

THE FACTORS AFFECTING PRODUCTIVITY AND PARENTAL
BEHAVIOR OF AMERICAN OYSTERCATCHERS IN TEXAS

by

Amanda N. Anderson, B.S.

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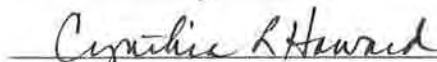
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by

Amanda N. Anderson


APPROVED BY


George Guillen, Ph.D., Chair


Cynthia Howard, Ph.D., Committee Member


Susan Heath, Ph.D., Committee Member


Dennis Casserly, Ph.D., Associate Dean


Zbigniew Czajkiewicz, Ph.D., Dean

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ABSTRACT

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BEHAVIOR OF AMERICAN OYSTERCATCHERS IN TEXAS

Amanda N. Anderson, M.S.
The University of Houston Clear Lake, 2014

Thesis Chair: Dr. George Guillen

The American oystercatcher (*Haematopus palliatus*) is considered a species of high concern because they exhibit low and variable annual productivity. Their reproductive success is highly sensitive to anthropogenic disturbances, predation, and weather events. There has been extensive research on Atlantic coast populations, but until recently, little was known about oystercatchers breeding in the Western gulf region. The objective of this study was to summarize productivity and document factors influencing daily survival and parental behavior. I monitored 80 breeding pairs and 144 nests during 2013 to 2014 along the Texas upper coast. Productivity was 0.51 chicks fledged per pair in 2013 and 0.59 in 2014. Variation in daily survival rates was best explained by seasonality, nest and brood age, and the abundance of laughing gulls (*Leucophaeus atricilla*). Nest and brood failures were caused by overwash, inclement weather, depredation, and starvation. I conducted focal observations on 60 nests and 38 broods to quantify parental behavior and determine if laughing gulls influenced their behavior. Incubation did not differ

significantly in the presence or absence of gulls. During chick rearing, roosting increased significantly when nesting gulls were absent. During both reproductive periods, vigilance increased significantly as the number of gulls increased. I calculated scaled mass indices for oystercatcher chicks, and determined that chick mass was significantly lower as gulls increased and when nesting gulls were present. This was the first study in the Western Gulf to quantify American oystercatcher behavior and document the negative effects of laughing gulls.

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INTRODUCTION

Shorebirds

Research over the last few decades has indicated that North American shorebird populations have declined for various reasons (Brown *et al.* 2001; Bart *et al.* 2007). Shorebird reproductive success is influenced by a suite of factors including nest site selection, food availability, predation risk, habitat disturbance, and inclement weather (Smith *et al.* 2007). They also exhibit fluctuating population dynamics due to generally low and variable reproductive rates, which makes them vulnerable to local extirpation (Brown *et al.* 2001). Furthermore, anthropogenic disturbances including habitat degradation and loss, and disturbance have negatively affected shorebird distribution and abundance (Brown *et al.* 2001; McGowan and Simons 2006; Bart *et al.* 2007). In order to conserve and manage shorebirds effectively for long term conservation, we need a comprehensive understanding of the influence of biotic and abiotic factors on individual species survival.

Life history and background information

American oystercatchers (*Haematopus palliatus*) have been identified as a species of high concern by U.S. Shorebird Conservation Plan and U.S. Fish and Wildlife Service (Brown *et al.* 2001; Clay *et al.* 2010). Oystercatchers exhibit low and variable annual productivity, and population estimates have documented declines across the Atlantic coast (Brown *et al.* 2001; Davis *et al.* 2001; McGowan and Simons 2006). Furthermore, oystercatchers are highly sensitive to disturbances including human activity, predation,

weather events, and habitat loss (McGowan and Simons 2006; Sabine *et al.* 2008). The National Fish and Wildlife Foundation has designated oystercatchers as a keystone species and has implemented a ten year business plan that provides resources and funding to increase oystercatcher populations by 30% (Clay *et al.* 2010). Oystercatchers are considered a keystone species because conservation efforts to protect this species will also benefit other coastal shorebird species that utilize similar habitat (American Oystercatcher Working Group *et al.* 2012).

American oystercatchers are large shorebirds (Figure 1) restricted to coastal habitats along the Atlantic and Gulf coast of the United States and both coasts in South America. They are the most widely distributed oystercatcher species in the Western hemisphere with an estimated population of 11,000 in the United States (Brown *et al.* 2005). In the Northern hemisphere, oystercatchers are short distance migrants and breed along the Atlantic coast from Maine to Florida and along the Gulf coast from Florida to Mexico (American Oystercatcher Working Group *et al.* 2012). Their winter range extends from New Jersey south towards the Gulf coast; and oystercatchers along the Gulf of Mexico are thought to be non-migratory (American Oystercatcher Working Group *et al.* 2012). An aerial survey across the specie's winter range estimated 477 individuals along the Texas coast in 2003 (Brown *et al.* 2005). Currently, there are no breeding season population estimates published for oystercatchers in the Gulf of Mexico states (American Oystercatcher Working Group *et al.* 2012).

American oystercatchers are long lived (10 to 15 years), monogamous shorebirds that exhibit delayed sexual maturity (Sanders *et al.* 2013). They feed exclusively on bivalves, mollusks, worms and other invertebrates inhabiting intertidal areas (American

Oystercatcher Working Group *et al.* 2012). Foraging bouts are highly influenced by the presence of exposed shellfish beds within intertidal areas (Sanders *et al.* 2013). American oystercatchers exhibit mate and nest site fidelity. Pairs along the Texas coast begin establishing breeding territories during January (American Oystercatcher Working Group *et al.* 2012). Oystercatchers are highly territorial and often display aggressive behaviors towards conspecifics when defending nesting and feeding territories (American Oystercatcher Working Group *et al.* 2012; Spiegel *et al.* 2012; Borneman 2013). They are ground nesters, and most nests in Texas are found on dredge spoil islands and shell rakes along salt marsh edges. Along the Atlantic coast, oystercatchers also nest on open beach, overwash flats, shell islands and dunes. Oystercatchers begin nesting as early as February on the Gulf coast, whereas nesting begins in April along the Atlantic coast (American Oystercatcher Working Group *et al.* 2012). Clutch size is one to three eggs and both adults incubate for 27 days until hatching. If early in the season, pairs may replace failed clutches during a single breeding season. Parents exhibit bi-parental care and semi-precocial chicks depend on adults for food and protection until they fledge at 35 days (Figure 1). Fledged chicks will continue to rely on adults for food provisioning for several more months (Hazlitt *et al.* 2002; Thibault *et al.* 2010; American Oystercatcher Working Group *et al.* 2012).

Parental attendance

American oystercatchers exhibit complementary sex roles and bi-parental care has been shown to increase nest and brood survival (Collins 2012). It is hypothesized that energetic demands are reduced when both adults invest in parental duties like incubation and chick rearing similarly (Collins 2012). Also, bi-parental care reduces the risk of

predation and permits adults to allocate additional time towards incubation and self-maintenance (Spiegel *et al.* 2012). Complimentary pairs are defined as those that coordinate roles in nest defense and rearing behaviors (Nol 1985; Collins 2012). During incubation, adults frequently leave their nests to chase conspecifics, other bird species, and mammals (Spiegel *et al.* 2012). Nol (1989) noted that when pairs encountered predators in the presence of newly hatched chicks, one adult would stay to guard the chicks while the other chased the predator away. She also found that as chicks aged, both adults would exhibit anti-predator behaviors toward potential predators and territorial displays towards other oystercatchers.

Reproductive success for avian species is influenced by the allocation of their time and energy into parental behavior (Hazlitt 2001; Palmer *et al.* 2001; Spiegel *et al.* 2012). The proportion of time adults spend incubating depends on their physiological condition, seasonality, predation risk, temperature, and food availability (Palmer *et al.* 2001; Spiegel *et al.* 2012). Activity around the nest also influences nest survival (McGowan and Simons 2006; Smith *et al.* 2007). Specifically, higher nest success was associated with birds taking fewer trips on and off the nest (McGowan and Simons 2006; Smith *et al.* 2007). McGowan and Simons (2006) argued that more nest activity cues predators onto the nest location. During chick rearing, brood success has been shown to be positively related to the amount of chick provisioning and chick guarding activity. (Groves 1984; Nol 1989; Thibault *et al.* 2010).

