Responses of American Alligators (Alligator mississippiensis) to Environmental Conditions: Implications for Population and Ecosystem Monitoring

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ABSTRACT: Accurate monitoring of wildlife populations is critical for species management and conservation. If management practices are based on inaccurate data, managers might not be implementing management strategies appropriately, which can have severe ecological consequences. We used a generalized linear mixed-model analysis to predict and explain the relative abundance of American Alligators (*Alligator mississippiensis*) within inland freshwater wetlands. Models were developed for three alligator age classes: hatchlings (\leq 30.5 cm total length [TL]), subadults (30.6–182.9 cm TL), and adults (\geq 183 cm TL). Independent variables included environmental parameters that we measured during nighttime surveys. We conducted 135 nighttime alligator surveys, and recorded 7689 observations of alligators in three study lakes. We found that the relative abundance of alligators is variable among age classes and lakes. Final models for each age classes as well. These results indicate that alligator occurrence and relative abundance is multifaceted and complex. Survey techniques should accurately quantify age- and populationspecific data. Managers and scientists should target particular age classes during surveys on the basis of prevailing environmental conditions.

Key words: Crocodilia; Habitat; Life history; Local environment; Texas; Wildlife management

POPULATION surveys are commonly used to collect data on activity, relative abundance, and population dynamics of reptiles and amphibians (Sun et al. 2001; Brown and Shine 2002; Pellet and Schmidt 2005). The rates at which active animals are encountered during surveys can exhibit large variation across an array of environmental scales (Brown and Shine 2002). Survey results are dependent upon seasonal events such as overwintering, migration, and the production and care of offspring (Brown and Shine 2002). Animal activity and encounter rates also might vary from day to day as the result of changes in environmental conditions (Walls 1983; Sun et al. 2001; Brown and Shine 2002; Altwegg et al. 2005).

American Alligators (Alligator mississippiensis) occur in the southeastern United States, and were declared an endangered species in 1967 (Conant and Collins 1998). The subsequent restoration of American alligator populations and their habitats throughout the southeastern United States has been attributed to strict harvest regulations, intensive management strategies, and wetland conservation (Thompson et al. 1984; Saalfeld et al. 2008). To maintain sustainable populations, alligator populations are regularly monitored using nighttime surveys (Chabreck 1966; Magnusson 1982; Thompson et al. 1984; Fujisaki et al. 2011). Harvest regulations and management strategies are based upon these survey results; therefore, their accuracy is essential to the sound management of the species and their ecosystems (Subalusky et al. 2009). American Alligators are frequently used as an indicator of ecosystem health and habitat restoration success (Rice et al. 2005; Mazzotti et al. 2009; Fujisaki et al. 2011; Ugarte et al. 2013). It is because of the integral role that alligators play as apex predators and habitat modifiers that they are highly useful as ecological indicators (Mazzotti and Brandt 1994; Mazzotti et al. 2009). Thus, alligator surveys are a valuable ecological management and monitoring tool because resulting data can reflect the status of not only alligator populations but also the quality of the ecosystems in which they occur. Little is known, however, about how these surveys are affected by variability in environmental factors such as weather, water quality, and lunar parameters. This relationship is especially important for surveys because activity of the target species can affect the detection of alligators (Chabreck 1966; Subalusky et al. 2009).

We evaluated the influence of environmental variables on the nighttime relative abundance of American Alligators. The objectives of our study were to determine: (1) which environmental factors are most influential on the relative abundance of alligators; (2) how these factors affect the detection of different age classes of alligators, and (3) methods to improve reliability of alligator surveys based on the first two objectives.

MATERIALS AND METHODS

Study Area

This study was conducted at Brazos Bend State Park $(BBSP; 29^{\circ}22.962'N, 95^{\circ}36.343'W, datum = WGS84), a$ 1982-ha park in Fort Bend County, Texas, USA. We surveyed seven lakes in the park (Fig. 1). Because of the small sample sizes of alligators observed in some lakes, we only used data from three lakes (Elm, Forty-Acre, and Pilant lakes) for data analysis. Although the three lakes are freshwater with similar aquatic plant communities, they differ in size, vegetation coverage, and alligator density (Table 1). Elm Lake is a heavily vegetated shallow-water lake (mean depth = 0.6 m) occupied by mostly juvenile and nesting female alligators (Table 1). Forty-Acre Lake has sparser vegetation, more deep-water areas (mean depth = 2.0 m), and a larger proportion of adult alligators (Table 1). Pilant Lake is similar to Elm Lake in terms of water depth but is the largest lake at the site (115.3 ha). Only 25% (29.1 ha) of the basin of Pilant Lake is likely usable by alligators on account of water levels and vegetation density (personal observation). These characteristics also severely limit the area that can be accurately surveyed using boats (Fig. 1). The area of Pilant Lake that was included in our study had little submerged aquatic vegetation, presumably

