

American alligator Population Genetics

The IUCN and the Crocodylian Specialist Group have stated that the preservation of genetic diversity is one of their main conservation objectives (IUCN, 1980; Thorbjarnarson et al., 1992). With that goal in mind, recent studies have focused on understanding the genetic structure of crocodylian populations. Currently, populations of the American crocodile (*Crocodylus acutus*), broad snouted caiman (*Caiman latirostris*), Nile crocodile (*Crocodylus niloticus*), West African crocodile (*Crocodylus suchus*), false gharial (*Tomistoma schlegelii*), Morelet's crocodile (*Crocodylus moreletii*), and the spectacled caiman (*Caiman crocodilus*) have been a part of studies focusing on population genetics. These studies report genetic differentiation among populations of crocodylians and a general trend of low genetic diversity within crocodylian populations (Amavet et al., 2007; Cunningham et al., 2016; de Oliveira et al., 2010; Dever et al., 2002; González-Trujillo et al., 2012; Hekkala et al., 2010; Marques et al., 2016; Mauger et al., 2017; Shafiei-Astani et al., 2015; Serrano-Gómez et al., 2016; Vandewoestijne et al., 2008; Velo-Antón et al., 2014; Versfeld, 2016).

The American alligator (*Alligator mississippiensis*) has also been a part of the increased focus on population genetics. The earliest American alligator genetic studies used allozymes and isozymes to examine the genetic variation. These early studies found low levels of genetic diversity (Adams et al., 1980; Gartside et al., 1977; Menzies et al., 1979). For example, Adams et al. (1980) reported an

2017; Oliveira et al, 2014; Olsson and Shine, 1997; Shine, 1988; Wu and Hu, 2010).

Crocodylians, which have widely varying population densities and degrees of male territoriality provide an excellent system to explore the evolutionary and ecological drivers that underlie the observed variation in frequency of multiple paternity (Amavet et al, 2008; Budd et al. 2015; Davis et al, 2001; Lafferriere et al, 2016; Lance et al, 2009; Lewis et al, 2013; Mcvay et al, 2008; Muniz et al. 2011; Ojeda et al, 2017; Oliveira et al, 2014; Wu and Hu, 2010). The frequency of multiple paternity observed across crocodylian taxa ranges from 32% in the Chinese alligator (*Alligator sinensis*) to 100% in black caiman (*Melanosuchus niger*) (Muniz et al. 2011; Wu and Hu 2010). Among crocodylians, it is not clear if the frequency of multiple paternity is driven by population density and/or mate encounter rate (Amavet et al, 2008; Budd et al. 2015; Davis et al, 2001; Lafferriere et al, 2016; Lance et al, 2009; Lewis et al, 2013; McVay et al, 2008; Muniz et al. 2011; Oliveira et al, 2014; Wu and Hu, 2010) though both have been suggested (Budd et al. 2015; Lafferriere et al, 2016).

The most thoroughly studied crocodylian species in terms of multiple paternity and mating behavior is the American alligator (*A. mississippiensis*) (Davis et al, 2001; Garrick and Lang, 1977; Joanen and McNease, 1971; Lance et al, 2009). However, because of the difficulty of observing mating activity in the wild, most research into mate selection dynamics has focused on captive

fitness advantages across sexes or is the product of population-specific parameters.

Methods

Site Description

This study was conducted on the South Island and Cat Island portions (6,033 ha) of the Thomas A. Yawkey Wildlife Center (YWC), a wildlife management area operated by the South Carolina (SC) Department of Natural Resources. The YWC alligator population is relatively closed, in that it is bordered by saltwater on all sides; the Atlantic Ocean to the east, Winyah Bay to the north, the Intracoastal Waterway to the west, and North Santee Bay to the south. This alligator population is well-characterized due to long-term (1970s to present) mark-recapture efforts resulting in a large database of alligator tissue, nesting, and morphometric data (Bangma et al., 2017; Hale et al., 2017; McCoy et al., 2015; Parrott et al., 2014; Wilkinson et al. 2016). However, information regarding the ongoing mark recapture studies was not available for this study.

Egg and Hatchling Collection

Alligator eggs were collected at YWC from 2011 to 2017. Helicopter surveys were used to locate nests from the air during the peak of the alligator nesting season in SC (early June-early July; Wilkinson, 1984). Nests were visited daily on foot until oviposition was confirmed. Fertility rates were determined by observing banding patterns (fertile eggs exhibit an opaque patch or band on the eggshell;

Ferguson, 1982). Eggs were collected within 48 hours of oviposition and transported to the Hollings Marine Laboratory (2011 – 2016) in Charleston, SC or the University of Georgia Savannah River Ecology Laboratory (2017) in Aiken County, SC where they were either necropsied as embryos or reared to hatching. In some cases, entire clutches of eggs were taken while at other nests only a subset (1-8 eggs) was collected (Table 1). In 2012, 2013, and 2017 twenty-seven full clutches were collected, maintained in damp sphagnum moss and reared until hatching. For all years in which eggs were allowed to hatch, eggs were checked twice daily for the initiation of hatching (“pipping”) and once hatchlings had pipped, they were removed from sphagnum and transferred to individual glass jars. Embryos that had not completed the hatching process within 48 hours of pipping were manually assisted in order to limit hatchling loss. Upon hatching, neonates were weighed and snout-vent length (SVL), total length, cloacal tail girth, and both head and snout length and width were measured. Scutes and/or chorioallantoic membrane were collected shortly after hatching. All tissue samples collected from hatchling alligators were immediately stored at -20° C upon collection.

A total of 1657 hatchlings were sampled from 151 nests. For 31 nests, we collected the entire clutch of eggs. For the remaining 120 nests, we collected a subset of the eggs (1-8 eggs).

Adult Alligator Capture and Sampling

NanoDrop Spectrophotometer ND-1000 (Thermo Scientific, Waltham, MA) and standardized to 20 ng/ μ l.

Microsatellite Development

We initially screened a subset of samples using the same microsatellite loci used by Lance et al. (2009). However, the YWC samples exhibited insufficient genetic variation for conducting parentage analyses (Lance, unpublished data). Therefore, we developed new microsatellite loci. We extracted DNA from one individual and prepared an Illumina paired-end shotgun library by shearing 1 μ g of DNA using a Covaris S220 sonicator and following the standard protocol of the Illumina TruSeq DNA Library Kit using a multiplex identifier adaptor index. Illumina sequencing was conducted on a HiSeq with 100 bp paired-end reads. Five million of the resulting reads were analyzed with the program PAL_FINDER_v0.02.03 (Castoe et al. 2012) to extract those reads that contained di-, tri-, tetra-, penta-, and hexanucleotide microsatellites. Once positive reads were identified, they were batched to a local installation of the program Primer3 (version 2.0.0) for primer design. To avoid issues with copy number of the primer sequence in the genome, loci for which the primer sequences only occurred one or two times in the five million reads were selected. Forty-eight potential loci that met this criterion were chosen. One primer from each pair was modified on the 5' end with an engineered sequence (CAG tag 5'-CAGTCGGGCGTCATCA-3') to enable use of a third primer in the PCR (identical to the CAG tag) that was

across all adult individuals using the same conditions described above with a touchdown protocol and highest annealing temperature of 58°C. Allele frequencies for these ten loci were estimated using all adults captured during the course of the study. We estimated the number of alleles per locus (k), observed and expected heterozygosity (H_o and H_e), mean polymorphic information content (PIC), the non-exclusion probability for the first parent (NE-1P), the non-exclusion probability for the second parent (NE-2P), and the non-exclusion probability for the parent pair (NE-PP) with Cervus 3.0.7 (Kalinowski et al. 2007). Tests for deviations from Hardy-Weinberg equilibrium (HWE) and for linkage disequilibrium were conducted using GENEPOP v4.0 (Rousset 2008). Characteristics of the loci are provided in Table 2. After determining that these 10 loci would provide the power needed for parentage analyses, we genotyped 1657 hatchlings across all 10 loci using the same conditions.