Additional factors including territory quality, food availability, and size and distance to foraging areas have also been shown to influence oystercatcher brood success (Nol 1989; Ens *et al.* 1992; Thibault *et al.* 2010). Nol (1989) and Hazlitt (2001)

suggested that optimal territory used by oystercatchers would allow an adult to be vigilant over their nesting territory while foraging simultaneously. Oyster reef exposure also influences provisioning rates. During low tides, McGowan and Simons (2006) found adults allocated more time towards foraging and locomotive behaviors. Hazlitt and Butler (2001) suggested that breeding pairs exhibiting site fidelity over multiple years and establishing breeding territories early in the season, may indicate high quality territory exists in the area that likely lead to higher reproductive success.

Daily nest and brood survival

Studies have demonstrated that daily nest and brood survival is influenced by the date of nest initiation, and that daily survival decreases as the breeding season progresses (Tjørve and Underhill 2008; Murphy 2010; Smith and Wilson 2010; Schulte 2012; Koczur 2013). A decline in nest survival over time may be explained by seasonal weather events and changes in temperature, food availability, human disturbance and predator activity (Ruthrauff and McCaffery 2005; Colwell *et al.* 2007; Schulte 2012). Semi-precocial young are particularly vulnerable to predation, starvation, and weather events within two weeks of hatching (Colwell *et al.* 2007; American Oystercatcher Working Group *et al.* 2012; Schulte 2012). Schulte (2012) and Hazlitt and Butler (2001) determined that oystercatcher chick mortality was the highest within the first week of hatching. Nest and brood age also affects daily survival rates. However, different studies have reported conflicting results where daily survival was found to be positively or negatively related to age (Colwell *et al.* 2007; Smith and Wilson 2010; Koczur 2013).

Sources of Mortality

Shorebird reproductive success and survival are influenced by a combination of factors including weather, resource availability, predators and anthropogenic disturbances (Peters and Otis 2005; McGowan and Simons 2006; Sabine *et al.* 2006). Researchers predict that waterbirds increase energy expenditure in response to human disturbance; which may consequently effect an individual's fitness (Peters and Otis 2005; Borgmann 2010). Human activity has been found to displace birds, cause mortality, reduce nesting habitat, alter behavior, and influence reproductive success (Burger and Gochfeld 1991; Brown *et al.* 2001; Borgmann 2010; Borneman 2013). American oystercatchers breed along coastal areas that are heavily influenced by human recreational activity, which is known to negatively affect reproductive success and alter behavior of oystercatchers along the Atlantic coast. (Davis *et al.* 2001; Peters and Otis 2005; McGowan and Simons 2006; Sabine *et al.* 2006; Sabine *et al.* 2008). Specifically, human disturbance has resulted in higher nest failure and chick mortality rates, and reduced incubation and brood attendance of oystercatchers along the Atlantic coast (Davis *et al.* 2001; McGowan and Simons 2006; Sabine *et al.* 2006). Furthermore, disturbance is linked to reduced foraging, roosting, and nest attendance, as well as; increased vigilance, flushing, and anti-predator defenses (Burger and Gochfeld 1991; Verhulst *et al.* 2001; Traut and Hostetler 2003; Peters and Otis 2005; McGowan and Simons 2006; Borneman 2013).

Several studies found incubation and foraging time decreased with frequent human activity near nest sites and foraging areas (Verhulst *et al.* 2001; Sabine *et al.* 2008). High human activity near nests has resulted in lower nest attendance and higher probabilities of depredation because nests' are left unattended more often and flushed

adults may cue predators onto the nest (McGowan and Simons 2006; Sabine *et al.* 2006). During foraging, chick provisioning rates decreased as the human disturber moved closer to adults (Verhulst *et al.* 2001). Although human disturbance is associated with lower reproductive success and altered oystercatcher behavior, there is limited evidence showing that humans are the direct cause for the species' decline (McGowan and Simons 2006). Researchers do not yet have a definitive quantitative understanding of the mechanisms that determine the influence of human presence on reproductive success (Peters and Otis 2005; McGowan and Simons 2006; Sabine *et al.* 2006). Besides anthropogenic disturbances, weather events and interaction with predators and competing avian species also influences oystercatcher productivity.

Predation has been the primary cause for nest failures where the sources of nest lost could be determined (Sabine *et al.* 2006; Schulte 2012; Denmon *et al.* 2013). Avian predation by raptors (*Falconiformes* spp.), fish crows (*Corvus ossifragus*), boat-tailed grackles (*Quiscalus major*) and gulls (*Larus* spp.) typically results in egg loss (Verboven *et al.* 2001; Sabine *et al.* 2006; Schulte 2012; Denmon *et al.* 2013). However, quantitative data is lacking on the relative frequency and importance of avian predation events (Verboven *et al.* 2001; Sabine *et al.* 2006; Schulte 2012; Denmon *et al.* 2013).

Mammalian predators like raccoons (*Procyon lotor*), feral cats (*Felis catus*), foxes (*Vulpes vulpes*), and mustelids (*Mustelidae* spp.) also feed upon eggs and chicks (McGowan and Simons 2006; Sabine *et al.* 2008; Schulte 2012). Researchers hypothesize that the frequency of predation by some mammal species (e.g. raccoons and feral cats) may be positively correlated with human activity (McGowan and Simons 2006; Sabine *et al.* 2008; Schulte 2012).

Inundation, also referred to as “overwash” of nesting sites during storm and high tide events is another major cause of nest failure (Sabine *et al.* 2006; Spiegel *et al.* 2012; Denmon *et al.* 2013). Strong storm events have been documented to eliminate most active nests during a breeding season (Schulte 2012).

Several studies have documented interspecific interactions between oystercatchers and gull species that affected reproductive success and food intake. Kleptoparasitism is a feeding strategy that various gull species exhibit that occurs on oystercatcher winter foraging sites (Martínez and Bachmann 1997; Tuckwell and Nol 1997; Khatchikian *et al.* 2002). Tuckwell and Nol (1997) found that kleptoparasitism occurred more often as the number of gulls increased. Additionally, oystercatchers foraged on smaller mussels and their intake rate decreased as gulls increased (Tuckwell and Nol 1997). Egg and chick predation by gulls is known to occur when oystercatchers nest near breeding gull colonies (Harris and Wanless 1997; Hazlitt 2001). Black oystercatchers (*H. bachmani*) that occupied territories adjacent to gull colonies had a smaller mean clutch size versus those nesting in territories with no gulls (Hazlitt 2001).

As an obligate coastal species, American oystercatcher habitat is threatened by coastal development and sea level rise. Wintering and breeding oystercatchers may be limited by habitat loss and degradation as a result of these threats (Clay *et al.* 2010). Coastal development has resulted in the direct loss of habitat (American Oystercatcher Working Group *et al.* 2012). Sea level rise is expected to have long term negative effects, and may reduce low lying coastal habitats used by breeding and wintering oystercatchers (Clay *et al.* 2010; American Oystercatcher Working Group *et al.* 2012). Additionally, storm events may increase with climate change, thus affecting barrier islands and

increasing overwash events (Clay *et al.* 2010). There is evidence that oystercatchers are shifting away from traditional nesting sites; and expanding their breeding range further north as the habitat changes (American Oystercatcher Working Group *et al.* 2012). For example, along the Atlantic coast there has been a decrease in barrier island nesting, and increase in dredge island and salt marsh nesting (Lauro and Burger 1989; American Oystercatcher Working Group *et al.* 2012). The shift between nesting habitat may also be attributed to greater predator abundance on barrier islands (McGowan and Simons 2005).

Conservation and management strategies

The American Oystercatcher Working Group and the American oystercatcher Conservation Plan have recommended multiple conservation strategies and actions for the species (Clay *et al.* 2010; American Oystercatcher Working Group *et al.* 2012). These include 1) identifying and conserving key wintering and breeding sites, along with crucial habitats and food resources used throughout the specie's range, 2) identifying potential habitat that may be utilized by oystercatchers in the future, 3) reducing or eliminating human disturbance and predators within protected areas before and during the breeding season to conserve and increase oystercatcher population, 4) monitoring population status and trends in order to evaluate the effectiveness of management strategies and 5) conservation and resource management entities must promote public education and gain public, state and federal support in implementing strategies.

As a long-lived species, oystercatchers exhibit highly variable but generally low reproductive rates (Davis 1999; Sabine *et al.* 2006; Schulte 2012). Therefore, oystercatchers would likely not recover quickly from significant population declines. Population viability is influenced by delayed maturity, juvenile recruitment, site fidelity

and regional factors (Davis *et al.* 2001; American Oystercatcher Working Group *et al.* 2012; Schulte 2012). It is difficult to determine the population status and whether survival and recruitment rates will sustain existing populations into the future. Juvenile recruitment strongly influences long term population dynamics; therefore, there is a critical need for monitoring and determining survival rates of post fledglings (Davis 1999; American Oystercatcher Working Group *et al.* 2012). Breeding attempts often fail during the chick rearing stage, but researchers have found it difficult to determine the cause and timing of chick mortality (Sabine *et al.* 2006; Schulte 2012). More research is needed to understand how various factors like chick age, habitat quality, disturbances, and parental behavior affect chick survival (Schulte 2012).

