse 1989). Crocodilian detection is influenced by environmental conditions including water and air

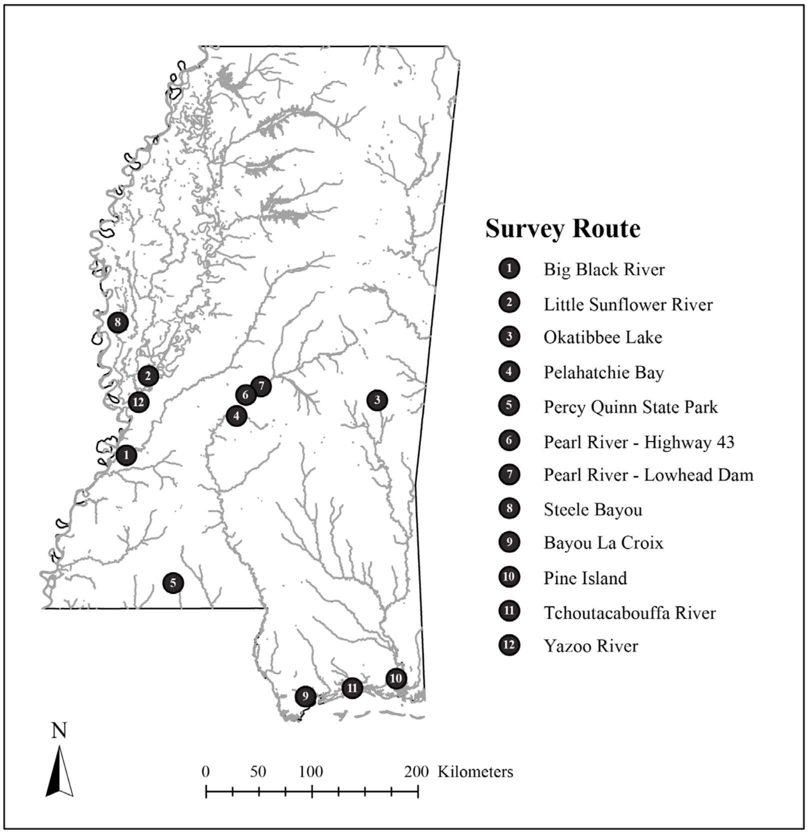

Figure 1. Map of American Alligator (*Alligator mississippiensis*) spotlight survey routes monitored during 1971–2016 in Mississippi, USA. Waterbodies and rivers (gray) were obtained from U.S. Geological Survey and Mississippi Automated Resource Information System (http://maris.state.ms.us).

temperature (Hutton and Woolhouse 1989), presence and density of vegetation (Cherkiss et al. 2006), observer variables such as spotlight intensity (Woodward and Marion 1978), and animal behavior (Pacheco 1996).

The American Alligator (*Alligator mississippiensis*) was historically common and widely distributed throughout the southeastern United States. Unregulated harvest, water pollution, and loss and degradation of wetland habitat reduced populations by the early 1900s across vast portions of their geographic range (McIlhenny 1935; Altrichter and Sherman 1999). The alligator was listed as an endangered species in 1967, yet the species was considered recovered by 1987 (Altrichter and Sherman 1999). Following delisting, some southeastern states continued monitoring programs, started alligator farms, established nuisance removal programs, and instituted regulated harvest seasons. The Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) initiated alligator spotlight surveys in 1971, but no study of this long-term monitoring program has been conducted.

We analyzed the MDWFP long-term alligator spotlight survey dataset to assess possible trends in counts as a proxy of population changes, provide insights on factors influencing its reliability, and to contribute information for the management and conservation of an ecologically important top predator. The first alligator hunt in Mississippi was permitted in 2005 and harvest pressure has been allowed to steadily increase with the assumption that alligator populations are stable or increasing statewide. We tested for a positive trend in alligator spotlight counts throughout the last 46 y across surveyed routes in Mississippi. In addition, we evaluated potential environmental covariates that could influence counts to assist future survey protocols. Further, we used survey data to determine whether annual counts capture within-season variation in alligator numbers. Lastly, we offer considerations for improvement of future crocodilian spotlight surveys.

Materials and Methods

Study site.—We selected the 1999–2016 dataset collected by MDWFP biologists and used 12 historical routes throughout the state of Mississippi with at least six surveys in the last 18 y for analysis (Fig. 1). Other surveys were conducted at some of these routes from 1971–1998. Route lengths were constant each year at individual sites but varied among sites (mean = 23.6 km; range, 6.4–55.2 km).

***Alligator survey protocols in Mississippi*.**—Alligator spotlight surveys were conducted by MDWFP personnel during the spring and summer months starting in 1971. Several routes were not surveyed during some years due to personnel issues and unpredictable water levels. In general, observers used a spotlight to detect alligator eyeshine while traveling on a boat in the center of a channel or along the shoreline of a water body. We used survey data collected during 1999 to 2016 for mixed model analyses and evaluation of covariates and incorporated earlier surveys for a separate trend analysis over time.

