

Evaluating the efficacy of capture as aversive conditioning for American alligators in human-dominated landscapes

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Abstract

As anthropogenic impacts on ecosystems increase, novel solutions are needed to mitigate increasing human–wildlife conflict. Aversive conditioning is one strategy that can reduce the risks of humans living alongside wildlife by modifying the behavior of animals through their experiences with humans. Although considered rare, American alligator (*Alligator mississippiensis*) attacks on humans most often occur in human-dominated landscapes and can be fatal. Our goal was to determine if capture and release protocols might serve as a form of aversive conditioning to reduce alligator tolerance of humans. Specifically, we compared the behavioral response of alligators to an approaching human for animals with 3 different levels of capture experience: alligators from a reference site where no captures occurred, alligators from a site where captures occurred that directly experienced capture and release, and alligators from the site where captures occurred that indirectly experienced capture and release (never captured but likely observed capture of others). We used a hurdle model and information-theoretic approach to evaluate support for 8 hypotheses regarding factors that influence alligator probability of flight in response to an approaching human and the flight initiation distance (FID) of alligators that did flee. Our hypotheses considered the effects of

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capture experience, exposure to non-capture (visual) surveys, alligator size, ambient temperature, and season. The best-supported models provided strong evidence that capture experience increased the probability of flight and, to a lesser extent, increased FID of alligators that did flee, but that the strength of the effect varied with alligator size or some correlate. Furthermore, the effect of capture may extend beyond animals with direct experience. Capture and release protocols can result in an aversive conditioning response in alligators, effectively reducing habituation to humans. Given the geographic limitations of our study, more work is necessary to determine whether the utility of aversive conditioning may be site-dependent, or similarly effective across a wider selection of developed landscapes.

KEYWORDS

Alligator mississippiensis, American alligator, aversive conditioning, coexistence, flight initiation distance, human-wildlife conflict, nuisance wildlife, South Carolina

Increasing anthropogenic impact on ecosystems requires novel solutions to address human-wildlife conflicts (Dickman 2010, Pooley et al. 2017, Bombieri et al. 2018). While humans often benefit from engaging with nature (Curtin and Kragh 2014), conflict occurs when wildlife negatively affect human well-being, particularly if animals pose a perceived or actual threat to people, property, or pets (Ngadan 2015, Kansky et al. 2016, Pooley et al. 2017, Bombieri et al. 2018). Wildlife managers often respond to reported threats with lethal removal or by translocating offending animals to areas with fewer people (Dickman 2010, Hayman et al. 2014). Translocation and, more so, lethal removal have been increasingly criticized as expensive, ephemeral, unsustainable, and unpalatable (Koval and Mertig 2004, Hayman et al. 2014, Miller et al. 2016, Breck et al. 2017, Pooley et al. 2017). Recent calls to improve wildlife management involve promoting coexistence to maintain viable populations, to conserve mature adults of slow-to-mature species, and to address the underlying causes of conflict for longer-lasting solutions (Janes 2004, Dickman 2010, Miller et al. 2016).

Coexistence management includes the use of behavior-based methods and public education to facilitate the ability of wildlife to persist in the presence of humans under a tolerable level of risk (Pooley et al. 2017, 2021). Aversive conditioning is one behavior-based method used to promote animal avoidance of humans, and thus may be a useful strategy to promote coexistence. Behavioral theory behind aversive conditioning assumes that animals in human-dominated areas are more tolerant of human presence through the process of habituation and thus are less likely to avoid humans after learning to associate humans with neutral consequences (Found et al. 2018, Much et al. 2018). More concerning, animals may become more likely to approach humans and exhibit nuisance behaviors if they associate humans with positive consequences (e.g., receiving food; Mazur 2010). Aversive conditioning aims to reduce an animal's tolerance towards humans through a process of sensitization by treating it with a non-lethal, negative experience associated with humans (Mazur 2010, Found et al. 2018). Several studies have demonstrated success of aversive conditioning in free-ranging mammals (shy and bold elk [*Cervus canadensis*] in a national park [Found and St. Clair 2018]; wild and food-conditioned black bears [*Ursus americanus*] in a national park [Mazur 2010]; shock-collared gray wolves [*Canis lupus*] in public and private lands [Hawley et al. 2009]), but there are few studies that test the application to other taxonomic groups.

Aversive conditioning may be useful for addressing the increasing number of human–alligator conflicts in coastal residential communities (Rhodes 1997, Eversole et al. 2014, Hayman et al. 2014, Skupien and Andrews 2017, Woodward et al. 2019). In South Carolina, a majority of nuisance alligator reports originate in populous areas (Rhodes 1997). While injurious human–alligator conflicts are considered rare, most of such incidents in South Carolina have occurred in Beaufort County (M. P. Hart, South Carolina Department of Natural Resources, personal communication), which is the state's sixth most populous county (human population in 2010 = 162,233) of the 28 counties within the alligator's range in South Carolina (U.S. Census Bureau 2012). Human–wildlife conflict is predicted to increase concomitantly with increasing human populations and human influence on landscapes into the future (Brackhane et al. 2018). Notably, there have been 3 documented fatal human–alligator conflicts in South Carolina, all occurring between 2016 and 2020 (Yee 2020). Managers often lethally remove alligators that are involved in attacks (i.e., when an alligator bites a human) or considered nuisances because of their behavior, location, and size (Rhodes 1997, Janes 2004, Hayman et al. 2014). Lethal removal of target alligators, either reactive or proactive, may be ineffective at preventing future negative human–alligator interactions because it does not address the underlying causes of human–alligator conflict (Dickman 2010, Hayman et al. 2014, Woodward et al. 2019). Captive studies indicate that crocodylians are capable of learning stimulus–response relationships (Davidson 1966, Augustine and Baumer 2012) and field observations suggest that crocodylians exposed to aversive experiences with humans exhibit greater avoidance of humans (Webb and Messel 1979, Pacheco 1996, Gramentz 2008, Marques et al. 2016), providing evidence that alligators may respond to aversive conditioning when applied strategically.

The overarching goal of our study was to investigate whether capture and release events might induce an aversive conditioning effect to reduce alligator tolerance towards humans in human-dominated landscapes. Our objectives were to compare the probability that an alligator will flee from an approaching human in a site where capture and release occurred over several years to that in a site where no capture and release occurred, and compare the flight initiation distance (FID) of alligators that do flee from an approaching human in the 2 sites. Our primary hypothesis was that increasing levels of capture experience would reduce alligator tolerance toward humans. We also considered the potential for other factors such as exposure to non-capture (visual) surveys, alligator size, ambient temperature, and season to influence alligator tolerance directly or moderate the effect of capture. Under our primary hypothesis, we predicted that probability of flight and FID would be greater at the site where capture events occurred, and that alligators with direct capture experience (i.e., that were captured) would exhibit the highest probability of flight and FID, followed by alligators with indirect experience (i.e., living in the site where captures occurred but were never captured), and finally alligators living in the site where capture events did not occur.

