


Article

Social Behavior Deficiencies in Captive American Alligators (*Alligator mississippiensis*)

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Abstract: Understanding how the behavior of captive American alligator (*Alligator mississippiensis*) congregations compares to wild congregations is essential to assessing the welfare of alligators in captivity. Wild alligator congregations perform complex social behaviors, but it is unknown if such behaviors occur in captive congregations as frequently. We observed the behaviors of a captive and wild congregation of American alligators in Florida, USA in January 2021. Social behaviors were, on average, 827% more frequent in the wild congregation than the captive, and the wild congregation had a richer repertoire of social behaviors, with growling and HOTA (head oblique tail arched) behaviors being particularly common. High walking, a nonsocial behavior, dominated the behavioral repertoire of the captive congregation (94% of behaviors, excluding feeding) and may be a stereotypy that can be used as an indicator of welfare. Both congregations experienced human disturbance and displayed flushing as a species-specific defense reaction. Captive environments differ from the wild with respect to size, structure, stocking density, resource availability, and human presence. These differences translate into behavioral differences between wild and captive congregations. We identified important behavioral differences between wild and captive alligator congregations that can serve as a platform for more detailed investigations of alligator welfare in captivity.

Keywords: alligator; animal welfare; behavioral observation; comparative; social behavior



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1. Introduction

The American alligator (*Alligator mississippiensis*) is a predatory species found throughout the Southeastern region of the United States [1]. Within Southern Florida, American alligators are both a keystone predator and an ecosystem engineer [2]. As of 2019, the International Union for Conservation of Nature lists the American alligator as a species “of least concern” [3]. Nonetheless, American alligators are categorized as a threatened species under the Endangered Species Act [4] due to their similarity in appearance to the threatened American crocodile (*Crocodylus acutus*). Thus, regulations in place for the protection of American alligators (hereafter referred to as alligators) also serve to protect American crocodiles [5].

Alligators perform complex social behaviors within congregate settings, both in the wild and in captivity. However, their social behavior between settings has not been compared in a singular study. Alligators can be successfully kept in a captive environment [6], but the behaviors of animals can differ in types and frequency performed when in captivity versus a natural environment [7].

Although there is a lack of published comparative studies in captive and wild alligators, there are extensive comparative behavioral studies that have been previously conducted on mammalian species. For example, chimpanzee (*Pan troglodyte*) groups in captivity increase their time spent grooming, but decrease their time spent foraging relative to wild groups [8]. Additionally, enclosure design and the number of human visitors that captive cotton-top tamarins (*Saguinus oedipus oedipus*) receive correlate with significant

differences in social interactions within the group [9]. These findings demonstrate that social behavioral discrepancies can occur between captive and wild animal congregations. As wild alligators commonly display social behavior, it is prudent to evaluate differences in social behavior between captive and wild alligator congregations [10].

While alligator social behavior has not been compared between captivity and natural settings, nesting behaviors have been compared between these settings. Rates of hatching and nesting successes in wild and captive individuals were closely correlated, denoting an insignificant difference between these groups [6]. However, congregation density and stocking rates were significantly different [6].

Interest in reptile welfare in captive settings has been growing and the similarity in reproductive success between captive and wild settings is positive but is only one dimension of welfare. Behavioral expression, both general and social, is also an indicator of animal health and wellbeing [7]. Alligator behaviors have been studied in a captive environment, but they have not been directly compared between wild and captive settings in a singular comprehensive study [6,10,11].

The objective of the current study was to assess social and general behavioral differences between alligator congregations in a captive and wild environment.

2. Materials and Methods

2.1. Wild Observation Site and Congregation

A congregation of wild alligators was observed at Myakka River State Park, Sarasota, Florida. The study site, known as the Deep Hole, is an area containing a large freshwater sinkhole located within the Park's protected Wilderness Preserve [12]. Human visitation is limited in the Wilderness Preserve to 30 permits per day to minimize interference. The area is open and free from tree cover, with the exception of a small cluster of trees on the Western basking area of the sinkhole (Figure 1). It provides alligators with a large prey supply and many suitable basking areas around the sinkhole [12]. The sinkhole connects the lower Myakka Lake and lower Myakka River [12]. During the dry season, when the alligators were observed, the sinkhole was approximately 41 m deep and approximately 90 m in diameter [12].



Figure 1. (a) The Deep Hole site in the Myakka Wilderness Preserve where wild alligators were observed. The body of water pictured is the sinkhole. (b) The captive enclosure at Croc Encounters, a wildlife sanctuary, where captive alligators were observed. The land area is utilized as basking space.

The Deep Hole site is occupied by a large congregation of alligators [12]. We estimated the congregation density by dividing the average number of individuals observed with binoculars each hour by the estimated area of the sinkhole (6362 m^2). On average, $0.0150 \text{ alligators/m}^2$ are found within the sinkhole. However, the alligators were not evenly distributed throughout the space, rather they were often clustered on or near the banks. Additionally, the number of alligators varied over time during our study, averaging 95 ± 4 individuals.

2.2. Captive Observation Site and Congregation

A congregation of captive alligators was observed at Croc Encounters, a wildlife sanctuary located in Tampa, Florida. This facility accepts and maintains various reptilian species which have been surrendered to the institution or taken in after being deemed nuisance wildlife. The alligator congregation was fed a dry crocodilian diet mix by passing groups on guided tours and Croc Encounters employees. Guided tours typically occur one to four times per day. The diameter of the captive enclosure was approximately 15.2 m, providing an estimated 182.4 m² area.

The captive congregation was composed of 84 adult alligators that varied in size, sex, and age; despite these differences, all were considered adults. The congregation density of 0.461 alligators/m² was higher at this site.

2.3. Behavioral and Environmental Data Collection

Two ethograms were created and used to quantify behavior of both the wild and captive alligator congregations. Both ethograms include behaviors previously described in the literature and some behaviors observed during pilot observations. The first ethogram consisted of “social” behaviors including bellowing, bellowing with water dancing, chumpfing, fighting, food theft, growling, hissing, head colliding, headslapping, raised posture, raised snout, roaring, HOTA (head oblique tail arched), and tail wagging (detailed descriptions of the behaviors and associated sources can be found in Table S1) [10,11]. HOTA posturing was included in the social behaviors ethogram due to its known function as a precursor to other social behaviors in a congregation and performance in conjunction with other social displays [11]. In a social context, this behavior can serve as a signifier of alertness [11]. The second ethogram consisted of “general” behaviors, including basking, death rolling, group feeding, group basking, high walking, individual feeding, and low walking (detailed descriptions of the behaviors and associated sources can be found in Table S2) [10,11]. Behavioral data were collected at each site for 5.5 h a day between 9:00 and 14:30 for seven continuous days at each site (38.5 total hours per site). The wild alligators were observed 5–11 January 2021 and the captive alligators 14–20 January 2021. During behavioral observations, the occurrence of behaviors from both the general and social ethogram were recorded with a time and date stamp. When the same behavioral event occurred multiple times in succession, the time interval was recorded and the number of times this behavior was performed. The identification of individual members of each congregation was not feasible. Therefore, behavioral states and events were recorded without the identification of the performing individual or individuals. However, the number of alligators performing these behaviors was recorded.

