Research on Species Distribution and Population Dynamics of the Reintroduced Chinese Alligators in Chongming Dongtan, Shanghai

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Executive Summary

The Chinese alligator is a critically endangered species that is endemic to China, with fewer than 200 individuals in the wild and over 13,000 in captivity. Reintroduction is crucial to restore its wild population, and Dongtan Wetland Park (DWP) in Shanghai is one of the reintroduction sites. However, the population size and viability were unclear due to inconsistent post-monitoring and lack of program evaluation. No further introduction or management plans were devised. Current literature also had little quantitative research on Chinese alligator habitat selection.

To understand DWP population status, this study first conducted population surveys using spotlight count. N-mixture models were employed to estimate the population size, and an average size of 54 individuals was calculated. Then, we examined the impact of environmental factors on Chinese alligator habitat selection in DWP by conducting habitat surveys and applied species distribution models. Finally, this paper used the software Vortex to identify factors influencing population growth and simulate population development. Vortex is commonly used for population viability analysis and has been used on crocodilian species.

We discovered that high vegetation coverage and a moderate presence of trees had a positive impact on alligator presence, while high mortality rates, low percentage of females breeding, and the percentage of males at birth exceeding 50% could severely hinder population growth. The viability analysis showed that the population is viable, and reintroduction may not be needed in the short term. Finally, we recommended that the park should construct more proper habitat with riparian cover and elevated ground for nesting females. Systematic and consistent monitoring should be established in DWP to provide long-term data. If monitoring shows low recruitment rates, reintroducing alligators from diverse genetic lineages should be considered.

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1. Introduction

The Chinese alligator (*Alligator sinensis*) is a species endemic to China that is listed as critically endangered by the International Union for Conservation of Nature (IUCN) and is classified as a national first-class protected species in China. This species is estimated to have a wild population of fewer than 200 individuals (Maqsood & Rong, 2019). Historically, the species was widely distributed along the lower Yangtze River. However, the wild population has sharply decreased since 1950s, mainly due to habitat loss, natural disasters, environmental pollution, and hunting (Ding & Wang, 2004). Currently, most of the remaining population in Anhui province live in fragmented habitats and are located close to human residences. Inbreeding depression and habitat loss remain as major threats to the wild population (Ding & Wang, 2004).

To protect Chinese alligators, captive breeding programs have been initiated since 1979 and have been highly successful (Jiang et al., 2006). The captive breeding programs have resulted in over 13,000 Chinese alligators currently in captive breeding sites (Maqsood & Rong, 2019). This large stock of captive-bred individuals enables the reintroduction of Chinese alligators, which is crucial for restoring the wild populations.

Chongming is the world's largest alluvial island (Thorbjarnarson & Wang, 2010) located in eastern China and within the municipality of Shanghai. The levees around the island have created non-tidal freshwater habitats that are suitable for Chinese alligators, and the island has the potential to hold one of the largest alligator populations in China (Thorbjarnarson & Wang, 2010). One reintroduction site, the Dongtan Wetland Park (DWP), is located at the eastern tip of Chongming Island. Six Chinese alligators were reintroduced in 2007 and another six in 2015. Nine of them survived and successfully reproduced in the park. However, consistent monitoring and evaluation to assess the effectiveness of the reintroduction in Dongtan have been lacking. While the two cohorts released in 2007 and 2015 were fitted with VHF radio transmitters, post-release monitoring stopped in 2009 and 2015 after the batteries ran out, and the transmitters detached from the alligators (Lv et al., unpublished). Systematic population surveys were conducted in 2014, 2015, and 2021. Other records were occasional sightings by park staff (Lv et al., unpublished). In 2021, a population survey was conducted in DWP, and 17 alligators were observed during the survey, including 8 adults, 1 subadult, and 8 juveniles (Lv et al., unpublished). The survey assumed a 60-70% detection probability according to literature and estimated there were 24-28 alligators in the park. (Lv, 2021). However, there was no previous research suggesting such a high detection probability in DWP, and detection probability of crocodilian species can vary from 17% to around 70% (Bayliss et al., 1986; Hutton et al., 1989; Balaguera-Reina et al., 2018; Cartagena-Otalvaro et al., 2020; Balaguera-Reina et al., 2021; Barao-Nobrega et al., 2022). Therefore, the 60-70% detection probability may not be applicable in DWP, and the estimate may not be accurate. Thus, there is a need to further evaluate the population viability and update the population size estimate.

Habitat restoration is essential for the success of the reintroduction, since Chinese alligator populations are most affected by habitat fragmentation and degradation, geographic separation, and pollution. (Maqsood & Rong, 2019). However, there is limited quantitative research on the habitat preferences of the Chinese alligator. Previous studies on habitat selection have largely focused on breeding sites (Wang et al., 2021; Wang et al., 2021; Zhang et al., 2006). In an extensive population survey conducted in Anhui province from 1999 to 2000, alligator habitats were classified into three categories: relict wetlands in valleys along principal river courses, ponds in tributary hill valleys, and artificial ponds (Thorbjarnarson & Wang, 2010). However, the survey did not further quantify the effects of environmental factors on habitat selection. One study has used a resource selection function to evaluate the relative importance of different environment variables (Wu et al., 2005). The study found that the shelter condition of banks had the greatest influence on habitat selection, while the presence or absence of islands and vegetation type had the smallest effects (Wu et al., 2005). However, the study relied on questionnaires with local villagers for presence and absence data, without conducting an extensive search or collecting precise location data. Additionally, the effects of roads and water depth may be important and yet not included in the study. Studies have shown that crocodiles are less abundant where human disturbance and road density are high (González-Trujillo et al., 2014; Yadav et al., 2022). Alligators require different water depths for activities. Young alligators need shallow water to hunt, and adult alligators prefer deeper water for breeding (Newsom & Howard, 1987). However, habitat suitability may decrease if water is too deep (Newsom & Howard, 1987). Therefore, further research is needed to better understand the habitat preferences of the Chinese alligator and the environmental factors that influence its habitat selection.

In this paper, we aim to answer the following questions: (1) What is the current distribution and size of the DWP population? (2) What are the most important factors influencing population growth, and how will the population change in the future? (3) What are the environmental factors that influence Chinese alligator habitat preference? To accomplish these objectives, we conducted population and habitat surveys throughout Dongtan Wetland Park. With N-mixture models we estimated the population size, accounting for detection probability. Furthermore, we utilized Vortex software to model DWP population development and analyze how the population changes with different reintroduction strategies. Generalized linear models (GLMs) were applied to analyze their habitat preferences. This research can enhance our understanding of Chinese alligator habitat preference and provide scientific evidence for future management and reintroduction in Dongtan Wetland Park.

2. Methodology

2.1 Study Sites

Dongtan Wetland Park is a man-made freshwater wetland located at the eastern tip of Chongming Island, the world's largest alluvial island at the mouth of the Yangtze River, covering 181 ha (Figure 1). The park is a popular public recreational area for hiking, cycling, and camping, featuring trails that reach most parts of the park. Ponds and canals extend throughout the park, some of which are surrounded by heavily managed landscapes such as artificial turfs and ornamental plantings, while others are in marshy areas that are not accessible to tourists. The freshwater in the park is controlled by a levee system around the island, with the water level remaining relatively stable, ranging from around 50 cm to 300 cm. The common reed (*Phragmites australis*) is the dominant species in the park and is often observed with cogon grass (*Imperata cylindrica*) along the banks. An invasive species, Canada goldenrod (*Solidago canadensis*), has recently occupied many areas in the park and has been used by alligators as nesting materials. To ensure an abundant food source for Chinese alligators, the park released a large number of snails, crabs, and fish as prey items for the alligators several times from 2015 to 2021(Yu, 2015; personal communication). The prey items existing in the park include crabs (*Eriocheir sinensis, Metaplax longipes*), aquatic insects, snails (*Bullacta exarata*), mollusks (*Moerella iribescens, Sinonovacula constricta*), shrimps (*Macrobrachium nipponense*), frogs, and snakes (Thorbjarnarson & Wang, 2010).