STUDY AREA

The study area included 2 island communities in Beaufort County in coastal South Carolina between 2009 and 2018 (Figure 1). The climate in coastal South Carolina is subtropical, with a long warm season from April to October and a short mild winter from December to February. Temperatures average 24.4°C to 32.2°C in the hottest month of July and 5.5°C to 15.5°C in the coldest month of January. Annual precipitation averages 1.2 m/year, and approximately 70% occurs during the warm season. The coastal zone and marine ecoregion where the study sites are located is characterized by elevations from sea level to 7.6 m and an abundance of tidal marshland and upland communities (South Carolina Department of Natural Resources [SCDNR] 2005a). Tidal marshlands are divided into saltmarsh, brackish marsh, freshwater marsh, and coastal impoundments (Wilkinson 1984). Upland vegetation communities include bottomland hardwoods, pine (*Pinus* spp.) woodlands, oak (*Quercus* spp.)–hickory (*Carya* spp.) or hardwood-dominated forest, mixed mesic hardwood, bald cypress (*Taxodium distichum*)–tupelo gum (*Nyssa sylvatica*) swamps, wet flatwoods, and grasslands. Development of metropolitan areas (e.g., Hilton Head Island–Bluffton,

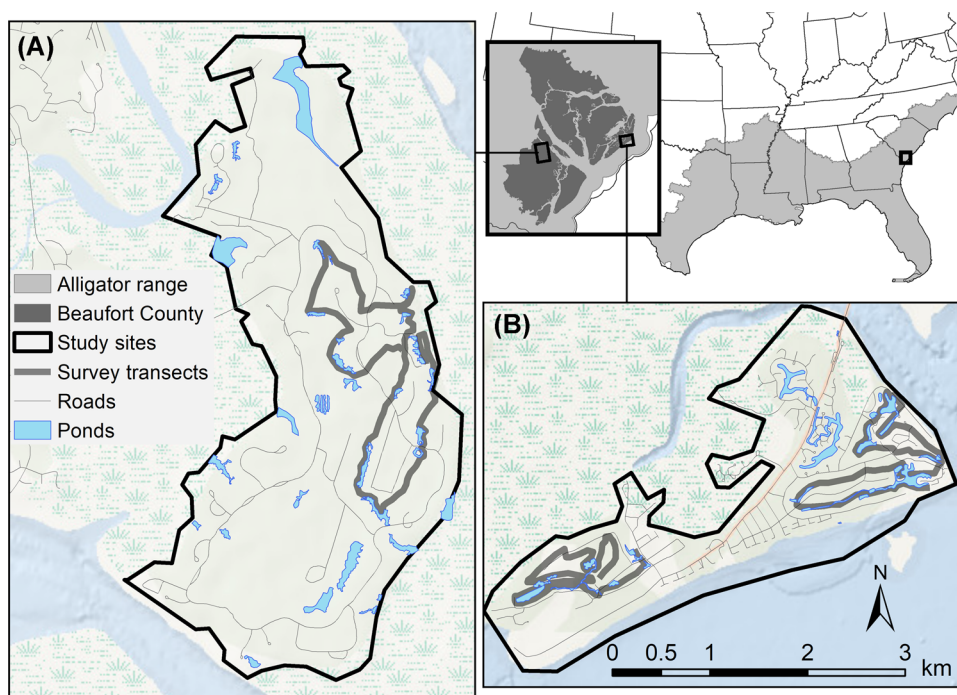


FIGURE 1 Study area for alligator visual surveys in Beaufort County, South Carolina, USA, 2009–2018. A) The treated site where alligators experienced capture events and regular visual behavioral surveys as part of a behavior monitoring program and B) the reference site where alligators were minimally exposed to capture events and surveys. We created maps using ArcGIS® software (Esri, Redlands, CA, USA).

Charleston-North Charleston) and introduction of ornamental vegetation has resulted in loss and fragmentation of native vegetation communities primarily along the coastline and on barrier islands. Wildlife communities include several mammals, a rich diversity of resident and migratory birds, herpetofauna, and fishes (SCDNR 2005b).

Study sites were Spring Island, a 12.33-km² nature preserve and low-density residential community, and Fripp Island, a 6.78-km² resort community on South Carolina's most seaward barrier island. Human residence in both of the study sites is highly seasonal, though the characteristics of that seasonality differ by site. Spring Island's peak residence occurs from fall through late spring, while Fripp Island's peak residence occurs from spring through summer. Freshwater features (e.g., natural and constructed ponds, inland marsh), which can serve as alligator habitat, make up approximately 5.92% of Spring Island and 3.69% of Fripp Island and the majority of water features on both islands occur within golf courses.

METHODS

Study design and behavioral surveys

We compared alligator behavioral responses in 2 golf course communities in coastal South Carolina that differed in historical occurrence of alligator capture and release events. Herein, we define a capture and release event for alligators as the targeted capture of an alligator by a human within sight of the alligator, restraint, application of physical marks or tags by humans, and release at the point of capture, collectively taking place over a range of

15 minutes to 1 hour from initial contact (e.g., hooking with snatch hook, snare application) to release. Though precautions are taken to ensure the physical well-being of each alligator, we assume that a capture event is somewhat traumatic to the animal. We considered Spring Island the treated site because capture and release events and subsequent behavioral observations for alligators were routinely performed since 2009 as a means to monitor alligator behavior in the community. We considered Fripp Island the reference site because alligator capture and release were absent barring the occasional lethal removal in response to substantiated nuisance complaint and intensive behavioral observations were minimally conducted at the time of this study. Alligators in the treated site had either directly (i.e., had been captured and released) or indirectly (i.e., never captured but were assumed to have observed other alligators being captured) experienced capture and release, while alligators in the reference site had never been captured and released on site.

To quantify alligator behavioral responses towards humans, we conducted repeat visual diurnal surveys along predefined, static, routes (i.e., transects) that were designed to facilitate visual access to water features on golf courses in each community (Figure 1). The lengths of the transects were 9.56 km at the treated site and cumulative 12.07 km at the reference site (5.51 km and 6.56 km at each of 2 golf courses). We conducted surveys an average of once per week at the treated site from June 2009 to September 2018 and at the reference site from November 2013 to June 2014. Although we did not conduct surveys in July to October at the reference site because of limited access to golf courses, July to October correlated with lower alligator sighting rates at the treated site in all years, suggesting that these months were not important for inference.