Additionally, at the wild site, human presence and activity were documented throughout the observational period. Human presences included the presence of park visitors in the vicinity, activities performed by the visitors, and any observed reaction by the alligators. At the captive site, we recorded every time a caretaker entered the interior area of the enclosure, any time a tour group approached the exterior area of the enclosure, and any observed reaction by the alligators. There was constant anthropogenic noise at this site that originated outside the sanctuary, particularly from a nearby interstate with heavy vehicle traffic.

Ambient air temperature and humidity were recorded every hour during the observation periods using a digital thermometer. At no time during the study was any contact made with an alligator in either congregation. Precautions were taken to minimize disturbance, including maintaining a minimum of approximately 30 m from all wild alligators, maintaining a non-disruptive tone when speaking, and minimizing speaking when possible [13]. At the captive location, there was glass separating the enclosure and viewing area. The observers were within 2 m of the glass and remained as still and quiet as possible. As alligators moved around the enclosure, their proximity to the observers varied.

2.4. Data Analysis

The mean \pm SE number of social behaviors performed per individual per hour for each congregation was calculated. Data from the 14:00–14:30 period were not included in this analysis because it was not a full hour. We then calculated the difference between the two means and conducted a permutation test using the statistical software R with the *perm* package [14,15]. The test shuffles the data between conditions (“Captive” and “Wild”) and calculates the difference in means for a set number of permutations ($n = 100,000$). The p -value, then, is the proportion of those 100,000 values that are greater than our observed value.

The difference in the frequency of the three most commonly observed social (growls, HOTA, and fighting) and general (high walk, flushing, and feeding) behaviors between congregations was compared using Wilcoxon Rank Sum tests. Because multiple comparisons were performed, a Bonferroni correction was used to adjust the alpha level to 0.0083.

To determine the influence of air temperature and human interactions on alligator behavior, all behavior types (social and general) were combined, and behavior/alligator/hour rates were calculated for each congregation. Data from the 14:00–14:30 period were not included in these analyses because it was not a full hour. Linear models were fitted to evaluate hourly trends in the frequency of alligator behaviors relative to air temperature and human interactions. Human interactions at the wild site included the occurrence of humans near the water and humans kayaking on the water. Human interactions at the captive site were quantified as the number of tour groups (there were no human visitors outside tour groups). Analyses and visualizations were performed in MATLAB unless otherwise stated [16].

3. Results

3.1. Social Behaviors

The mean number of social behaviors performed per individual per hour was 0.0942 ± 0.0245 (mean \pm SE) for the wild site and 0.0112 ± 0.0027 for the captive site. Of the 100,000 differences in means calculated by the permutation test, none were equal to or greater than the difference in means observed in the current study (0.083). Therefore, the mean number of social behaviors was significantly higher for the wild congregation than the captive congregation ($p < 0.001$) (Figure 2).

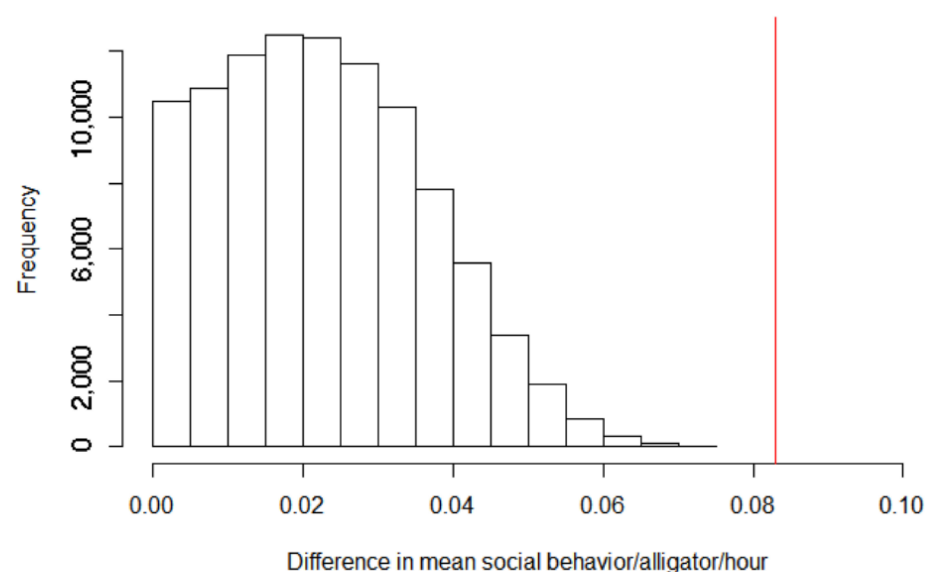


Figure 2. Frequency histogram of the 100,000 permutations of difference in mean social behavior/alligator/hour. This parameter was calculated by subtracting the mean number of social behaviors

per alligator per hour in the captive congregation from the same value in the wild congregation. The permutations are created by randomly resampling the observed data to create hypothetical mean social behavior/alligator/hour for each congregation and the difference in means between congregations is calculated. All 100,000 permutations were higher than the observed difference in means (red vertical line at 0.083).

In total, 320 social behaviors were observed at the wild site and 42 at the captive site. The mean number of social behaviors performed by each congregation per hour was higher at the wild site (8.71 ± 2.41 social behaviors/hour) than at the captive site (0.94 ± 0.23 social behaviors/hour). This increase in behaviors performed across sites indicates that, on average, the wild alligators performed 827% more social behaviors than the captive alligators during the observational periods of this study (Figure 3).