2.2 Species Distribution

2.2.1 Population Survey

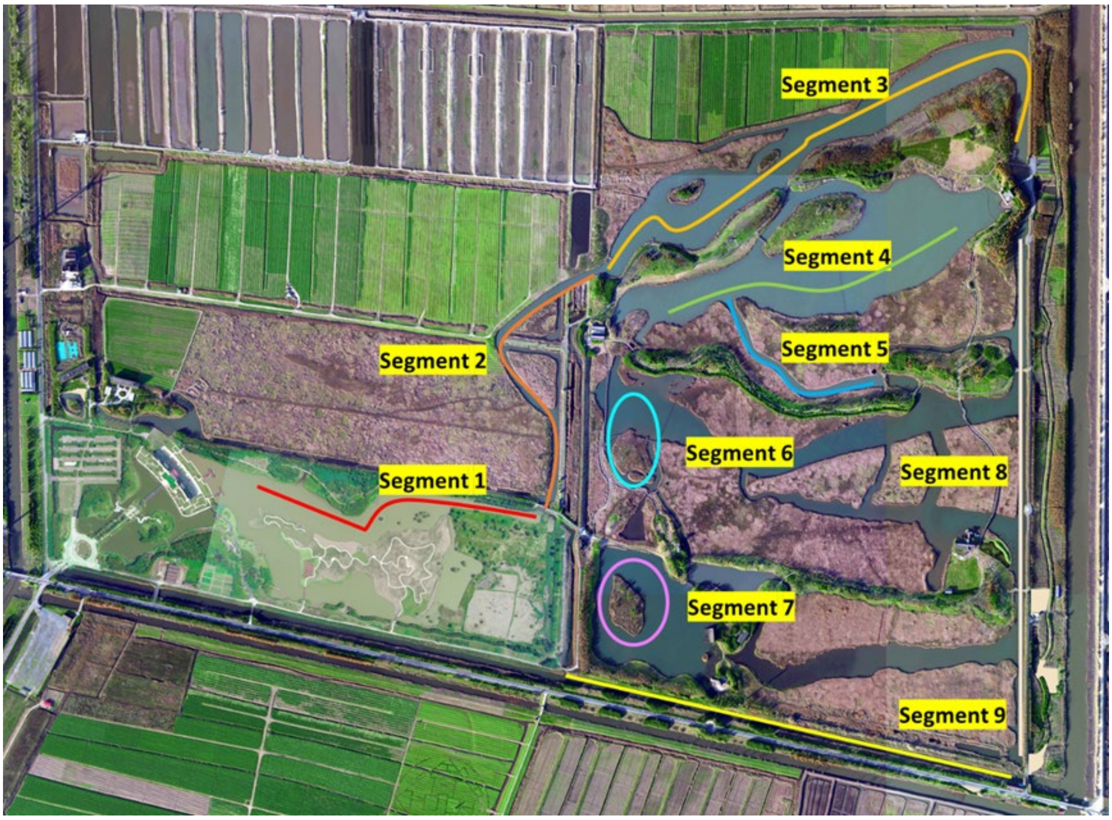


Figure 1. The segments where the surveys were conducted.

Spotlight counts and transect surveys were conducted in the 2022 summer (25-27 July and 5-7 August) to determine the number of alligators and their distribution in the park. We carried out 5 daytime transect surveys and 6 spotlight counts at night. As shown in Figure 1, we divided the park into 9 segments based on their connectivity and characteristics. Each segment was surveyed at least three times during the whole survey period, except for segment 5, which was only surveyed twice. Segment 6 was a fenced area and the reintroduction spot in 2015. Six alligators were released into the area for transition but many of them have escaped and dispersed into other areas of the park. During the day, we walked along the transects in DWP and used binoculars to look for alligators. We conducted both pedestrian and waterway searches in the nocturnal spotlight counts. We had multiple groups searching at the same time to reduce double-counting. One group walked along the trails and another one or two groups of people used an electric boat and kayaks to search for the reflective eye-shines through the DWP waterways. The alligators were classified into different age groups based on their total length (TL): adult (TL > 120 cm), subadult (TL = 101-120 cm), and juveniles (TL < 101 cm) (Lv et al., unpublished). When we observed an alligator, we tried to get as close as possible to identify their age group and location.

Drones and direct searches were conducted to find alligator nests. During mating season, female alligators use surrounding plants to make a nest mount, which is usually visible from the air. We utilized drones to look for alligator nests throughout the park. Potential nests were identified and verified by conducting a field inspection. We opened the nest and checked the presence of eggs. Subsequently, cameras were installed near the nests to observe and monitor breeding activities.

2.2.2 Habitat Survey

We conducted plant surveys across the park. We placed a total of 61 5m-by-5m plots near where the alligators were present and absent. Within each 5m plot, we created a 1m-by-1m subplot to survey the understory species. For each sub-plot, we selected three plants, reed, Canada goldenrod, and cogon grass to measure their coverage and abundance. These three species were most common in the park, and there were concerns from the park staff about whether the presence of Canada goldenrods, an invasive species, would affect the Chinese alligators. We also recorded the coverage of other grass and shrub species. We then chose three individuals representing the average condition of each species and measured their heights. We recorded the presence of trees and classified the abundance into four categories within a 20-meter radius from the center of the 5m plot. If there were no trees within 20 meters, then we gave it an index of 0. We then labeled 0-1 trees 1, 3-6 trees as 2, and >6 trees as 3. We also measured the water depth, pH, and salinity across the park. For each plant sample point, a 100m buffer was created, and the water depths measured within the buffer were averaged for that point. The waterway width and the distance from the sample to the roads were measured using Google Earth. The height from land to water is also considered a crucial factor because Chinese alligators create tunnels for their survival, especially in winter, which requires a certain height from the water surface (Thorbjarnarson & Wang, 2010). We measured the height from the survey point to the water surface using a range finder.

2.2.3 Data Analysis

Generalized linear models (GLM) were applied in R to analyze the relationship between environmental factors and alligator presence and absence. We first examine the correlation between all the variables. For variables that have a correlation above 0.7, we tested different combinations and used AIC as criteria to find the best variables to include in the model. Then, the forward, backward, and both direction stepwise regressions were employed to find the best model.

2.3 Population Estimation

To estimate the population size, we applied the N-mixture models (Royle, 2004). The N-mixture model was first proposed to estimate population size for spatially and temporally repeated surveys, accounting for imperfect detection. It has already been used in several studies to estimate Crocodilian population size from spotlight counts (Cartagena-Otalvaro et al., 2020; Balaguera-Reina et al., 2021; Barao-Nobrega et al., 2022). The method assumes that the number of individuals we observed at each site and sampling time follows a binomial distribution and was determined by the actual population and detection probability. The actual population is assumed to follow a prior distribution, for example, the Poisson distribution which assumes that the animals distribute randomly in space (Royle, 2004). However, the assumption may not be valid in some cases. Other prior distributions, such as negative binomial distribution and zero-inflated Poisson distribution have also been used (Cartagena-Otalvaro et al., 2020; Balaguera-Reina et al., 2021; Barao-Nobrega et al., 2022). Detection probability and abundance can also be modeled from environmental covariates (Royle, 2004).