Each time we visually detected an alligator along the transect, we recorded individual characteristics of the animal and its behavior in response to a standardized trial that involved approach by a human subject (one of our survey team). We conducted a trial only if there was a clear line of sight between the human subject and the alligators' eyes and if an alligator could be approached close enough to elicit a response or to within 5 m. If we detected multiple alligators of the same size in the same location that were indistinguishable, we randomly selected 1 alligator per estimated size class pre-defined by 30.5-cm intervals (e.g., <30.5 cm, 30.5–61 cm, 61.1–91.5 cm) in each cluster on which to conduct a trial. Prior to beginning each trial, we approximated total length (i.e., length from the tip of the snout to the tip of the tail, ± 15 cm), noted unique marks, and recorded the treatment group based on capture experience (e.g., reference, indirectly treated, directly treated) of each alligator. At the treated site, we defined alligators as directly treated if a systematic mark (e.g., series of notched tail scutes) or a plastic, numbered cattle tag was visible (on nuchal or tail scutes) and as indirectly treated if there was no evidence of a mark or tag on the alligator's body. For some observations, an alligator's capture experience was unknown because of poor visibility of marking areas (i.e., alligator neck or tail partially submerged or in thick vegetation). In these cases, we inferred capture experience based on the observation date, location, and size of the alligator following 2 rules: if we observed an alligator of similar size and with known capture experience in the same location within 2 weeks of an unknown experience observation, we assumed the 2 alligators were the same individual, but if we did not observe any alligators of similar size in the same location within 2 weeks or observed ≥ 2 alligators of similar size with differing capture experience (i.e., ≥ 1 tagged and ≥ 1 untagged) in the same location within a month of the unknown experience alligator observation, we were unable to infer capture experience. We omitted from further analysis all records of alligators for which we could not infer as indirect or direct capture experience.

To determine alligator tolerance towards humans, in each trial 1 member of the survey team (usually T. M. Murphy) walked in a direct path toward an alligator at a normal walking pace. The surveyor stopped walking when the alligator reacted (e.g., moving toward or away from the observer), at which point they measured and recorded the straight-line distance between the observer and alligator with a rangefinder (Nikon Aculon 6 × 20 Laser Rangefinder, Melville, NY, USA). In cases where the alligator did not react, the surveyor walked toward the alligator until reaching what we defined to be a minimum safe distance (1 m) from the alligator. To determine the probability of an alligator fleeing from the surveyor, we coded each alligator response using a binary response variable such that 0 indicated the alligator did not move away from the surveyor (i.e., non-responses, inquisitive approaches) and 1 indicated the alligator moved away from the surveyor (i.e., flights). To determine FID, we used the straight-line

distance between the surveyor and alligator at the time of response for alligators that fled from the surveyor. Under our definition of tolerance, we considered alligators with a 0 response to an approaching human to be maximally tolerant, whereas alligators with a 1 response were positioned along a spectrum of tolerance, where the degree of tolerance and FID were negatively correlated. That is, alligators with lower FID were more tolerant of humans than alligators with higher FID.

Data analysis

We used a hurdle model approach and multi-model framework to investigate the relative support for multiple hypotheses on factors that influence alligator tolerance of humans in developed areas. Briefly, a hurdle model approach allows binary response data and intensity response data to be analyzed separately (Zuur et al. 2009). In the first half of our hurdle model approach, we fit a candidate set of mixed-effect logistic regression models (using a logit link function) to our data with a binary response (e.g., flight or no flight from an approaching human). This step facilitated our ability to evaluate support for hypotheses concerning factors that would influence the probability that an alligator would flee from an approaching human (i.e., probability of flight). In the second half of our modeling approach, we subset our data to include only those observations in which an alligator did flee from an approaching human and investigated factors associated with FID. We formatted FID as an integer by rounding each value to the nearest 1 m (truncated negative binomial distribution) and fit our data to a candidate set of mixed-effect generalized linear mixed models using a log link function. We treated individual alligator observations as the sampling unit and defined random effects as unique alligator identities in all candidate models. We assigned unique alligator identities based on unique markings or by a unique combination of size, location, and a number following a protocol (available in Supporting Information). Because our knowledge regarding alligator identity was imperfect, we made an effort to evaluate the potential effect of error in our assignment of capture experience based on inference. To do so, we performed 3 separate analyses using 3 levels of increasing conservatism: records with known and inferred capture experience ($n = 1,475$), only records with known capture experience ($n = 1,427$), and only records with known capture experience and, for directly treated animals, confirmed identities based on tag or scute markings ($n = 1,255$). We fit all models using the `glmmADMB` package (version 0.8.3.3; Skaug et al. 2016) in Program R (version 4.0.2; R Core Team 2020).

We considered the effects of 5 predictor variables on alligator tolerance of humans in developed areas (Table 1). We screened continuous variables for correlation before analysis and evaluated support for inclusions of nonlinear forms of variables (e.g., log-linear, quadratic) by visual inspection of plotted data. We scaled all continuous variables to have a mean of 0 and standard deviation of 1 prior to model fitting.

We defined and fit a virtually identical candidate set of 8 *a priori* and hypothesis-driven models for each portion of our hurdle model analysis (Table 2; predictions available in Supporting Information). Because of the longevity of alligators and their ectothermic nature, we anticipated potentially important effects of alligator age, season, and time of day on alligator tolerance of humans, even though these factors were not the primary focus of our investigation. To account for their potential effects, we included alligator length (a general proxy for age; Wilkinson et al. 2016, Lawson et al. 2020), a quadratic ($x + x^2$) form of day of year (a proxy for season), and time of day (a proxy for ambient temperature) in all of the candidate models, and the simplest (base) model assumed these were the only factors associated with the response (model 1, Table 2). Seven additional models expanded on the base model by including various combinations of treatment and survey exposure (Table 2). Because all directly treated alligators fled, we were unable to consider indirect and direct capture experience separately when modeling probability of flight and thus pooled indirectly and directly treated groups into a single treated group (Table 1). Thus, the models that included treatment (models 2, 4, 5, 6, 8, Table 2) differed between probability of flight and FID.

We used an information-theoretic approach and Akaike's Information Criterion (AIC) to evaluate the relative support for each model in 6 separate candidate model sets (i.e., probability of flight and FID candidate

TABLE 1 Summary of covariates considered in modeling probability of flight and flight initiation distance (FID) of American alligators in 2 coastal communities in South Carolina, USA, 2009–2018.

Covariate	Description	Summary	Predicted effect
Fixed effect covariates			
Treatment (probability of flight)	2-level categorical variable used to model probability of flight representing alligators' capture experience (reference vs. treated). Alligators with indirect and direct experience were classified as treated.	$n_{\text{reference}} = 439$ $n_{\text{treatment}} = 1036$	+
Treatment (flight initiation distance)	3-level categorical variable used to model flight initiation distance representing alligators' capture experience (reference vs. indirectly treated vs. directly treated).	$n_{\text{reference}} = 439$ $n_{\text{indirect}} = 535$ $n_{\text{direct}} = 501$	+, ++
Survey exposure	Cumulative number of days we visited a site for FID surveys (days).	$\bar{x} = 97$ (1–276)	±
Alligator length	Estimated length (m) from the tip of the snout to the tip of the tail; proxy for alligator age.	$\bar{x} = 1.66$ (0.20–3.66)	±
Day of year	Day of the year that observations took place represented by an integer between 1–365 (days).	$\bar{x} = 163$ (2–365)	±
Time of day	Time of day that observations took place represented by a whole number between 0–24 and the proportion of minutes in an hour (hr).	$\bar{x} = 13.05$ (6.33–20.08)	+
Random effect covariates			
Identification	Random effect variable describing the marks or tags on alligators with direct capture experience or a combination of an alligator's capture experience, size, and location.		

model sets for each of 3 levels of analysis). We calculated AIC corrected for small sample size (AIC_c) and ranked models using the `bbmle` package (version 1.0.23.1; Bolker and R Development Core Team 2020). We based inference on the 95% confidence model set based on cumulative AIC_c model weight (Burnham and Anderson 2002). In the case that ≥ 1 model made up the 95% confidence set, we discuss competing models individually.