Starting in 1999, surveys were conducted from May to August during clear nights with no recent thunderstorms or heavy rainfall, and where wind speed did not exceed 10 km/h. Water temperature, wind velocity, and cloud coverage were collected locally at each site using a thermometer and visual estimation. Precipitation during the previous 24 h (hereafter, rainfall) was obtained from the nearest weather station before each survey. Water level was visually estimated or water gage height obtained from the nearest U.S. Geological Survey station and categorized into an ordinal variable as: very low (1), low (2), average (3), high (4), and very high (5; http://waterdata.usgs.gov/nwis). We obtained data on the fraction of the moon illuminated at midnight of every survey night (http://aa.usno.navy.mil/data/docs/MoonFraction.php). Surveys began after sunset with start times ranging between 1930 and 2230 and ended by 2125 and 0225, depending on route length. Average survey time across all routes was 142 min (range, 32–325 min). Survey teams used a boat-mounted GPS unit to track survey route and length (km), store starting and ending coordinates, and record location of each observation.

Survey teams usually consisted of a driver/navigator, data recorder, and two trained observers. Approximately 74% of surveys used two 1-million candle power handheld lights. Almost half (46%) of surveys used a 75-horsepower motor and a 5-m boat combination. The driver maintained a constant speed of approximately 10 km/h, which was monitored using the GPS unit. Observers recorded eyeshine of individual alligators and placed each detection into size classes (i.e., over or under 1.8 m) based on visual estimation of snout length as an index for total length (Chabreck 1966). Alligators in this area of their range are expected to attain sexual maturity when approximately 1.8 m in total length (Chabreck 1963). The driver diverted from the survey route to confirm size estimations when needed before returning to the survey route.

***Analysis of survey data*.**—We used surveys among routes to examine effects of covariates on counts and assess general trends from 1999–2016. We tested for multicollinearity among explanatory variables and scaled variables by subtracting the mean and dividing by the standard deviation for each observation. We used Poisson generalized linear mixed models (GLMMs) using function overdisp.glmer in package RVAideMemoire in Program R (Hervé 2015) and found evidence of overdispersion. Therefore, we used negative binomial GLMMs with function glmer.nb in package lme4 of Program R (Bates et al. 2014) to model alligator counts. We estimated model overdispersion using the ratio of the sum of squares of Pearson residuals to residual degrees of freedom (Ganio and Schafer 1992). Further, we used route as a random effect and year, Julian date, start time, route length, water temperature, rainfall, cloud coverage, wind velocity, moon phase, and water level as fixed effects. Other route-level variables including light intensity and boat motor horsepower had low variation in the dataset and we did not include them as covariates. We included a null model with the random effect and a global model with all explanatory variables for model selection. We constructed an additional 30 models based on combinations of variables without interaction terms. 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 within two units of the most supported model (Burnham and Anderson 2002). We used the MuMin package in Program R to perform multi-model inference (Bartoń 2014). Finally, we evaluated significance of fixed effects at $\alpha = 0.05$.

We did not use size class as an observation level covariate in modeling the survey counts due to the amount of missing data given approximately 14% of all detections identified size estimation as unknown. However, we used a regression approach to determine changes in mean detected proportion of immature-sized (estimated size under 1.8 m) versus mature (estimated size over 1.8 m in total length) individuals across surveys over time. In another analysis, we also used separate linear regressions at each route to evaluate the potential of increasing alligator observation density per kilometer over survey years including the earlier counts as well (i.e., 1971–2016).

Lastly, we examined within-season variation in alligator counts during summer (1 July to 14 August) of 2013 by conducting separate surveys from MDWFP on the Pearl River - Ratliff Ferry to Highway 43 (n = 6) and Pelahatchie Bay (n = 4) alligator survey routes. We performed separate surveys on different nights but followed the same protocol to assess within-season variation. We used a non-parametric Wilcoxon Signed Rank test due to low sample sizes to determine whether alligator counts from the annual MDWFP survey differed from the mean count of our test surveys. We conducted statistical analyses using program R (R Core

Team 2017) and means reported with ± 1 standard deviation (SD).

Results

During 1999–2016, 5,121 alligator observations were recorded from 124 surveys conducted at 12 sites across Mississippi. Counts from all surveys at six sites recorded 4,128 alligator observations during 1971–2016. For standardized surveys, alligator nightly counts averaged 21.2 ± 6.0 for the Big Black River, 22.0 ± 10.8 for Little Sunflower River, 15.0 ± 6.5 for Okatibbee, 40.8 ± 9.1 for Pelahatchie Bay, 20.3 ± 9.7 for Percy Quinn State Park, 126.5 ± 30.2 for Pearl River Hwy 43, 37.1 ± 14.3 for Pearl River Lowhead Dam, 24.9 ± 5.9 for Steele Bayou, 17.7 ± 2.7 for Bayou La Croix, 97.8 ± 34.0 for Pine Island, 26.3 ± 17.1 for Tchoutacabouffa River, and 48.0 ± 24.4 for Yazoo River. Mean environmental conditions included water temperature of 29° C (range, 20–37° C), rainfall 0.4 ± 0.9 cm (range, 0–5.1 cm), wind speed 3.7 ± 3.2 km/h, fraction of the sky covered by clouds 0.3 ± 0.3, and fraction of the moon illuminated 0.5 ± 0.3. Also, 59% of surveys were conducted under average water level conditions and fewer than 6% were conducted during the very high and very low water level categories.