American oystercatchers in Texas

The Texas Parks and Wildlife Department considers American oystercatchers to be a priority species. The Gulf Coast Bird Observatory (GCBO) began investigating the status of oystercatchers along the Texas coast in 2011 through a grant from the National Fish and Wildlife Foundation. This project includes color banding, nest monitoring, observing movement patterns, and identifying threats to the Western Gulf population. Based on initial observations, Dr. Susan Heath has documented multiple causes for nest failures including overwash, chick starvation, and predation by mammals and laughing gulls (*Leucophaeus atricilla*). The estimated productivity along the upper coast for the previous 2011-2012 was 0.78 chicks fledged per pair, 0.20 chicks fledged per pair (S. Heath *pers. commun.*). Low productivity in 2012 was attributed to multiple high tide events that overwashed many nests and chicks. Furthermore, limited food availability as a result of little reef exposure during high tide events, consequently led to chick starvation.

There are indications that Texas oystercatchers exhibit high site fidelity because *ca.* 85% of the birds banded in 2012 were present in the 2013 field season (S. Heath *pers. commun.*).

Study objectives and hypothesis

The primary objective of my study included evaluating the influence of selected variables on 1) American oystercatcher productivity and 2) parental behavior. First, I aimed to summarize the productivity of American oystercatchers in 2013 and 2014 breeding seasons. Secondly, I hypothesized that the variation in nest and brood success was influenced by 1) timing of nest initiation, 2) laughing gull density, 3) parental behavior, and 4) territory size. Lastly, I hypothesized that parental behavior and chick body condition was negatively influenced by the number of laughing gulls and the presence of nesting laughing gulls.

METHODS

Study site

This study was conducted along the upper Texas coast in West Galveston Bay, Bastrop Bay and Drum Bay (Figure 2-3). The region contains numerous dredge spoil islands, natural estuarine islands, salt marshes, and intertidal oyster reef. There is significant human development and high recreational activity along Galveston Island and Follets Island. The Gulf Intracoastal Waterway (GIWW) also runs through the study area. Numerous barges, tug boats, and recreational vehicles use the GIWW.

The primary nesting substrate for the American oystercatcher in Texas is shell hash located on various islands. Intertidal oyster reefs, primarily consisting of Eastern

oysters (*Crassostrea virginica*) occur throughout the adjacent shallow bays and provide foraging habitat for oystercatchers. The dominant vegetation along the fringe and interior portions of these islands consists of smooth cordgrass (*Spartina alterniflora*), saltwort (*Salicornia spp.*), and sea ox-eye daisy (*Borrchia frutescens*). Other nesting colonial waterbird species commonly observed within the study sits include laughing gulls, brown pelicans (*Pelecanus occindentalis*), tern species (*Laridae spp.*), and heron species (*Ardeidae spp.*). Potential nest predators within the region include laughing gulls, raccoons, opossum (*Didelphis virginiana*) feral cats, coyotes (*Canis latrans*), raptors, and Western diamondback rattlesnake (*Crotalus atrox*). Small dredge spoil islands also experience overwash during high tide and storm events. Many of the islands are easily accessible to recreational boaters and fishermen.

Field Procedures

Surveys and monitoring. The study period extended from February to August in 2013 and 2014. Surveying and monitoring occurred twice a week in West Galveston Bay and once a week in Drum Bay and Bastrop Bay. I monitored nests to estimate breeding pair distribution, survival, and productivity. I conducted nest surveys from February to June to locate breeding pairs and nests. Monitoring continued through July until all surviving chicks had fledged. The surveying and monitoring was conducted by boat and birds were observed with 10 x 42 binoculars. I attempted to locate and observe every oystercatcher nest within the study area. I initially located incubating adults and those exhibiting defensive behaviors, and then searched the areas by foot to locate nests (Figure 4). Nest location was determined with a handheld global positioning system (GPS). I also recorded the adult color bands, egg number, and date found. I numbered eggs with a non-

toxic sharpie in order to determine whether there were newly laid eggs or eggs disappeared over the life of the nest. If the nest contained < 3 eggs, I checked the nest in the following visit to verify final egg number. I restricted time within nesting territories to less than 10 minutes.

I revisited nests again in subsequent weeks to verify whether the nest was active or had failed. Nests were considered active if I observed a bird incubating. If neither adult was incubating or displayed defensive behaviors before the estimated hatch date, I verified whether the nest had failed and attempted to determine the cause of failure. Evidence of nest failure included absence of eggs, unviable or cracked eggs, overwash of nesting area, and nest scrape disturbance.

I also employed motion activated game cameras and continuous video monitoring at *ca.* 15% of nests to document avian or mammalian predation. Camera monitored nests included those located on the mainland or islands accessible to predators, or nests surrounded by nesting gulls. If the nests failed, Dr. Heath reviewed the pictures and video to confirm the predation event. I used an incubation period of 27 days to estimate hatch date (American Oystercatcher Working Group *et al.* 2012) and those that hatched, were considered successful nests'. Evidence of a successful nest included direct observation of chicks or adults carrying food items within the territory. If this evidence was not observed, I approached the nesting area to search for chicks. If adults exhibited defensive behaviors such as flying and triple alarm calling, I assumed chicks were present and left the area to prevent further disturbance. I continued to monitor chicks after hatching and considered a chick successful if it survived to 35 days or when capable of sustained flight (American Oystercatcher Working Group *et al.* 2012). I considered a brood unsuccessful

if chicks were found dead before 35 days of age, adults did not exhibit defensive behaviors at the hatching date, or chicks were not seen for ≥ 2 weeks before they were capable of sustained flight.

Time activity budgets. I conducted behavioral observations of adult pairs during the incubation and chick rearing periods. Each focal animal observation or Time Activity Budget (TAB) consisted of a twenty minute sampling period, in which I recorded a behavior every fifteen seconds. Observation sessions occurred from land if possible or by boat when necessary using binoculars and a 20 x 60 spotting scope (Figure 5). I attempted to observe both adults simultaneously, but if an adult went out of sight for five consecutive minutes, I discontinued the observation period on that adult. I continued to observe the other adult unless it too went out of sight for greater than five minutes. I monitored pairs across three diurnal temporal blocks: morning (8:00-10:30), mid-day (10:30-13:00), and late afternoon (13:00-15:30). I conducted observations at a minimum of 50 m away, and moved further away if I suspected observer disturbance based on changes in bird behavior (Rave and Baldassarre 1989; Thibault *et al.* 2010). I did not randomly sample pairs because of logistical and time constraints. The opportunity to observe pairs depended on tide levels, weather, access to islands, and observation points. Also, the pairs I selected to observe in a single day depended on which time block a pair needed to be observed in, and whether the nest or brood was still active. In most instances, I did not complete consecutive observations on a pair within a single day. I completed TABs on as many nests as possible during the incubation period, and attempted to observe every pair with chicks due to small sample size and unpredictability of chick survival.

I documented twenty-one behaviors for the incubation and chick rearing periods, and defined and categorized behaviors based on previous studies by Purdy and Miller 1988; Rave 1989; Peters and Otis 2005; Sabine *et al.* 2008. I categorized behaviors into the following for both reproductive periods: incubation (i.e., incubating-roosting, incubating-vigilant, shading eggs), self-maintenance (i.e., preening, bathing, stretching, bill dipping), rest (i.e., roosting, standing, laying), forage (searching, probing, handling), locomotion (i.e., flying, walking, running), vigilance (i.e. standing-vigilant, laying-vigilant), agonistic (i.e., agonistic, fly-agonistic, walk-agonistic, run-agonistic), and chick care (i.e. brooding, chick feeding) (Table 1). Intra and interspecific interactions frequently caused oystercatchers to exhibit agonistic and vigilant behaviors. When this occurred, I coded the causes of these behaviors as laughing gulls, other oystercatchers, other bird species, humans, or observer.

Laughing gull surveys. I monitored and inventoried laughing gulls (hereafter gulls) in order to determine whether they affected oystercatcher parental behavior and reproductive success. I recorded the occurrence of nesting gulls and estimated the number of loafing and nesting gulls within the areal extent of what I considered an oystercatcher's nesting territory. Territory was defined as an area of shell hash and/or adjacent intertidal area in which there was evidence of reproductive activities and defense by a single oystercatcher pair (Hazlitt 2001; Steenhof and Newton 2007). I considered entire islands, such as small dredge spoils that were occupied by a single breeding pair as a territory.