We used the pcount() function from the “unmarked” R package to conduct the analysis. Due to the small sample size of the count data, we only included one or two variables each time for detection and abundance covariates, respectively. Though vegetation coverage and water depth are two widely used variables in many N-mixture models for crocodilian population estimation and proven to affect detection probability or abundance (Yadav et al., 2022; Cartagena-Otálvaro et al., 2020; Barao-Nobrega et al., 2022; Bayliss et al., 1986), the vegetation cover and water depth are relatively homogenous on the segment scale in DWP, therefore, they were excluded from the analysis. We chose one variable, the waterway width, for the detection probability (Yadav et al., 2022; Bayliss et al., 1986), and three variables, the waterway width, the height to water, and water area, as abundance covariates. The height to water was categorized into low, medium, and high levels. Table 1. Shows the models we used.

Table 1. The models used for Poisson and Zero-inflated Poisson distributions.

Models	Observation	Abundance
Null	~1	~1
Model1	water width	water area + water width
Model2	water width	height to water + water width
Model3	water width	water area + height to water
Model4	water width	water width
Model5	water width	water area
Model6	water width	height to water
Model7	~1	water area + water width
Model8	~1	height to water + water width
Model9	~1	water area + height to water
Model10	~1	water width
Model11	~1	water area
Model12	~1	height to water
Model13	w_width	~1

Based on the distribution of the count data collected, we utilized both Poisson (P) and Zero-inflated Poisson (ZIP) as prior distributions and compared the AIC within each distribution. All models with least AIC and a delta AIC less than 2 were selected to predict the total population size. To determine the parameter K, the maximum count of each site, we first calculated the carrying capacity of DWP. In previous studies on the wild Chinese alligator population in Anhui province, an average density of 1.535 alligators per hectare was estimated (Ding et al., 2001; Thorbjarnarson & Wang, 2010). The area of DWP is 181 ha, and therefore we assumed the carrying capacity to be 278. Then based on the different sizes, we calculated the carrying capacity of each segment and used the medium value, 17, as the parameter K in the models. Finally, we used the predict() function to estimate the abundance for each segment and sum them up to calculate the total abundance of the park.

2.4 Population Modeling

The software Vortex was employed to predict the DWP population growth and investigate influencing factors. We conducted literature review and also included unpublished past DWP population surveys to obtained parameter values on Chinese alligators. However, due to the discontinuity of these population surveys, there are still many parameters on which we could not obtain accurate data. These parameter values were extrapolated from other crocodilian species and then on which we conducted a sensitivity analysis.

2.4.1 Basic scenario

The modeling time is set to 100 years according to Chaves et al., 2016 and Brook et al., 2002, and each model will be run 1000 times. Because 9 of the 12 reintroduced alligators survived, if the population size is less than 9, then the reintroduction is considered a failure. So, when the number of individuals declines below 9, the population was defined as extinct in our analysis.

2.4.2 Inbreeding depression

Inbreeding depression could be a threatening factor for Chinese alligators, given their habitats are highly fragmented and the isolated populations are usually very small (Thorbjarnarson et al., 2002). Though studies have shown that inbreeding between Chinese alligators can cause lower fertility and a higher rate of malformation (Ding et al., 2001; Ding et al., 2004; Wu et al., 1999; Wu et al., 2006), no research has investigated the lethal equivalents. We used a value of 5 for lethal equivalents, which was extrapolated from the American alligator, the closest relative to the Chinese alligator (Brook et al., 2002).

2.4.3 Reproduction

The mating system of Chinese alligator is polygynous (Thorbjarnarson & Wang, 2010). According to Chen (2003), male alligators reach sexual maturity between 5 and 6 years old and females 6~7 years old in captivity. The assumption is that they may not have the chance to reproduce in the first year of maturity (Chen, 2003). Therefore, we assumed that for DWP population, males first reproduced at 7 years old and females at 8 years old. The Chinese alligator can live up to 60 years and reproduce in the fifties in captivity (Thorbjarnarson & Wang, 2010). From previous surveys conducted in DWP, the largest known nest consisted of 32 eggs. Assuming a viability of 85%, then the maximum number of hatchlings per brood would be 27 (Lv et al., unpublished). The sex ratio of wild Chinese alligators was observed to be 4.5:1 in the wild (Zhao et al., 2013). So, in the model, we assumed that 20% of the hatchlings were males.

2.4.4 Catastrophes

Based on the records of DWP from 2008 to 2016, one flooding occurred in 2016 and submerged 2 of the 3 nests. One extreme low-temperature event occurred in 2014 and led to clutch failure. We assumed that the frequency of both flood and low temperature was 11%. A flood event would lead to a 67% clutch failure rate of all nests and reduced the survival rates to 95% of the normal rates (Wu, 2004). In case of a low-temperature event, all nests were assumed to fail. No data was found on the impacts of low temperatures on Chinese alligator survival rates, so we assumed it to be the same as the flooding events.

2.4.5 Carrying capacity

The carrying capacity of DWP was estimated from the population surveys conducted in Anhui province in 1999 and 2000. The 1999 survey produced a density of 1.28 alligators per ha. And the 2000 survey produced a new density of 1.79/ha (Ding et al., 2001). We took the average and used 1.535/ha for the baseline model. So, the DWP was estimated to have a carrying capacity of 278 alligators.

2.4.6 Mortality rates

The discontinuous survey in DWP almost made it impossible to estimate the mortality rates for each age. We collected mortality data from past DWP surveys and various literature on crocodilian population viability analysis using Vortex, for Chinese alligators and other species (Wu, 2004; Chaves et al., 2016; Brook et al., 2002). In an unpublished DWP population paper, a population survey was conducted in 2014 during which the researchers discovered 2 subadults and 4 large juveniles. These alligators were presumed to be born in 2008 and 2012 because reproduction was observed during these years. Assuming 48 eggs hatched during the two nesting events, then the survival rate would be 12.5% (Lv et al., unpublished). Because the cohort from 2012 would be 2 years old, and the cohort from 2008 would be 6 years old in 2014. We took the average and assumed the survival rate from age 0 to age 4 is 12.5%. In our 2022 summer survey, we observed 3 juveniles that were born last year. Assuming the nest has an average of 24 hatchlings, then the mortality of the first-year juvenile would be 87.5%. Another Chinese alligator Vortex modeling derived its mortality rates from the conclusion of Webb's book, *Australian Crocodiles*, that only 1% of the freshwater and saltwater crocodilian hatchlings can survive to adulthood in the wild (Wu, 2004; Li et al., 1996). However, these mortality rates may be problematic when applied to the scenarios in Dongtan Wetland Park. To choose the proper mortality for the base model, we modeled the population using from 2007 to 2022 different mortality rates from the literature and surveys. Thus, we could identify the best mortality rate that could lead to the most accurate estimate of population size observed in 2022. Table 3 lists the 5 mortality rates we used. M1 was the mortality rates used in Wu 2004. M2 was based on the DWP survey in 2014 which assumed the survival rate from age 0 to age 4 is 12.5%. The mortality after age 4 in M2 is same to that in M1. The mortality of age 0~1 in M3 was the average of M1, M2, and our 2022 summer survey. The rest of M3 was the average of M1 and M2. M4 was calculated by averaging M3 and the mortality of American alligator from Brook et al., 2002. Finally, we mixed different mortality rates in M5 and assumed the mortality of adults was as low as 3% (Brook et al., 2002).