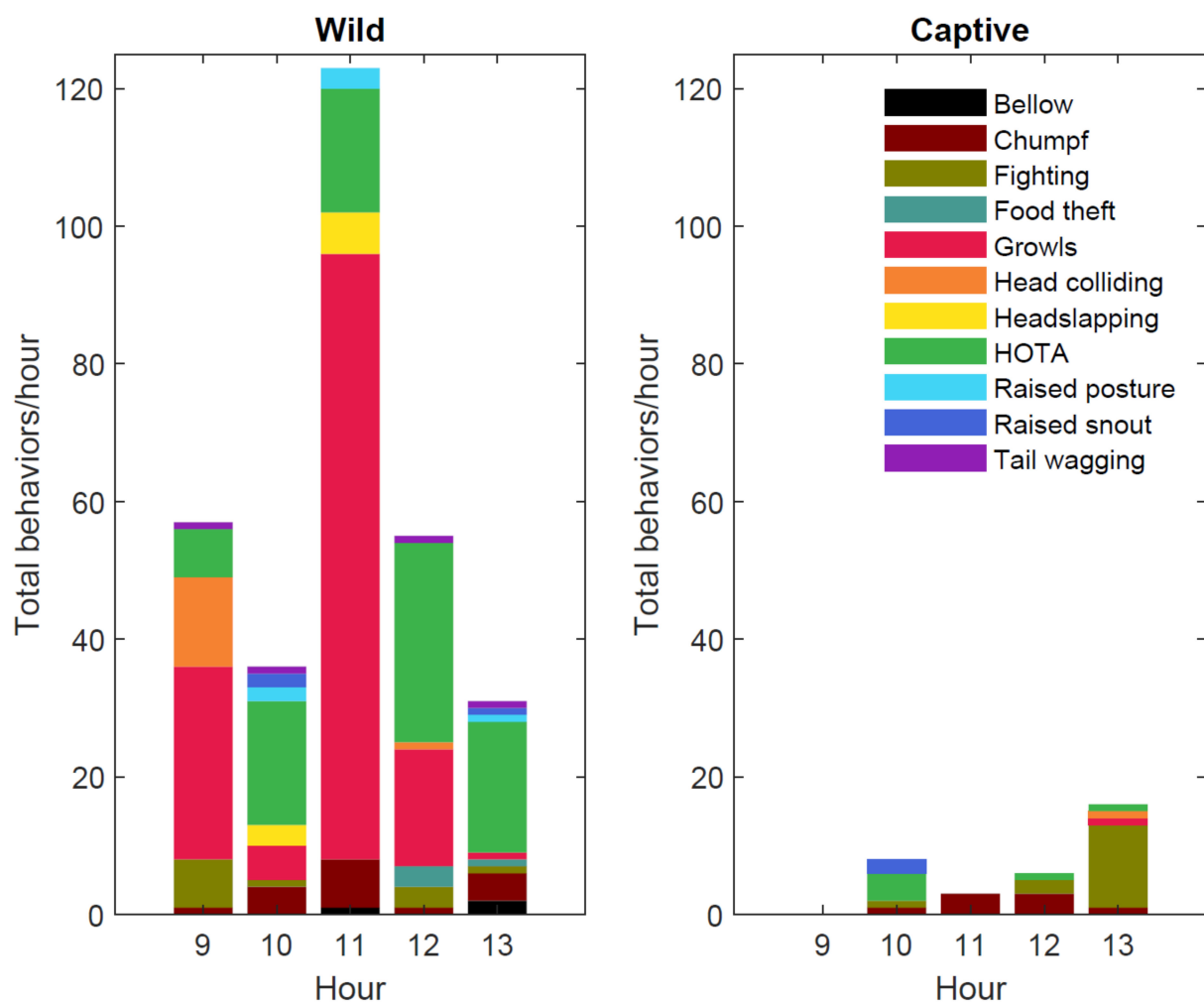


Figure 3. Total number of specific social behaviors (color-coded) during each hour of the day summed across days. The social behavior of the wild congregation is represented on the left and the social behavior of the captive congregation on the right. The y-axis limits are the same for both plots to facilitate comparison of the frequency of social behaviors between the wild and captive congregations. Proportions of general behaviors performed within the wild and captive congregations can be found in Table 1.

The most frequently observed social behavior performed within the wild congregation was growls (46.6% of social behaviors; $n = 149$) and the second most frequently observed social behavior was HOTA posturing (30.0% of social behaviors; $n = 95$) (Table 1). Growls (Z

= 3.54, $p < 0.0001$) and HOTA ($Z = 5.32$, $p < 0.0001$) were observed significantly more often in the wild congregation compared to the captive congregation (Figure 4). Growl choruses, in which multiple individuals growl in close succession, occurred in the wild congregation but not the captive. Within the captive congregation, fighting (50% of social behaviors; $n = 21$) was the most frequently observed social behavior followed by chumpfing (21.4% of social behaviors; $n = 9$) (Table 1). Fighting was the only social behavior observed more often at the captive site than the wild site ($n = 21$ at the captive site and $n = 10$ at the wild site), however the difference was not statistically significant. Roar and water dance were the only social behaviors not observed at either site.

Table 1. The proportion of each social behavior at each site, presented as the percentage of each type of social behavior divided by the total number of social behaviors performed at that site with behavior counts in parentheses ($n = 320$ for the wild site and $n = 42$ for the captive site; data collected 09:00–14:30).

| Behavior Performed | Wild Site | Captive Site |
|--------------------|----------------------|---------------------|
| Bellow | 0.94% ($n = 3$) | 0.00% ($n = 0$) |
| Chumpf | 5.31% ($n = 17$) | 21.43% ($n = 9$) |
| Fighting | 3.13% ($n = 10$) | 50.00% ($n = 21$) |
| Food theft | 1.25% ($n = 4$) | 0.00% ($n = 0$) |
| Growl | 46.56% ($n = 149$) | 2.38% ($n = 1$) |
| Head colliding | 3.75% ($n = 12$) | 2.38% ($n = 1$) |
| Headslapping | 2.81% ($n = 9$) | 0.00% ($n = 0$) |
| HOTA | 29.69% ($n = 95$) | 19.05% ($n = 8$) |
| Raised posture | 1.88% ($n = 6$) | 0.00% ($n = 0$) |
| Raised snout | 3.44 % ($n = 11$) | 4.76% ($n = 2$) |
| Roar | 0.00% ($n = 0$) | 0.00% ($n = 0$) |
| Tail wagging | 1.25% ($n = 4$) | 0.00% ($n = 0$) |
| Water dance | 0.00% ($n = 0$) | 0.00% ($n = 0$) |