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FIG. 1.—Lakes that were surveyed for Alligator mississipiensis at Brazos Bend State Park, Texas, USA, from 16 August 2012 to 10 July 2013. Figure includes both surveyed and nonsurveyed lake area.

because of water-level fluctuations. Predominant aquatic plants that occur in all lakes include common water hyacinth (*Eichhornia crassipes*), alligator weed (*Alternanthera philoxeroides*), coontail (*Ceratophyllum demersum*), hydrilla (*Hydrilla verticillata*), smartweed (*Polygonum spp.*), American

TABLE 1.—Lake-specific characteristics of Pilant, Elm, and Forty-Acre lakes at Brazos Bend State Park, Needville, Texas, USA, calculated from nighttime population surveys of *Alligator mississippiensis*.

		Lake	
	Pilant	Elm	Forty-Acre
Size (ha)	29.1	34.2	16.3
Alligator relative density (alligators/ha)	0.3	3.5	2.6
Hatchlings (%)	0	36	27
Subadults (%)	50	34	30
Adults (%)	50	29	45

lotus (*Nelumbo lutea*), wild rice (*Zizania aquatica*), common duckweed (*Lemna minor*), cattail (*Typha* spp.), and Chinese tallow (*Triadica sebifera*).

Alligator Surveys

Population characteristics were determined by conducting nighttime surveys along designated transects in each lake following the methods of Chabreck (1966), Thompson et al. (1984), and Webb et al. (2006). Each survey was conducted from a 5.5-m airboat at 6–8 km/h and using two 200,000 candle power spotlights. Observers were positioned in boat seats that were elevated 1.5 m above the water surface. An estimation of total length (TL) of each alligator was determined by estimating the distance from the eyes to the tip of the snout in inches; this length is known to correlate with TL in feet (Chabreck 1966). Accuracy of this method across all observers was >90% as verified by previous surveys in which visually estimated length was compared with actual length. We converted TL estimates to centimeters and classified alligators into three age classes on the basis of these values: hatchlings (TL \leq 30.5 cm), subadults (30.6–182.9 cm TL), and adults (TL \geq 183 cm; Hutton 1989; Saalfeld et al. 2008). If observers were unable to determine the TL, individuals were recorded as unknown in TL.

We conducted surveys on each lake during four consecutive nights each month during a 12-mo period (16 August 2012–10 July 2013). We completed each night's survey of the three study lakes in approximately 6 h. Each 4-d survey period was randomly selected within a given month, and survey nights began approximately 1 h after sunset. Lake order was randomly selected each night. We calculated lake size (ha), relative density of alligators (individuals/ha), and proportion of individuals within each of the three life-history stages for each of the three lakes.

Weather parameters were measured at the start of each night's survey using a Kestrel 3500 weather meter (http:// www.kestrelmeters.com) and included air temperature ($^{\circ}C$), relative humidity (%), dew point (°C), barometric pressure (hPa), maximum wind velocity (km/h), and mean wind velocity (km/h). We monitored rainfall daily at BBSP with a stationary rain gauge. We obtained information on moon phase, altitude of meridian, distance of the moon from the earth, and percent moon illumination from the closest monitored area (Houston, Texas) to our study site (http:// www.timeanddate.com). We measured the following hydrologic parameters from each lake during each survey period: temperature, conductivity, salinity, total dissolved solids (TDS; measured with an EcoSense EC300 conductivity and salinity meter, YSI Inc., Yellow Springs, Ohio), dissolved oxygen (DO; measured with a EcoSense DO 200 dissolved oxygen meter, YSI Inc.), turbidity (measured with a Global Water Instruments portable turbidity meter, Global Water, Gold River, California), and pH (measured with a HACH pH meter, HACH Co., Loveland, Colorado).

Statistical Analyses

Alligator count data were modeled assuming a negative binomial distribution with a generalized linear mixed model (PROC GLIMMIX; Schabenberger 2005) with SAS® 9.3 software (SAS Institute, Inc. 2011) to develop models using environmental parameters as independent variables. Because of a large number of zero counts of hatchlings in Forty-Acre Lake, our analyses from this particular lake were based on a log (count + 1) analysis of variance of a general linear model; back-transformed means and asymmetric SE are presented (Sokal and Rohlf 2012). Models were used to explain variation in the relative abundance of alligators for each size class. We used a reverse selection process to determine individual parameter contribution based on type III effects to each model (i.e., all parameters were put into the model and the least significant parameters were removed one at a time until all remaining parameters provided a significant $[P \le 0.05]$ and unique contribution to the model). Significance level for each parameter was determined from *F*-tests on type III effects, which calculate the significance of each parameter after variation attributable to all other parameters in the model has been taken into account. Therefore, we determined the independent relationship of the number of alligators observed to each significant model parameter, and accounted for multicollinearity among parameters. Partial regression coefficients in multiple regression models with correlated independent variables can be difficult to interpret, however, and do not necessarily reflect the inherent effects of individual variables, but rather their marginal (or partial) effect (Kutner et al. 2004).