Maternal Genotype Comparison and Genotyping Error Rate

Hatchling alligator genotypes were initially screened using the Program Gerud 2.0 to test that each clutch could be explained by a single maternal genotype (Jones 2005). The genotypes of clutches that could not be explained by a single maternal genotype were examined for unexpected alleles. If an unexpected allele occurred at one locus, the allele was considered to be a mutation and the allele calls for that hatchling at the locus were excluded from future analysis. If an individual contained two or more alleles that prevented the clutch

used to determine intra-clutch relatedness as well as the likely number of sires (Jones and Wang 2010). Colony uses a maximum likelihood full pedigree analysis to assign individuals into either full-sibling or half-sibling categories (Jones and Wang 2010). If a clutch contains individuals who are half-siblings then multiple paternity is determined to have occurred (Jones and Wang 2010, Lafferriere et al. 2016). Colony runs were conducted under the “high precision” likelihood while incorporating the estimated genotyping error rate of 5%.

Our power to detect multiple paternity was tested with Gerudsim 2.0 (Jones 2005). Gerudsim 2.0 uses provided allele frequencies, clutch size, number of males contributing to a clutch, the number of offspring sired by each male, as well as whether or not the maternal genotype is known, to simulate potential clutch genotypes, maternal genotypes, and paternal genotypes. These simulated genotypes are then passed to Gerud 2.0 to test if Gerud 2.0 is able to accurately re-create the correct paternal and maternal genotypes (Jones 2005). We simulated 39 egg clutches sired by three males with one male contributing to 24 eggs, another male contributing to 10 eggs and the final male contributing to 5 eggs. With a known mother, 11 eggs needed to be sampled in order to accurately recreate the paternal genotypes 75% of the time. Without a known mother and 11 eggs sampled, we were able to accurately recreate the paternal genotypes 70% of the time. As a result, our estimates of multiple paternity are likely to be underestimates.

function lmer from the package “lme4” (Bates et al. 2007). P-values were extracted from these models using the function summary from the “lmerTest” R packages (Kuznetsova et al. 2017). Within R, the function “rcorr” within the package Hmisc was used to perform a Pearson’s correlation test on maternal size and paternal size (Harrell and DuPont, 2012; R Development Core 2017). The function “moran.I” within the R package ltools to perform a Global Morans I test was used to determine the degree of spatial autocorrelation between multiply sired and singly sired nests (Kalogirou, 2016; R Development Core, 2017). For nests with multiple paternity, a Wilcoxon ranked sums test was used to compare the contributions from the primary males and secondary males at nests sired by two or three males. All variables were considered significant at P-values of less than 0.05.

Results

Parentage and Clutch Characteristics

Of the 151 nests examined, we assigned a mother to 78 and at least one father to 38. For 28 nests, we assigned both maternity and a paternity. The majority of maternity assignments matched the female that was caught at the nest (81%). However, at 15 nests, the female captured at the nest was determined not to be the maternal female. Three pairs were found to have mated with each other across multiple years (Table 2). No cases of multiple paternity were detected within nests that had been sired by the same pair across years.

tested if larger males were also mating with larger females but detected no significant correlation between paternal and maternal size (Pearson's correlation coefficient = 0.12, $p= 0.54$, Figure 1). Multiple paternity was confirmed for only three nests for which a known male was identified as the sire of the nest; therefore, the relationship between male size and multiple paternity could not be examined. Together, these data suggest that male size is a determinant of reproductive success.

Multiple Paternity

Based on our simulations we determined that the probability of accurately detecting the number of sires when we collected eight or fewer eggs was less than 70%. Therefore, we excluded nests with eight or fewer eggs from our analyses of multiple paternity. This removed all nests collected in 2011, 2015 and 2016 and a total of 116 nests were excluded from our multiple paternity analysis. We detected multiple paternity at 11 (35%) of the 35 remaining nests, and rates of multiple paternity varied across years with an average of 43.5% per year (Table 1). Within multiply sired nests, we detected up to three males contributing to a clutch. For 80% of multiply sired nests there was a primary male that was responsible for $\geq 50\%$ of the hatchlings in the clutch (Figure 2). We next asked if paternal contribution from a tertiary male detracts from the proportion of eggs sired by either the primary or secondary male. Interestingly, the primary male sired an average of 74.5% of the clutch when there were two sires, but only 57 %

not sire larger clutches or have higher fertilization rates, suggesting that the advantage of territoriality among larger males is more mating opportunities but perhaps not higher quality mates. In captive studies, female alligators were found to preferentially mate with larger males (Joanen and McNease, 1971). This appears to extend to wild populations as we saw no size-assortative mating but did find that only males > 2.86 m in TL sired offspring. In Louisiana, male alligators as small as 1.83 m in total length produce sperm during the mating season (Joanen and McNease, 1980). It is possible that while these males are physiologically capable of mating, they are excluded from entering the breeding population by the larger males or by female selection (Joanen and McNease, 1971; Garrick and Lang, 1977; Hamlin et al. 2011). Adult males with an SVL of 135 cm or less display seasonal increases in testosterone (T), similar to larger males, until late March. After which, T concentration in smaller males decreases, whereas T concentrations in larger males continues to increase into April (breeding season) and remained much higher through June (Hamlin et al. 2011). This physiological observation is consistent with smaller males being excluded from the breeding population, and is perhaps mediated through social interactions with larger, more dominant males.

Our study represents the first study to describe multiple paternity in the American alligator outside of Louisiana (RNWR). Multiple paternity occurred in 25% to 75% of nests examined from 2012 to 2017 with an average of 43% of

through mating scars (Fitze et al. 2005). Male harassment could explain multiple paternity in American alligators given that we observed decreases in clutch fertility and hatchling size indicating an overall cost to females of mating multiply. Contrary to this idea are other observational studies indicating that female alligators are able to reject male advances and will even kill potential male suitors (Joanen and McNease, 1971; Garrick and Lang, 1977). Though, in these studies the rejected or killed males were smaller than the males we detected within the breeding population at YWC (Garrick and Lang, 1977, Joanen and McNease, 1971). It is possible that once a male reaches a certain size, females are no longer able to avoid mating. The role of male harassment within American alligator mating dynamics remain unclear and require further study.

Our study was able to document three cases in which the same parent pair sired nests across years. These results are similar to the findings of Lance et al. (2009) with the exception that our study found no cases of mate fidelity and multiple paternity within the same clutches. Mate fidelity is often explained with three hypotheses; males assist in parental care in order to increase their own reproductive success, males defend females from rival males to ensure paternity, or females adopt monogamy in order to gain some advantage from the male (Bull, 2000). Male parental care has not been documented in the American alligator, and while males will defend a territory, females will interact with multiple males during a breeding season (Garrick and Lang, 1977, Joanen and McNease, 1971).

Introduction

The maintenance of genetic diversity is a key component of population viability and conservation. The loss of genetic variation has been correlated with reduced individual fitness and with increased extinction risk (Reed and Frankham, 2003; Reed et al., 2007; Vandewoestijne et al, 2008). For example, studies on the wolf spiders in the genus *Rabidosa* correlated lower genetic diversity within a population to lower fecundity and offspring survivorship to sexual maturity (Reed, 2007; Reed et al. 2007). These effects can be particularly pronounced in recently recovered species, which often have experienced a genetic bottleneck (Frankham, 1995; Nei et al., 1975). The genetic diversity within a population can be influenced by several factors including demographic history and isolation from other populations (Levin, 1970; Mayr, 1942; Mayr, 1970; Nei et al., 1975; Wright, 1943). Populations may become isolated because of geological features, distance from other populations, or because of an impermeable habitat matrix (Mayr, 1970). Identifying the factors influencing population isolation is challenging but imperative for effective conservation (Frankham, 1995).