I was able to conduct direct nest counts in small gull colonies (≤ 30 nests) to compare with my count of individuals. However, direct nest counts were not feasible in

large colonies because it disturbed not only gulls, but other nesting species. Areal surveys were conducted in which I counted all gulls occupying foraging territory, shell hash within a nesting territory, and those 10 m from the shell hash/vegetation line.

Gulls were counted when an oystercatcher nest was found, when it hatched or when a nest or brood failed. Gulls were also counted during a TAB. Gulls were counted by two observers, Dr. Heath and I on all occasions. I used the average of these counts as my estimate of gull density. In several cases I neglected to count gulls for a nest or TAB. To avoid removing them from the data set, I used the average of all gull counts I recorded throughout the season for that nest and TABs. I also identified whether gulls were nesting when an oystercatcher nest was found and at hatch or failure.

I utilized ArcGIS (ESRI 2010) to spatially depict data collected in the field and determine the size of oystercatcher nesting territories. I digitized the observed nesting territory data collected in the field on aerial overlays of the survey area to determine the area (ha) of nesting territory and assess whether nesting territory size is related to reproductive success.

Capture and banding. The American Oystercatcher Working Group initiated a color banding program in 1999 to learn about demographics, movement patterns, and habitat requirements of the birds. The working group maintains a database for researchers to enter and search for records of banded oystercatchers. Each state participating in the banding program is represented by a unique color leg band so researchers can determine where the oystercatcher was banded. I used U.S. Geological Survey stainless steel leg bands and PVC maroon color bands with unique alphanumeric codes for each bird (Figure 1). I attempted to band every chick that survived to 25 days, with a preferred age

of 30 to 35 days. I captured adults by employing a whoosh net in combination with oystercatcher decoys and recorded vocalizations (Figure 6). I also employed a box trap to capture incubating adults (Figure 7). I captured chicks by hand or with a hand net. During banding, I took morphometric measurements of each chick. I used digital calipers to measure culmen to the nearest millimeter, a metal wing ruler to measure unflattened wing chord length to the nearest millimeter, and a digital spring scale to measure weight in grams (Figure 8a-c). I physically estimated subcutaneous fat within the furculum region and assigned a fat score ranging from 1 to 5 (Meissner 2009) (Figure 9). A score of 1 indicated small traces of fat and very concave, while 5 indicated fat filling the entire furculum region and convex (Meissner 2009). I re-sighted banded birds during the entire study period to record survival, habitat use, and breeding pair fidelity.

Statistical analysis

Daily nest survival. Previous studies have used the Mayfield method for determining apparent nest survival, in which nest survival was the proportion of successful nests to unsuccessful nests (Dinsmore *et al.* 2002). This method assumes that successful and unsuccessful nests are found with equal probability; however, true nest survival is overestimated when failed nests go undetected, and the timing of hatch or loss may not be determined exactly (Dinsmore *et al.* 2002). Many ornithological studies now use Program MARK to model daily survival rates of nests' and broods' as a function of yearly and seasonal variation, nest age, and other covariates (Dinsmore *et al.* 2002). I used Program MARK to determine daily nest and brood survival for oystercatchers (White and Burnham 1999; Dinsmore *et al.* 2002). The daily survival rate (DSR) is calculated from nest observation days and the time of failure is assigned to an interval of

observation days so the exact failure date is not needed. Daily survival is the likelihood of a nest surviving one day. The nest survival model requires five pieces of information for each nest. They include: 1) the day the nest was found, 2) the last day the nest was checked alive, 3) the last day the nest was checked, 4) the fate of the nest (0 = successful, 1 = failed), and 5) the number of nests that were successful or failed. In the case of brood survival, the day the nest hatched, the last day a chick was seen alive and checked, and the fate of the chick were used in the analysis. I standardized the days within the breeding season, in which Day 1 represented the first day a nest was found and the first day a nest hatched. I used a 27 day incubation period and considered a nest to be successful if at least one egg hatched. Brood survival was the probability of at least one chick in a brood surviving to 35 days.

Program MARK allows temporal variation and individual covariates to be incorporated into candidate nest survival models. Program MARK builds and evaluates competing models of DSR using Akaike's Information Criteria (AIC). I used the Akaike's information criterion for small samples (AIC_c) to determine the best fitting model for daily nest and brood survival (Burnham and Anderson 2002). I considered models with ΔAIC_c values < 2 to be top competing models (Burnham and Anderson 2002). Model covariates whose 95% confidence limits did not include zero were considered statistically significant results.

First, I ran a simple model of constant daily nest survival. Constant daily survival (S.) is the default model in which DSR is assumed to be constant across all nests and all dates. Next, I incorporated temporal variation by modeling the main effects of a linear (LT) and quadratic (QT) time trend on DSR. The linear time was used because daily

survival typically decreases across the nesting season (Dinsmore *et al.* 2002). A quadratic time trend reflects a bimodal pattern that occurs with re-nesting (Dinsmore *et al.* 2002). Lastly, I added covariates to the best temporal model. From the linear model, parameter estimates are constrained to be linear functions of covariates. I hypothesized there were several covariates explaining the variation in nest and brood success and they included the following: territory size, number of gulls, presence or absence of nesting gulls, and nest and brood age. The number of gulls I counted at lay and hatch were used as the gull number covariate.

I modeled site fidelity with constant survival to determine if nest and brood survival differed when one or two adults occupied a territory for two consecutive years. Site fidelity was modeled separately because many birds are unbanded, and nests' with an unbanded adult would have to be excluded from the main analysis incorporating the time trend and individual covariates. I assigned nests and broods to one of two groups for site fidelity (Table 2).

Time activity budgets and behavior. I used Mann-Whitney and Kruskal-Wallis in Minitab® statistical package to examine differences in frequency of behaviors under the influence of four variables including 1) number of gulls, 2) absence or presence of gulls, 3) absence or presence of nesting gulls and 4) nest fate. Nest fate was categorized as fail or hatch and brood fate was no fledge or fledge. I created two classification schemes for gull density that were used to evaluate the influence of this variable on nest and chick rearing behaviors. First, I created class intervals of gull densities following Sturges (1926) method and displayed the class intervals in histograms. The histograms were asymmetrical, so I manipulated the category bins until there was a closely symmetrical

distribution of categories. The gull categories for incubation were (0-75 - low, 76-300 - high) and (0-49 - low, 50-99 - medium, 100-300 - high). The gull categories for chick rearing were (0-60 - low, 61-230 - high) and (0 - low, 1-40 - medium, 41-230 - high).

I examined differences in median values of behaviors for nest fate, presence or absence of gulls, and the various gull abundance classes using Mann-Whitney or Kruskal-Wallis. If significant differences were detected, the Dunn's multiple comparisons analysis was conducted to determine which group was different. I examined the incubation and chick rearing periods separately and each bird was considered a sample. I analyzed the proportion of time spent per behavior category by totaling the individual behaviors comprising a category for each sample (Table 1). To avoid a preponderance of zeros, I excluded the incubating adult when analyzing non-incubating behaviors and the non-incubating adult when analyzing incubation. I used Kruskal-Wallis and Mann-Whitney to determine if behaviors differed between time of day (morning, mid-day, afternoon) and chick age (1 to 20 days, 21 to 45 days). I used a histogram to categorize chick age and manipulated the category bins until there was a symmetrical distribution of chick ages. I considered $P < 0.05$ to be significant.

I utilized cluster analysis (CA) to group nests and broods based on similarity in lay date, chick age, behavior, number of gulls, nesting gulls, and territory size. The CA method used the Euclidean distance metric and Wards linkage method. All variables were standardized prior to cluster analysis. After classification, I generated median values of the variables for each group which was determined by CA.

I also utilized principle component analysis (PCA) to construct linear combinations of these variables to assess the relative importance of the variables and

identify those that explained the majority of differences between cluster groupings. I plotted the distribution and median values of these components, and then examined the loading and score biplots to determine if any patterns were associated with the groupings. I considered principle component loadings > 0.40 to be significant based on recommendations by McGarigal *et al.* 2000.

Body condition indices. I calculated scaled mass indices for oystercatcher chicks banded in 2013-2014 to determine if the presence of gulls explained variation in body condition. Many researchers have stated that body condition is a measure of the energetic reserves available for use by individuals in their daily processes (Colwell *et al.* 2007; Tjørve and Underhill 2008; Virzi 2008; Smith and Wilson 2010). Condition indices are calculated to reflect the health of an individual. A commonly used index is body mass, but mass is not independent of structural size. In order to separate mass of nutrient reserves from structural components, body mass is scaled to a structural measurement to remove size related variation (Colwell *et al.* 2007; Virzi 2008; Smith and Wilson 2010).