Explanatory variables were not highly correlated; values of the correlation matrix were < |0.30|. Results of the Poisson GLMM with route as random effect exhibited overdispersion ($\hat{c}$ = 4.317; P < 0.001). We used a negative binomial distribution for the additional dispersion parameter to address overdispersion. Inclusion of route as a random effect in the models was supported by comparing marginal r^2 (0.06), or the variance explained by fixed effects, and conditional r^2 (0.94) considering fixed and random effects, for the global model (Nakagawa and Schielzeth 2013). One of 32 candidate models exhibited $\Delta AIC_c < 2$ (Table 1).

The top model included year as a positive effect, suggesting an increasing alligator count for routes (Table 2). Wind and rainfall had a negative effect on counts, whereas water temperature had a positive effect (Table 2). Predicted number of alligators per standardized survey (1999–2016) derived from the top model (Fig. 2) indicated mean count increased 70% (i.e., 24 to 41 alligators per survey) across all routes from 1999 to 2016. Density of alligator observations per kilometer based on all surveys (1971–2016; Fig. 3) increased significantly over time for Little Sunflower ($F_{1,16}$ = 18.28, P < 0.001, adjusted r^2 = 0.504), Okatibbee Lake ($F_{1,19}$ = 22.69, P < 0.001, adjusted r^2 = 0.520), Pelahatchie Bay ($F_{1,15}$ = 15.68, P = 0.001, adjusted r^2 = 0.479), and Pearl River - Highway 43 ($F_{1,22}$ = 72.77, P < 0.001, adjusted r^2 = 0.757), but not for Bayou La Croix ($F_{1,26}$ = 0.67, P = 0.421) and Percy Quinn ($F_{1,14}$ = 1.42, P = 0.253). Mean proportion of detected immature-sized animals did not exhibit a linear relationship over time ($F_{1,40}$ = 1.387, P = 0.246; Fig. 4). Counts of alligators in MDWFP surveys did not differ for either route from the test surveys (Pelahatchie Bay: V = 9, P = 0.250 and Ratliff Ferry: V = 10, P = 1.000).

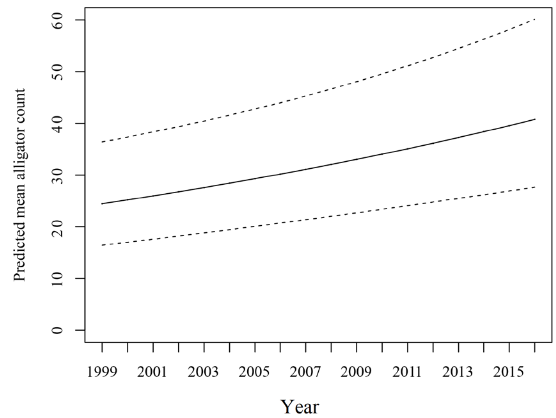

Figure 2. Predicted mean count of American Alligators (*Alligator mississippiensis*) per spotlight survey for all routes by year (1999–2016) for the top model (solid line) and the 95% prediction interval (dotted lines) in Mississippi, USA.

Table 1. Results from negative binomial generalized linear mixed models from candidate set with delta $AIC_c \leq 3$ and the null and global models to describe American Alligator (*Alligator mississippiensis*) counts of spotlight surveys in Mississippi, USA, 1999–2016. Route is the single random effect in all mixed models. The global model along with listed covariates also included Julian date, route start time, route length, cloud coverage, moon phase as fixed effects. 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_c) and number of units from the top model is denoted by ΔAIC_c. Weight of support for each model is given by w_i in a total of 1. All covariates are scaled (mean = 0, SD = 1). Water temperature is abbreviated water temp.

Model	df	Log L	AIC_c	ΔAIC_c	w_i
year + wind + rainfall + water temp	7	-486.09	987.1	0.00	0.38
year + wind + rainfall	6	-488.31	989.3	2.20	0.13
year + wind + rainfall + water temp + water level	8	-486.06	989.4	2.24	0.12
year + wind + water temp	6	-488.42	989.6	2.42	0.11
global model	14	-481.53	994.9	7.77	0.01
intercept only	3	-499.84	1005.9	18.75	0.00