2.4.7 Initial population size

To be conservative, the initial population size was based on the number of individuals observed during our survey in 2022, which was 21 individuals. The juveniles were all assumed to be from last year's nests. The subadults found may range from 3 to 5 years old, because no reproduction monitoring was conducted from 2017 to 2020, some nests may not be detected. Three of the adults were likely to be the surviving individuals of the 2007 reintroduction, and six were from 2015. The rest of the adults observed were presumed to be from the 2008, 2012, and 2016 nests. A 4:1 sex ratio was assumed for unknown individuals.

2.4.8 Future reintroduction scenarios

We modeled different reintroduction scenarios to find the best reintroduction strategies. The assumption is that we will introduce a large number of alligators in one single event. As the population grows, the alligators will disperse into the nearby bird reserve and canals on the island. The bird reserve next to DWP has different sections. The sections adjacent to the park consist of 509 ha. Therefore, the carrying capacity in the park and nearby bird reserve was set to 1000 for reintroduction scenarios. We modeled three events of introducing 10, 30, and 50 individuals at year 5, respectively. The age was set to 5 to 6 years old, with a sex ratio of 4:1.

2.4.9 Software and parameters selection

Vortex is a widely used population modeling software and has been used on different crocodilian species, including the Chinese alligator (Chaves et al., 2016, Wu, 2004). In a study comparing different population viability analysis software, the authors found the predictions were highly concordant (Brook et al., 2000). Vortex also allows individual-based models, which can include inbreeding depression in the analysis. While some other software such as INMAT, RAMAS/Metapop, and RAMAS/Stage are matrix-based programs that are not able to consider such effects (Bach et al., 2009). Since multiple studies have demonstrated that inbreeding depression is a potential threat to the Chinese alligator population and could lead to lower fertility and higher malformation, we chose Vortex for our analysis (Ding et al., 2001; Ding et al., 2004; Wu et al., 1999).

3. Results

3.1 Population Survey

We had a total of 45 sightings of the alligators and 3 nests during our survey. Some alligators were repeatedly observed at the same location over different survey occasions.

Segments 2 and 8 had the most stable presence of alligators. We found alligators in almost every survey around the same spot. Two adult females occupied segment 2 where they chose to nest this summer. At least three hatchlings from last year were confirmed in this area. Though segment 1 and segment 3 were connected to segment 2, no alligators were found in these canals. Two adults were observed only in one of the three survey nights at the eastern end of segment 9. But the closely located channel (segment 8), at the eastern edge of the park, had the most stable population with at least two adults. A maximum of 5 individuals were observed at segment 8, with two of them classified as subadults. One nest and a guarding female were found here this summer. Two adults were sighted repeatedly on two survey nights at segment 5, and a subadult was found in segment 4 during one of the survey nights. Based on their usual appearance location, we estimated there were around 20 to 22 individuals observed in this summer survey, including 3 juveniles, 4 subadults, and 13 ~ 15 adults. And the three nests all successfully hatched by September.

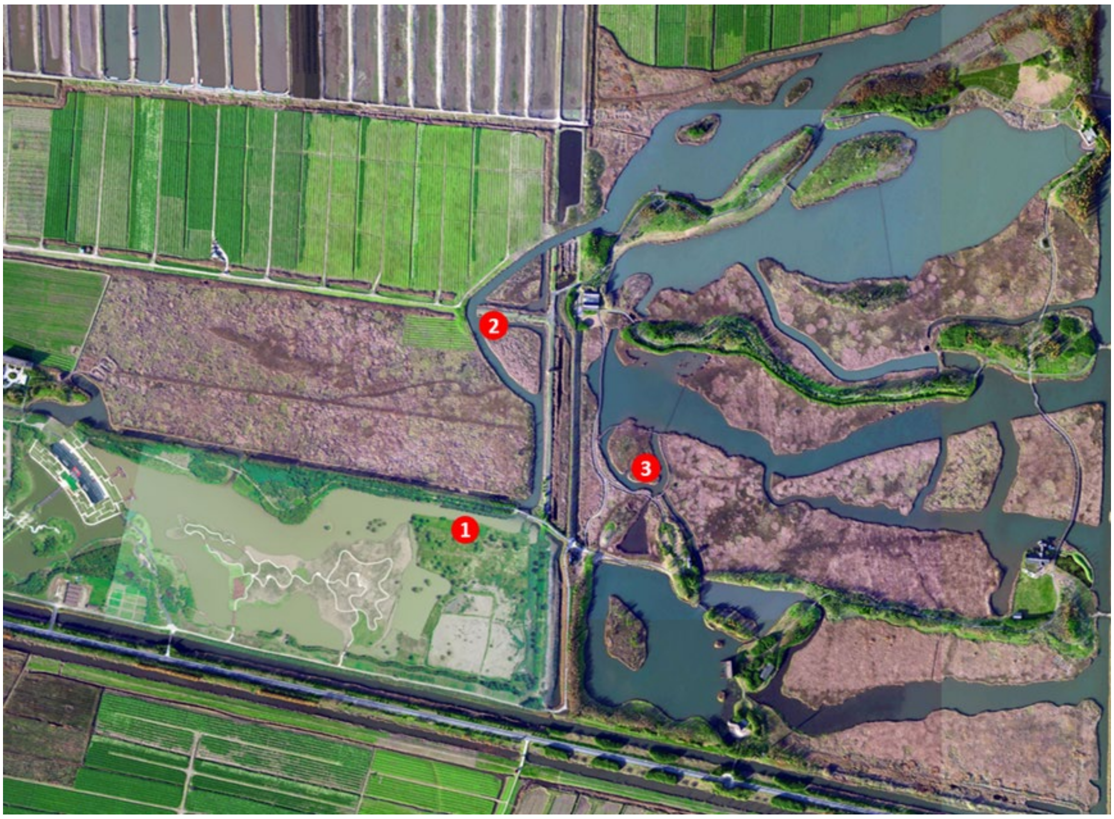


Figure 2. Locations of the three nests.

Nest 1 was the first nest constructed in this location, while the other two nesting locations had been used in previous years. Two of the nests (nest 2 and 3) were mostly made of Canada goldenrods, and Nest 1 was mostly made of reeds. The two goldenrod nests were smaller than the reed nest, with a mean diameter and height of 115cm and 20cm, while the reed nest had a diameter of 134cm and a height of 38cm. We found eggs in the goldenrod nests but not in the reed nests, however, a following visit in September found eggshells around the nest, revealing that it was an active nest and produced hatchlings.

3.2 Species Distribution

Figure 3 shows the differences between environmental factors where alligators were present and absent. Our analysis revealed that the coverage of the three wetland plants (reed, Canada goldenrod, and cogon grass) and a moderate tree abundance had a positive effect on Chinese alligator presence. The likelihood of alligator presence increased as plant coverage increased ($p = 0.00578$). When 1-3 trees were present within 20 meters of a sample plot, the possibility of alligator presence also increased significantly compared to when the trees were absent ($p = 0.00408$). Although the effect of 4-6 trees remained positive, it was not statistically significant ($p = 0.07768$), and the coefficient for more than 6 trees was smaller and not significant ($p = 0.22920$). Interestingly, we found that the percentage of reed and the total density of the three wetland plants were negatively associated with alligator presence ($p = 0.006$ and $p = 0.01967$, respectively), indicating that the Chinese alligators were less likely to be present in areas with high weed percentage or vegetation density. These findings seem to contradict our previous result on the positive relationship between alligator presence and plant coverage, but it is possible that the type of vegetation or other factors may be responsible for these differences, which will be discussed in detail. Finally, although height to water and water depth was thought to be important predictors, our analysis did not find a significant relationship between these variables and alligator presence ($p = 0.11807$ for water height, $p = 0.133$ for water depth).