I followed the methods of Peig and Green (2009) to determine a scaled mass index for oystercatcher chicks. They employed the standardized major axis (SMA) regression between mass (y) versus length (x) log transformed data to estimate a scaling exponent (or the slope of the best fit line). I did not have the software to complete a SMA, so based on their recommendation I performed an OLS regression on the log transformed M-L data in Microsoft Excel 2013. I used the following equation to calculate a scaled mass index:

$$M = M_i \left[\frac{L_0}{L_i} \right]^{b_{sma}}$$

where M_i and L_i are the body mass and linear body measurements of individual i ; b_{sma} is the scaling exponent; L_0 is the arithmetic mean value of L for the study population, and M is the predicted body mass for the individual. The scaling exponent (b_{sma}) was calculated by dividing the slope from the OLS regression by the Pearson's r correlation coefficient. I used the Pearson's correlation method in Minitab® statistical package to determine if bill or wing was more correlated with weight. Wing length was more correlated with weight ($r = 0.594$ vs. $r = 0.509$).

I used independent, two-tailed T-tests in Minitab® statistical package to quantify the effects of gulls on scaled mass indices. The variables I examined included the absence or presence of nesting gulls and number of gulls. I analyzed several categories of gull numbers to determine if a threshold was evident. I categorized gull numbers into absent (0 gulls), present (> 0 gulls), a low number of gulls (0-20; 0-40), and a high number of gulls (21-140; 41-140). I also used a T-test to determine whether the presence or absence of other nesting bird species on oystercatcher territory explained variation in mass indices. I considered test results significant if $P < 0.05$. Prior to conducting the T-test, I tested the data set for normality and outliers using the Anderson-Darling and Grubbs tests'. I tested for equal variances between groups using Levene's test and assumed equal variances if $P > 0.05$. Since oystercatcher chicks were banded at various ages, I used the Tukey's test to determine if mass indices differed significantly between two age classes (23 to 32 days) and (33 to 42 days). I used histograms to categorize chick age and selected two categories that closely resembled a symmetrical distribution.

RESULTS

Nest Survival

I monitored 80 breeding pairs and 144 nests during the two year study period (Table 3). Seventy-eight percent of nests ($n = 113$) were located in Galveston Bay and the remaining 22% of nests ($n = 31$) were located in Drum and Bastrop Bays (Table 4). Fifty-six percent ($n = 81$) of nests were first nest attempts, and 44% ($n = 63$) were re-nest attempts. The majority of pairs only made one re-nest attempt ($n = 46$) and the percent of nests that hatched decreased as the number of re-nest attempts increased (Table 5). Clutch size ranged from 1-3 eggs and the average clutch size was 2.4 ($n = 126$ clutches of known size). Average clutch size for first nest attempts was 2.6 ($n = 76$) and lower for re-nests at 2.06 ($n = 50$). A nesting attempt was defined as a nest with at least one egg. In cooperation with Dr. Susan Heath, I banded a total of 54 oystercatchers; 20 adults and 44 chicks (USGS band permit 23712; UHCL IACUC 12.008.R1).

The nesting season, from first nest initiation to last nest hatched or last nest or brood failure, was 142 days in 2013. I found the first nest on 27 February 2013 and the last nest on 1 June 2013. The mean nest initiation date was 11 April 2013. The nesting season was 148 days in 2014. I found the first nest on 10 February 2014 and the last nest on 23 June 2014. The mean nest initiation date was 8 April 2014.

The mean nest initiation for first nest attempts in 2013 was 25 March and earlier in 2014 (20 March). The majority of first nest attempts were initiated in March for both

study years. The mean nest initiation for re-nest attempts in 2013 was 11 May and earlier for 2014 (7 May). The majority of re-nest attempts occurred in May for both study years.

Eighty nests failed in 2013-2014 combined. I could not identify the cause of failure for 47.25% of nests (Table 6). Known and unknown predation events accounted for 30.99% of nest failures. Known depredation events were those verified by motion activated camera or video monitoring and included feral cat, gull, and coyote. Unknown predation events were not captured on camera and I assumed a predation event had occurred based on evidence within the nesting area (i.e. digging in nest scrape, cracked egg near nest cup, rattlesnake presence). Overwash and weather related causes accounted for 21.13% of failures. I predicted that approximately 5% of nest failures were related to human disturbance. For example, I observed oystercatchers not incubating when a wade fisherman or boat approached the nesting site, consequently leaving the eggs vulnerable to weather and predation.

I estimated hatching success to be 40% ($n = 57$). Hatching success was defined as at least one egg hatched (American Oystercatcher Working Group *et al.* 2012). As previously stated, daily nest survival is defined as the likelihood of a nest surviving one day. Constant daily nest survival was 0.968 (SE 0.003). The probability of nest survival to hatching during the 27 day incubation period was 0.418 (SE 0.003).

Variation in nest survival was best explained by a linear time trend plus the additive effect of nest age (Table 7). As the nesting season progressed and nests' aged, daily survival rates decreased (Figure 11). The next best model included the additive effects of the remaining covariates ($< 2 \Delta AIC_c$) (Table 7). Survival was a function of the number of gulls, territory size, and the presence of nesting gulls, but support for the

covariates was weak (95% confidence intervals overlapped zero). Daily survival rate decreased with increasing territory size ($\beta_i = -0.085$, CL = -0.419, 0.248). Daily survival rate decreased as the number of gulls increased (Figure 12). When nesting gulls were present, daily survival increased ($\beta_i = 0.178$, CL = -0.384, 0.739)

When survival was held constant, daily survival was higher when one adult rather than two occupied the same territory for two consecutive years, but support was statistically insignificant ($\beta_i = 0.162$, CI = -0.398, 0.721).

Productivity

Productivity was 0.51 chicks fledged per pair in 2013 and 0.59 chicks fledged per pair in 2014 (Table 3). Forty-four chicks fledged from the 54 broods I monitored across 2013-2014. The percentage of clutches that fledged chicks in 2013-2014 was 43.5%. The majority of pairs fledged one chick ($n = 20$), while 9 pairs fledged two chick broods, and 2 pairs fledged three chick broods. The number of pairs fledgling a chick was greater in the absence of nesting gulls ($n = 26$) versus in the presence of nesting gulls ($n = 6$).

Overall, first nest attempts were more frequently ($n = 26$) successful (fledged ≥ 1 chick) compared to re-nest attempts ($n = 6$). In both seasons, 7 pairs re-nested after brood loss and one of these pairs fledged a chick. Re-nest attempts were initiated when broods were lost at 3 to 11 days old.

I could not document many causes of chick mortality. I was able to find 4 chick carcasses, and Figure 10 depicts two chicks that died during a cold front. There were three instances of fledgling mortality in both seasons. A breeding pair on South Deer lost a fledgling to disease in both seasons. During monitoring, we discovered that both chicks were severely emaciated. One chick was brought to a rehabber and died from West Nile

virus shortly thereafter, and the second chick had disappeared the following week. I hypothesized that another fledgling died in 2014, evident by the fledgling's disappearance from the adult pair approximately a month after their chick fledged.

Constant daily brood survival was 0.985 (SE 0.003). The probability of at least one chick surviving to fledging or 35 days was 0.591 (SE 0.003).

Variation in brood survival was best explained by a quadratic time effect and the addition of the number of gulls (Table 8). The model indicated that daily survival rates decreased as the season progressed and the number of gulls increased (Figure 13-14).

The next best model included the nesting gull covariate (2.32 ΔAIC_c units above).

Nesting gulls appeared to decrease daily survival, but not significantly ($\beta_i = -0.839$, CL = -1.690, 0.011). Adding all covariates to the quadratic time effect did not improve the model (Table 8). Brood survival appeared to be positively related to brood age, but the relationship was insignificant ($\beta_i = 0.033$, CL = -0.010, 0.076).

Brood survival was positively related to territory size, but not significantly ($\beta_i = 0.628$, CL = -0.591, 1.847). When survival was held constant, daily survival was higher when both adults occupied the same territory for two consecutive years, but was statistically insignificant ($\beta_i = 0.162$, CL = -0.398, 0.721).

Time activity budget

I conducted 249 time activity budgets and 18,540 behavioral observations on 60 nests during the incubation period in 2013-2014. During incubation, pairs engaged predominantly in incubation behaviors (52%) (Table 9). All other behaviors, such as foraging, self-maintenance, resting, locomotion, vigilance, and agonistic were much less

frequent. Resting (16%) occurred more often than self-maintenance (10%) and vigilance (8%). All other behaviors accounted for 14% of observations.