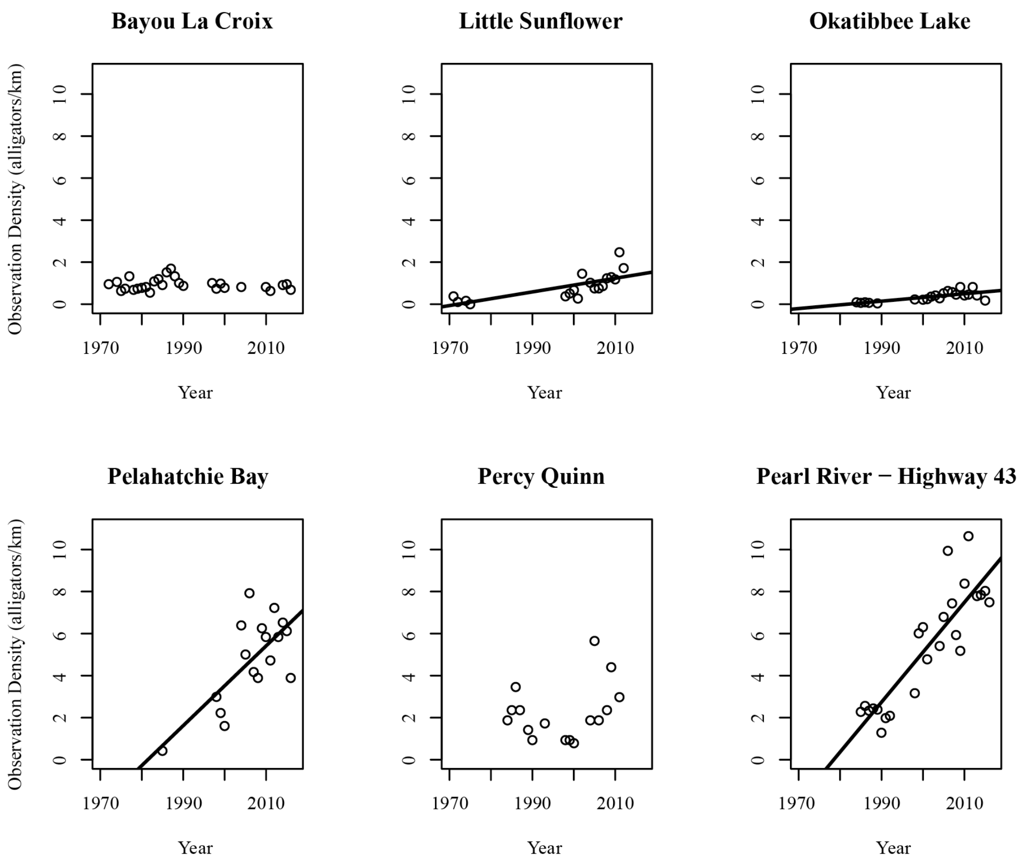

Figure 3. Observation densities of American Alligators (*Alligator mississippiensis*; open circles) across routes by year (1971–2016) of spotlight surveys in Mississippi, USA. Linear regression tested positive trends over time where significance is at α = 0.05 (solid line).

Discussion

Counts of alligators detected on spotlight surveys generally increased across routes in Mississippi during the study period (1971–2016). The observed positive response of alligator counts could represent an actual population increase and reflect the conservation benefits accrued from species protection and wetland conservation policies. Endangered species protection and wetland conservation and restoration practices started in the early 1970s when alligator populations were very low. We think that increasing alligator counts observed in our long-term monitoring reflect continual recovery from the combined effects of decades of protection of the species and its wetland habitats in Mississippi. Increasing abundance as a result of species recovery has been suggested in other portions of the range of alligators (Brandt 1991; Altrichter and Sherman 1999). However, this pattern may not be consistent across the present range of the species given tolerance limits (e.g., ambient temperature) at the northern edge of the geographic range (Dunham et al. 2014). In fact, two of six long-term routes in Mississippi did not show a positive trend and exhibited no linear relationship in counts over time. This finding suggests conservation actions may have site-specific effects; thus, long-term monitoring programs might benefit from the addition of multiple sites in various habitats. An alternative explanation for the observed positive trend is improved detection of animals over time as surveys were conducted by increasingly experienced observers. However,

Table 2. Negative binomial generalized linear mixed model coefficients from top model to describe American Alligator (*Alligator mississippiensis*) counts of spotlight surveys in Mississippi, USA, 1999–2016. Route is the single random effect in the mixed model. All covariates are scaled (mean = 0, SD = 1). Water temperature is abbreviated water temp.

Parameter	β	SE	Pr(>|z|)	2.5%	97.5%
intercept	3.48	0.19	<0.001	3.07	3.89
year	0.14	0.03	<0.001	0.08	0.20
wind	-0.08	0.03	0.015	-0.15	-0.02
rainfall	-0.07	0.03	0.027	-0.12	-0.01
water temp	0.08	0.04	0.032	0.01	0.15

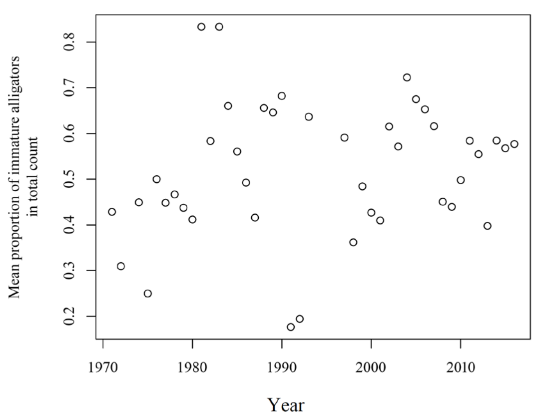

Figure 4. Mean proportion of the detected population of American Alligators (*Alligator mississippiensis*) under 1.8 m in total length (immature size) across routes of spotlight surveys in Mississippi, USA did not exhibit a linear relationship by year (1971–2016).

observers were not held constant throughout the many years of monitoring. Specifically, 12 routes across the state included different individuals and combinations of observers nearly every year. Also, it is important to note that light intensity was not recorded for surveys before 1999. Older surveys may not have had spotlights as powerful as the 1 million candle-power spotlights consistently used starting in 1999. However, we do not believe that this is a likely explanation for an increasing pattern over time because the trend we found is linear, is evident in the analysis of the standardized surveys alone, and is apparent even for routes with narrow-channel rivers, streams, and passes where detectability may be more constant regardless of spotlight intensity.