Because our sampling strategy involved data collection on four successive days each month, we modeled possible nonindependence with a first-order autoregressive process for the residuals using "day within month" as a subject effect. We calculated a pseudo- R^2 (Heinzl and Mittlbock 2003) for each model to determine the amount of variation in the number of alligators observed that could be explained by our independent variables; these values were used as measures of model goodness of fit for each lake and dependent variable, and were not compared across models or dependent variables (IDRE 2014). We determined differences in levels of categorical variables that were included in the models (i.e., moon phase, water level, season, and time period) through the use of least-squares mean separation, and considered means statistically different if $P \leq 0.05$. For each age class, we evaluated the generalizability of our results by comparing those models developed from analyses using data from all lakes combined with those based on analyses that were lake specific.

We calculated mean values of environmental parameters for each lake and used the general linear model procedure (PROC GLM; Littel et al. 2006; SAS Institute, Inc. 2011) to compare environmental parameters between lakes. Tukey's honestly significant difference test was conducted when significant *F*-tests were detected (P < 0.05).

Results

Alligator Relative Abundance

We conducted 135 of 144 (i.e., survey 3 lakes, 4 times per month for 12 consecutive months) scheduled surveys among the lakes incorporated into our data analysis. Because of logistical reasons (e.g., boat mechanical failure, unsafe weather conditions) nine of these individual surveys were not conducted on scheduled nights; however, surveys were conducted during each scheduled survey period. We recorded 7689 observations of individual alligators during the study. Overall, we observed age classes of alligators in nearly equal proportions, with hatchlings, subadults, adults, and alligators of unknown size comprising 23%, 24%, 24%, and 29% of the observed individuals, respectively.

We developed 11 models, one for each age class by lake and for all lakes combined to examine the influence of the environmental parameters on the relative abundance of alligators (Tables 2–4).

Weather Parameters

Air temperature, dew point, relative humidity, and barometric pressure were similar among the three lakes $(F_{2,131} = 0.06, P = 0.94; F_{2,125} = 0.01, P = 0.99; F_{2,131} =$ 1.73, $P = 0.18; F_{2,131} = 0.04, P = 0.96$, respectively; Table 5). However, average wind speed was different among lakes $(F_{2,131} = 17.69, P < 0.001;$ Table 5), and was higher at Elm Lake than at either Pilant or Forty-Acre lakes. Air temperature, cloud cover, relative humidity, rainfall, and maximum wind gust were the least significant variables in

TABLE 2.—Regression coefficients (± 1 SE), *P*-values, and pseudo– R^2 for the Elm Lake model that predicts relative abundance of three size classes of *Alligator mississipiensis* at Brazos Bend State Park, Needville, Texas, USA. Variables having indicated values are significant ($P \le 0.05$), whereas missing values indicate nonsignificant model parameters.

						L	ife-history sta	ıge					
			Adult				Subadult				Hatchlings		
Model	df	F	Р	Slope	df	F	Р	Slope	df	F	Р	Slope	
Dew point	_	_	_	_	_	_	_	_	1,34	13.0	0.001	0.07 ± 0.02	
Conductivity	1,38	34.9	< 0.001	0.013 ± 0.002	1,35	8.1	0.007	0.02 ± 0.006			_		
Salinity	1,38	35.3	< 0.001	-19.7 ± 3.32	1,35	9.4	0.004	-33.7 ± 11.0	1,34	17.23	> 0.001	-8.71 ± 2.10	
Dissolved oxygen	1,38	102	< 0.001	0.11 ± 0.01	1,35	8.7	0.006	0.12 ± 0.04					
Turbidity	1,38	6.84	0.013	0.010 ± 0.004		_	_		_		_	_	
Water temperature			_		1,35	4.26	0.046	0.12 ± 0.06	_		_		
Moon distance	1,38	32.00	< 0.001	-0.008 ± 0.001	1,35	10.0	0.003	-0.009 ± 0.002	1,34	19.68	< 0.001	-0.019 ± 0.004	
Moon phase			_		4,35	3.35	0.020	_	4,34	6.95	< 0.001		
Water level	1,38	13.1	< 0.001	_		_	_	_	1,34	5.58	0.003	_	
Class parameters ^a				Mean			Ν	lean			Mean		
Moon phase:													
First atr.				_			33.9	$\pm 3.68^{A}$		$\begin{array}{r} 41.64 \pm 5.73^{\rm A} \\ 10.96 \pm 6.14^{\rm A} \end{array}$			
Third atr.				_			32.50	$\pm 6.43^{A}$					
Full				_			28.75	$\pm 3.40^{A}$		4	0.06 ± 9.4	17 ^A	
Super				_			3.27	$\pm 1.98^{B}$			6.21 ± 2.5	50^{B}	
New				_			36.97	$\pm 5.78^{A}$		4	1.42 ± 6.8	89 ^A	
Water level:													
Normal				19.3 ± 1.03^{B}				_		3	2.83 ± 9.0	00^{A}	
Low			\$	$28.3 \pm 2.14^{\text{A}}$				_		1	4.17 ± 2.7	2^{B}	
Intercept			\$	2.13 ± 0.44			1.21	± 1.37			5.28 ± 1.0)5	
Pseudo- R^2				0.85			0	0.66			0.63		