To evaluate fit of models in the 95% confidence model sets, we estimated marginal and conditional R^2 for probability of flight models and visually inspected plots of residuals versus fitted values and versus each covariate in the model for FID models (Zuur and Ieno 2016). We evaluated performance of both probability of flight and FID models using a cross validation procedure with new observations collected from the same sites from March 2019 to July 2020 following the same protocol (Zuur and Ieno 2016). We calculated the estimated probability of flight for 192 ($n_{\text{reference}} = 139$, $n_{\text{treatment}} = 53$) FID trials using models in the 95% confidence set. We used a receiver operating characteristic curve (ROC) where we predicted a well performing model would have an area under the curve (AUC) ≥ 0.7 . For FID models, we calculated estimated FID for 97 ($n_{\text{reference}} = 46$, $n_{\text{indirect treatment}} = 26$, $n_{\text{direct treatment}} = 25$) FID trials in which the alligator fled using models in the 95% confidence set. We examined the correlation between observed and estimated FID using simple linear regression where we predicted a well performing model would yield a statistically significant ($P < 0.05$) positive correlation between observed and estimated FID.

TABLE 2 Mathematical expression of 8 hypotheses for the effects of capture experience, exposure to surveys, alligator size, and temporal effects on American alligator tolerance of humans in 2 coastal communities in South Carolina, USA, 2009–2018. Using a hurdle model approach, an alligator's binomial response (e.g., flight or no flight) to an approaching human is estimated as probability of flight (PF) separately from the flight initiation distance (FID) for alligators that did flee.

Model	Response variable	Model
1	PF and FID	~alligator length + day of year ² + time of day + identification (ID)
2a	PF	~treated + alligator length + day of year ² + time of day + ID
2b	FID	~indirectly treated + directly treated + alligator length + day of year ² + time of day + ID
3	PF and FID	~survey exposure + alligator length + day of year ² + time of day + ID
4a	PF	~treated + survey exposure + alligator length + day of year ² + time of day + ID
4b	FID	~indirectly treated + directly treated + survey exposure + alligator length + day of year ² + time of day + ID
5a	PF	~(survey exposure × alligator length) + day of year ² + time of day + ID
5b	FID	~(survey exposure × alligator length) + day of year ² + time of day + ID
6a	PF	~(treated × alligator length) + day of year ² + time of day + ID
6b	FID	~(indirectly treated × alligator length) + (treated × alligator length) + day of year ² + time of day + ID
7	PF and FID	~(treated × survey exposure) + alligator length + day of year ² + time of day + ID
8a	PF	~(treated × alligator length) + (survey exposure × alligator length) + day of year ² + time of day + ID
8b	FID	~(indirectly treated × survey exposure) + (treated × alligator length) + (survey exposure × alligator length) + day of year ² + time of day + ID

RESULTS

We performed 1,475 FID trials on alligators (reference = 439, treated = 1,036). Approximately half of the trials (50.8%) occurred between March and May though we distributed survey effort throughout the year. The mean estimated length of observed alligators across the study was 1.66 ± 0.96 m (SD; range = 0.20–3.66 m). For the 1,285 observations in which we recorded alligator activity at the time of encounter, 78.8% were basking (Figure S1, available in Supporting Information). At the treated site, directly treated alligators made up 48.4% of our observations, and we positively identified 60% of directly treated alligator observations to 41 individuals in capture records. We could not assign the remaining 40% of records from directly treated alligators to a unique individual and assigned identities based on capture experience, size, and location.

The majority (74.6%) of our trials resulted in alligators that fled from an approaching human, and median FID was 27 m ($\bar{x} = 32.3 \pm 28.5$ m). For observations in which alligators did not flee from an approaching human ($n = 374$), the alligator approached the observer on 9 occasions. Depending on treatment group, 31.9–100% of basking alligators fled, and 97.2–100% of alligators in the water fled (Figure S1). At the reference site, 33.5% of observations were flight responses with a median FID of 4 m ($\bar{x} = 5.6 \pm 5.8$ m) for alligators that did flee. At the treated site, 92% of observations were flight responses with a median FID of 33 m ($\bar{x} = 36.5 \pm 28.4$ m) for alligators that did flee. Within the treated site, indirectly treated alligators fled in 84.7% of FID tests and median FID was 16 m ($\bar{x} = 25.4 \pm 25.8$ m), while 100% of directly treated alligators fled from an approaching human with a median FID of 43 m ($\bar{x} = 46.5 \pm 26.9$ m).

Probability of flight

In all 3 levels of analysis, the AIC_c 95% confidence set was composed of the same 2 candidate models (Table 3). The first-ranked and second-ranked models carried an average of $69.2 \pm <0.01\%$ and $30.1 \pm <0.01\%$ of AIC_c model weight, respectively. Marginal R^2 indicated fixed effects explained approximately 60% of the variation in data for both models and our model validation (using the first- and second-ranked models from the first-level analysis) procedure indicated reasonable predictive ability (Table 3). Estimated beta coefficients for covariates in each model were similar across all levels of analysis (Figure 2). For simplicity, we restrict our focus to results from the first-level (i.e., least conservative) analysis, which included records with known and inferred capture experience.

Estimates from the first-ranked model indicated that probability of flight varied with capture experience, exposure to neutral encounters with humans, alligator size, season, and time of day (Figure 2). While the first-ranked model was less parsimonious than the second-ranked model, evidence ratios indicated 2.23 times more support for the first-ranked model over the second-ranked model. Coefficients associated with the treated \times alligator length interaction provided strong evidence that alligator response to capture depended on the size of the alligator being observed. The treated site was associated with higher probability of flight than the reference site and the effect size increased as alligator size increased (Figure 3A). For example, probability of flight for a 1-m and 3-m-long alligator at the treated site was 2.57 and 11.11, respectively, times greater than that of a similarly sized alligator at the reference site. Coefficients associated with the survey exposure \times alligator length interaction suggested that the direction and intensity of non-capture survey exposure effects varied with site and alligator size. Probability of flight was always high at the treated site, but at the reference site it increased with increasing survey exposure for smaller alligators and decreased for larger alligators (Figure 4A–C). For example, at the treated site probability of flight for a 2-m-long alligator with no previous survey exposure was 0.99 (95% CI = 0.94–1.00) and remained high with increasing alligator size regardless of survey exposure. At the reference site, small alligators (1 m) were 1.42 times more likely to flee at 36 weeks of survey exposure than at 4 weeks of survey exposure, while large alligators (3 m) were 3.50 times more likely to flee at 4 weeks of survey exposure than at 36 weeks of survey exposure. Confidence intervals for coefficients associated with the survey exposure \times length interaction overlapped zero, indicating uncertainty in the true effect (Figure 2). Coefficients associated with a quadratic form of day of year had relatively large associated standard errors but suggested that probability of flight was highest at the end of summer (28 Sep; Figures 2 and 3B). Similarly, coefficients associated with time of day had large associated standard errors but suggested that probability of flight may have increased throughout the day (Figures 2 and 3C).