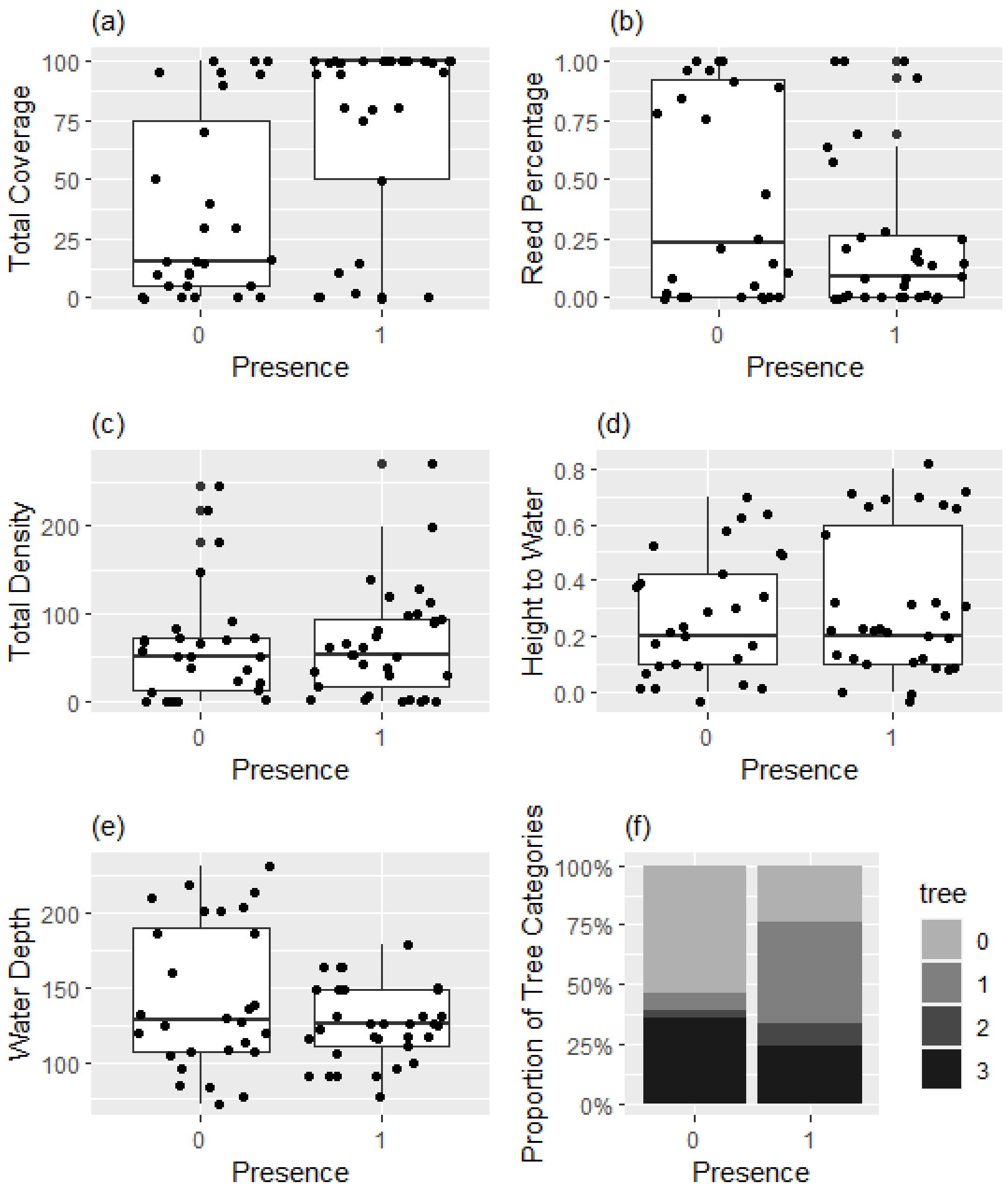


Figure 3. Environmental factors where alligators were present and absent. (a) shows the positive relationship between plant coverage and alligator presence. Reed percentage (b) and total density (c) had a negative relationship with alligator presence. The relationship of height to water (d) and water depth € with alligator presence was not significant. (f) shows the proportion of different tree categories within presence and absence groups.

3.3 Population Estimation

The N-mixture models produced six best-fitting models as shown in Table 2. The models showed that waterway width had a negative effect on detection probability and a positive effect on abundance at each segment. From each model, the average abundance at each segment were estimated, ranging from 5.8 to 6.4 (Table 2). The population size of the park calculated by the models ranged from 52.2 to 57.6 (Table 2). Then, we took the average of all the models and calculated 54 individuals for the DWP population size.

Table 2. The best model summaries for population estimation. The covariates are listed for detection (det) and abundance (abun). A mean abundance at each segment was calculated for each model. Population is the total population size of the park.

Model	Distribution	AIC	Coefficient	*p*	Mean (SE)	Population
det(water width), abun(~1)	Poisson	90.48	-0.026	0.0274	5.799 (3.916)	52.1876
det(~1), abun(water width)	Poisson	91.4	-0.0198	0.0404	6.398 (3.116)	52.1876
det(water width), abun(water width)	Poisson	92.47	-0.0281 0.00203	0.374 0.9426	5.964 (5.755)	53.67212
det(water width), abun(~1)	ZIP	90.48	-0.026	0.0274	5.799 (3.916)	52.1876
det(~1), abun(water width)	ZIP	91.4	-0.0198	0.0404	6.398 (3.116)	57.58642
det(water width), abun(water width)	ZIP	92.47	-0.0281 0.00203	0.374 0.9426	5.964 (5.755)	53.67212