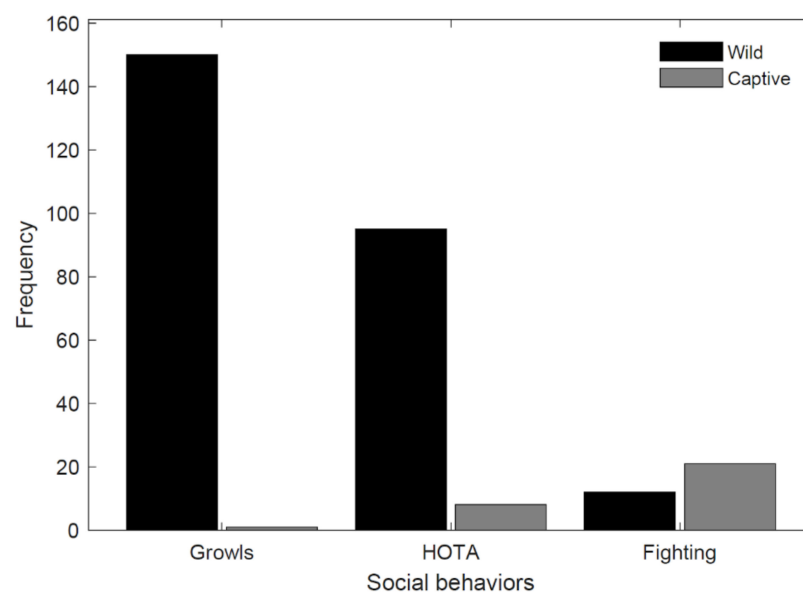


Figure 4. The frequency of the three most commonly observed social behaviors compared between the captive and wild congregations.

3.2. General Behaviors

At the wild site, a total of 422 general behaviors were recorded. The most frequently observed general behavior within the wild congregation was flushing (72.27% of general behaviors; $n = 305$ at the wild site and 2.70% of general behaviors; $n = 74$ at the captive site), which most often occurred at the same time as human visitor presence at the Deep Hole site. The death roll behavior was recorded at the wild site while no instances were observed at the captive site ($n = 3$ at the wild site and $n = 0$ at the captive site). At the captive site, 2736 general behaviors were recorded. The most frequently observed general behavior within the captive congregation were individuals performing high walks (Figure 5; Table 2). In total, 1973 individual instances were observed of high walking (72.11% of general behaviors; $n = 1973$).

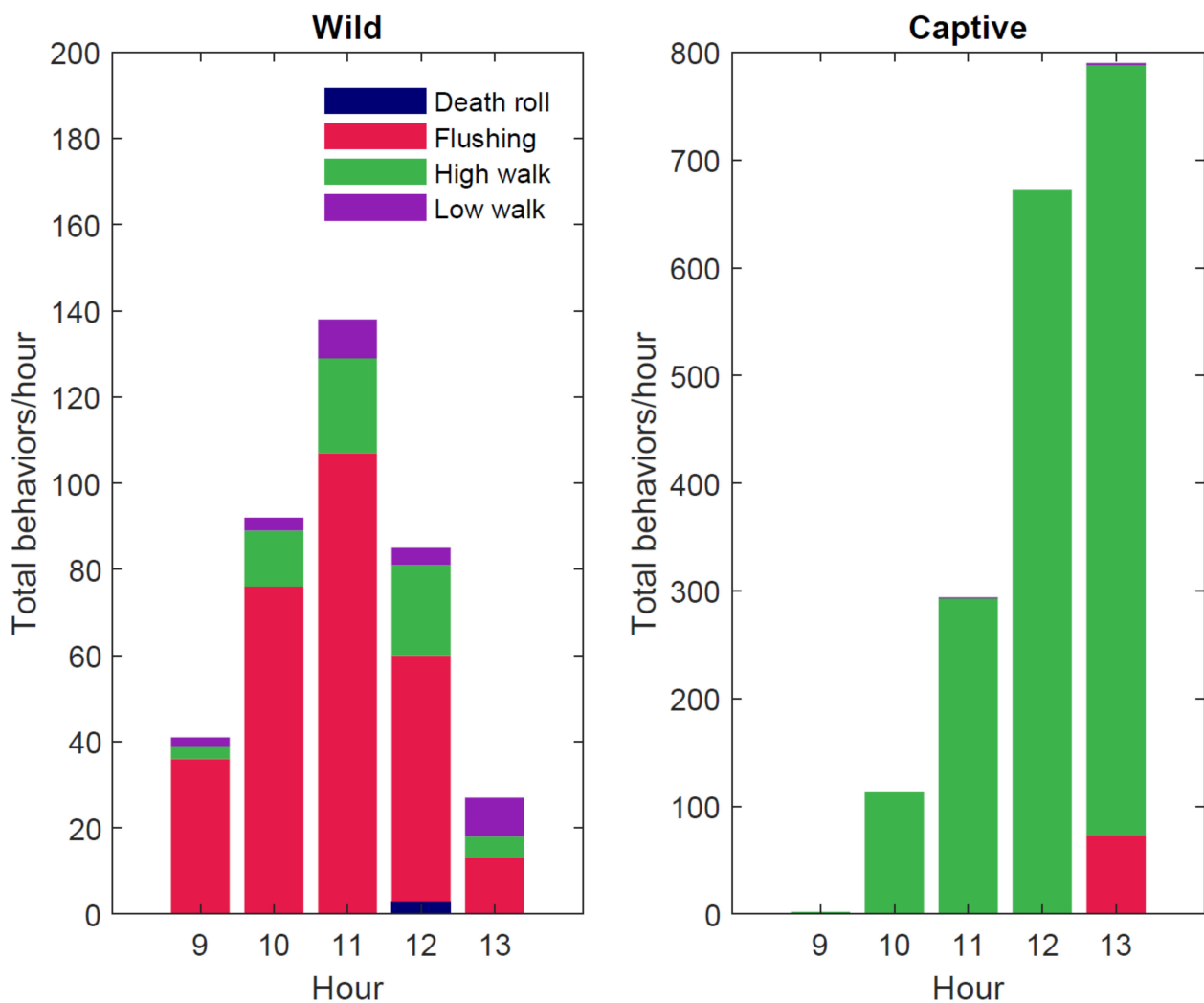


Figure 5. The total number of specific general behaviors (color-coded) during each hour of the day summed across days. The general behavior of the wild congregation is represented in the left plot and the general behavior of the captive congregation in the right plot. Note that the y-axis limits are different between the wild and captive congregation plots. Feeding is excluded because food offerings only occur between 11:30 and 13:27 in the captive congregation, whereas in the wild feeding may occur at any time.