The second-ranked model was identical to the top-ranked model, with the exception that it lacked a survey exposure \times length interaction. Coefficients for terms that were shared between the first-ranked and second-ranked models were similar and produced nearly identical inference (Figure 2).

Flight initiation distance

In all 3 levels of analysis, the same candidate model (model 8b, Table 2) carried the majority of the AIC_c model weight ($\bar{x} = 99.9 \pm <0.01\%$). Estimated beta coefficients for covariates from the top model were highly similar across all levels of analysis (Figure 2). Visual inspection of residuals indicated adequate model fit and our model validation (using the first-ranked model from the first-level analysis) procedure indicated reasonable predictive ability ($\beta = 0.35$, $P < 0.01$, $R^2 = 0.18$, $df = 96$). For simplicity, we restricted our focus to results using the first level (i.e., least conservative) analysis, which included records with known and inferred capture experience.

Estimates from the top-ranked model indicated that FID varied with capture experience, exposure to neutral encounters with humans, alligator size, season, and time of day (Figure 2). Coefficients associated with the treated \times alligator length interaction provided moderate evidence that the effect of capture experience on FID depended on

TABLE 3 Model ranking criteria for the 95% confidence set of models used to evaluate support for hypotheses concerning factors associated with the probability that American alligators will flee from humans in 2 coastal communities in South Carolina, USA, 2009–2018 using various subsets of data reflecting 3 levels of data conservatism to account for errors in identity assignment. Level 1 (least conservative) included alligators with inferred capture experience ($n = 1,475$). Level 2 included only alligators with confirmed capture experience (e.g., direct or indirect) based on the presence and absence of tags or marks but not confirmed identities ($n = 1,427$). Level 3 (most conservative) included only alligators with confirmed capture experience and confirmed identities for those with direct experience ($n = 1,255$). All models not included carried <0.01% Akaike weight. Area under the curve (AUC) is only reported for models used to describe inference.

Model	Log-likelihood	K ^a	AIC _c ^b	ΔAIC _c	w _i ^c	Marginal R ^{2d}	Conditional R ^{2e}	AUC
Level 1—least conservative								
8a: $\sim(\text{treated} \times \text{alligator length}) + (\text{survey exposure} \times \text{alligator length}) + \text{day of year}^2 + \text{time of day} + \text{ID}$	-466.3	10	952.8	0.0	0.69	0.60	0.72	0.74
6a: $\sim(\text{treated} \times \text{alligator length}) + \text{day of year}^2 + \text{time of day} + \text{ID}$	-469.1	8	954.4	1.6	0.31	0.59	0.71	0.74
Level 2								
8a: $\sim(\text{treated} \times \text{alligator length}) + (\text{survey exposure} \times \text{alligator length}) + \text{day of year}^2 + \text{time of day} + \text{ID}$	-465.1	10	950.3	0.0	0.70	0.60	0.72	
6a: $\sim(\text{treated} \times \text{alligator length}) + \text{day of year}^2 + \text{time of day} + \text{ID}$	-467.9	8	952.0	1.7	0.30	0.59	0.71	
Level 3—most conservative								
8a: $\sim(\text{treated} \times \text{alligator length}) + (\text{survey exposure} \times \text{alligator length}) + \text{day of year}^2 + \text{time of day} + \text{ID}$	-458.5	10	937.1	0.0	0.79	0.59	0.69	
6a: $\sim(\text{treated} \times \text{alligator length}) + \text{day of year}^2 + \text{time of day} + \text{ID}$	-461.8	8	939.8	2.7	0.21	0.57	0.68	

^aNumber of parameters.

^bAkaike's Information Criterion corrected for small sample size.

^cAkaike weight.

^dMarginal R² represents variance explained by fixed effects only. We considered marginal R² > 0.7 indicative of good model fit.

^eConditional R² represents variance explained by both fixed effects and random effects (alligator identification [ID]).

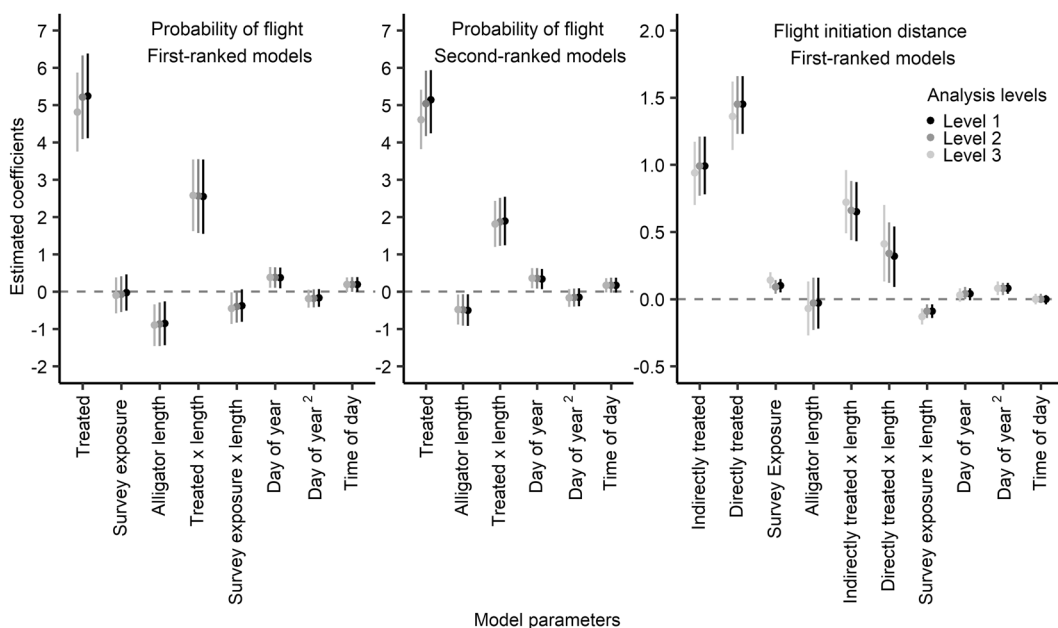


FIGURE 2 Comparison of beta estimates and 95% confidence intervals regarding the effects of capture experience, survey exposure, alligator size, day of year, and time of day on the probability that American alligators will flee from humans and the flight initiation distance of alligators that do flee when approached in 2 coastal communities in South Carolina, USA, 2009–2018, calculated using 3 levels of data conservatism. Level 1 included alligators with inferred capture experience. Level 2 included only alligators with confirmed capture experience (e.g., direct or indirect) based on the presence and absence of tags or marks but not confirmed identities. Level 3 included only alligators with confirmed capture experience and confirmed identities for those with direct experience.