3.4 Population Modeling

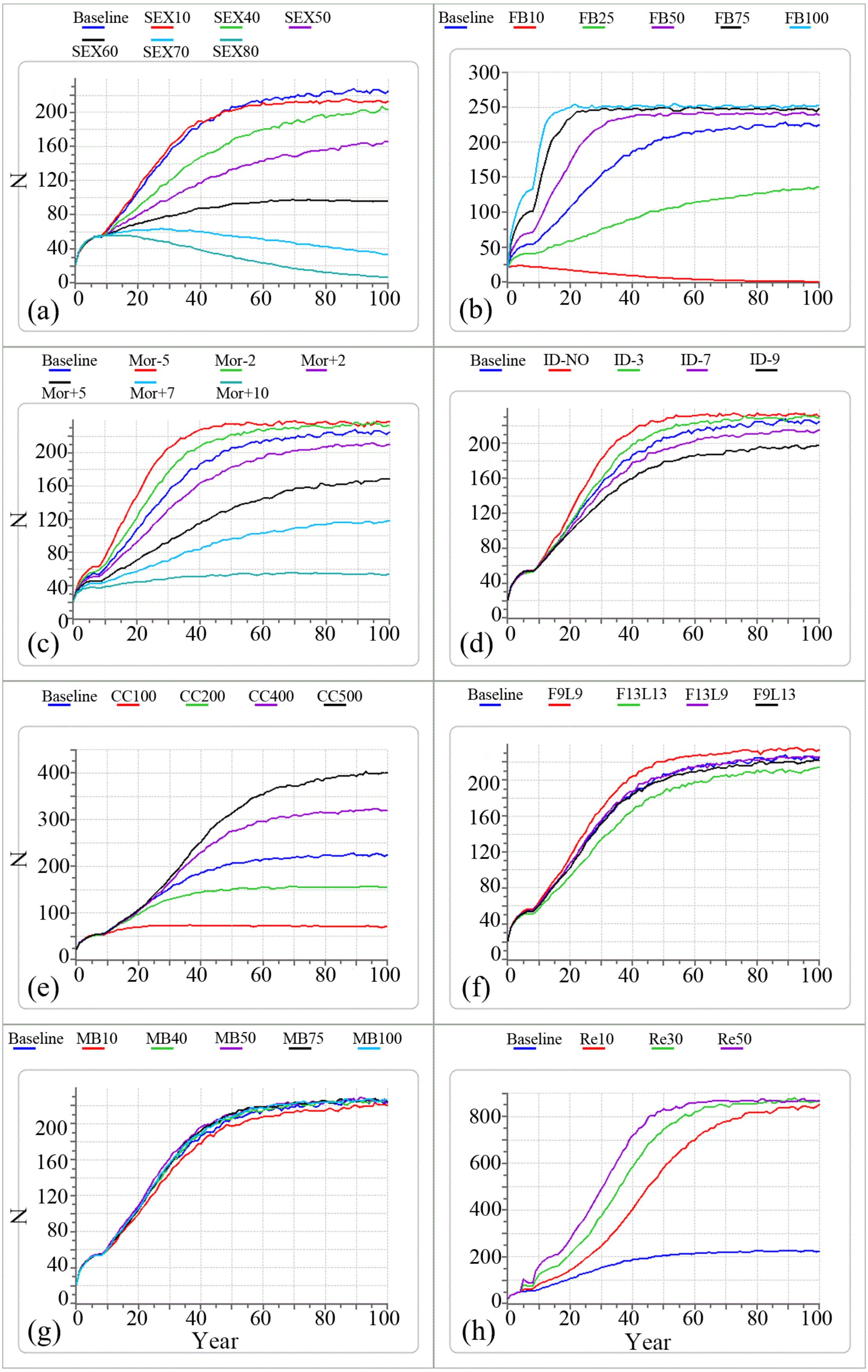
We tested 5 different sets of mortality rates, collected and averaged from past surveys and literature (Wu, 2004; Lv et al., unpublished; Brook et al., 2002; Chaves et al., 2016). Table 3. shows the mortality rates and the predicted population sizes of the models in 2022. We chose the mortality from M4 as the mortality rate for our baseline model, with an averaged population size of 23, similar to our observation.

Table 3. The different sets of mortality (M1~M5) for each age used to stimulate the population growth from 2007 to 2022. The 2022 population shows the resulting population size in 2022 of each mortality rate.

Age	M1	M2	M3	M4	M5
0~1	80	75	81	72	81
1~2	70	30	50	46	50
2~3	50	20	35	30	35
3~4	40	10	25	25	25
4~5	10	10	10	17.5	17.5
5~6	10	10	10	17.5	17.5
6~7	10	10	10	15	17.5
7~8	10	10	10	6.5	15
After 8	10	10	10	6.5	3
2022 Population	8.85	25.67	12.41	22.26	12.19

The parameter values of the baseline model and sensitivity analysis are listed in Appendix Table 1. The results of sensitivity analysis and reintroduction are shown in Figure 4 and Appendix Table 2. The baseline model showed that the DWP population would reach a population size of 225 in 100 years with an extinction probability of 1.4%. Inbreeding depression had limited effects on the population compared to the baseline model (Figure 4d). The model with the highest inbreeding depression setting, lethal equivalents of 9, only increased the extinction probability to 4.4%. Removing inbreeding depression from the model did not improve extinction risk nor population size.

Sex ratio at birth (the percentage of males at birth) and the percentage of females breeding had the greatest impact on population (Figure 4a, 4b, Appendix Table 2). The population size decreased to only 14 individuals as the percentage of males at birth increased from 20% to 90%, with an extinction risk of 98%. The baseline model, when 20% of the hatchlings were male, had the highest population size of 226 in 100 years compared to other sex ratios (Appendix Table 2). The extinction probability had a sharp increase when the percentage of males at birth exceeded 50%. The extinction risk for the percentages of males of 50%, 60%, 70%, and 80% were 4.4%, 14.6%, 40%, and 76.6%, respectively. The population size increased, and extinction risk decreased as more females participated in breeding activities. When there were more than 50% of the females participating in breeding, the extinction risk was close to zero. But when the percentage decreased to 25%, the extinction risk increased to 16.8%. And if that continues to decrease to 10%, the population will have an extinction probability as high as 98.5% (Appendix Table 2). Different from the percentage of females participating in breeding, the percentage of males breeding did not have much impact on population growth. All the scenarios, from 10% to 100% of males breeding all produced similar extinction probability around 2% (Figure 4g, Appendix Table 2).



Baseline SEX10 SEX40 SEX50
SEX60 SEX70 SEX80
N
(a)
Baseline FB10 FB25 FB50 FB75 FB100
(b)
Baseline Mor-5 Mor-2 Mor+2
Mor+5 Mor+7 Mor+10
N
(c)
Baseline ID-NO ID-3 ID-7 ID-9
(d)
Baseline CC100 CC200 CC400 CC500
N
(e)
Baseline F9L9 F13L13 F13L9 F9L13
(f)
Baseline MB10 MB40 MB50 MB75 MB100
N
Year
(g)
Baseline Re10 Re30 Re50
Year
(h)

Figure 4. Vortex modeling results. (a) shows the sex ratio at birth (male percentage). (b) is the percentage of females breeding (FB). (c) shows the different mortality rates (Mor). (d) is inbreeding depression (ID). (e) is carrying capacity (CC). Catastrophes (f) and the percentage of breeding males (MB, g) have limited impacts. The catastrophes include flooding (F) and low temperature (L) occurring at different frequencies. For instance, F9L13 means flooding and low temperature have a frequency of 9% and 13%, respectively. (h) shows the reintroduction (Re) compared to baseline.

The changes in carrying capacity (Figure 4e) and catastrophe frequency (Figure 4f) led to little changes in extinction probability. Though when carrying capacity was decreased to 100, and the population only have around 71 individuals, the extinction risk was only 3.9%. When the carrying capacity was 500, the population size would increase to 402. The catastrophes of flooding and low temperature did not influence the population much, though the extinction probability was slightly higher. It was 2.7%, when the frequency of low temperature events was 13%, compared to when the frequency of the flooding events was 13%, the extinction risk was 1.9% (Appendix Table 2).

While the decrease in mortality improved little extinction risk, the increase in mortality led to sharp decrease in population size (Figure 4c). When the mortality rates decreased by 5%, the extinction probability only improved from 1.4% to 1.3%, but with a 5% increase in mortality, the risk would increase to 10%. When the mortality increased by 7% and 10%, the extinction probabilities were 20.4% and 44.9%, respectively (Appendix Table 2).

Reintroducing 10, 30, and 50 Chinese alligators at year 5 would lead to similar outcomes (Figure 4h), around 865 population size and 0 extinction probability, in the 100-year timespan (Appendix Table 2).

4. Discussion

4.1 Population Survey

The population in the park consisted of at least 20 individuals in 2022, supported by our summer survey, and the total size was estimated to be around 54 alligators by the N-mixture model, including adults, subadults, and juveniles. Compared with past surveys and sightings, the adult population was relatively stable, but we were able to detect more subadults. The sightings of subadults have been lacking in the park. There could be two possible explanations. First is that the survival rate of juveniles is low, so there may just be very few subadults. Or maybe it is difficult to detect them due to their smaller size and secretive nature.