The American alligator (*Alligator mississippiensis*) has recently recovered from endangered status and is currently actively managed across its range (Ross, 1989). Population genetics studies of the American alligator suggest an East-West split and two populations; one encompassing Georgia, Florida, and South Carolina and one including Alabama, Louisiana, and Texas (Adams et al., 1980;

estuary is spread across numerous North Carolina counties but we only collected samples from Hyde and Dare county. Lake Waccamaw is a large freshwater Carolina bay located in south central North Carolina within Columbus County. The lake is a part of the Lake Waccamaw State park and is managed by the North Carolina Division of Parks and Recreation.

South Carolina

We included two populations in South Carolina: the Thomas A. Yawkey Wildlife Center and from Lakes Marion and Moultrie. The Thomas A. Yawkey Wildlife Center is located in Georgetown County, South Carolina and is a series of three barrier islands located along the coast of South Carolina. The islands are bordered by the Atlantic Ocean to the east, Winyah Bay to the north, the Intracoastal Waterway to the west, and North Santee Bay to the south. Lake Marion and Lake Moultrie are two man made reservoirs located in central South Carolina. While these lakes span multiple counties in South Carolina, we only collected samples from Clarendon County and Berkeley County. Lake Marion flows into Lake Moultrie and the two lakes are only separated by a distance of three miles. Therefore, for this study alligators from Lake Marion and alligators from Lake Moultrie were considered a part of the same population.

Georgia

The two populations sampled in Georgia are Sapelo Island and at the Joseph E. Jones Ecological Research Center at Ichauway. Sapelo Island is a barrier island

located along of the coast of Georgia located entirely within McIntosh County. The island is currently managed by the Georgia Department of Natural Resources. The Joseph E. Jones Ecological Research Center at Ichauway is an ecological research center located in Baker County, Georgia. The Joseph E. Jones Ecological Research Center has been the site of long-term ecological studies since 1991. This population is unique to our study in that this population lies within the Gulf of Mexico watershed.

Florida

The sampled populations from Florida include Guana Lake and Silver Lake. Guana Lake is located on the Atlantic coast of northern Florida. It is a man-made saltwater lake and is a part of the larger Guana Tolomato Matanzas National Estuarine Research Reserve. Silver lake is located in central Florida within Lake County. Silver lake is a naturally occurring freshwater lake.

Sample Collection

We captured alligators using multiple methods including baited-trip snare traps, walk-through traps, snare poles, and snatch hooks (Cherkiss et al. 2004; Murphy et al., 1983; Wilkinson 1994, Wilkinson et al. 2016). Table 6 described the locations and years in which we collected samples. Samples from the Joseph E. Jones Ecological Research Center were collected from 2009 until 2010 as a part of other studies examining the movement and ecology in inland alligator populations (Subalusky et al., 2009). Samples from Sapelo Island, Guana Lake,

add eight unknown bases to the end of DNA strands. This was done in order to detect PCR duplicates. Itru-5 external tags were added in a 50 μ L volume (10 μ L 5X kapa Hifi Buffer, 15 μ M dNTP's, 25 μ M itru-5 8N primer, 300 ng of pooled DNA, 17.5 μ L water, 1 unit of Kapa Hifi Polymerase). Kapa Hifi buffer and polymerase were provided by Roche Holding AG (Basel, Switzerland). Itru-5 external tags were added using an Applied Biosystems GeneAmp 9700 Thermo Cycler to perform one cycle of denaturation at 98°C for one minute, annealing at 60°C for 30 seconds, and elongation at 72°C for six minutes. Itru-7 external tags were immediately added after the addition of the itru-5 tags. The addition of the itru-7 was performed in at 50 μ l volume (10 μ L 5X kapa Hifi Buffer, 15 μ M dNTP's, 25 μ M P5 primer, 25 μ M itru-7 primer, 200 ng of pooled DNA, 20 μ L water, 1 unit of Kapa Hifi Polymerase). Itru-7 external tags were added using an Applied Biosystems GeneAmp 9700 Thermo Cycler to perform six cycles of PCR consisting of an initial denaturation at 98°C for two minutes, followed by six cycles of denaturation at 98°C for 20 seconds, annealing at 60°C for 15 seconds, and elongation at 72°C for 30 seconds, followed by a final elongation at 72°C for five minutes.

We prepared two libraries of 96 individuals, used a BluePippin (Sage Science, Beverly, MA, USA) to select fragments between 100 – 600 bp, and sequenced them on an Illumina NextSeq device using a 150 Cycles PE75 Mid Output flow cell at The Georgia Genomics and Bioinformatics Core.

“populations” commands within stacks. Harvester indicated that our data were best explained by two clusters. Samples were clustered based on which library they had been sequenced in. In order to determine how library biases may be influencing our results, the commands “ref_map” and “populations” were re-run with the libraries being analyzed separately rather than together. Our analyses resulted in 17819 loci from library one and 30944 loci from library two. Harvester indicated that five clusters are the most likely number of clusters from library two and four clusters are the most likely number of clusters for library one. No clear pattern of cluster is evident for the populations in either library.

RADcap

After processing, an average of 1,370,274 reads remained per individual. 3,267 loci were found using the “ref_map” and “populations” commands within stacks. After removing loci that contained repeated sequences or were linked to other loci, 716 loci remained. A total of 1432 capture probes were designed and produced by Arbor Biosciences.

Discussion

It is important to note that our study found a strong library bias with the program Structure clustering samples according to the library in which they were sequenced. Library biases has been reported from another study examining the effectiveness of ddRAD techniques to population genetic analysis (DaCosta and Sorenson, 2014). One potential explanation for this bias in our data could be that

the libraries were sequenced independently on different dates. Library two was prepared in September 2018 while library one was prepared in December 2018 and library two was sequenced in November 2018 while library one was sequenced in March 2019. DaCosta and Sorenson (2014) found inconsistent recovery of loci across different sequencing runs. While the explanations for this inconsistency vary, the end result would explain why when both libraries were analyzed together, the samples clustering according to the library in which they were sequenced.

In order to help alleviate some of these issues, we are currently in the process of using sequence capture methods such as RADcap (Hoffberg et al., 2016). RADcap allows to the consistent recovery of the same loci across sequencing runs and between individuals. RADcap also allows for the selective sequencing of the most informative loci. We were able to find 3,267 potential loci shared across populations in Louisiana, South Carolina, and Florida. Of these only 716 were found to be unlinked and without repetitive sequences. Our future studies focusing on the population genetics of the American alligator will be able to use these loci and baits in order to ensure consistent recovery of the same loci across sequencing runs and between individuals.

occurred in 25% to 75% of nests examined from 2012 to 2017, with an average of 43% of examined nests in a year having multiple paternity. This average closely aligns with the average occurrence of multiple paternity at the Rockefeller National Wildlife Refuge (Davis et al., 2001; Lance et al., 2009). Clutch fertility was lower, on average, in multiply sired nests than in singly sired nest but there was no difference in average clutch size, hatchlings length, hatchlings mass, or hatchling body condition. Given the lack of observable differences between multiply sired offspring and singly sired offspring, and the decrease in average clutch fertility, potential explanations for these results include that multiple paternity in alligators may be driven by a population parameter such as density or mate encounter rate. Unfortunately, population estimates for YWC or RNWR are unavailable. However, both populations occur in vastly different habitats suggesting that habitat characteristics may not be an important determinant in the occurrence of multiple paternity within the American alligator.

These effects of low genetic diversity can be particularly pronounced in recently recovered species, which often have experienced a genetic bottleneck (Frankham, 1995; Nei et al., 1975). The genetic diversity within a population can be influenced by several factors including demographic history and isolation from other populations. Previous studies on the populations genetics of the American alligator have demonstrated an East West phylogeographic split within the American alligator range (Davis et al., 2001; Davis et al., 2002; Glenn et al. 1998;

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Table 1. The number of clutches and hatchlings sampled during each year of the study and the results regarding multiple paternity.