^a For class parameters within a life-history stage, mean values followed by the same capital letter within a column are not significantly different (P > 0.05).

models for the relative abundance of alligators; none of these variables emerged as a significant parameter in any of the models. Barometric pressure was incorporated as a significant variable in only two models—one hatchling model and one adult model—and exhibited a positive relationship with the relative abundance of alligators in both (Tables 3 and 4). Dew point had a positive relationship in the Elm Lake hatchling model (Table 2). Average wind speed occurred as a significant variable in the Pilant Lake model and had a negative relationship with the relative abundance of subadult alligators (Table 4).

Moon Parameters

Moon parameters frequently occurred as significant variables in the models for the relative abundance of alligators (Tables 2 and 3). However, altitude of the meridian and percent moon illumination were not incorporated as significant variables. Moon distance was significant in the Elm Lake models for each life-history stage (Table 2) and the Forty-Acre Lake subadult model (Table 3). Moon distance was negatively related to the relative abundance of adult, subadult, and hatchling alligators in Elm Lake. Additionally, in Forty-Acre Lake, the relative abundance of subadult alligators was negatively related to moon distance. Moon phase was a significant parameter in the Elm Lake models for subadult and hatchling alligators (Table 2) and the models for Forty-Acre Lake for all life-history stages (Table 3). The relationship between the relative abundance of alligators and moon phase type was variable.

Water Parameters

Water temperature and TDS were similar among the three lakes ($F_{2,131} = 0.31$, P = 0.74; $F_{2,131} = 0.64$, P = 0.53,

respectively; Table 5). However, values for water conductivity, salinity, DO, turbidity, and pH differed among the lakes $(F_{2,131} = 19.25, P < 0.001; F_{2,131} = 7.20, P = 0.001; F_{2,131} = 13.01, P < 0.001; F_{2,131} = 6.13, P = 0.003; F_{2,131} = 14.76, P < 0.001$, respectively; Table 5). Water parameters appeared to influence alligator relative abundance more often than any of the weather or moon variables (Tables 2–4). DO, turbidity, TDS, and pH appeared to be relatively poor indicators of alligator relative abundance, as these variables were incorporated into relatively few of the possible models (Tables 2–4). Water temperature was frequently incorporated as a significant model parameter and had a positive relationship with the relative abundance of alligators in the Elm Lake model for subadults, the Forty-Acre models for adults and hatchlings, and Pilant Lake model for adults (Tables 2-4). Salinity exhibited a negative relationship with the relative abundance of alligators of all size classes in all Elm Lake models. Salinity displayed a negative relationship in the adult and subadult models, but a positive relationship with the relative abundance of hatchlings, in Forty-Acre Lake (Table 3). In the Elm Lake models, conductivity was positively related to adult and subadult relative abundance. Water conductivity was negatively related to the relative abundance of adult and subadult alligators in the Forty-Acre Lake models (Table 3).

DISCUSSION

The nighttime relative abundance of alligators appears to be highly variable in relation to subject age class, lake, and environmental parameters. When we combined lakes into one analysis, the ability to explain and predict the fluctuations in the relative abundance of alligators was greatly reduced. This highlights the variable influences that TABLE 3.—Regression coefficients (± 1 SE), *P*-values, and pseudo– R^2 for the Forty Acre Lake model that predicts relative abundance of three size classes of *Alligator mississipiensis* at Brazos Bend State Park, Needville, Texas, USA. Variables having indicated values are significant ($P \le 0.05$), whereas missing values indicate nonsignificant model parameters.