I conducted 187 time activity budgets and 13,976 observations on 38 broods during the chick rearing period in 2013-2014. During chick rearing, pairs engaged predominantly in resting (35%) and vigilance (29%) behaviors (Table 9). Foraging and chick feeding accounted for 13% of observations. Self-maintenance, locomotion and agonistic behaviors accounted for the remaining observations (23%). Pairs engaged in more self-maintenance, foraging, and agonistic behaviors during chick rearing than incubation.

Agonistic behaviors during the incubation and chick rearing periods were primarily caused by the presence of gulls and other oystercatchers (Figure 15). Gulls caused agonistic behaviors more than other oystercatchers during the incubation period, while the reverse was observed during chick rearing. The presence of other bird species were the next most common cause of agonistic behaviors.

Cluster analysis and Principle Component analysis

Incubation period. Based on the results of cluster analysis, I identified three groupings of nests (Table 10) (Figure 16). After examining the PCA plots, I found there were several characteristics associated with these nest groups (Figure 17). Oystercatchers in group 3 were early to mid-season nesters and had the greatest occurrence of incubation (Table 10). Nesting gulls were absent, and they occasionally had loafing gulls on their territories. Oystercatchers in group 2 were late season nesters and engaged in more agonistic, vigilant and roosting behaviors (Table 10). They had nesting gulls and high numbers of gulls on their territories. Oystercatchers in group 1 were early season nesters

and had the greatest occurrence of vigilance and locomotion (Table 10). No nesting gulls were present, but the number of loafing gulls ranged from low to high. Hatching success was higher for cluster 3 (71.4%) than clusters 1 (39.4%) and 2 (29.4%).

I generated and analyzed five principle components (PC) and PC1 through PC3 explained 52.8% of the variation in the original data matrix (Table 11). The variation in PC1 was primarily explained by incubation, locomotion, and vigilance (Figure 17). Lay date, roosting, and nesting gulls were the variables with the highest loading coefficients and explained the greatest amount of variation along the PC2 axis (Figure 17). Finally, PC3 was best explained by locomotion, vigilance, agonistic, and foraging behaviors (Table 11).

Chick rearing. Cluster analysis identified two clusters of similar broods (Table 12) (Figure 18). After examining the PCA plots, I determined there were several characteristics associated with the groups (Figure 19). Oystercatchers in group 1 engaged in more roosting and foraging behaviors (Table 12). Nesting gulls were absent, and they occasionally had loafing gulls on their territories. Oystercatchers in group 2 engaged in more agonistic, vigilant, locomotive, and chick care behaviors (Table 12). They had nesting gulls and high numbers of gulls on their territories. Chick age was similar between clusters. Brood success was higher for cluster 1 (95.2%) than cluster 2 (35.3%).

Five principle components were generated with PC1 through PC3 explaining 60.2% of the variation in the original data matrix associated with chick rearing (Table 13). The variation in PC1 was best explained by vigilance, roosting, number of gulls, and nesting gulls (Figure 19). Chick age, foraging, and locomotion were the components

driving PC2 (Figure 19). Finally, PC3 was best explained by chick age, chick care, and agonistic behaviors (Table 13).

Behavior

Roosting and vigilance were the only behaviors that differed significantly between successful and unsuccessful nests and broods (Table 14). Oystercatchers with successful nests roosted significantly less than those with failed nests ($P = 0.042$) (Table 15). Although not significant, incubation and self-maintenance occurred more often when nests were successful (Table 15). Pairs that fledged a chick roosted significantly more than pairs that did not ($P = 0.031$) (Table 17). Oystercatchers that did not fledge a chick were significantly more vigilant than those that did ($P = 0.009$) (Table 17).

Behaviors exhibited during the incubation period did not differ significantly in the absence or presence of nesting gulls (Table 16). Although not significant, oystercatchers engaged less in incubation and self-maintenance, and more in roosting in response to gulls (Table 15). Roosting, chick care, and vigilance differed significantly when nesting gulls were present during the chick rearing period. Roosting increased when no nesting gulls were present ($P = 0.013$) (Table 17). Vigilance and chick care increased significantly in the presence of nesting gulls (Table 16-17).

During incubation, vigilance only differed significantly when there were ≥ 100 gulls. Specifically, vigilance was significantly higher when there were 100-300 gulls present versus 0-49 and 50-99 gulls (Figure 20). Although not significant, incubation and self-maintenance decreased, and roosting increased as the number of gulls increased (Table 15). During chick rearing, vigilance was the only behavior that exhibited

significant differences between gull numbers. Vigilance increased as the number of gulls increased ($H_2 = 11.11$, $P = 0.004$) (Figure 21).

Body condition

I found no significant differences between the age classes ($P > 0.05$). The scaled mass indices were normal and no outliers were present ($P > 0.05$).

I found significant differences in scaled mass indices between the absence and presence of gulls ($P = 0.012$). Mass indices were higher when gulls were absent than when gulls were present (Table 18). As the number of gulls decreased, indices increased significantly (Table 18). Indices also differed significantly in the presence or absence of nesting gulls and indices were higher when nesting gulls were absent (Table 18). Mass indices did not differ significantly in the absence or presence of other nesting species ($P = 0.289$).

DISCUSSION

Nest survival

The proportion of nests hatching (40%) in 2013-2014 was similar to what Koczur (2013) found along the central and upper Texas coast in 2011-2013. Compared to previous years, hatching success was higher than 2012 (30%), but considerably lower than 2011 (56%). On the Atlantic coast, hatching success has been variable, but generally lower. In North Carolina, Davis *et al.* (2001) and Schulte (2012) documented a 32% and 28% hatching success rate. In Georgia, Sabine *et al.* (2006) reported a hatching success rate (45%) similar to my findings.

My constant DSR (0.968) and probability of hatching (0.418) was similar to Koczur (2013) findings for oystercatchers along the Texas coast. On the Atlantic coast, DSR has varied among studies. Sabine *et al.* (2006) and Borneman (2013) reported similar DSR of 0.979 and 0.966. Schulte (2012) estimated a lower DSR (0.950) and probability of hatching (0.28). Similarly, Davis *et al.* (2001) reported a DSR of 0.928 and 0.133 probability of hatching.

During this study, I found that nest survival was primarily influenced by the nest initiation date and nest age. I determined that daily survival rates decreased as the season progressed. Several studies have found that nest survival varied seasonally and begin to decline by mid-season (Smith and Wilson 2010; Schulte 2012; Koczur 2013). There are several factors that may explain this relationship. As the season progresses, nests become vulnerable to heat stress, high tide events, and disturbance by recreationalists. During the study, strong southerly winds from April through June frequently caused high tide events that resulted in several occurrences of synchronous nest loss. Furthermore, the arrival of colonial nesting species like laughing gulls, brown pelicans, and waterbird species in mid-April may have strongly affected oystercatcher hatching success. For example, birds that nested near the mean initiation date of March 25th had 49% hatching success, while the hatching success of those nesting after this date was 32%. Johnson and Walters (2008) and Tjørve and Underhill (2008) found that birds initiating clutches early in the season also had higher hatching success. The temporal variation may also explain why re-nesting attempts were less successful. The mean initiation date for re-nesting was early May, and hatching success was 30%.

I found that daily survival decreased as a nest aged, but many studies have found nest age to be positively related to daily survival (Klett and Johnson 1982; Smith and Wilson 2010). A positive relationship may indicate that as a nest ages, it becomes increasingly valuable to adults; and the adults will allocate more time towards incubation and nest defense (Smith and Wilson 2010). My findings are consistent with those by Johnson and Walters (2008) and Koczur (2013). Johnson and Walters (2008) suggested that a negative relationship between DSR and nest age may be related to site experience. They found that when western sandpipers had more than two years of site experience, DSR varied less as a nest aged.

Nest survival was higher when only one adult occupied the territory for two consecutive years. My analysis of site fidelity was not consistent with other studies. Hazlitt and Butler (2001) found that hatching success was higher when black oystercatcher pairs occupied territories for two seasons. Johnson and Walters (2008) determined that nest survival was higher for western sandpipers (*Calidris mauri*) that had prior breeding site experience. My results may be skewed because unbanded birds were excluded from the analysis because I could not determine if the same bird had consecutively occupied the territory.