Year	Total Clutches Sampled	Full Clutches	Hatchlings Collected	Multiply Sired Clutches (%)
2011	10	0	66	-
2012	11	8	267	2 (25%)
2013	20	9	305	4 (44%)
2014	19	4	110	3 (75%)
2015	19	0	135	-
2016	44	0	319	-
2017	28	10	455	3 (30%)
Total	151	31	1657	12

Table 2. The forward and reverse primer sequence used for each microsatellite loci used in the analysis as well as the repeated sequence motif for each loci. Each sequence includes the CAG forward primer and the pigtailed reverse primer.

Loc i	Primer Sequence 5' -> 3'	Moti f
Alm i 8	F: CAGTCGGGCGTCATCACCTTAATTATGAATTATCCGGA GGG R: GTTTAATCCTCCCTGACATTTCCC	ATC T (56)
Alm i 19	F: CAGTCGGGCGTCATCAGCAGACTCTAGAGCATTTAGAA TAGTCC R: GTTTC AAGTCAGGTTCACTTGTATCTAAACTAGC	ATC T (52)
Alm i 26	F: CAGTCGGGCGTCATCAGAACCAGTAAGTGCCCTCCC R: GTTTCGAAACAGAAGTCACACATCCC	ATC T (68)
Alm i 30	F: CAGTCGGGCGTCATCATTAGACCCTGTTGCCCATCC R: GTTTGCCCTCTTCTTCATCATGCC	ATC T (60)
Alm i 32	F: CAGTCGGGCGTCATCATGTCTGGCCTGGAAAGATCC R: GTTTGGGAGTACCTGCCTGTTCCC	ATC T (56)
Alm i 34	F: CAGTCGGGCGTCATCAGGAGTGCAGATGTCCAGG R: GTTTGTTCGGACCAGCAGCACC	ATC T (48)
Alm i 39	F: CAGTCGGGCGTCATCAAGTCTCCCTACACACAGGG R: GTTTGCAGTCAGGGACAGACTACC	ATC T (52)
Alm i 40	F: CAGTCGGGCGTCATCAGGCTCTGTGCATCTTGCTCC R: GTTTGGTATGGGATGCTAAGCCC	ATC T (64)
Alm i 46	F: CAGTCGGGCGTCATCATTGTTTCCTATCTTTCCTCCC R: GTTTGAGAACACTTCAACGTTTCC	ATC T (56)

Alm **F:**CAGTCGGGCGTCATCAGGAGTTCTCTGATGATCCTATCC ATC
i 47 C T
R: GTTTATTGGAGGATGTCATTGGG (64)

Table 3. Details on the loci used for parentage analysis and multiple paternity detection. H_o is the observed heterozygosity, H_e is the expected heterozygosity, PIC is the mean polymorphic information content, NE-1P is the non-exclusion probability for the first parent, NE-2P is the non-exclusion probability for the second parent, and NE-PP is the non-exclusion probability for the parent pair.

Loci	k	H_o	H_e	PIC	NE-1P	NE-2P	NE-PP	Error Rate
Almi 8	12	0.81	0.814	0.791	0.530	0.355	0.169	0.04
Almi 26	11	0.797	0.815	0.789	0.539	0.364	0.183	0.02
Almi 30	20	0.839	0.841	0.822	0.476	0.31	0.134	0.07
Almi 34	15	0.813	0.851	0.833	0.458	0.296	0.125	0.08
Almi 47	9	0.667	0.67	0.627	0.732	0.557	0.362	0.06
Total	-	-	-	-	0.046	0.0066	0.00188	0.05

Table 4. The nests in which mate fidelity occurred. (5), 1264-1278. *Molecular*

Year	Nest ID	Female	Male
2016	13_2016	CF-35	CG-18
2017	35_2017	CF-35	CG-18
2013	7_2013	BE-02	BF-05
2015	3_2015	BE-02	BF-05
2012	3_2012	CF-40	CI-28
2016	1_2016	CF-40	CI-28
2017	24_2017	CF-40	CI-28

Table 5. An AICc table of the AICc scores, Delta AICc and model weight of each model used to examine the effect of male morphometrics on the number of nests each male sired.

Formula	AICc	ΔAICc	Weight
Nest Sired~SVL+Tail Girth	72.8818	0	0.56
Nest Sired~SVL	73.38822	0.50642	0.44
Nest Sired~Total Length+Tail Girth	87.31301	14.43121	0
Nest Sired~Tail Girth	89.35854	16.47674	0
Nest Sired~Total Length	94.09322	21.21142	0
Nest Sired~ Ratio of SVL to Tail Girth	125.482	52.6002	0
Nest Sired~ Ratio of Total Length to Tail Girth	125.8006	52.9188	0

Table 6. The location and years in which samples were collected

Population	State	Type	Years Collected
Albemarle Sound	NC	Coastal	2011-2015
Lake Waccamaw	NC	Inland	2017
Thomas A. Yawkey Wildlife Center	SC	Coastal	2011-2017
Lake Marion/ Lake Moultrie	SC	Inland	2017
Sapelo Island	GA	Coastal	2011-2014
Joseph E. Jones Ecological Research Center	GA	Inland	2009-2010
Guana Lake	FL	Coastal	2011-2014
Silver Lake	FL	Inland	2011-2014

Table 7. Sequences of each internal and external tag used per sample.

Sample ID	Library	Itru-5 Internal Tag 5' -> 3'	Itru-7 Internal Tag 5' -> 3'	External Itru-7 Tag 5' -> 3'
SAM153	1	CCGAATAT	CTAACGC	TGTTTCGAG
SAM240	1	TTAGGCAAT	CTAACGC	TGTTTCGAG
SLV120	1	AACTCGTCAT	CTAACGC	TGTTTCGAG
SLV141	1	GGTCTACGTAT	CTAACGC	TGTTTCGAG
WA3716	1	GATACCAT	CTAACGC	TGTTTCGAG
WA3810	1	AGCGTTGAT	CTAACGC	TGTTTCGAG
MUSC101	1	CTGCAACTAT	CTAACGC	TGTTTCGAG
CG59	1	TCATGGTCAAT	CTAACGC	TGTTTCGAG
SAM179	1	CCGAATAT	TCGGTACC	TGTTTCGAG
SAM247	1	TTAGGCAAT	TCGGTACC	TGTTTCGAG
SLV121	1	AACTCGTCAT	TCGGTACC	TGTTTCGAG
SLV157	1	GGTCTACGTAT	TCGGTACC	TGTTTCGAG
WA3718	1	GATACCAT	TCGGTACC	TGTTTCGAG
WA3812	1	AGCGTTGAT	TCGGTACC	TGTTTCGAG
CF29	1	CTGCAACTAT	TCGGTACC	TGTTTCGAG
CG61	1	TCATGGTCAAT	TCGGTACC	TGTTTCGAG
SAM180	1	CCGAATAT	GATCGTTGC	TGTTTCGAG
SAM249	1	TTAGGCAAT	GATCGTTGC	TGTTTCGAG