Our results indicated no change in proportion of detected mature-sized and immature-sized individuals over time. Given that alligators are long-lived, relatively slow-growing, and reach sexual maturity when 8–16 y old, detecting changes in abundance and population structure could take decades of monitoring (Brandt 1991; Wilkinson et al. 2016). Moreover, these demographic responses require an approach where information is collected from populations with a segment of known individuals (i.e., capture-mark-recapture/resight). While our study included 46 y of information, observer estimates of body size may be inaccurate without species- or site-specific correction curves (Magnusson 1983). In addition, missing data exist in our dataset often due to alligator submergence prior to obtaining a visual to estimate size. It is unknown how these issues affect the reliability of using spotlight counts to investigate temporal changes in demography. We suggest these results be taken in context and encourage further research focused on this topic. Also, there may be body size-based differences in detection probabilities arising from habitat use patterns, thus biasing our observations. For instance, hatchlings could be difficult to detect given the appearance of a smaller eyeshine and their disproportionate use of difficult to survey habitats (i.e., tree roots and marsh habitats) for protection from larger predatory alligators. Further, smaller subdominant individuals may be relegated to shallower sections of greater cover and avoid the deeper waters on the main channels used by the largest and more aggressive alligators, where surveys generally occur (Strickland et al. 2016). Hatchlings may also be more susceptible to changes in weather and might retreat or remain submerged, further influencing detection (Eversole et al. 2015). In addition, differences in wariness between size classes may affect detectability (Woodward and Marion 1978).

Our top model included variables for environmental conditions directly related to alligator detection and encounter rate. Increasing wind velocity and recent rainfall had negative effects on counts. Wind impairs the ability of observers to detect alligators as moving water may obscure or hide eyeshine (Woodward and Marion 1978). Also, wind and rain negatively affect emergence rates as crocodilians seek shelter from inclement weather and high winds (Pacheco 1996; Bugbee 2008). Turbidity from recent precipitation and wave action associated with wind and rain events also limit alligator feeding activity (Murphy 1977). Conversely, increasing water temperature had a positive effect on counts. Effect of water temperature on alligator activity and emergence rates varies, depending on season and its relation to air temperature (Woodward and Marion 1978; Bugbee 2008). However, the effect is greater for water temperature than air temperature and for colder periods than warmer periods (Woodward and Marion 1978). Stratification of survey effort by season, as done in our monitoring program, and within-seasonal shifts may help account for the complexity of the interaction of temperature and alligator behavior. However, more controlled studies are needed to investigate the impact of specific environmental variables (e.g., water temperature, flow rates, wind) on emergence and detection rates of alligators during spotlight surveys. In addition, our long-term dataset does not include high or extreme values for some of the covariates (e.g., wind and rainfall); this likely means that our findings are underestimates of their true effects on counts.

Several variables not retained in the top model have been reported to affect alligator spotlight counts in other studies. Higher water levels affect movement patterns (i.e., encounter rates) by providing a larger area for alligators (especially subadults) to disperse while foraging or avoiding predation (Woodward and Marion 1978; Woodward et al. 1996; Webb et al. 2009). Our study dataset exhibited low variation in water level, limiting our ability to detect its effects on counts. Also, increased percentage of moon illuminated has been shown to negatively impact counts due to increased moonlight reflection off the water impairing observers (Woodward and Marion 1978). However, the relationship of alligator activity to moon parameters is complex and involves changes in foraging efficiency due to illumination (Eversole et al. 2015).

Validating spotlight counts as indices for population estimation and for assessing changes in population sizes would improve their reliability as a monitoring tool for crocodilians (Vincent et al. 1991; Jennelle et al. 2002). We encourage this effort, even though some researchers challenge obtaining reliable population sizes as an ultimate aim and emphasize tracking multiple indicators of ecological change, including relative abundance (Morellet et al. 2007; Strickland et al. 2008). Some authors reject the usefulness of indirect approaches such as spotlight counts and their relationship to population abundance (Collier et al. 2013), but others have validated the information gained from their use on terrestrial mammals such as ungulates (Garel et al. 2010) and carnivores (Gerht 2002). For crocodilian spotlight surveys, validation is limited, appears to be site-specific, and may require several different survey techniques (Murphy 1977; Brandt 1991; Woodward et al. 1996). Arguably the best approach to reliable estimates of population size is capture-mark-recapture methods; however, they are expensive, labor-intensive, and assumptions are difficult to meet (Buckland et al. 2000). Methods that allow estimates of population sizes with a measure of certainty across a wide geographic range at a low cost, such as distance sampling, could be an option for new monitoring programs though logistics of sampling varying habitat types and availability biases are still major concerns. Furthermore, the best justification for validation would be its ability to mitigate or quantify the availability bias.