Table 2. The proportion of each general behavior at each site, presented as the percentage of each type of general behavior divided by the total number of general behaviors performed at that site with behavior counts in parentheses ($n = 422$ for the wild site and $n = 2736$ for the captive site; data collected 09:00–14:30).

| Behavior Performed | Wild Site | Captive Site |
|--------------------|----------------------|-----------------------|
| Deathroll | 0.71% ($n = 3$) | 0.00% ($n = 0$) |
| Feeding | 2.61% ($n = 11$) | 25.07% ($n = 686$) |
| Flushing | 72.27% ($n = 305$) | 2.70% ($n = 74$) |
| High walk | 18.01% ($n = 76$) | 72.11% ($n = 1973$) |
| Low walk | 6.40% ($n = 27$) | 0.11% ($n = 3$) |

High walking ($Z = -4.21$, $p < 0.0001$) was observed significantly more often in the captive congregation compared to the wild congregation (Figure 6). Flushing ($Z = 4.55$, $p < 0.0001$) was observed significantly more often in the wild congregation compared to the captive congregation (Figure 6). The frequency of feeding events was not statistically compared between congregations, because feeding is regulated by caretakers in the captive setting.

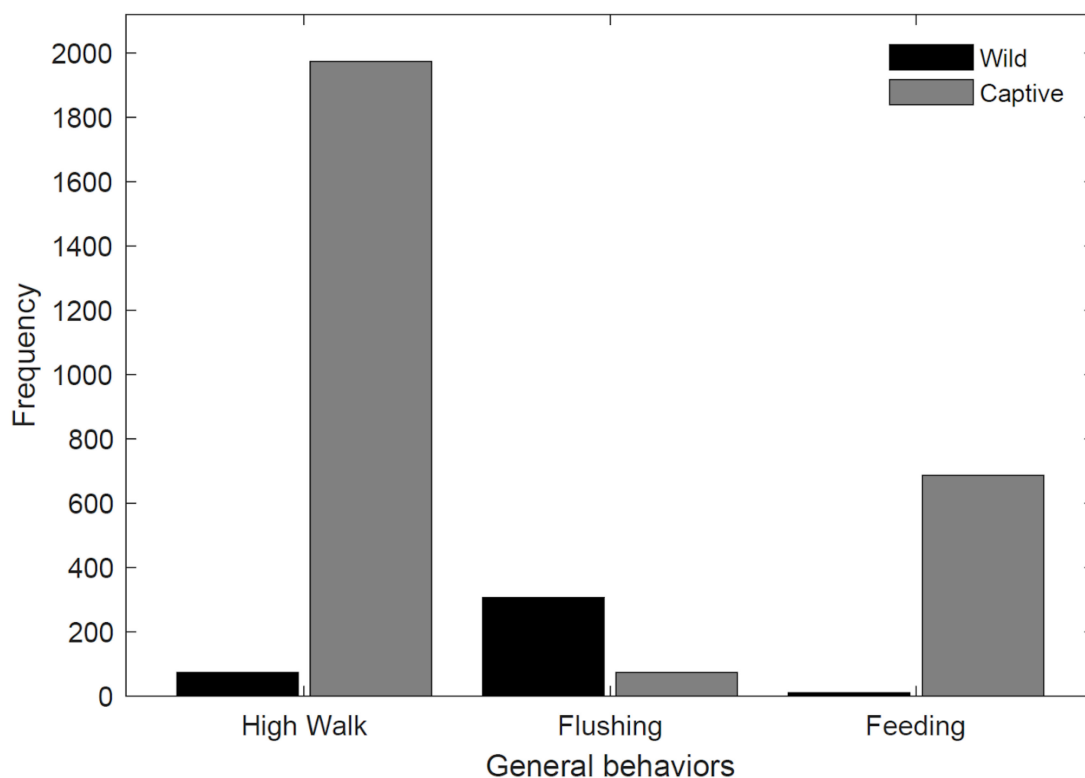


Figure 6. The frequency of the three most commonly observed general behaviors compared between the captive and wild congregations. Feeding opportunities in the captive congregation are regulated by caretakers.

3.3. Environmental and Human Impacts on Behavior

The frequency of behavioral events, including both social and general behaviors, generally increased from 9:00 to 12:00 and then decreased in the wild congregation (Figure 7A). In the captive congregation, the frequency of behavioral events increased from 9:00 to 14:00 (Figure 8A).