SLV122	1	AACTCGTCAT	GATCGTTGC	TGTTTCGAG
SLV158	1	GGTCTACGTAT	GATCGTTGC	TGTTTCGAG
WA3723	1	GATACCAT	GATCGTTGC	TGTTTCGAG
WA3841	1	AGCGTTGAT	GATCGTTGC	TGTTTCGAG
MUSC209	1	CTGCAACTAT	GATCGTTGC	TGTTTCGAG
YK45	1	TCATGGTCAAT	GATCGTTGC	TGTTTCGAG
SAM182	1	CCGAATAT	AGCTACACTC	TGTTTCGAG
SAM250	1	TTAGGCAAT	AGCTACACTC	TGTTTCGAG
SLV123	1	AACTCGTCAT	AGCTACACTC	TGTTTCGAG
SLV160	1	GGTCTACGTAT	AGCTACACTC	TGTTTCGAG
WA3744	1	GATACCAT	AGCTACACTC	TGTTTCGAG
WA3845	1	AGCGTTGAT	AGCTACACTC	TGTTTCGAG
MUSC93	1	CTGCAACTAT	AGCTACACTC	TGTTTCGAG
YK49	1	TCATGGTCAAT	AGCTACACTC	TGTTTCGAG
SAM191	1	CCGAATAT	ACGCATC	TGTTTCGAG
SAM255	1	TTAGGCAAT	ACGCATC	TGTTTCGAG
SLV124	1	AACTCGTCAT	ACGCATC	TGTTTCGAG
SLV161	1	GGTCTACGTAT	ACGCATC	TGTTTCGAG
WA3755	1	GATACCAT	ACGCATC	TGTTTCGAG
WA8258	1	AGCGTTGAT	ACGCATC	TGTTTCGAG

MUSC94	1	CTGCAACTAT	ACGCATC	TGTTTCGAG
YK54	1	TCATGGTCAAT	ACGCATC	TGTTTCGAG
SAM222	1	CCGAATAT	GTATGCAC	TGTTTCGAG
SAM290	1	TTAGGCAAT	GTATGCAC	TGTTTCGAG
SLV126	1	AACTCGTCAT	GTATGCAC	TGTTTCGAG
SLV162	1	GGTCTACGTAT	GTATGCAC	TGTTTCGAG
WA3757	1	GATACCAT	GTATGCAC	TGTTTCGAG
WA8265	1	AGCGTTGAT	GTATGCAC	TGTTTCGAG
MUSC95	1	CTGCAACTAT	GTATGCAC	TGTTTCGAG
CG86	1	TCATGGTCAAT	GTATGCAC	TGTTTCGAG
SAM223	1	CCGAATAT	CACATGTCC	TGTTTCGAG
SAM292	1	TTAGGCAAT	CACATGTCC	TGTTTCGAG
SLV127	1	AACTCGTCAT	CACATGTCC	TGTTTCGAG
SLV163	1	GGTCTACGTAT	CACATGTCC	TGTTTCGAG
WA3764	1	GATACCAT	CACATGTCC	TGTTTCGAG
WA8267	1	AGCGTTGAT	CACATGTCC	TGTTTCGAG
MUSC218	1	CTGCAACTAT	CACATGTCC	TGTTTCGAG
CG92	1	TCATGGTCAAT	CACATGTCC	TGTTTCGAG
SAM225	1	CCGAATAT	TGTGCACGAC	TGTTTCGAG
SAM299	1	TTAGGCAAT	TGTGCACGAC	TGTTTCGAG

SLV128	1	AACTCGTCAT	TGTGCACGAC	TGTTTCGAG
SLV165	1	GGTCTACGTAT	TGTGCACGAC	TGTTTCGAG
WA3765	1	GATACCAT	TGTGCACGAC	TGTTTCGAG
WA9800	1	AGCGTTGAT	TGTGCACGAC	TGTTTCGAG
MUSC216	1	CTGCAACTAT	TGTGCACGAC	TGTTTCGAG
CI27	1	TCATGGTCAAT	TGTGCACGAC	TGTTTCGAG
SAM227	1	CCGAATAT	GCATCAC	TGTTTCGAG
SAM320	1	TTAGGCAAT	GCATCAC	TGTTTCGAG
SLV129	1	AACTCGTCAT	GCATCAC	TGTTTCGAG
SLV166	1	GGTCTACGTAT	GCATCAC	TGTTTCGAG
WA3772	1	GATACCAT	GCATCAC	TGTTTCGAG
BF7	1	AGCGTTGAT	GCATCAC	TGTTTCGAG
CG34	1	CTGCAACTAT	GCATCAC	TGTTTCGAG
YK53	1	TCATGGTCAAT	GCATCAC	TGTTTCGAG
SAM228	1	CCGAATAT	ATGCTGTC	TGTTTCGAG
SAM323	1	TTAGGCAAT	ATGCTGTC	TGTTTCGAG
SLV134	1	AACTCGTCAT	ATGCTGTC	TGTTTCGAG
SLV167	1	GGTCTACGTAT	ATGCTGTC	TGTTTCGAG
WA3777	1	GATACCAT	ATGCTGTC	TGTTTCGAG
MUSC191	1	AGCGTTGAT	ATGCTGTC	TGTTTCGAG

CG36	1	CTGCAACTAT	ATGCTGTC	TGTTTCGAG
MUSC143	1	TCATGGTCAAT	ATGCTGTC	TGTTTCGAG
SAM233	1	CCGAATAT	CATGACCTC	TGTTTCGAG
SAM326	1	TTAGGCAAT	CATGACCTC	TGTTTCGAG
SLV135	1	AACTCGTCAT	CATGACCTC	TGTTTCGAG
SLV172	1	GGTCTACGTAT	CATGACCTC	TGTTTCGAG
WA3780	1	GATACCAT	CATGACCTC	TGTTTCGAG
MUSC96	1	AGCGTTGAT	CATGACCTC	TGTTTCGAG
CG4	1	CTGCAACTAT	CATGACCTC	TGTTTCGAG
GTM124	1	TCATGGTCAAT	CATGACCTC	TGTTTCGAG
SAM239	1	CCGAATAT	TGCAGTGAGC	TGTTTCGAG
SLV119	1	TTAGGCAAT	TGCAGTGAGC	TGTTTCGAG
SLV137	1	AACTCGTCAT	TGCAGTGAGC	TGTTTCGAG
SLV173	1	GGTCTACGTAT	TGCAGTGAGC	TGTTTCGAG
WA3791	1	GATACCAT	TGCAGTGAGC	TGTTTCGAG
MUSC97	1	AGCGTTGAT	TGCAGTGAGC	TGTTTCGAG
CG50	1	CTGCAACTAT	TGCAGTGAGC	TGTTTCGAG
GTM122	1	TCATGGTCAAT	TGCAGTGAGC	TGTTTCGAG
AP10	2	CCGAATAT	CTAACGC	CCAAGCAA
AP33	2	TTAGGCAAT	CTAACGC	CCAAGCAA

AP9	2	AACTCGTCAT	CTAACGC	CCAAGCAA
GTM174	2	GGTCTACGTAT	CTAACGC	CCAAGCAA
IC304	2	GATACCAT	CTAACGC	CCAAGCAA
IC408	2	AGCGTTGAT	CTAACGC	CCAAGCAA
SAB10	2	CTGCAACTAT	CTAACGC	CCAAGCAA
SAD3	2	TCATGGTCAAT	CTAACGC	CCAAGCAA
AP12	2	CCGAATAT	TCGGTACC	CCAAGCAA
AP34	2	TTAGGCAAT	TCGGTACC	CCAAGCAA
GTM132	2	AACTCGTCAT	TCGGTACC	CCAAGCAA
GTM177	2	GGTCTACGTAT	TCGGTACC	CCAAGCAA
IC306	2	GATACCAT	TCGGTACC	CCAAGCAA
IC411	2	AGCGTTGAT	TCGGTACC	CCAAGCAA
SAB11	2	CTGCAACTAT	TCGGTACC	CCAAGCAA
SAD4	2	TCATGGTCAAT	TCGGTACC	CCAAGCAA
AP13	2	CCGAATAT	GATCGTTGC	CCAAGCAA
AP36	2	TTAGGCAAT	GATCGTTGC	CCAAGCAA
GTM138	2	AACTCGTCAT	GATCGTTGC	CCAAGCAA
GTM178	2	GGTCTACGTAT	GATCGTTGC	CCAAGCAA
IC312	2	GATACCAT	GATCGTTGC	CCAAGCAA
IC413	2	AGCGTTGAT	GATCGTTGC	CCAAGCAA