Using boats and kayaks has improved detection of alligators, especially in places less accessible by foot and in large water areas. We confirmed the presence of alligators in places previously thought with no alligators when we changed to boats. It suggests that despite our extensive search, there could still be undetected individuals, since Chinese alligators are shy and likes to hide in their tunnels. Meanwhile, there were a few waterways we could not access during the survey, where presence of alligators could be possible.

According to past nest survey records, it was the first time that three nests were discovered in one summer and all successfully hatched. We were concerned about the small goldenrod nest, because it might be harder for the females to chew the plants, might not provide enough insulation from the hot weather and lead to clutch failure. But the results indicate that no negative impacts from Canada goldenrod on reproduction as a nesting material.

4.2 Species Distribution

Our analysis shows that the high understory coverage and the moderate coverage of trees have positive effects on Chinese alligator presence. Other studies have also shown that high understory coverage can provide shelter and food availability for crocodilians (Wu et al., 2005; Cartagena-Otalvaro et al., 2020). A certain number of trees present is shown to be preferred by alligators. Possibly the trees provide more shade and canopy coverage. However, as the number of trees continues to increase, its effects are less and not significant. One possible explanation is that the roots may prevent the alligators from digging tunnels.

The percentage of reeds and total density of the three plants were found to be negatively associated with presence of alligators and both results were significant. The results seem counterintuitive since denser and more vegetation should provide more coverage. The reason may be that the total density is highly correlated with the density of cogon grass ($cor > 0.7$). However, the cogon grass in our survey were found to have very thin stems and tend to fall close to ground, providing little coverage. The reeds, though were outmatched in number, can provide more coverage than the cogon grass. The higher density of cogon grass may indicate high total density, but lower reed percentage, and therefore lower coverage, leading to less alligator presence. The absence of Canada goldenrod in the best model suggests that this species does not affect the presence of Chinese alligators.

The height from land to water surface has a positive but not significant relationship to alligator presence. Alligators usually require a certain height to build nests and dig tunnels, but our analysis did not specifically investigate their relationship, due to the small number of nests and the difficulty finding underground tunnels. The alligators could be present for other reasons, such as resting or hunting, leading to non-significant results. Water depth was also considered to impact alligators, because juveniles usually need shallow water to hunt, and deep water may hinder their activities, even for adults. The model did show a negative relationship, though not significant. This is probably due to the relatively homogenous water depth in the park, mostly ranging from around 100cm to 200cm. Only a few areas have a shallow depth around 70cm, and the deepest depth we measured is 268cm.

4.3 Population Estimation

One of the limitations of our population estimation was the small dataset which contained many not available values (NAs) since most of time we were not able to sample the all the waterways in one single night. This limited the number of variables we could add in our models. Dongtan Wetland Park is only 181 hectare and has a relatively homogenous environment, which also presented challenges when choosing covariates and their values to represent different segments. In future population estimations, different choices of segments and covariates may be tested. For instance, in our survey, we divided the northern route into segment 1, 2, and 3 because alligators were only found in segment 2 even though they are connected. It is possible that alligators prefer the narrower segment 2 canal or are too few to disperse into segment 1 and 3. However, the N-mixture model results indicate that alligators are present in these two segments but are not detected, which may lead to an overestimation of the population size. Segments 4 and 5 are determined based on their different water width, even though they are connected. The two adults we observed in this area seemed to stay at segment 4 for most of the time but occasionally move between these two segments. Therefore, future models may group segment 1, 2, and 3 into one segment and view segments 4 and 5 as one. There are also possible movements between segment 6 and 7. The detailed designation of the segments and potential movements between segments, possible but unlikely to be frequent during one survey season, could lead to an overestimation of the population size. Therefore, we advise caution when using 54 as the population size, rather, it seems more reasonable to view it as an upper bound for the DWP population. Future research may try to find a better way to separate the park into segments and conduct long-term consistent surveys.

4.4 Population Modeling

High male percentage at birth and low percentage of females breeding may lead to higher extinction risk. A decrease in the breeding female percentage may lead to fewer nesting activities, which is likely to hinder population growth as crocodilian species usually experience high mortality during hatchling and juvenile phases. If low recruitment is combined with high male percentage at birth, it will probably lead to further decrease in female numbers and reproduction activities. Nesting locations are also important for reproduction to success. Female alligators usually built nests close to water and on higher ground, so females can carry water to cool the nests and prevent flooding (Zhang et al., 2006; Thorbjarnarson et al., 2001; Wang et al., 2021a; Wang et al., 2021b). One of the three nests we discovered this year was 0.3 meters higher than water, and two other nests had a height to water around 0.6 meters. However, many marsh areas in the park have very low elevation. They are either inundated or only 10-20 centimeters above water, unsuitable for nest construction. Trials and roads are usually built on high ground. Though our species distribution model indicated that the distance to road didn't affect alligator presence, these high grounds may not be suitable for nesting because they could be easily accessible by visitors. As the population in DWP grows, the lack of breeding sites may be a limiting factor for breeding females. If the percentage of females participating in breeding is low, population may drop quickly or possibly become extinct, even when the mortality is not high. Understanding the sex ratio and the percentage of breeding females in the DWP population are essential. However, these two parameters are difficult to calculate because it is difficult to determine the sex of all alligators. Reproduction and nesting activities may serve as an indicator of population status, which is already used for some species such as American alligator (Chabreck, 1966; Platt, 2021). Now, with the deployment of drones in nest researching, it is much more efficient than researching the whole park by foot or boat.

Contrary to the percentage of females breeding, the percentage of males breeding has little effects on population growth, probably due to the polygynous mating system. Therefore, though we have no data on the percentage of males breeding in DWP, and there is great uncertainty in the value we used, it may not affect our results. Although the percentage of males breeding have little effects on population size, male density may be a more essential role in population growth. A study on captive Chinese alligator demonstrated that male density was more likely to constrain population growth rather than population density (Zhao et al., 2019). When the male density reached 83.14 individuals per hectare in captivity, the population growth stopped. It was recommended that male density best to be maintained around 40.5 per hectare (Zhao et al., 2019).

Inbreeding depression and catastrophes have some impacts on population, though it is not prominent. To our surprise, even under our highest inbreeding depression value, the extinction risk is close to zero, with only a small decrease in the population size. The results may be due to the low mortality values we applied in the model. As the population reaches a certain size, the effects of inbreeding depression may become weaker compared to smaller populations. However, it is not wise to dismiss the negative impacts of inbreeding depression under other circumstances. For example, inbreeding depression may have larger effects on population when mortality rates are higher or over a longer time, for instance, in 200 years.

Similar to inbreeding depression, catastrophes have limited impacts on DWP population. However, we only considered events that happened in the past, with climate change, the type and frequency of extreme events may increase in the future. For instance, we encountered extreme hot weather in the summer of 2022, even the lowest daily temperature can reach 35 Celsius during some days with a daily highest temperature of around 40 degrees. The proper incubation temperature range for Chinese alligators is from 28 to 35 degrees (Thorbjarnarson & Wang, 2010; Fang & Fang, 2015; He et al., 2002). A nest will hatch more females under high temperatures since alligator sex is temperature-determined (Thorbjarnarson & Wang, 2010; Fang & Fang, 2015). Although our modeling results showed that more females are beneficial for population growth, it may lead to severer inbreeding depression if the offspring only come from a few males. Moreover, extreme events, such as flooding, low temperature, and high temperature, could lead to more clutch failure, which may be detrimental for the population. With climate change, this issue should be further investigated.