Reliable estimates of diving and emergence (surfacing) rates is an important parameter that will improve abundance estimates derived from crocodilian spotlight survey counts. Availability bias of submerged animals missed during a survey is an important issue facing crocodilian spotlight surveys (Marsh and Sinclair 1989; Braulik et al. 2012). Though spotlight surveys generally determine effects of environmental covariates on counts without accurate measures of availability bias, estimates from analytical approaches (i.e., distance sampling methods and strip transects) will only represent the available (i.e., surfaced) portion of the population. Available emergence estimates for alligators are highly variable and environmental and demographic characteristics influencing this behavior have not been well-studied (Woodward et al. 1996; Bugbee 2008; Nifong et al. 2014).

Our analyses and its assumptions only allowed examining alligator population trends over time, and we were not able to obtain estimates of population size. The reliability of the MDWFP alligator monitoring program would benefit from validation and new survey protocols that account for imperfect detection and modeling important covariates. For instance, double observer or seasonally replicated hierarchical modeling approaches would improve information collected by the alligator monitoring agencies across the Southeastern U.S. (Shirley et al. 2012). In addition, adopting a stratified spotlight survey design incorporating habitat types and management regime (i.e., harvest pressure) might improve the inferential ability of this monitoring program and be an enhanced approach to monitor alligator populations over time (O'Brien and Doerr 1986). However, it is important to avoid disrupting the integrity of the existing long-term alligator monitoring dataset from extensive methodological modifications that would preclude comparisons of temporal trends. This could be resolved by retaining sites with significant amounts of data and introducing new sites within a targeted stratum.

Current alligator surveys conducted by most state agencies are restricted to the spring and summer months. We are uncertain how counts outside this time period might improve population assessments given the relative inactivity of alligators during the colder months and greatly increased activity during the spring breeding season. Our results indicated no difference in counts from MDWFP annual surveys and trial surveys conducted to assess within-season variation. This suggests existing MDWFP survey protocols (e.g., standardizing wind and rainfall) and current sampling regime may account for environmental variation of counts. Although observed counts did not differ from our trial surveys, some MDWFP routes exhibited large variation in counts between years. Based on this finding, conducting replicate surveys within a year may improve the ability to account for environmental sources of variation influencing alligator encounter rates and detection. Replicate surveys for each route would allow future analyses to better incorporate the possible influence of the many covariates currently recorded by MDWFP personnel, especially when modeling covariates by body size class.

The impact of development, habitat fragmentation, and change in water temperature and precipitation patterns because of climate change on wetland ecosystems may represent future environmental stressors for alligator populations. Alligator management practices including recreational harvest and removal of nuisance animals will benefit from reliable information on populations and temporal trends. Therefore, implementing robust survey techniques that improve abundance estimates with associated precision measures will improve the capabilities of MDWFP to monitor and manage alligator populations and may serve as a model to other conservation agencies in the southeastern U.S. and international organizations monitoring other crocodilian species.

Acknowledgments.—Funding was provided by Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP; award number 14-16-0009-1543) and Berryman Institute (award number 10-7400-0471-CA). We are grateful to Scott Edwards of MDWFP for project support and coordination. We thank Ashley Gary and Linda Taylor of MDWFP for sorting and entering hard copy data for computer analysis. Bruce Leopold, Jerry Belant, and Marcus Lashley provided comments to an earlier version of this manuscript. Katherine Strickland designed the study site map. Andrew Smith and Sid Godfrey provided valuable assistance in the field along with dozens of other volunteers that assisted with surveys over the 46 y of data collection. Fieldwork was conducted under the auspices of protocol 12-016 from the Institutional Animal Care and Use Committee of Mississippi State University. The use of trade, firm, or product names is for descriptive purposes only and does not constitute endorsement by the U.S. Government.

Literature Cited

Altrichter, M., and P.M. Sherman. 1999. Distribution and abundance of the American Alligator in the Welder Wildlife Refuge, Texas. Texas Journal of Science 51:139–146.

Anderson, D.R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Bartoń, K. 2014. MuMIn: multi-model Inference. R package version 1.10. http://cran.r-project.org/package= MuMIn.

Bates, D., M. Maechler, B. Bolker, S. Walker, R.H.B. Christensen, H. Singmann, and B. Dai. 2014. lme4: linear mixed-effects models using eigen and S4. R package version 1.1–7. https://github.com/lme4/lme4/ http://lme4.r-forge.r-project.org/.

Brandt, L.A. 1991. Long-term changes in a population of *Alligator mississippiensis* in South Carolina. Journal of Herpetology 25:419–424.

Braulik, G.T., Z.I. Bhatti, T. Ehsan, B. Hussain, A.R. Khan, A. Khan, U. Khan, K.U. Kundi, R. Rajput, P. Reichert, et al. 2012. Robust abundance estimate for endangered River Dolphin subspecies in South Asia. Endangered Species Research 17:201–215.

Buckland, S.T., I.B.J. Goudie, and D.L. Brochers. 2000. Wildlife population assessment: past developments and future directions. Biometrics 56:1–12.