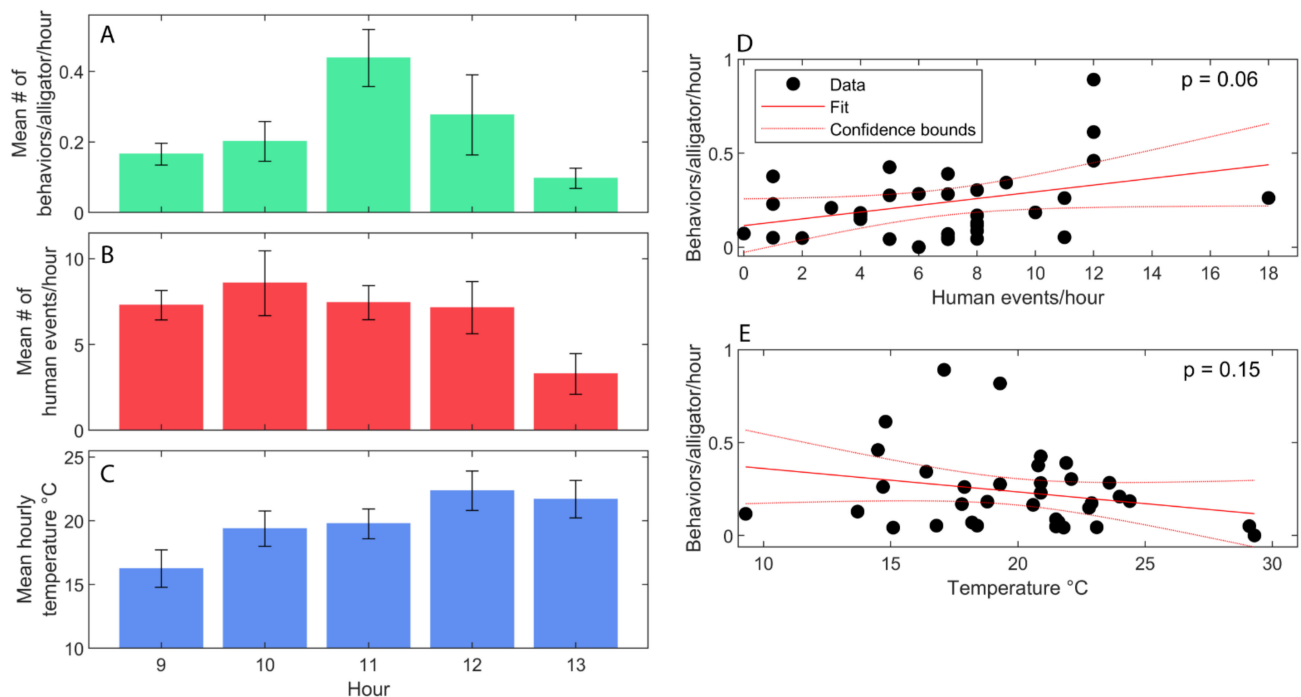


Figure 7. A comparison of trends in behavior, human interactions, and temperature by hour in the wild congregation. (A) The mean (\pm SE) number of behaviors (including social and general) divided by group size per hour by hour of day. (B) The mean (\pm SE) number of human events (including humans walking near the water or kayaking) per hour by hour of day. (C) The mean (\pm SE) hourly temperature ($^{\circ}$ C) by hour of day. (D) Relationship between the frequency of alligator behavior compared to the frequency of human events. The solid line represents a fitted linear model with the dashed lines representing the 95% confidence interval. (E) Relationship between the frequency of alligator behavior compared to the air temperature. The solid line represents a fitted linear model with the dashed lines representing the 95% confidence interval.

Human presence at the wild site (from land or water) generally decreased from the morning to the afternoon (Figure 7B). Aggressive social behaviors were not observed in association with human presence at the wild site. Instead, the wild alligators were often recorded flushing due to human presence. Flushing bouts, that involved more than one alligator, in response to human interaction occurred an average of 9.9 times per day at the wild site. A mean of 43.9 individual alligators flushed per day in response to human activity at this location.

At the captive site, tour groups only occurred between 11:00 and 14:00 (Figure 8B). At the captive site there was an increase in aggressive social behaviors between the alligators, such as fighting, when a human caretaker had entered and exited the enclosure. While the caretaker was present inside the enclosure, the alligators showed defensive behavior that included but was not limited to hissing, posturing, and flushing. The mean period of time between the caretaker exiting the enclosure and the first sign of aggressive social interactions between the alligators was 10 min.

The mean hourly temperature at the wild site was 20.3 ± 0.6 $^{\circ}$ C and the mean hourly humidity level was 46.6%. The mean hourly temperature at the captive site was 17.3 ± 0.5 $^{\circ}$ C and the mean hourly humidity level was 52.5%. Temperature generally increased from 9:00 to 14:00 at both sites (Figures 7C and 8C).

At the captive site, there was a positive correlation between human presence and the frequency of alligator behavioral events, but no statistically significant correlation at the wild site (Figures 7D and 8D). There was also a positive correlation between the frequency

of alligator behavioral events and air temperature at the captive site, but no statistically significant correlation at the wild site (Figures 7E and 8E).

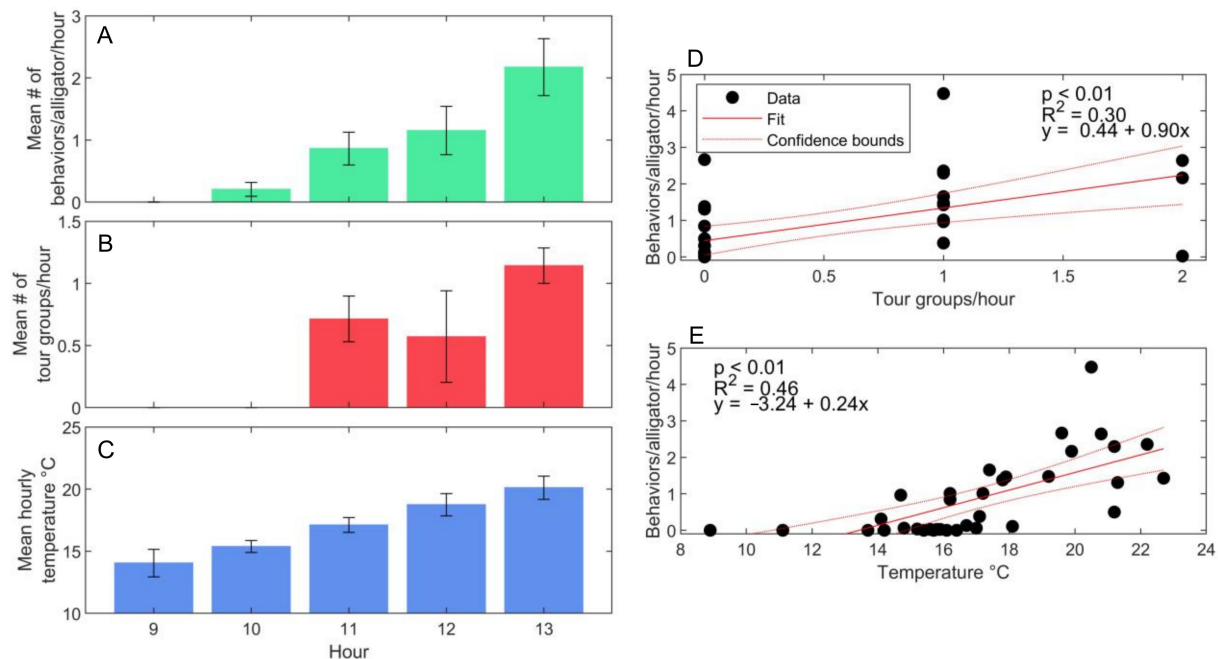


Figure 8. A comparison of trends in behavior, human interactions, and temperature by hour in the captive congregation. (A) The mean (\pm SE) number of behaviors (including social and general) divided by group size per hour by hour of day. (B) The mean (\pm SE) number of tour groups per hour by hour of day. (C) The mean (\pm SE) hourly temperature ($^{\circ}$ C) by hour of day. (D) Relationship between the frequency of alligator behavior compared to the frequency of tour groups. The solid line represents a fitted linear model with the dashed lines representing the 95% confidence interval. (E) Relationship between the frequency of alligator behavior compared to the air temperature. The solid line represents a fitted linear model, with the dashed lines representing the 95% confidence interval.