SAB2	2	CTGCAACTAT	GATCGTTGC	CCAAGCAA
SAD5	2	TCATGGTCAAT	GATCGTTGC	CCAAGCAA
AP17	2	CCGAATAT	AGCTACACTC	CCAAGCAA
AP47	2	TTAGGCAAT	AGCTACACTC	CCAAGCAA
GTM140	2	AACTCGTCAT	AGCTACACTC	CCAAGCAA
GTM188	2	GGTCTACGTAT	AGCTACACTC	CCAAGCAA
IC313	2	GATACCAT	AGCTACACTC	CCAAGCAA
IC414	2	AGCGTTGAT	AGCTACACTC	CCAAGCAA
SAB3	2	CTGCAACTAT	AGCTACACTC	CCAAGCAA
SAD6	2	TCATGGTCAAT	AGCTACACTC	CCAAGCAA
AP18	2	CCGAATAT	ACGCATC	CCAAGCAA
AP48	2	TTAGGCAAT	ACGCATC	CCAAGCAA
GTM142	2	AACTCGTCAT	ACGCATC	CCAAGCAA
GTM190	2	GGTCTACGTAT	ACGCATC	CCAAGCAA
IC328	2	GATACCAT	ACGCATC	CCAAGCAA
IC415	2	AGCGTTGAT	ACGCATC	CCAAGCAA
SAB4	2	CTGCAACTAT	ACGCATC	CCAAGCAA
SAD7	2	TCATGGTCAAT	ACGCATC	CCAAGCAA
AP19	2	CCGAATAT	GTATGCAC	CCAAGCAA
AP49	2	TTAGGCAAT	GTATGCAC	CCAAGCAA

GTM143	2	AACTCGTCAT	GTATGCAC	CCAAGCAA
GTM193	2	GGTCTACGTAT	GTATGCAC	CCAAGCAA
IC330	2	GATACCAT	GTATGCAC	CCAAGCAA
IC416	2	AGCGTTGAT	GTATGCAC	CCAAGCAA
SAB5	2	CTGCAACTAT	GTATGCAC	CCAAGCAA
SAD8	2	TCATGGTCAAT	GTATGCAC	CCAAGCAA
AP23	2	CCGAATAT	CACATGTCC	CCAAGCAA
AP50	2	TTAGGCAAT	CACATGTCC	CCAAGCAA
GTM148	2	AACTCGTCAT	CACATGTCC	CCAAGCAA
GTM195	2	GGTCTACGTAT	CACATGTCC	CCAAGCAA
IC37	2	GATACCAT	CACATGTCC	CCAAGCAA
IC418	2	AGCGTTGAT	CACATGTCC	CCAAGCAA
SAB6	2	CTGCAACTAT	CACATGTCC	CCAAGCAA
SAD9	2	TCATGGTCAAT	CACATGTCC	CCAAGCAA
AP24	2	CCGAATAT	TGTGCACGAC	CCAAGCAA
AP51	2	TTAGGCAAT	TGTGCACGAC	CCAAGCAA
GTM156	2	AACTCGTCAT	TGTGCACGAC	CCAAGCAA
GTM205	2	GGTCTACGTAT	TGTGCACGAC	CCAAGCAA
IC402	2	GATACCAT	TGTGCACGAC	CCAAGCAA
IC44	2	AGCGTTGAT	TGTGCACGAC	CCAAGCAA

SAB7	2	CTGCAACTAT	TGTGCACGAC	CCAAGCAA
SAD10	2	TCATGGTCAAT	TGTGCACGAC	CCAAGCAA
AP25	2	CCGAATAT	GCATCAC	CCAAGCAA
AP52	2	TTAGGCAAT	GCATCAC	CCAAGCAA
GTM160	2	AACTCGTCAT	GCATCAC	CCAAGCAA
GTM206	2	GGTCTACGTAT	GCATCAC	CCAAGCAA
IC404	2	GATACCAT	GCATCAC	CCAAGCAA
IC441	2	AGCGTTGAT	GCATCAC	CCAAGCAA
SAB8	2	CTGCAACTAT	GCATCAC	CCAAGCAA
SAD11	2	TCATGGTCAAT	GCATCAC	CCAAGCAA
AP26	2	CCGAATAT	ATGCTGTC	CCAAGCAA
AP54	2	TTAGGCAAT	ATGCTGTC	CCAAGCAA
GTM167	2	AACTCGTCAT	ATGCTGTC	CCAAGCAA
GTM241	2	GGTCTACGTAT	ATGCTGTC	CCAAGCAA
IC405	2	GATACCAT	ATGCTGTC	CCAAGCAA
IC443	2	AGCGTTGAT	ATGCTGTC	CCAAGCAA
SAB9	2	CTGCAACTAT	ATGCTGTC	CCAAGCAA
SAD12	2	TCATGGTCAAT	ATGCTGTC	CCAAGCAA
AP28	2	CCGAATAT	CATGACCTC	CCAAGCAA
AP7	2	TTAGGCAAT	CATGACCTC	CCAAGCAA

GTM170	2	AACTCGTCAT	CATGACCTC	CCAAGCAA
IC26	2	GGTCTACGTAT	CATGACCTC	CCAAGCAA
IC406	2	GATACCAT	CATGACCTC	CCAAGCAA
SAB0	2	AGCGTTGAT	CATGACCTC	CCAAGCAA
SAD10	2	CTGCAACTAT	CATGACCTC	CCAAGCAA
SAM000	2	TCATGGTCAAT	CATGACCTC	CCAAGCAA
AP32	2	CCGAATAT	TGCAGTGAGC	CCAAGCAA
AP8	2	TTAGGCAAT	TGCAGTGAGC	CCAAGCAA
GTM173	2	AACTCGTCAT	TGCAGTGAGC	CCAAGCAA
IC301	2	GGTCTACGTAT	TGCAGTGAGC	CCAAGCAA
IC407	2	GATACCAT	TGCAGTGAGC	CCAAGCAA
SAB1	2	AGCGTTGAT	TGCAGTGAGC	CCAAGCAA
SAD2	2	CTGCAACTAT	TGCAGTGAGC	CCAAGCAA
SA_M1	2	TCATGGTCAAT	TGCAGTGAGC	CCAAGCAA