						1	life-history sta	ge				
			Adult				Subadult				Hatchlings	
Model	df	F	Р	Slope	df	F	Р	Slope	df	F	Р	Slope
Barometric pressure	_	_	_			_	_	_	1,32	9.28	0.005	0.06 ± 0.02
Conductivity	1,33	53.35	< 0.001	-2.64 ± 0.36	1,32	4.47	0.043	-1.92 ± 0.91		_	_	
Salinity	1,33	61.23	< 0.001	-57.45 ± 7.34	1,32	4.91	0.034	-38.42 ± 17.34	1,32	57.4	< 0.001	29.04 ± 3.83
Turbidity	_		_		1,32	17.28	< 0.001	-0.23 ± 0.054	1,32	9.93	0.004	-0.14 ± 0.04
Total dissolved solids	1,33	52.97	< 0.001	4.10 ± 0.53	1,32	4.43	0.043	2.97 ± 1.41		_	_	
Water temperature	1,33	9.08	0.005	0.03 ± 0.01				_	1,32	36.74	< 0.001	0.34 ± 0.06
Water level	2,33	3.53	0.041		2,32	7.18	0.003	_	2,32	7.75	0.002	
Moon distance	_		_		1,32	23.23	< 0.001	-0.02 ± 0.003		_	_	
Air temperature	_		_					_	1,32	4.45	0.043	-0.12 ± 0.06
Moon phase	4,33	19.04	< 0.001		4,32	10.76	< 0.001	—	4,32	3.69	0.014	
Class parameters ^a			Ν	Mean			Mea	in			Mean ^b	
Moon phase												
First qtr.			16.70	$\pm 1.24^{AB}$			$7.56 \pm$	0.94^{A}		2	2.21 ± 1.7	, 2.7 ^B
Third qtr.			12.94	$\pm 2.34^{B}$			$4.17 \pm$	1.05^{B}		2	1.67 ± 1.9	, 3.7 ^{AB}
Full			18.58	$\pm 4.26^{A}$			$1.45 \pm$	$0.61^{\rm C}$		2	2.22 ± 1.6	2.9^{B}
Super			3.82	$\pm 0.86^{\circ}$			$1.85 \pm$	0.78°		5	5.96 ± 4.3	, 8.2 ^A
Nnew			19.35	$\pm 2.18^{A}$			$6.51 \pm$	1.39^{A}		5	5.07 ± 4.0	, 6.3 ^A
Water level												
Above			20.08	$\pm 7.38^{A}$			$0.97 \pm$	0.63^{B}		3	3.49 ± 2.1	5.5^{AB}
Low			6.47	$\pm 1.09^{B}$			$8.32 \pm$	2.15^{A}		1	$.93 \pm 1.6$, 2.3 ^B
Normal			14.76	$\pm 2.43^{A}$			$5.47 \pm$	1.50^{A}		5	5.36 ± 4.7	, 6.1 ^A
Intercept			0.863	± 1.40			$19.93 \pm$	5.01		-6	52.4 ± 18.1	1
Pseudo-R ²			0).83			0.8	4			0.92	

^a For class parameters within a life-history stage, mean values followed by the sam ^b Because of asymmetric values, this column is reported as mean –SE, +SE.

weather and water-quality parameters have on alligators from one lake to the next. The combination of factors that are present in one lake can be much different from what occurs in another; therefore, how the relationships are expressed might be dependent on habitat and other ecological factors present. Each life-history stage of *A. mississipiensis* is affected by the environment differently (Mazzotti and Brandt 1994), and thus separate models are

TABLE 4.—Regression coefficients (± 1 SE), *P*-values, and pseudo– R^2 for the Pilant Lake model that predicts relative abundance of three size classes of *Alligator mississipiensis* at Brazos Bend State Park, Needville, Texas, USA. Variables having indicated values are significant ($P \leq 0.05$), whereas missing values indicate nonsignificant model parameters.

						Life-h	istory stage					
_			Adult				Subadult		_	Hato	chlings	
Model	df	F	Р	Slope	df	F	Р	Slope	df	F	Р	Slope
Barometric pressure	1,37	18.2	< 0.001	0.27 ± 0.06	1 30	4.6		-0.23 ± 0.11	_	—	—	—
Turbidity	1,37	26.7	<0.001	1.01 ± 0.20				0.25 = 0.11	_	_	_	_
Air temperature Distance	4,57				1,39 1,39	$\frac{-}{4.54}$	0.039 0.047	0.048 ± 0.022 -0.005 \pm 0.002	_	_	_	_
Water temperature Water level	1,37	69.3 	<.001	0.60 ± 0.07	2,39	13.8	<0.001		_	_		_
Class parameters ^a				Mean			Mear	1		Me	an	
Water level: Normal Low Very low							4.4 ± 0 4.1 ± 0 0.81 ± 0).98 ^A).46 ^A).23 ^B			-	
Moon phase First qtr. Third qtr. Full Super New Intercept Pseudo- R^2				$\begin{array}{c}78 \pm 0.85^{AB} \\ 0.37 \pm 0.25^{AB} \\ .50 \pm 1.30^{A} \\ .12 \pm 0.10^{C} \\ 0.27 \pm 0.18^{C} \\ .343 \pm 65.3 \\ 0.83 \end{array}$).53			-	