Bugbee, C.D. 2008. Emergence dynamics of American Alligators in Arthur R. Marshall Loxahatchee National Wildlife Refuge: life history and application to statewide alligator surveys. M.Sc. Thesis, University of Florida, Gainesville, Florida, USA. 115 p.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd Edition. Springer-Verlag, New York, New York, USA.

Caughley, G. 1977. Analysis of Vertebrate Populations. John Wiley and Sons, Brisbane, Australia.

Chabreck, R.H. 1963. Methods of capturing, marking, and sexing alligators. Proceedings of the Southeastern Association of Game and Fish Commissioners 17:47–50.

Chabreck, R.H. 1966. Methods of determining the size and composition of alligator population in Louisiana. Proceedings of the Southeastern Association of Game and Fish Commissioners 20:105–112.

Cherkiss, M.S., F.J. Mazzotti, and K.G. Rice. 2006. Effects of shoreline vegetation on visibility of American Crocodiles *Crocodylus acutus* during spotlight surveys. Herpetological Review 37:37–40.

Collier, B.A., S.S. Ditchkoff, C.R. Ruth, and J.B. Raglin. 2013. Spotlight surveys for White-tailed Deer: monitoring panacea or exercise in futility? Journal of Wildlife Management 77:165–171.

Da Silveira, R., W.E. Magnusson, and J.B. Thorbjarnarson. 2008. Factors affecting the number of caimans seen during spotlight surveys in the Mamirauá Reserve, Brazilian Amazonia. Copeia 2008:425–430.

Dunham, K., S. Dinkelacker, and J. Miller. 2014. A stage-based population model for American Alligators in northern latitudes. Journal of Wildlife Management 78:440–447.

Eversole, C.B., S.E. Henke, D.B. Wester, B.M. Ballard, and R.L. Powell. 2015. Responses of American Alligators to environmental conditions: implications for population and ecosystem monitoring. Herpetologica 71:37–45.

Fujisaki, I., F.J. Mazzotti, R.M. Dorazio, K.G. Rice, M. Cherkiss, and B. Jeffery. 2011. Estimating trends in alligator populations from nightlight survey data. Wetlands 31:147–155.

Ganio, L.M., and D.W. Schafer. 1992. Diagnostics for overdispersion. Journal of the American Statistical Association 87:795–804.

Garel, M., C. Bonenfant, J. Hamann, F. Klein, and J. Gaillard. 2010. Are abundance indices derived from spotlight counts reliable to monitor Red Deer populations? Wildlife Biology 16:77–84.

Gehrt, S.D. 2002. Evaluation of spotlight and road-kill surveys as indicators of local raccoon abundance. Wildlife Society Bulletin 30:449–456.

Hervé, M. 2015. RVAideMemoire: diverse basic statistical and graphical functions. R package version 0.9-45-2. https://cran.r-project.org/web/packages/RVAideMemoire/index.html.

Hutton, J.M., and M.E.J. Woolhouse. 1989. Mark-recapture to assess factors affecting the proportion of a Nile Crocodile population seen during spotlight counts at Ngezi, Zimbabwe, and the use of spotlight counts to monitor crocodile abundance. Journal of Applied Ecology 26:381–395.

Jennelle, C.S., M.C. Runge, and D.I. MacKenzie. 2002. The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. Animal Conservation 5:119–120.

Johnson, D.H. 2007. In defense of indices: the case of bird surveys. Journal of Wildlife Management 72:857–868.

Magnusson, W.E. 1983. Size estimates of crocodilians. Journal of Herpetology 17:86–88.

Marsh, H., and D.F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. Journal of Wildlife Management 53:1017–1024.

Mazzotti, F.J., G.R. Best, L.A. Brandt, M.S. Cherkiss, B.M. Jeffery, and K.G. Rice. 2009. Alligators and crocodiles as indicators for restoration of Everglades ecosystems. Ecological Indicators 9:S137–S149.

McIlhenny, E.A. 1935. The Alligator's Life History. Christopher Publishing House, Boston, Massachusetts, USA.

Morellet, N., J.M. Gaillard, A.J.M. Hewison, P. Ballon, Y. Boscardin, P. Duncan, F. Klein, and D. Maillard. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. Journal of Applied Ecology 44:634–643.

Murphy, T.M. 1977. Distribution, movement, and population dynamics of the American Alligator in a thermally altered reservoir. M.Sc. Thesis, University of Georgia, Athens, Georgia, USA. 64 p.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Nifong, J.C., R.L. Nifong, B.R. Silliman, R.H. Lowers, L.J. Guillette, J.M. Ferguson, M. Welsh, K. Abernathy, and G. Marshall. 2014. Animal-borne imaging reveals novel insights into the foraging behaviors and diel activity of a large-bodied apex predator, the American Alligator (*Alligator mississippiensis*). PLoS ONE 9:1–11. https://doi.org/10.1371/journal.pone.0083953.

O'Brien, T.G., and P.D. Doerr. 1986. Night count surveys for alligators in coastal counties of North Carolina. Journal of Herpetology 20:444–448.