the size of the alligator being observed. While the reference site had consistently lower FID across all alligator size classes, the effect size of direct and indirect capture experience increased as alligator size increased (Figure 3D). For example, FID for indirectly and directly treated 1-m-long alligators was 1.71 and 3.41 times greater, respectively, than that of a similarly sized alligator at the reference site. In contrast, FID for indirectly and directly treated 3-m-long alligators was 6.71 and 6.63 times greater, respectively, than that of a similarly sized alligator at the reference site. Coefficients associated with the survey exposure × alligator length interaction provided weak evidence that alligator response to increasing survey exposure depended on the size of the alligator being observed (Figure 2). Briefly, increasing survey exposure was associated with increasing FID for smaller alligators, but was not associated with a notable change in FID for larger alligators, though there was considerable uncertainty regarding overall effects of survey exposure (Figure 4D–F). Coefficients associated with a quadratic form of day of year and time of day had relatively large associated standard errors. While there was no meaningful effect of time of day on FID, we observed slight evidence suggesting that FID may have been lowest in late spring (25 May; Figures 2 and 3E, 3F).

Post hoc analysis of alligator size effects

Given the relatively long timespan over which data were collected at the treated site (9 yr), alligator size was at least partially confounded with the timespan over which individual alligators were exposed to capture events. To help clarify whether the effects of alligator size that we observed were the result of learning over time or size-associated

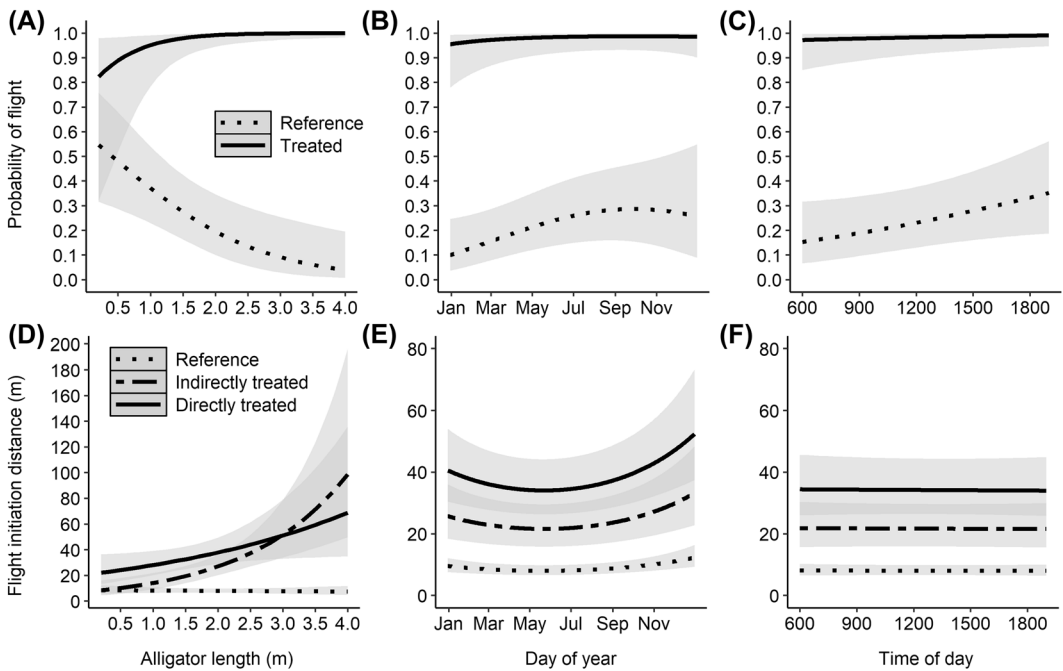


FIGURE 3 Associations between alligator probability of flight (A–C) and flight initiation distance (D–F) in response to an approaching human and an alligator's capture experience and size (A, D), the day of year the survey was conducted (B, E), and the time of day the survey was conducted (C, F) in 2 coastal communities in South Carolina, USA, 2009–2018, based on the first-ranked models. The bold lines represent the model-predicted trend with 95% confidence intervals shaded in grey. Predictions were based on fixed effects only and calculated while holding other terms in the model at their mean observed value (alligator length = 1.66 m, survey exposure = 97 days, day of year = 12 Jun, and time of day = 1302). Note variation in y-axes.

variation in responsiveness to capture events, we leveraged the longitudinal nature of data from the treated site to compare short-term and long-term effects of capture on alligator probability of flight.

Our short-term analysis was aimed at understanding the effects of treatment in the 9-month period following onset of capture events and behavior monitoring efforts and involved constraining the sampling window for the treated site to the first 214 days of visual surveys to coincide with the 214 days over which observations were collected at the reference site ($n = 121$ treated observations, $n = 439$ reference observations). Our long-term analysis was aimed at understanding the cumulative effect of long-term treatment and involved constraining the sampling window for the treated site to be identical to the period when observations were recorded at the reference site (Nov 2013–Jun 2014; $n = 117$ treated observations, $n = 439$ reference observations). For each scenario, we fit data to candidate models to estimate probability of flight, ranked models with AIC, and calculated predictions using top-ranked models. We did not include FID in our *post hoc* analyses because the subsamples of data did not include sufficient observations of indirectly and directly treated alligators.

The top-ranked models in our short-term and long-term analyses were identical in structure to the first-ranked model in our primary analysis (model 8a), but model coefficients, and thus inference, differed. Our short-term analysis suggested that within the first year following onset of aversive conditioning via alligator capture, probability of flight declined as alligator size increased at reference and treated sites (Figure 5A). Results from our long-term analysis indicated that probability of flight declined with size at the reference site but was consistently near 1.0 regardless of size at the treated site (Figure 5B), consistent with our main results.