^a For class parameters within a life-history stage, mean values followed by the same capital letter within a column are not significantly different (P > 0.05).

		Air temperature (°C)	Water temperature (°C)	Wind speed (km/h)	Dew point (°C)	Relative humidity (%)	Barometric pressure (hPa)	Conductivity	Salinity	Total dissolved solids	Dissolved oxygen	Turbidity	Hq
Elm	Mean \pm 1 SE	$22.4 \pm 0.8^{\rm A}$	$23.4 \pm 0.8^{\rm A}$	$0.6 \pm 0.1^{\mathrm{A}}$	$18.0 \pm 1.1^{\mathrm{A}}$	$79.0 \pm 1.8^{\Lambda}$	$1015.9 \pm 0.7^{\rm A}$	$256.4 \pm 19.0^{\rm A}$	$0.1 \pm 0.01^{\rm A}$	$0.2 \pm 0.03^{\rm A}$	$10.3 \pm 0.9^{\rm A}$	$50.9 \pm 1.3^{\mathrm{A}}$	$7.4 \pm 0.3^{\Lambda}$
	Minimum	11.8	15.4	0.0	-4.4	45.0	1006.3	148.7	0.1	0.1	2.7	23.2	3.6
	Maximum	30.5	31.4	3.3	25.6	92.0	1027.3	520.0	0.3	1.0	19.4	54.9	11.2
Forty-Acre	$Mean \pm 1$ SE	$22.7 \pm 0.8^{\rm A}$	$23.6 \pm 0.9^{\rm A}$	0.8 ± 0.2^{B}	$17.8 \pm 1.1^{\rm A}$	$74.0 \pm 2.0^{ m A}$	$1016.1 \pm 0.8^{\rm A}$	$278.0 \pm 3.5^{\rm A}$	0.1 ± 0.01^{B}	$0.2 \pm 0.002^{\rm A}$	27.4 ± 3.5^{B}	$54.4 \pm 0.4^{\rm B}$	8.8 ± 0.2^{B}
	Minimum	6.0	11.2	0.0	-1.7	38.5	1006.4	243.0	0.1	0.16	0.1	52.8	5.25
	Maximum	29.8	31.1	4.1	26.9	92.1	1029.4	316.2	0.2	0.21	84.0	59.8	10.9
Pilant	$Mean \pm 1 SE$	$22.77 \pm 0.9^{\rm A}$	$22.7 \pm 0.8^{\rm A}$	$0.6 \pm 0.1^{\rm B}$	$17.1 \pm 1.1^{\rm A}$	$75.0 \pm 2.2^{\rm A}$	$1016.1 \pm 0.7^{\rm A}$	178.0 ± 7.1^{B}	$0.1 \pm 0.0^{\rm B}$	$0.2 \pm 0.04^{\rm A}$	$10.7 \pm 3.0^{\rm A}$	54.2 ± 0.2^{B}	$6.7 \pm 0.3^{\rm A}$
	Minimum	9.2	13.4	0.0	-4.4	3.3	1006.5	129.5	0.1	0.08	0.1	52.05	3.5
	Maximum	30.5	30.3	3.3	25.6	89.5	1028.8	276.8	0.1	1.0	71.1	57.65	10.1

more informative when presented for each stage. Site- and age-specific responses to environmental conditions also have been detected in other species such as snakes (Henderson and Hoevers 1977; Sun et al. 2001) and mammals (Härkönen et al. 1999). Foraging activity might differ between age classes of alligators because their life history, and more specifically diet, are known to differ by age (Brandt 1991; Saalfeld et al. 2008; Fujisaki et al. 2009). As noted by Sun et al. (2001), the determinants of activity patterns of reptiles are highly complex and generalizations might not be possible within a given ecosystem. Weather parameters (e.g., dew point, barometric pressure,

Weather parameters (e.g., dew point, barometric pressure, and wind speed) appeared as significant variables in hatchling models possibly because hatchling alligators are more susceptible to changes in weather patterns than larger alligators. This might partially explain why there were no significant effects on the number of adult and subadult alligators in relation to weather in the Elm and Forty-Acre lakes models. Hatchling alligators may retreat or exhibit increased submergence rates during times when weather conditions are not optimal. This subsequently results in a decrease in the number of hatchling alligators seen by survey observers and therefore affects the outcome of hatchling alligator relative abundance.