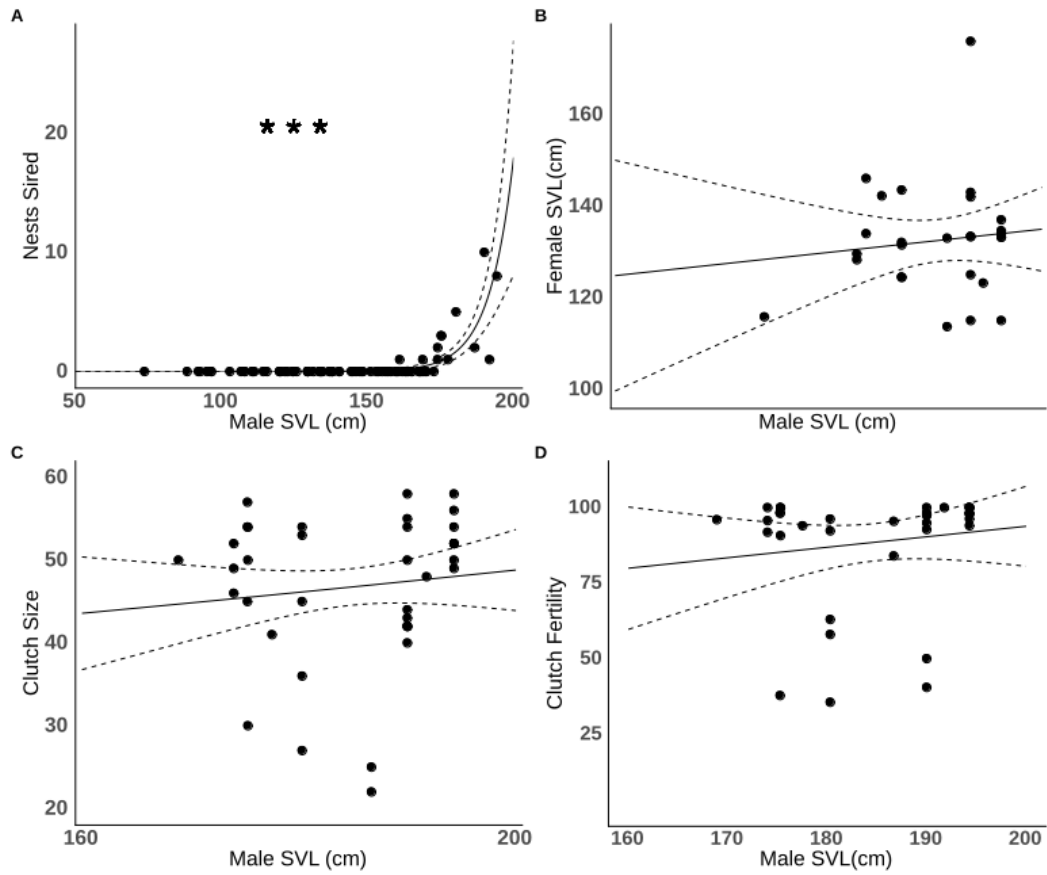


Figure 1. Relationships between male snout-vent length and (A) the number of nests sired, (B) size of female mate, (C) clutch size and (D) clutch fertility. Asterisks indicate significant results.

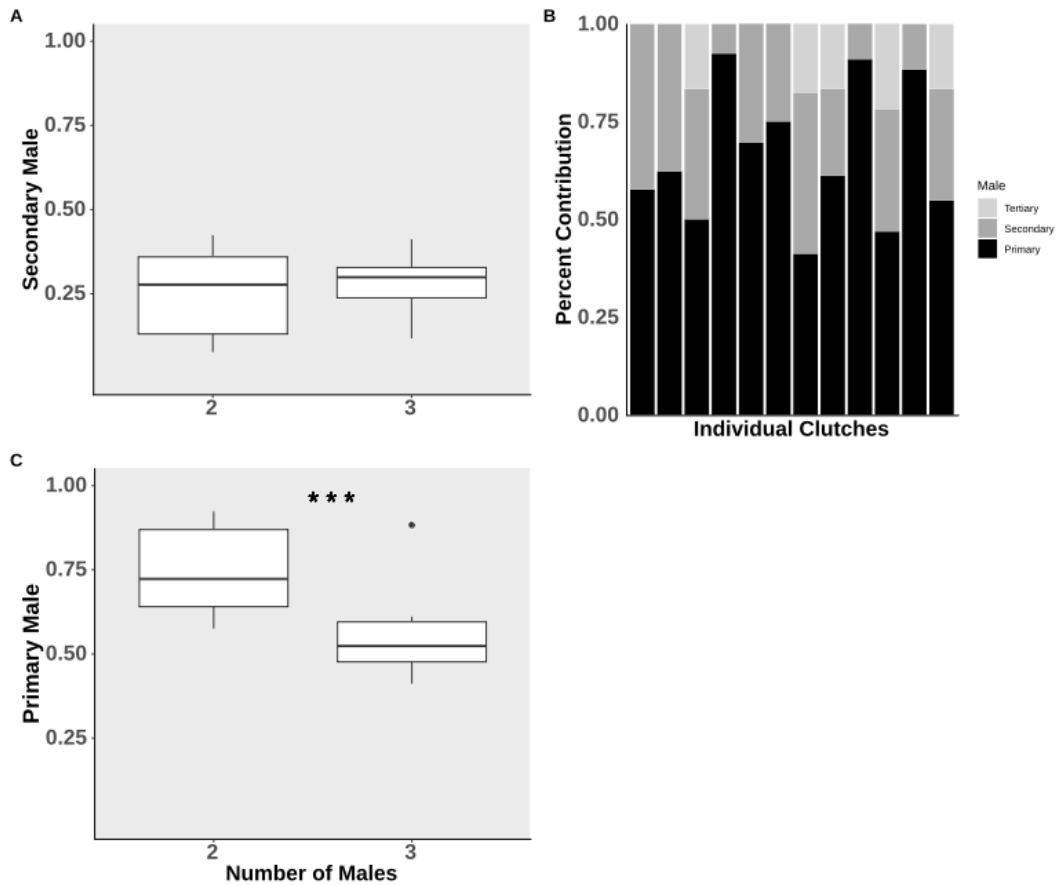


Figure 2. Examination of male contributions to nests with (A) the distribution of contributions across secondary males, (B) the distributions of contributions across primary, secondary and tertiary males, and (C) the distribution of contributions across primary males. N= 35. Asterisks indicate a significant difference.

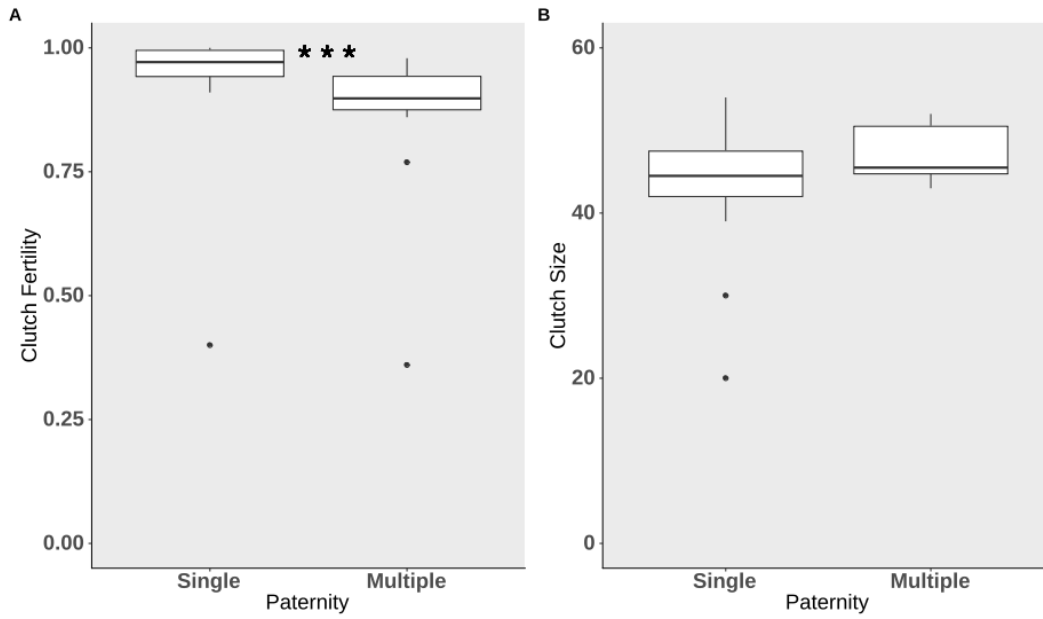


Figure 3. Relationships between fitness related traits and multiple paternity including (A) clutch fertility and (B) clutch size across singly sired and multiply sired nests. N= 35. Asterisks indicate significant results.