Oystercatchers occupying larger territories were typically breeding on larger islands, and my findings of lower nest survival associated with larger territories are consistent with Atlantic coast studies. On the Atlantic coast, hatching success was higher on isolated islands than large barrier islands. For instance, Virzi (2008) reported lower hatching success on barrier islands (5.8%) than on salt marsh and dredge spoil islands (37%). Similarly, McGowan *et al.* (2005) estimated hatching success on dredge spoil

islands as 45% and 11% on barrier islands. Many Atlantic coast studies have attributed differences in nest survival to higher predator abundance on large islands.

Mammalian predation has been documented as the leading cause of predator mortality in many studies on the Atlantic coast (American Oystercatcher Working Group *et al.* 2012). McGowan and Simons (2005) found that the absence of mammalian predators on dredge spoil islands accounted for higher nest survival than on barrier islands. In Massachusetts, Murphy (2010) reported 67% hatching success when predators were absent. In my study, breeding sites that are accessible to mammalian predators generally yielded more variable hatching success. I documented several instances of nest predation by mammals, and these nests were located on the mainland or on islands connected to the mainland by intertidal oyster reefs. During separate low tide events, we observed a raccoon and coyote reaching an island via the reef. Furthermore, large islands within the study site supported large nesting colonies of laughing gulls, brown pelicans, tern and wading bird species. The abundance of competing species of nesting birds appeared to influence the behavior and reproductive success of oystercatchers. There were numerous instances when I observed oystercatchers flushing and displaying agonistic behaviors towards other bird species approaching their nesting site. I also documented kleptoparasitism by nesting forster terns' s and gulls when an oystercatcher adult returned to feed its chick.

Nest failures

I was not able to directly document most nest failures and had to rely on indirect evidence. Failures that were reported as unknown generally represent nests where predation, weather events, and human disturbance were the suspected causes of failure.

northerly storms bring cold fronts during February and March, and several failures likely occurred when eggs were exposed to cold temperatures. Many nests were overwashed during high tide and storm events.

Based on my observations, egg predation by rattlesnakes and coyotes are also likely causes of some of the observed nest failures. For example, I observed several occasions of coyote near different islands, and did not find eggs in the following nest checks. On the larger islands western diamondback rattlesnakes are present. On one island it is very likely that a breeding pair lost two nests' to rattlesnake predation based on visually documenting the rattlesnake near the nest during my nest monitoring and little evidence of nest scrape disturbance.

Although brown pelicans do not predate nests, their activity along the shell hash where nests were found may have destroyed nests. Brown pelicans frequently came very close to stepping on nests. On two occasions, I observed a non-incubating adult oystercatcher engaging in a standoff with a brown pelican that had approached the nest site. This response may indicate that oystercatchers perceive brown pelicans as a threat because of previous interspecific interactions. Denmon *et al.* (2013) previously documented twenty-one instances of incubating oystercatchers reacting to brown pelicans along the Atlantic coast.

Recreationalists may have been indirectly related to several incidences of nest failure. Incubating oystercatchers would often flush from their nests' when boaters or wade fisherman were near the islands. Unattended nests result in eggs being exposed to potentially lethal ambient temperatures and higher risk of depredation by gulls. On the Atlantic coast, human activity near breeding sites has shown to alter oystercatcher

behavior and reduce nest attendance, consequently affecting reproductive success (Davis *et al.* 2001; Verhulst *et al.* 2001; McGowan and Simons 2006; Sabine *et al.* 2008). I did not document humans directly causing nest failures, but believe two oystercatcher nests were destroyed when humans were recreating on islands in Drum Bay. In the subsequent nest check, not only did I find human garbage, but it was evident that humans were walking around the island.

Brood survival

The number of chicks fledging in 2013 (0.51) and 2014 (0.59) was higher than 2012 (0.21), but lower than 2011 (0.81) (Koczur 2013). On the Atlantic coast, productivity is highly variable and has ranged from 0 to 1.48 (Clay *et al.* 2014). Oystercatcher productivity in Texas seems relatively high compared to Atlantic coast states. In North Carolina from 1998-2009, annual productivity was 0.32 (Clay *et al.* 2014). Sabine *et al.* 2006 reported 0.46 productivity in Georgia.

My constant DSR (0.985) and probability of fledging (0.591) was similar to previous findings by Koczur (2013) for oystercatchers along the Texas coast. Also, studies from the Atlantic coast have yielded similar results. In North Carolina from 1998-2009, daily brood survival was 0.981 and the probability of fledging was 0.471 (Clay *et al.* 2014). Sabine *et al.* 2006 estimated daily survival to be 0.991 and the probability of fledging was 0.329 in Georgia.

Daily brood survival was primarily influenced by the hatching date and daily survival decreased as the season progressed. As discussed earlier, this negative relationship may be influenced by colonial nesting birds, weather, and predator abundance. The probability of chick predation increases when gulls begin nesting and

mammalian presence increases as the season progresses. It is highly likely that cold fronts early in the season increased food availability and consequently the probability of fledging. Frequent northerly winds early in the nesting season cause extreme low tide events within the bays, and results in greater reef exposure over long periods of time. As mentioned previously, southerly winds beginning in April cause prolonged high tide events and reduce reef exposure. I recorded several instances of mortality in older chicks (> 2 weeks) during high tide events. Typically, the probability of fledging increases as chicks' age and they become decreasingly vulnerable to threats (Colwell 2007, Schulte 2012). I believe that decreased food availability during high tide events contributed to the starvation of these chicks.

Brood survival increased as a chick aged and these finding are consistent with other studies by Colwell *et al.* 2007, Schulte 2012, and Koczur 2013. Oystercatcher chicks are semi-precocial and they depend on their parents for food and protection from weather and predators. For shorebird species with precocial young, high mortality occurs soon after hatching (Colwell *et al.* 2007). Schulte (2012) found that chick mortality was highest during the first week after hatching. Groves (1989) and Hazlitt and Butler (2001) also found similar results for black oystercatchers. On a study of Eurasian oystercatchers (*H. ostralegus*), Ens *et al.* (1992) determined that chick mortality predominantly occurred within 10 days of hatching.

Sources of chick mortality

I did not document many causes of direct mortality to chicks and believe that predation and inclement weather were the primary sources of mortality. I suspected coyote predation occurred on an island where a game camera had captured a coyote

visiting the nest the night of hatching. The camera showed two chicks had hatched, but only one chick was verified in the subsequent nest check. Approximately three weeks later, the second chick had disappeared too and it's likely that the coyote continued visiting the nesting territory. Several instances of chick mortality occurred during cold fronts with high northerly winds when newly hatched chicks were likely exposed to cold temperatures and rain. As mentioned previously, high tide events may have caused chick starvation later in the season.

Time activity budgets

As expected, pairs spent most of their time incubating during nest rearing, which is consistent with other studies and characteristic of bi-parental care (Byrkjedal 1985; Kersten 1996; Collins 2012; Spiegel *et al.* 2012). Incubation bouts are influenced by foraging opportunities and disturbances (Purdy and Miller 1988; Sabine *et al.* 2008; Spiegel *et al.* 2012). Black oystercatchers incubated continuously when high tides prevented foraging, and exhibited short incubation bouts at low tide so both adults could forage (Purdy and Miller 1988; Spiegel *et al.* 2012). Furthermore, long incubation bouts are suggested to be an effective anti-predator strategy that minimizes the risk of predation (Smith *et al.* 2007; Sabine *et al.* 2008). I found nest departures were due to mate switching, human disturbance and defense against predators or conspecifics. Typically, oystercatchers left nests when boats approached islands, or to chase and attack intruders. Lastly, data collected during this study and other studies supports the hypothesis that incubation behavior is directly related to nest success (McGowan and Simons 2006; Collins 2012). Although, incubation was not significantly related to nest fate, there was a

positive relationship between the occurrence of successful nests and longer incubation times.

Following incubation, resting and self-maintenance behaviors occurred more often than the remaining behavior categories. Collins (2012) and Sabine *et al.* 2008 found that American oystercatchers on the Atlantic coast spent similar time in self-maintenance, but less time resting. On the other hand, Byrkjedal (1985) found golden plovers (*Pluvialis apricaria*) spent similar time resting. Preening and bathing are critical for maintaining good condition of feathers, and I expected oystercatchers to allocate sufficient time towards self-maintenance. While incubating, oystercatchers were vigilant 38% of the time and roosted only 7% of time. When adults were relieved from incubating, they would typically begin roosting or preening. Incubation is less energetically demanding than chick rearing, but constant allocation towards vigilance may affect energy reserves and explain why roosting occurred so often. The frequency of self-maintenance and roosting behaviors could also be influenced by food availability.