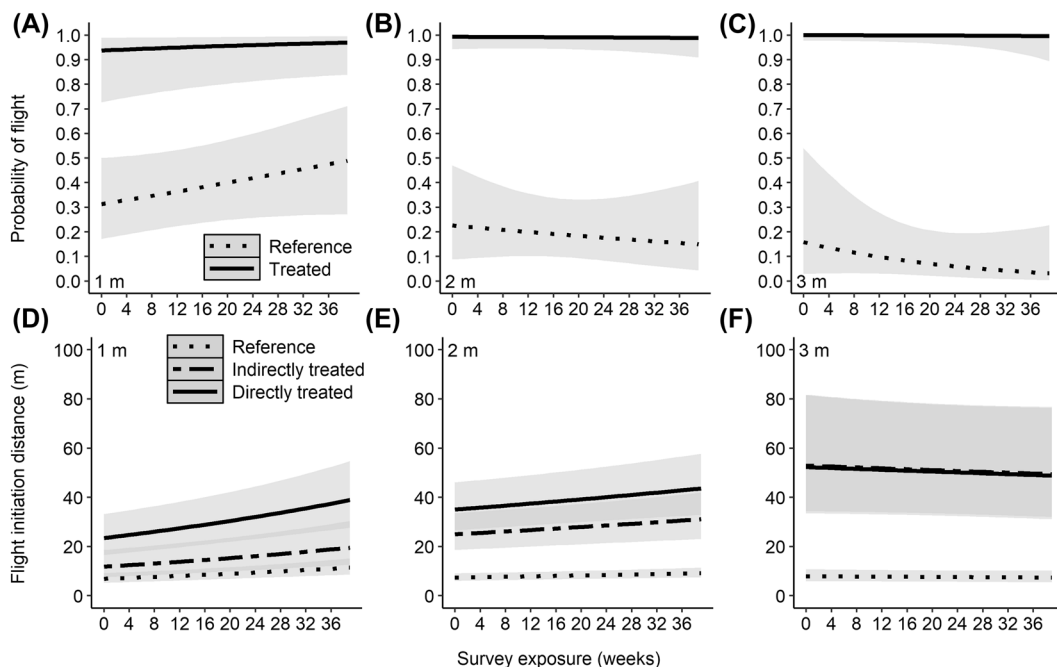


FIGURE 4 Estimated association between alligator probability of flight (A–C) and flight initiation distance (D–F) in response to an approaching human and an alligator's capture experience and the cumulative number of days visual flight initiation distance surveys had been conducted for 1-m (A, D), 2-m (B, E), and 3-m-long alligators (C, F) in 2 coastal communities in South Carolina, USA, 2009–2018, based on the first-ranked models. The bold lines represent the model-predicted trend with 95% confidence intervals shaded in grey. Predictions were based on fixed effects only and calculated while holding other terms in the model at their mean observed value (day of year = 12 Jun, and time of day = 1302).

DISCUSSION

In this study, we sought to determine if capture and release events could influence alligator tolerance of humans (estimated by probability of flight and FID in response to an approaching human) in human-dominated landscapes. Our results supported our hypothesis that an alligator's tolerance of humans can be influenced by capture experience and, to a lesser degree, repeated neutral experiences with humans, but that the degree and direction of their influences are dependent on alligator size or some correlate (e.g., age, prior accumulated experience). Our results can advance understanding how human actions influence alligator behaviors and can be used to develop strategies intended to facilitate coexistence between alligators and humans in human-dominated landscapes.

While our study is not experimental and cannot determine direct causation, the observed inverse relationship between alligator size and probability of flight between sites is consistent with our hypothesis that alligator behavior around humans depends on accumulated experiences (Sih et al. 2004, Bejder et al. 2009). In our study, alligator size was at least partially confounded with the timespan over which individual alligators were exposed to capture events. Collective results from our main analysis and *post hoc* data exploration led us to conclude that the interaction between alligator length and capture experience we observed was an artifact of the relatively long timespan over which treatment occurred at Spring Island (9 yr) and the longevity of alligators. More explicitly, capture experience appears to affect all size classes of alligators similarly over short time spans, but repeated aversive experiences can continue to reduce at least some individual alligators' tolerance of humans resulting in older members of a population exhibiting relatively low tolerance. We suspect increased probability of flight reflects

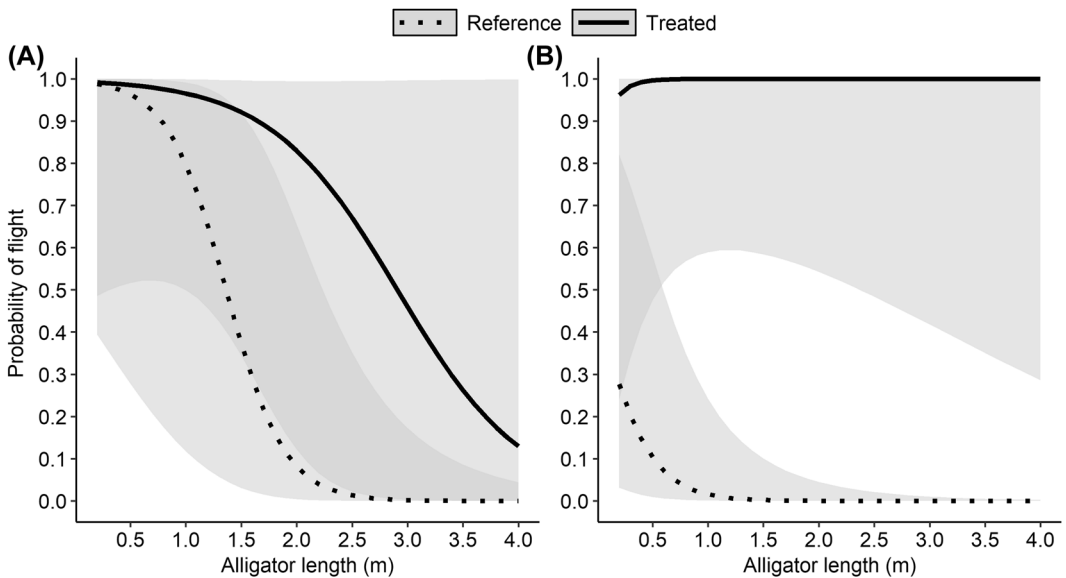


FIGURE 5 *Post hoc* analyses to control for A) days since study initiation at the treated site by extracting observations collected over the first 214 days to coincide with the length of time over which observations were collected at the reference site, and B) the period when observations were collected at both sites by extracting data at the treated site to include only those dates that overlapped with observations taken at the reference site when estimating alligator probability of flight in 2 coastal communities in South Carolina, USA, 2009–2018.

heightened anti-predator strategies to prevent future costly interactions, assuming that alligators perceive capture and release events as an escape from a predator (Whittaker and Knight 1998, Bejder et al. 2009, Bucklaew and Dochtermann 2021). These patterns are consistent with the theory that capture and release events can stimulate sensitization (i.e., a learning process in which animals increase their reactions to an associated stimulus to reduce the likelihood of experiencing risk or to reduce the costs if a risk is experienced) resulting in an aversive conditioning response (Sih et al. 2004, Bejder et al. 2009).