The negative effect of salinity on the relative abundance of alligators in Elm Lake might be related to prey abundance and availability. Salinity can be limiting to some crocodilian species by disrupting normal osmoregulation (Dunson and Mazzotti 1989); however, the salinity levels observed in this study (0.1-0.2%) were well within the known range of tolerance for alligators (<15%; Mazzotti 1983; Lauren 1985). It is more likely that the salinity levels observed affected biota at lower trophic levels (Nielsen et al. 2003), as slight change in salinity can cause these organisms to delay or cease reproduction, or lay dormant as propagules (Williams 1985; Brock et al. 2003). The effects on activity of organisms at lower trophic levels likely have cascading effects as farreaching as apex predators such as A. mississipiensis. We believe that the same rationale explains the relationship between conductivity and the relative abundance of alligators because conductivity and salinity are usually highly correlated (McNeil and Cox 2000); however, our analysis highlights the individual contribution of each parameter, regardless of correlations with other parameters. The agespecific relationships between alligators and salinity and conductivity do not follow intuitive trends and are difficult to interpret. The size and sign of a given partial regression coefficient in a model can be affected by other variables in the model (Chen 2012). Factors that we did not measure might be affecting how the relationships between these parameters and the relative abundance of A. mississipiensis are expressed.

This same phenomenon was observed between the relative abundance of alligators and TDS as well as turbidity. It remains unknown why adult alligators have this unique relationship with TDS (regardless of its source), but it appears to be substantial in its effects on the relative abundance of adult alligators in Forty-Acre Lake. Additionally, it is possible that turbidity has an effect on the foraging ability of hatchlings and subadults by reducing their ability to locate prey items, thereby reducing their relative abundance levels during times of high turbidity. High turbidity alters populations of aquatic organisms (Henley et al. 2000; Trebitz et al. 2007). It would be interesting to pursue this idea further and specifically test the effect of turbidity on alligator sensory ability to verify our hypothesis.

As DO levels increase, so do the relative abundances of adult and subadult alligators, a finding that might relate to decreased submergence rates of individuals in these two lifehistory stages. If alligators spend more time at the surface when DO concentrations are high, this might explain increased observer detection rates under these conditions. The underlying causes of this behavior were not tested in this study; however, the increased detectability might also be the result of an increase in foraging behavior as the result of an increased prey activity and availability in lakes having high DO values.

Studies of other crocodilian species have found that abundance had no relationship with moon phase (Larriera and Del Barco 1992; Pacheco 1996). In contrast, Woodward and Marion (1978) found that the availability of moonlight during warm-weather months was positively correlated with the number of alligators counted during survey periods. However, this relationship was not examined across different age classes of alligators. Our results indicate that moon phase and distance of the moon from the earth might influence the relative abundance of alligators. The relationship of alligator abundance to changing moon distance and phase seems complex, and there is little information available over how crocodilians are affected by changes in moon parameters. Perry and Fisher (2006) suggested that moonlight increases predation risk of prey species and that in response the activity of many invertebrates increases during dark or newmoon nights. Some reptiles not only increase activity during the new moon, but their consumption of prey is highest following these dark conditions (Bouskila 1995, 2001; Tsairi and Bouskila 2004). In Forty-Acre Lake we found that, except during the new-moon phase, the relative abundance of hatchling alligators was lowest when that of adult and subadult alligators was highest. We infer from this relationship that hatchlings are likely avoiding the larger (possibly predatory) alligators, as well as other predators, during times when their relative abundance is highest.

Water temperature affects the relative abundance of alligators during nighttime surveys (Woodward and Marion 1978; Lutterschmidt and Wasko 2006); our study appears to be the first to quantify the influence of this variable across different size classes of alligators. Bugbee (2008) found that alligators were less likely to emerge as water temperature increased, which differs from our results and those of Woodward and Marion (1978) and Lutterschimdt and Wasko (2006). We found that water temperature had a positive relationship with the relative abundance of hatchling alligators in Forty-Acre Lake, but not in Elm Lake. This might be because, although the mean water temperature was almost identical between Elm (23.4°C) and Forty-Acre (23.6°C) lakes, temperatures during Forty-Acre Lake surveys $(11.2-31.1^{\circ}C)$ were more variable than those of Elm Lake (15.4–31.4°C). Although water temperature was not a significant variable in the Elm Lake model, a threshold minimum temperature required to produce an effect on the relative abundance of hatchlings might not have been reached. Hatchlings in Forty-Acre Lake might spend more time in maternal dens during times of lower water temperatures, thus reducing their likelihood of detection.