4. Discussion

Social behaviors were consistently observed more often at the wild site than the captive site (Figures 2 and 3; Table 1). In particular, growls and HOTA were observed more often in the wild congregation than the captive (Figure 4). The wild congregation also exhibited a more diverse social behavior repertoire compared to the captive congregation (Figure 3; Table 1). More general behaviors were observed in the captive congregation, but the increase in the performance of general behaviors resulted from the prevalence of a single behavior, high walking, which dominated the behavioral repertoire of the captive congregation (Figures 5 and 6; Table 2). Contrary to high walking, flushing occurred more often in the wild congregation. The frequency of behavioral events of the captive congregation was influenced by human presence (Figure 8).

The difference in population size between congregations is unlikely to account for the observed differences in social behavior. Although there were typically more alligators at the wild site, the average difference in the number of individual alligators ($n = 11$ which is 12.3%) is small relative to the difference in the frequency of observed social behaviors (7.8/hour which is 827% more social behaviors in the wild congregation). Additionally, the differences in behavior extended far beyond frequency. In the wild congregation, 11 types of social behaviors were observed, while 6 types of social behaviors were observed within the captive congregation. Of particular interest is the prevalence of growling in the wild congregation, but not the captive (Figure 4). Growling is hypothesized to be used for multiple social purposes and may occur in conjunction with or as a component of

another social behavior [10,11]. Growling can be used by female individuals as a response to courtship attempts or aggression, although mating behaviors may not have been as prevalent in the mid-January season in which this study was conducted [11]. However, this behavior has been recorded by other researchers as most often being performed by males as a courtship or defensive behavior [10,11]. Growling can also moderate more aggressive behavior like fighting. While the increased fighting in the captive congregation was not statistically significant, it is important to consider the occurrence of growling relative to fighting. In the wild congregation, growling was markedly more prevalent than fighting (14.9 growls:fighting) than in the captive congregation (0.05 growls:fighting) (Table 1). Joanen and McNease (1971) observed three out of five large adult male alligators experienced an increase in the occurrence of aggressive behaviors over the time that they were living in a captive environment. That observed increase in aggressive behavior, along with our findings that fighting was the most commonly performed social behavior by individuals in the captive congregation, suggests that some aspect of the captive environment is influencing the alligators' aggression levels [6]. In the current study, the differences in congregation density, habitat structure, and agitation by the entrance of caretakers into captive enclosures may be the cause of increased aggression in the captive congregation.

The most striking difference in general behavior was the prevalence of high walking in the captive congregation ($n = 1973$ at the captive site and $n = 76$ at the wild site). Considering both general and social behaviors (excluding feeding), high walking represents 94% of the observed behaviors in the captive congregation. The elevated high walking behavior at the captive site may be related to overcrowding and space limitation in the captive congregation (the wild site is approximately 35 times the size of the captive site). High walking was observed in the captive congregation on the land area of the enclosure and typically occurred during basking hours. It was necessary for individual alligators to perform the high walking behavior during basking hours in order to maneuver over other alligators on land, though high walking also occurred when not maneuvering over other alligators. The large difference in congregation density for each site ($0.0150/\text{m}^2$ for the wild site and $0.461/\text{m}^2$ for the captive site) resulted in less area available for basking at the captive site than the wild site (Figure 9). High walking in the captive congregation was akin to wandering; this opposes the wild congregation, where alligators typically walked directly from the water to a specific spot for basking. The performance of stereotypic behaviors, like the excessive high walking in the captive congregation, is typically attributed to environmental stress and a lack of adaptation in individual captive animals [17]. Stereotypic behaviors, such as high walking without a clear destination can have negative metabolic consequences beyond the energetic cost of the movement itself, as such activities result in excess post-exercise oxygen consumption (energy continues to be consumed after initial locomotive activities) [18].

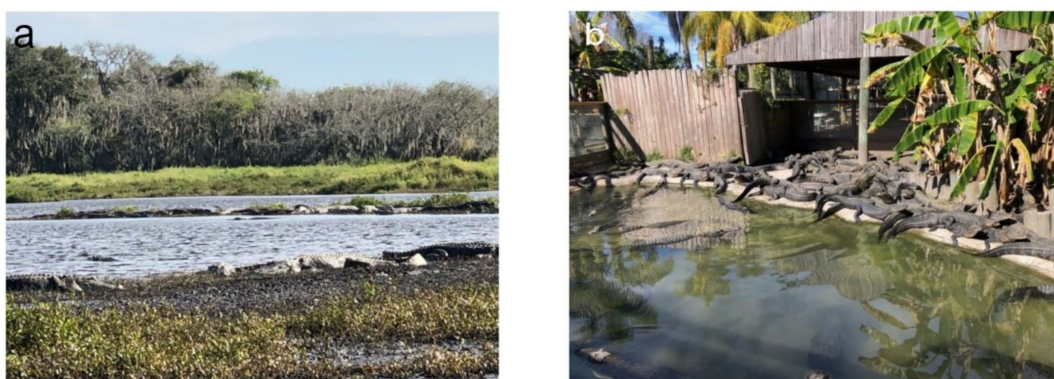


Figure 9. (a) The basking area of the wild site. (b) The basking area of the captive enclosure, showing the typical spacing of individual alligators during basking hours.

The space limitations of the captive enclosure also affected spatial organization of the alligators. At the wild site, alligators commonly arranged themselves based on a size hierarchy, with the largest alligators in the Western and Southern basking areas surrounding the sinkhole whereas the smaller individuals would often be observed basking on the Eastern shoreline. Alternatively, at the captive site, the basking arrangement was in a large pile and there did not appear to be a noticeable size hierarchy or organization in the basking spots. Additionally, direct contact between alligators was commonly observed at the captive site, but not in the wild. Forms of direct contact included alligators forming tightly packed basking piles rather than spaced out groups. Movement is also impacted by the limited area such that alligators commonly crawled over each other, both in basking areas and in the shallow pond (approximately 2 m deep compared to 41 m depth at the wild site) [12]. Stress, as measured through differences in plasma corticosterone levels, has been observed to increase in individual alligators with higher stocking densities in captive environments and decrease in individual alligators in wild environments [19]. Increased stress levels as a result of higher stocking density in the captive site could be a contributing factor to a decrease in social behaviors observed within the captive congregation when compared to the wild congregation.

Differences in the level of confinement may also contribute to behavioral differences observed between congregations. Alligators in an estuary environment exhibit high individual variation in daily movement distance, but travel on average 0.7 to 3.2 km per day [20]. The observed wild site has a larger area than the captive enclosure and has connections with the greater Myakka watershed. The connected open space within the wild site permitted the wild congregation unrestricted movement and migratory opportunities not available to the captive congregation.