Pacheco, L.F. 1996. Wariness of caiman populations and its effect on abundance estimates. Journal of Herpetology 30:123–126.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Shirley, M.H, R.M. Dorazio, E. Abassery, A.A. Elhady, M.S. Mekki, and H.H. Asran. 2012. A sampling design and model for estimating abundance of Nile Crocodiles while accounting for heterogeneity of detectability of multiple observers. Journal of Wildlife Management 76:966–975.

Strickland, B.A., F.J. Vilella, and J.L. Belant. 2016. Scale-dependent habitat selection and size-based dominance in adult male American Alligators. PLoS ONE 11:1–16. https://doi.org/10.1371/journal.pone.0161814.

Strickland, B.K., S. Demarais, and P.D. Gerard. 2008. Variation in mass and lactation among cohorts of White-tailed Deer. Wildlife Biology 14:263–271.

Tracey, J.P., P.J.S. Fleming, and G.J. Melville. 2005. Does variable probability of detection compromise the use of indices in aerial surveys of medium-sized mammals? Wildlife Research 32:245–252.

Vincent, J.P., J.M. Gaillard, and E. Bideau. 1991. Kilometric index as biological indicator for monitoring forest Roe Deer populations. Acta Theriologica 36:315–328.

Webb, K.K., A.F. Zuur, G.E. Calkins, and J.P. Duguay. 2009. Habitat use of American Alligators in east Texas. Journal of Wildlife Management 73:566–572.

Wilkinson, P.M., T.R. Rainwater, A.R. Woodward, E.H. Leone, and C. Carter. 2016. Determinate growth and reproductive lifespan in the American Alligator (*Alligator mississippiensis*): evidence from long-term recaptures. Copeia 104:843–852.

Woodward, A.R., and W.R. Marion. 1978. An evaluation of factors affecting night-light counts of alligators. Proceedings of the Southeastern Association of Game and Fish Commissioners 32:291–302.

Woodward, A.R., K.G. Rice, and S.B. Linda. 1996. Estimating sighting proportions of American Alligators during night-light and aerial helicopter surveys. Proceedings of the Southeastern Association of Game and Fish Commissioners 50:509–519.

Bradley A. Strickland received his B.S. in 2011 for Environmental Biology from Berry College in Mt. Berry, Georgia, USA, which holds the title for the largest contiguous campus in the world at over 109 km2. In 2015, he completed his M.S. in Wildlife Sciences at Mississippi State University in Starkville, Mississippi, USA, investigating American Alligator spatial ecology and population estimation in Mississippi rivers. He has also participated in a National Science Foundation Research Experience for Undergraduates at the University of Minnesota in St. Paul, Minnesota, USA, to study invasive earthworm ecosystem impacts, surveyed endangered mussels and fish species in Georgia, and coordinated a long-term juvenile bull shark monitoring program. Currently, he is a Ph.D. Candidate at Florida International University in Miami, Florida, USA, studying how predators influence community structure and ecosystems beyond their namesake roles of eating and scaring prey. His doctoral work as an Everglades Foundation Fellow investigates the influence predators have on bottom up processes through nutrient recycling and physical engineering. (Photographed by Katherine Strickland).

Francisco J. Vilella is Assistant Unit Leader at the Mississippi Cooperative Fish and Wildlife Research Unit of the U.S. Geological Survey, and Professor of Conservation Biology in the Department of Wildlife, Fisheries and Aquaculture at Mississippi State University in Starkville, Mississippi, USA, where he conducts research in conservation biology and tropical ecology. Francisco received his B.S. in Biology from the University of Puerto Rico at Mayaguez, Puerto Rico, USA, a M.S. in Biology from Hofstra University, Hempstead, New York, USA, and a Ph.D. in Wildlife and Fisheries Science from Louisiana State University, Baton Rouge, Louisiana, USA. His research has focused on population and community ecology, as well as habitat restoration and management. Besides his research in the southeastern U.S., Francisco has conducted research in the Caribbean islands and South America. In addition to his position at Mississippi State University, Dr. Vilella holds Adjunct Professor appointments at the University of Puerto Rico, Universidade Norte Fluminense in Campos dos Goytacazes, Rio de Janeiro, Brazil, and Universidad Nacional de Córdoba in Córdoba, Córdoba, Argentina. (Photographed by Steve Dinsmore).

Ricky D. Flynt received his B.S. degree in Forestry/Wildlife Management from Mississippi State University (MSU), Starkville, Mississippi, USA, in 1991. While attending MSU he was a Cooperative Program Student working for the Mississippi Wild Turkey Cooperative Research Project assisting with field work on four M.S. thesis projects related to wild turkeys (1989–1991). He has previously worked for the Denver Wildlife Research Center of the U.S. Department of Agriculture/Animal and Plant Health Inspection Service located in Starkville, Mississippi, USA, where he researched bird depredation on aquaculture facilities in the Mississippi Delta (1991–1993). He is a Wildlife Biologist and Law Enforcement Officer with the Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP; 1993–present). He currently serves as the Alligator/Furbearer/Nuisance Wildlife Program Coordinator for the MDWFP. He previously served as an Area Manager and Associate Biologist managing habitats for deer, wild turkey, waterfowl, quail, and other small game species on MDWFP Wildlife Management Areas. (Photographed by Corey Hunt).