The models for adult and subadult alligators in Pilant Lake were not similar to any of the other models. Specifically, weather parameters contributed more variation to the relative abundance of alligators in the models for Pilant Lake than in any of the models for Elm and Forty-Acre lakes. We believe this is likely an effect of how habitat features specific to Pilant Lake influence environmental variables and the relative abundance of alligators. The area of Pilant Lake that was included in our surveys is shallow in most areas, has little aquatic vegetation, and is more susceptible to fluctuations in water level (personal observations). It is likely that subadult alligator relative abundance decreased with an increase in average wind speed on account of increased submergence rates. These findings are similar to those of Pacheco (1996) in Bolivia that indicated that Black Caiman (Melanosuchus niger) abundance was negatively influenced by an increase in wind speed. Additionally, Bugbee (2008) found that wind speed had a negative relationship with emergence rates of alligators during nighttime surveys. This relationship likely affects the ability of observers to detect alligators when wind speeds are high.

The relative abundance of subadult alligators in Pilant Lake increased at higher water levels. Our finding corroborates with several studies suggesting that habitat suitability declines as water-level fluctuations become more unpredictable (Kushlan and Jacobson 1990; Webb et al. 2006; Mazzotti et al. 2009). Because adult alligators were usually found along the portion of the survey transect that retained water, even when water levels in Pilant Lake were low, water level did not have an effect on the relative abundance of adult individuals. Conversely, subadult alligators were usually found along other parts of the survey transect that were shallow and more subject to water-level fluctuations. Subadult alligators were probably forced to occupy less than optimum areas on account of competition with adults for higher-quality habitat (i.e., inundated areas). This most likely resulted in subadult individuals either increasing submergence rates (an avoidance behavior that decreases detection by observers), or leaving the area to find more suitable areas inundated by water or where there was less competition with adults.

We observed more hatchling alligators in Elm Lake during times of normal water levels than when water levels were low. Interestingly, the relationship of adult alligators and water level was the opposite of that with hatchling alligators. Similar to subadult individuals in other lakes, hatchling alligators might be exhibiting avoidance behavior during times that adult alligators are the most active. When water levels are low in Elm Lake, the availability of shallow vegetated areas in which hatchlings can hide is greater. This could decrease observer detection of hatchling alligators.

Implications

Our results show that the relative abundance of alligators is a multifaceted and highly variable ecological characteristic. These results have several implications in terms of alligator management, ecosystem monitoring, and environmental change—a one-size-fits-all management approach may not be the best strategy for *A. mississippiensis*. Improved development of the concepts related to the management of alligator populations is important because *A. mississippiensis* is an apex predator, a keystone species and ecosystem engineer that helps maintain ecosystem integrity through direct and indirect interactions with other species (Mazzotti et al. 2009).

From a management perspective, our data are useful in identifying the environmental conditions that have the greatest impact on survey accuracy. Furthermore, if survey efforts target specific life-history stages, managers can better manage those efforts on the basis of current or forecast environmental conditions. Age-specific surveys will produce more accurate population estimates that can better inform management practices. For example, current harvest regulations are based entirely on estimates of alligator population size and nest density. With increased accuracy available from surveys that are specific to life-history stages, managers can adjust harvest limits accordingly. Closely monitored alligator populations can sustain regulated harvest with negligible effects as long as management practices are properly implemented (Gibbons et al. 2000).

From a research perspective, considering our findings can allow researchers to better assess treatment effects in wetland habitats (e.g., Mazzotti et al. 2009; Fujisaki et al. 2009; Ugarte et al. 2013) by using more accurate alligator monitoring techniques. This will produce not only more reliable results than would be available from broad-scale techniques, but will also provide a more in-depth understanding of wetland ecology and management.

Population changes in response to environmental variation are difficult to detect (Gibbons et al. 2000); therefore, studies of naturally occurring populations and communities are invaluable for understanding normal population trends (Tinkle 1979). Documenting how American Alligators respond to environmental conditions can aid in understanding wetland function, and how managers and scientists can further rely on this species as an indicator of ecosystem health. As alteration of wetland habitats continues to threaten biodiversity, scientists need to identify not only causes of species and habitat declines, but also ways to manage and reverse them. American Alligators are valuable in this regard because the species integrates responses to changes in the ecosystem in ways that are easy to interpret (Schiller et al. 2001; Doren et al. 2009; Mazzotti et al. 2009).

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