While human presence and interactions are generally considered confounding variables in behavioral studies, human presence and interactions with captive animals is commonly intrinsic to housing animals in a captive setting. As such, maintaining a typical pattern of human presence during the study period is important for evaluating behavioral differences between alligators living in wild versus captive conditions. Human presence influenced alligator behavior in both congregations, but the type of influence and magnitude differed. Territorial interactions, which were observed as fighting behaviors between individual alligators within the captive congregation, were observed most often after a caretaker entered the enclosure. A caretaker's entrance always elicited multiple hisses from the alligators, as well as flushing behaviors. Human-induced behavioral changes have been observed in other captive reptiles, such as disruption in social hierarchical perching behaviors of black spiny-tailed iguanas (*Ctenosaura similis*) when humans are close and make eye contact with the iguanas [21]. In the wild congregation, hissing was not observed in response to human presence. The typical response in the wild congregation was flushing and could occur in response to indirect human presence, such as loud speaking voices, humans walking in basking spots, aircrafts traveling overhead, and kayaks traveling through the sinkhole. Conversely, indirect human presence outside of the enclosure was not an observable agitator in the captive site. When humans entered the enclosure there was a more pronounced disturbance to the captive congregation's behavior compared to the wild congregation's reaction to humans. The differences in response to humans could in part be related to proximity between humans and alligators. At the wild site, the distance between human observers and individual alligators was more variable than the captive site. In rare instances, visitors were observed violating park rules to get in close proximity to the wild alligator congregation, at times standing or kneeling within one or two meters of an alligator. In contrast, the captive site had a large barrier that kept tour groups at least three meters from the alligators, maintaining a predictable distance between the guests and the alligators. Both the wild and captive congregations responded to human disturbance when basking by flushing. Alligators are more vulnerable on land, therefore flushing into the water is prudent when disturbed [22]. The consistent presentation of flushing across

context when disturbed suggests flushing may be a flight-based species-specific defense reaction to disturbance [23].

Flushing in response to anthropogenic disturbance interrupts basking, which is essential for an alligator to maintain proper homeostatic internal body temperature and the elevated body temperature common to reptiles [24,25]. The maintenance of elevated body temperature during basking hours in reptiles has multiple benefits for the health of individuals, including the performance of typical behaviors and the continuation of normal species-specific growth patterns [22]. The performance of a flushing behavior displaces an individual for a period of time and can therefore negatively impact the individual's energy budget, placing limitations on the performance of other activities [22]. Interruptions to basking behaviors also cause interruptions to the non-rapid eye movement stages of sleep in alligators, [24]. Behaviors like basking are commonly influenced by temperature in crocodilians and indeed we observed a positive correlation between the frequency of behavioral events and temperature at the captive site (Figure 8) [25,26]. Human presence had a more pronounced effect on the frequency of behaviors performed within the captive congregation (Figure 8).

Measuring behavioral differences between wild and captive congregations is only one potential measure of captive animal welfare and should be interpreted with caution [7]. We identified differences between behavior of captive and wild alligators, but welfare requires multiple indices to build a robust picture [27–29]. Ideally, both physiological and behavioral measures should be used, such as cortisol levels, autonomic response, circadian patterns, changes in behavioral repertoire, and stereotypies [30]. We suggest the diminished frequency of social behaviors, impoverished social behavior repertoire, and pronounced occurrence of stereotypies in the captive congregation likely represents compromised welfare. Further study of alligator welfare in captivity is warranted and should consider, in particular, incorporating physiological measurements, non-winter seasons, different congregation densities, and tracking individual differences in behavior.

Concern for reptile welfare in zoos has been growing and includes developing methods to improve welfare [31–33]. One avenue for improving animal welfare is enrichment, such as changes to habitat structure, adding olfactory cues, active food searches, and behavioral training for cognitive stimulation [33–36]. Enrichment methods can decrease stereotypies in captive animals and should be evaluated for improving captive alligator welfare [37,38]. In a study regarding the behavior of captive green sea turtles, researchers discovered that general behaviors impact social behaviors [39]. Food enrichment decreased aggressive behavior displayed and significantly reduced the number of bite wounds inflicted by tank mates [39]. The findings of that study indicate that a change in the general behaviors performed, such as artificially simulated food foraging behavior, by captive reptiles can have a connective relationship with social behaviors performed towards one another [39].

Animal welfare is an important consideration when keeping animals in captivity and care should be taken to assess their welfare and develop species-specific solutions to address deficits [29,36,40]. For example, in the case of American alligators, which display patterns of travel in a natural environment, it is essential to maximize space for the performance of natural locomotive behavior [20].

Despite concerns regarding the welfare of alligators in certain captive environments, there are numerous benefits of captive care of alligators. First, captive environments provide an alternative to euthanizing or relocating nuisance alligators that have come in conflict with humans [41]. Relocation of the alligators is not always successful at resolving the conflict because of the tendency of relocated alligators to travel back to original capture sites [42]. Captive alligators which are kept by private owners and surrendered can also be provided with a living environment if they are unable to be released when habituated to or raised in a captive environment [41]. Second, alligators in captivity provide unique opportunities for scientific research that are not feasible with wild populations. For example, captive research of alligators led to the discovery of a new species of mycoplasma bacteria that causes high mortality rates, and an antibacterial treatment was developed [43]. Third,

alligators in captivity offer excellent educational opportunities. Education on wildlife conservation is very commonly taught to the public in zoos and aquariums, with particular programs increasing awareness, avoidance of harmful behaviors towards animal species conservation, and supportive behaviors towards species conservation [44]. Hands-on educational intervention in conservation-related education within zoos and related institutions have been found to retain information learned after an initial educational experience [45,46]. Frequent visitation to zoos increases visitor attitudes, perceptions, and subsequent actions towards the conservation of animal species [47]. Learning experiences from educational intervention on species conservation continue to influence some individuals after the initial lesson [46].

5. Conclusions

Captive alligators, at our study site, displayed fewer social behaviors than wild alligators and wild alligators displayed more variety in social behaviors. These differences may occur because of a range of factors, such as differences in stocking density, enclosure structure and size, human proximity and variation in human behavior, and behavioral variation in individual alligators. Captive alligators also exhibit high-walking stereotypy behaviors that may indicate compromised welfare and warrant consideration of enrichment methods to improve welfare. Building on our behavioral findings in the future by incorporating physiological measures will provide a more complete picture of alligator welfare in captivity.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jzbg3010011/s1>, Table S1: Social behavior ethogram; Table S2: General behavior ethogram.

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