Our results suggest that alligators might be capable of learning a conditioned response (flee) indirectly by observing another alligator's experience. We observed heightened avoidance behaviors for alligators that had not directly experienced capture but lived in the treated site, suggesting that animals can learn to avoid or tolerate risk without their own direct experiences. Similar results are reported where animals become trap-shy or avoid researchers after witnessing other animals in their population being captured (Bustard 1968) or when elk that experience a herd member being taken in a hunt behaviorally adapt to reduce their exposure to hunting pressure (Thurfjell et al. 2017). In an experimental study, Indian mynahs (*Acridotheres tristis*) that witness conspecifics experiencing an aversive event (being captured and handled by humans) exhibit behaviors consistent with increased wariness despite their lack of direct aversive experience (Griffin and Boyce 2009). In observations of mobbing behaviors by American crows (*Corvus brachyrhynchos*) towards a conditioned stimulus, the majority of scolding birds had not been captured themselves (Marzluff et al. 2010, Cornell et al. 2012). If evidence for indirect learning continues to be supported in future studies, it could suggest that only a portion of alligators in a population need to undergo aversive conditioning to elicit desired population-level behavior changes. Low probability of flight at the reference site suggests alligator behavior towards humans over time is context-dependent, and primarily shaped by the nature of interactions, rather than just the frequency of interactions between alligators and humans. Declining probability of flight with increasing alligator size at the reference site and early in the course of aversive conditioning at the treated site (see *post hoc* results) suggest that alligators may undergo habituation towards humans in the absence of significant aversive experiences with humans. In

contrast to sensitization, habituation occurs as a result of repeated experiences with a stimulus that is not followed by any kind of reinforcement (e.g., reward, injury), shaping animal behavior to minimize future reactions to that stimulus (i.e., become nonreactive; Whittaker and Knight 1998, Bejder et al. 2009, Bucklaew and Dochtermann 2021). If alligators innately perceive humans as predators, sensitization and habituation could explain why small (i.e., young) alligators at the reference site demonstrated increased avoidance of humans (higher probability of flight) in response to survey exposure over short time scales, but that alligators generally stopped avoiding humans over longer time scales (i.e., as they grew and accumulated non-aversive experience). Similar context-dependent responses of wildlife to humans have been observed across a wide range of taxa. For example, crocodylians in areas where they were hunted, captured for research, or otherwise disturbed by humans were less approachable (i.e., sensitization) than those in less disturbed areas (i.e., habituation), and older animals were less approachable than younger animals (sensitization; Webb and Messel 1979, Pacheco 1996, Gramentz 2008, Marques et al. 2016). Elk were more vigilant on public lands where hunting occurs (i.e., sensitization) than in national parks where they encounter large crowds of people but are not hunted (i.e., habituation; Ciuti et al. 2012), and females have been suspected to learn from prior experience and alter movement rates and resource use to specifically avoid human hunters (sensitization; Thurfjell et al. 2017). Collectively, our results add to a growing body of work highlighting that the ways in which animals experience humans can influence their behavior as a result of learning.

While our results support sensitization in response to aversive experiences and habituation in response to benign experiences, other short- and long-term factors beyond the scope of our study may have influenced alligator behaviors. Long-term exposure to disturbance, such as development or a high degree of human presence, can result in populations with bold baseline behaviors (e.g., personalities) if shy animals (those that exhibit greater escape or lower risk-taking behaviors) move to less-disturbed areas or are not able to thrive as well as bold animals (Carrete and Tella 2010, Miranda et al. 2013). Short-term human behaviors that promote tolerance (e.g., feeding wild animals) and long-term processes that shift the population toward bolder behaviors could exacerbate nuisance human-wildlife interactions (Orams 2002, Newsome and Rodger 2008, Found 2019). Bold personalities might predispose animals towards tolerant behaviors and might also reduce the effectiveness of strategies aimed to manipulate behavior (Found and St. Clair 2018, Found 2019). The degree to which site-level differences (other than those which we explored) may have influenced our results remains somewhat unclear and future research should more directly investigate changes in alligator behavior across a range of human disturbances to account for differences in baseline behaviors associated with humans.

Capture experience had a more predictable association with probability of flight than FID, though the reason for this remains unclear. For example, the probability of flight model had better predictive ability for additional observations than the FID model based on model validation results. Flight initiation distance could be more difficult to predict because of the influence of individual differences in alligator behavior that interact with site-level factors or alligator experiences in their environments. While animal behavior is influenced by experiences, behavior is also partly determined by innate temperaments or personalities (Sih et al. 2004, Found and St. Clair 2018).

Additional work may be warranted to investigate the potential implications of our results for future alligator population monitoring. While our study design was not designed to explicitly investigate whether capture events influence our ability to detect alligators, we did identify increased probability of flight during diurnal surveys when humans approached alligators. Thus, it is plausible the capture and release efforts could negatively affect alligator detectability in areas where monitoring protocols rely on visual encounters with alligators, especially during diurnal periods (Mancini et al. 2015). The degree to which aversive conditioning effects described herein influence nocturnal responses of alligators to humans remain unclear but warrants further exploration, especially because nighttime surveys are one of the most widespread and common methods for monitoring crocodylian populations (Skupien and Andrews 2017). In golf courses like those examined in this study, vegetation was often sparse and rarely limited visual access to popular basking areas from long distances. In areas where thick riparian vegetation visually conceals much of the basking habitat and where surveyors must be relatively close before alligators are visually accessible, increased probability of flight might pose a challenge for monitoring. In cases where sensitization

to the presence of humans is undesirable, capture and detection methods that minimize interactions between alligators and humans, such as baited traps (Murphy and Fendley 1975) and remote cameras (Merchant et al. 2018), might be preferred.

MANAGEMENT IMPLICATIONS

While our results provide preliminary evidence that capture events can produce an aversive conditioning effect for alligators in some scenarios, there are several limitations to our study, and we encourage managers to consider several factors before investing in aversive conditioning in other systems. Increasing probability of flight through aversive conditioning might be useful when alligator interactions are problematic (e.g., alligators can be approached too closely). For addressing human-wildlife conflict, we recommend that others consider the current state of human-alligator interactions in a local population and if aversive conditioning is an appropriate action to meet the needs of the local human and alligator populations. First, we do not recommend aversive conditioning to address food-conditioned alligators that are attracted to humans because our observations did not include animals that were obviously food-conditioned. We also only assessed alligator responses towards an approaching adult human and cannot say with confidence that a similar effect would extend to children or pets. Managers may also be interested in the effect of microhabitat characteristics (e.g., vegetation, water depth) on alligator behavior, but we lack this information as most of our reported encounters were of basking alligators on mowed grass. Second, we encourage managers to investigate the role of human behaviors in the development of nuisance alligator behaviors to develop strategies to prevent the need for aversive conditioning. Third, because intensive alligator capture efforts might be costly, time intensive, and logistically difficult for some organizations, and our study was limited to only 2 study localities, we recommend small-scale pilot studies to evaluate the baseline state of alligator behavior if a management goal is to reduce alligator tolerance of closely approaching humans (i.e., increase probability of flight). We also recommend following any aversive conditioning protocol with additional surveys to monitor changes in alligator behavioral responses to humans. Finally, we recommend concentrating monitoring and conditioning efforts in spring (e.g., Mar-Jun in the USA) because this time period was aligned with low probability of flight, low FID, and high alligator activity in this system. Thus, the spring season is likely the time of year when humans and alligators are interacting most often and when sample sizes from visual surveys or attempted conditioning are likely to be highest. Despite potential drawbacks, aversive conditioning may help promote human-alligator coexistence while also preserving the large alligators that are most likely to be perceived as nuisance animals.

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CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

Handling and observation of alligators was conducted under research permits issued by the South Carolina Department of Natural Resources and in accordance with Clemson University Institutional Animal Care and Use protocols 2016-059 and 2019-068.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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