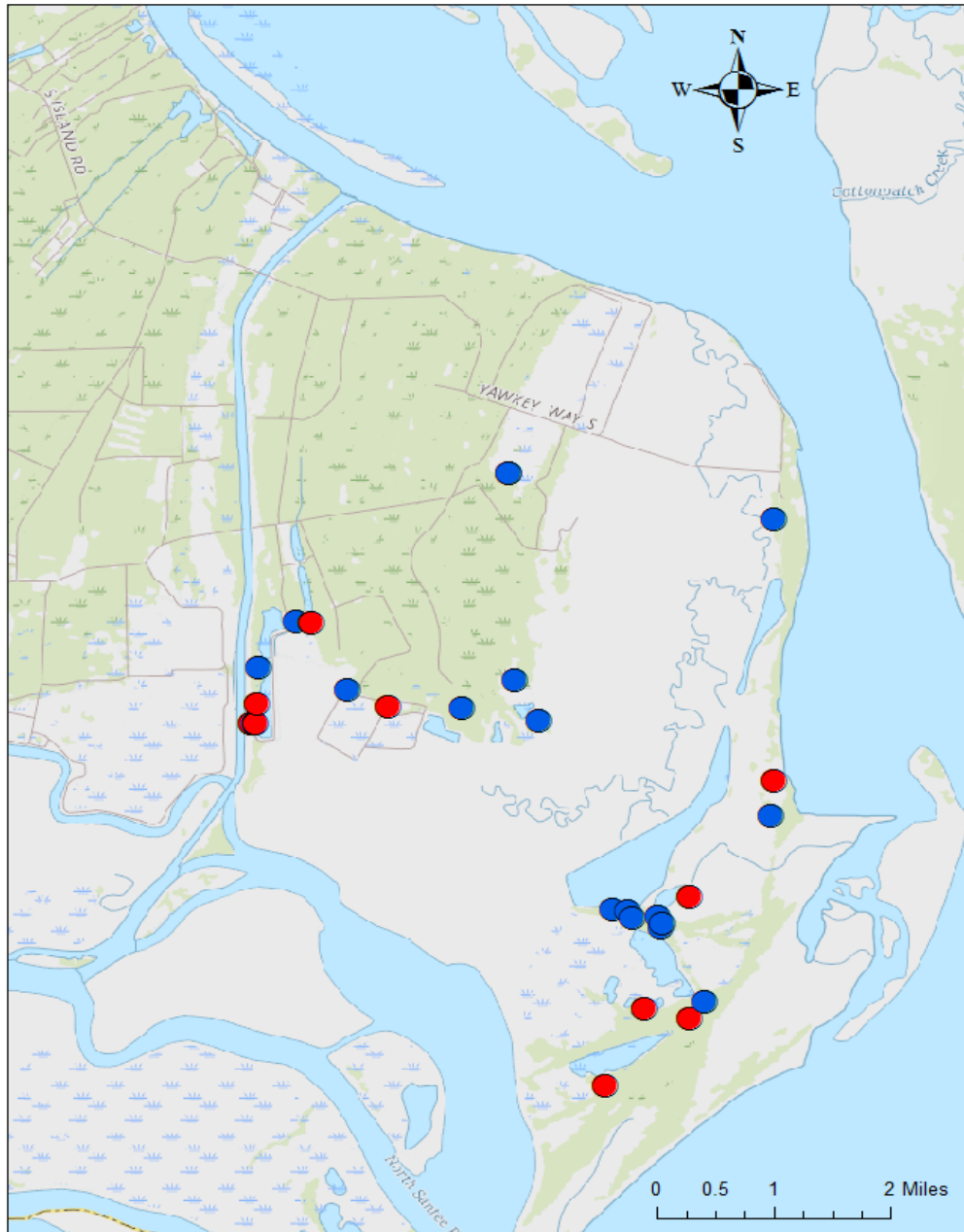


Figure 4. Map of YWC with points indicating nests for which the entire clutch was sampled (N= 35) Blue points represent nests that were singly sired and red points represent nests that were multiply sired.

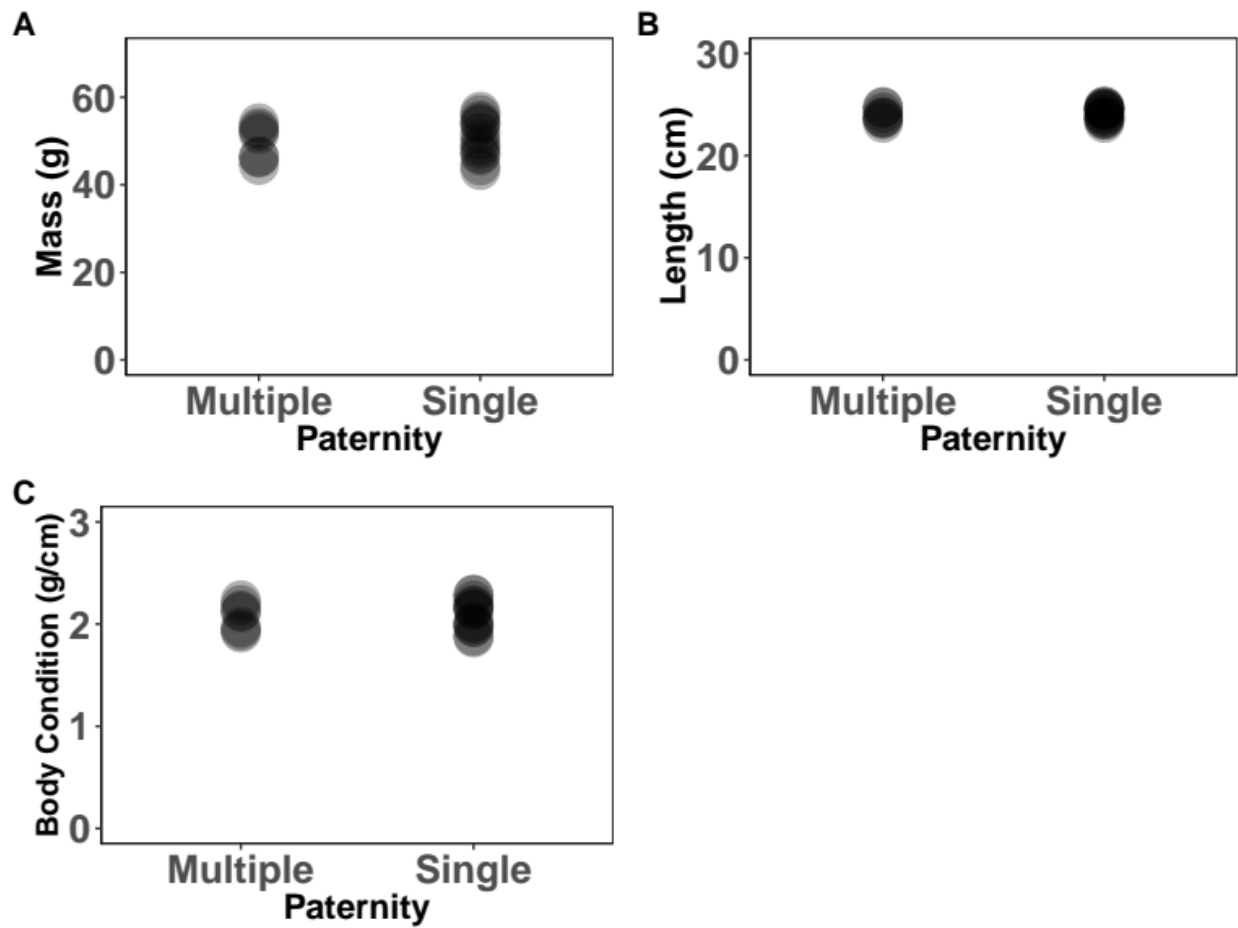


Figure 5. Relationships between hatchling phenotypes and patterns of paternity with (A) hatchling mass (B) hatchling length and (C) body condition across singly sired and multiply sire nests. Each point represents one clutch. N=35. Asterisks indicate significant differences.



Figure 6. Map of sampled alligator locations. Orange dots represent one population that was included in the analysis of population connectivity.