The results indicated that improving carrying capacity would not reduce extinction probability but can increase population size. The density we used in the model, however, may not represent the highest density which population can reach in the wild. The Anhui populations, from which the density was calculated, were small and may not have reached carrying capacity themselves, suggesting the carrying capacity in Dongtan may exceed 278. Therefore, carrying capacity is not the limiting factor for the current DWP population since the baseline model suggested that the population will not reach the carrying capacity until 70 years later.

Mortality is one of the variables on which we have little data, and yet may impact the population significantly. There are several limitations regarding the choice of baseline mortality. Firstly, the mortality rates from other literature may not be applicable in DWP because DWP is a relatively artificial environment while the literature from which the mortality rates were extracted often focuses on population in the wild. Secondly, mortality rates calculated from the past DWP survey paper (Lv et al., unpublished) have much uncertainty, because the data was calculated from one single survey season and may underestimated the mortality of juveniles. During our communications with the park staff, we learned that they often observed hatchlings from the previous year, after the first winter when they would spend with their mother. But the juveniles were rarely sighted after the second winter when they needed to survive on their own, which may indicate high mortality of second-year juveniles. The modeling results showed that mortality rates lower than baseline did not lead to bigger population size or lower extinction risk, probably limited by carrying capacity. But as the mortality becomes larger than baseline, the population demonstrates more sensitivity and may plunge quickly. Therefore, mortality should remain one of the focuses of future monitoring.

Our population survey and the baseline model indicated a stable adult population in the park with a low extinction risk. Therefore, reintroduction may not be necessary to sustain the population in the short term. However, there are uncertainties in the modeling. If mortality rates of juveniles and subadults remains high and population growth is slow, reintroducing alligators around 5-7 years old and at a 4:1 sex ratio may facilitate growth. Reintroduction could also be considered to expand the population beyond DWP. Adjacent to the park lies the Chongming Dongtan Nature

Reserve, which was established in 1998 and declared a national migratory bird reserve in 2005 (Thorbjarnarson & Wang, 2010). The nature reserve consists of 241.5 km^2 and is considered a potential habitat for Chinese alligators (Lv et al., unpublished). Therefore, in the reintroduction scenarios, we assumed that as the population reaches a certain density, it would disperse into surrounding areas, such as the National Bird Reserve adjacent to the park or waterways scattering the island. In fact, a few sightings of Chinese alligators dispersed from the park have been confirmed in the bird reserve and other parts of the island, though these individuals were later captured and returned to the park. The reintroduction modeling suggests that under the baseline conditions, a small number of reintroduced alligators can lead to huge increase in population. Therefore, it may not be efficient to introduce a large number of alligators, for instance, 100 individuals, in a single event. Reintroducing too many alligators may not be beneficial if dispersion is slow, since excessive male density can halt reproduction (Zhao et al., 2019). Radio tracking and dispersion may be worth investigating in the future to facilitate reintroduction. What's more, the social aspect seems to be an important limiting factor for reintroduction. We have conducted an explorative social-economic survey following our summer fieldwork. We conducted interviews and questionnaires with tourists in the park and local people. Most of them were unaware that Chinese alligators were in the park and were concerned about reintroducing them to the whole island and potential human-wildlife conflicts. One interesting result is that some people, even though they were approved of Chinese alligator conservation and fond of them, did not want to reintroduce them outside the park as well, because they were afraid that people would harm these alligators.

4.5 Recommendation

Our modeling results confirmed the essential role of breeding females and mortality rates, therefore, the priority should be establishing a systematic and consistent survey method for monitoring and collecting more data, especially should focus on reproduction and survival of hatchlings and subadults. Multiple teams, possibly three teams, should operate at the same time to cover all the segments because it is hard for a boat to navigate across all the channels. The park may set up kayak stations near different waterways for convenience. During our survey, we found that carrying kayas to different canals was labor intensive and time consuming. An established survey method can also help better to predict the population size using N-mixture models. We recommend that as the population grows, the park should construct more suitable habitat for nesting. The park may construct higher grounds near water with vegetation, providing cover for nests and shelter from visitors.

The population modeling revealed that the DWP population is relatively viable, and reintroduction in the park may not be necessary within the short term. Long-term monitoring can be instrumental in the development and success of reintroduction programs. If recruitment rates are sluggish, strategies such as introducing additional breeding females from diverse genetic lineages should be considered to mitigate the potential deleterious effects of inbreeding depression. If considering reintroduction for areas outside DWP, social perspective may play a bigger role rather than habitat. Future studies may focus on social surveys, community engagement, and education. Many local people rely on fishing and aquaculture, which may induce human-wildlife conflicts. The fishing nets set by fisherman can drown alligators, and alligators may eat shrimps and crabs raised by people. Banning fishing nets and stipends are possible solutions, but it requires extensive communication and collaboration between scientists, local people, and government, which may be the next step.

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Appendix

Table 1. The values used in sensitivity analysis.

Parameters Changed	Baseline Values	New values
Inbreeding depression (lethal equivalents)	5	No inbreeding 3 7 9 10
sex ratio in birth - % in male	20	40 50 60 70 80
% adult female breeding	36	10 25 50 75 100
% adult male breeding	21.9	10 40 50 75
Carrying Capacity	278	100 100 200 400 500
Catestrophe Frequency	flood: 11% low temp: 11%	flood: 9% low temp: 9% flood: 13% low temp: 13% flood: 13% low temp: 9% flood: 9% low temp: 13%

Mortality rates	Decrease by 2% for all age groups Decrease by 5% for all age groups Increase by 2% for all age groups Increase by 5% for all age groups Increase by 7% for all age groups Increase by 10% for all age groups

Table 2. Vortex modeling results. ID is inbreeding depression. SEX is the male percentage at birth. FB and MB mean the percentage of females and males breeding. CC is carrying capacity. F stands for flood, and L is low temperature. Re is reintroduction. PE is the probability of extinction. N.all averages all repetition results, including the extinct ones.

Scenario	PE	N.all	SD.N.all.
Baseline	0.014	225.2	57.49
ID-NO	0.018	230.13	55.85
ID3	0.017	228.61	55.45
ID7	0.033	215.68	68.18
ID9	0.044	197.09	76.54
SEX10	0.068	213.55	74.98
SEX20	0.02	225.76	58.06
SEX30	0.014	219.71	58.76
SEX40	0.019	202.94	68.57
SEX50	0.044	165.19	82.89
SEX60	0.146	95.8	78.88
SEX70	0.4	32.89	43.83
SEX80	0.766	6.3	11.62
SEX90	0.98	0.66	2.26
FB10	0.985	0.44	3
FB25	0.168	134.96	95.3
FB50	0.004	237.89	47.83
FB75	0.002	247.98	45.32
FB100	0.001	251.68	41.76
MB10	0.023	220.34	60.89
MB40	0.023	224.62	59.59

MB50	0.021	222.48	58.77
MB75	0.023	224.11	60.03
MB100	0.02	226.29	58.29
CC100	0.039	70.16	24.47
CC200	0.029	155.22	45.37
CC400	0.028	319.66	92.16
CC500	0.024	401.69	115.46
F9L9	0.006	233.8	47.66
F13L13	0.034	214.94	68.76
F13L9	0.019	225.91	57.9
F9L13	0.027	221.4	62.53
Mortality-5	0.013	238.61	50.53
Mortality-2	0.011	232.75	49.46
Mortality+2	0.036	210.69	68.83
Mortality+5	0.1	168.93	88.71
Mortality+7	0.204	118.83	92.54
Mortality+10	0.449	53.19	72.79
Re10	0.007	853.51	174.32
Re30	0	861.66	157.61
Re50	0	870.97	152.72