As expected, pairs predominantly engaged in vigilant behaviors during chick rearing which is consistent with other studies on American oystercatchers by Sabine *et al.* 2008 and Collins (2012). Either one or both adults would exhibit vigilance while standing or laying near a chick, presumably chick guarding. Byrkjedal (1985) observed that at least one adult golden plover was always chick guarding. I determined that even when oystercatchers exhibited significantly more vigilance, they did not always fledge a chick. This may have been related to poorer parental performance and gull presence, or because I did not document the true cause of chick mortality.

Though, only 3% of observations were agonistic behaviors, pairs exhibited them more often during chick rearing than incubation. Collins (2012) found that oystercatcher brood success was positively related to agonistic behaviors. Other oystercatchers and gulls were the major causes of agonistic behavior, but differed depending on the reproductive period. During incubation, nearly 50% of the agonistic occurrences were towards gulls. These findings are not surprising considering that gulls are the major predatory threat to eggs and chicks. During chick rearing, the frequency of agonistic occurrences was similar for gulls and conspecifics. Territory disputes were very common when several breeding pairs were occupying an island. I also documented a suite of bird species that elicited agonistic responses including: great blue heron (*Ardea Herodias*), great egret (*Ardea alba*), willet (*Tringa semipalmata*), tri-colored heron (*Egretta tricolor*), ruddy turnstone (*Arenaria interpres*), grackle species (*Quiscalus spp.*), peregrine falcon (*Falco peregrinus*) and tern species. On the Atlantic coast, Denmon *et al.* (2013) observed oystercatchers responding to great egret, tri-colored heron, willet, and grackles.

I was surprised that foraging and chick care behaviors only accounted for 13% of observations because many studies have found that these behaviors occurred more often (Byrkjedal 1985; Kersten 1996; Collins 2012). My research was not focused on documenting foraging behavior, which is a likely reason why the time spent foraging was underestimated for several reasons. First, I did not include tidal phase in my statistical analysis of behaviors. As mentioned before, tide levels and amount of reef exposure highly influences oystercatcher foraging behavior. Though I conducted TABs at various tidal phases, the observations were not scheduled around low tide events when foraging

opportunities are greater for oystercatchers. Secondly, because of logistical constraints, I did not conduct observations at sunrise or dusk, which are times of high foraging activity for birds.

Chick age may also explain some of the variability in adult behaviors. As chicks age, they become more independent and parents allocate less time toward chick attendance and possibly more time for themselves (Byrkjedal 1985; Colwell *et al.* 2007; Collins 2012).

There are other factors that may have affected bird behavior that I did not evaluate due to limited resources. First, the sex of adults has been shown to influence the quantity of oystercatcher parental investment (Purdy and Miller 1988; Palmer *et al.* 2001). Depending on the gender, an adult will allocate time towards incubation and nest disproportionately. For example, large bodied females typically incubate more, while males initiate nest defense behaviors (Purdy and Miller 1988; Nol 1989). American oystercatchers exhibit sexual dimorphism, but there is a large range of overlap so I was not able to verify sex of every adult. Secondly, flushing off the nest affects nest success (Smith *et al.* 2007). I did not measure whether flushing was related to nest success because flushing events were inconsistently documented. Finally, I did not measure nocturnal behavioral patterns, so I may have underestimated behaviors that oystercatchers engage in at night such as incubation, roosting, and predator defense.

Daily survival and laughing gulls

Daily nest survival decreased as the number of gulls increased, but not significantly. Only one gull predation event was verified by camera, but there was evidence that suggested gulls are a major threat to eggs. Adults were frequently agonistic

at gulls near their nests' and I found eggs with holes within the nest site. I believe that gulls were predating eggs when nests were left unattended. Hazlitt (2001) found that black oystercatcher pairs nesting near glaucous-winged gull (*L. glaucescens*) colonies had significantly smaller clutch sizes than pairs without adjacent gulls and attributed these results to egg predation by gulls.

Conversely, nest survival slightly increased in the presence of nesting gulls; however, hatching success was still higher (41%) when nesting gulls were absent than when they were present (33%). The size of colonies and the proximity to nesting gulls may explain these findings and suggest a density dependent threshold. Large islands within the study site supported high density nesting colonies, while small dredge spoils typically supported ≤ 20 gull nests'. Oystercatcher pairs may be capable of effectively defending against several gulls versus a large aggregation of gulls. This may also support why daily survival was higher on smaller territories.

The top model for brood survival during this study included the number of gulls. Daily survival decreased significantly as the number of gulls increased. The presence of nesting gulls decreased daily survival, but not significantly. However, substantially more pairs ($n = 26$) fledged a chick in the absence of nesting gulls than in the presence of nesting gulls ($n = 6$). A study on European oystercatchers found that breeding success was only higher in areas with very low numbers of gulls (Harris and Wanless 1997). Magella and Brousseau (2001) also found that chick predation by herring gulls (*L. argentatus*) was the major factor explaining low reproductive success of common terns (*Sterna hirundo*). Additionally, O'Connell (2003) confirmed that black skimmers

(*Rynchops niger*) and terns breeding on islands with nesting gulls experienced higher rates of gull disturbance than those breeding on islands lacking nesting gulls.

Body condition and laughing gulls

Chick body condition was lower when nesting gulls were present and as the number of gulls increased. Many studies relate body condition to an individual's energetic state and overall fitness (Peig and Green 2009; Schamber *et al.* 2009). Furthermore, Tella *et al.* (2001) suggested that chick fledging weights are positively correlated with juvenile survival for many species. My results showed changes in parental behavior were associated with breeding near nesting gull colonies. Although not statistically significant, foraging decreased in the presence of nesting gulls and as the number of gulls increased. The stressful conditions of breeding near a large colony may result in more parental allocation towards chick guarding and less towards chick attendance, and ultimately compromise chick body condition. A study on colonial penguins found that higher breeding densities around a nest site negatively affected offspring condition because adults invested more in nest defense and less in chick attendance (Tella *et al.* 2002).

Poor chick body condition may influence the probability of an oystercatcher surviving their first non-breeding season. Intraspecific competition between adults and juveniles on wintering sites may force individuals in poor condition to disperse to lower quality habitat (Barbraud *et al.* 2003). Based on personal observations, juvenile oystercatchers tend to roam within the bays and feed together on the reefs. Adult and juvenile oystercatchers also flock during the winter and I have observed both cohorts feeding near each other. I witnessed intraspecific interactions on multiple instances. First,

when juveniles attempted to feed on a breeding pair's feeding territory and secondly, when both cohorts were feeding together on unclaimed reefs. During these periods of interaction, adults elicited agonistic reactions when juveniles encroached on their active foraging area.

Based on banding re-sights, we are aware that juvenile oystercatchers disperse along the central and upper coasts. I feel that oystercatchers also disperse to other areas like Louisiana and Mexico, but little is known about juvenile dispersal patterns along the Gulf coast. Barbraud *et al.* (2003) found that dispersal rates increased when juvenile flamingos were in good condition. If juvenile oystercatchers are displaced from natal sites and forced to roam along the Gulf coast, body condition may be a key variable that predicts their probability of survival.

Body condition does not reflect true physiological conditions, and unverified indices must be used with caution. Many studies recommend making repeated measures and validating indices with some physiological measure like total body fat or protein (Peig and Green 2009). A causal relationship between gulls and lower chick body condition cannot be inferred because I did not measure all variables that may influence body condition. Many studies have determined that oystercatcher reproductive success is influenced by foraging (Nol 1989; Ens *et al.* 1992; Kersten 1996; Thibault *et al.* 2010). I did not measure parental foraging rates, food items, and the area or location of feeding territories. Food availability is also influenced by tide levels and amount of reef exposure. Lastly, brood size and sibling rivalry may also explain variation in body condition. Groves (1984) found weight differences between siblings in two chick broods, with the larger sibling exhibiting more dominance.

Parental behavior and laughing gulls

I found that many behaviors during incubation were not significantly influenced by nesting gulls or the number of gulls. However, parental vigilance did increase significantly when there were ≥ 100 gulls. This supports my hypothesis that a density dependent threshold of gulls exist, in which parental behavior begins to be significantly affected when gulls reach a certain density. Also, my findings demonstrate that oystercatchers nesting near high density of gulls are allocating time differently than oystercatchers nesting near fewer gulls.

I found that oystercatchers with successful nests roosted significantly less than those with failed nests, which may be influenced by gulls. Although not significant, they roosted more in response to gulls. As mentioned previously, it appears that oystercatchers within a stressful environment may have to roost more to maintain their energy stores. It may also be a strategy to reduce nest site activity and prevent gulls from cueing onto the nest site location. Even though I did not find significant differences between incubation occurrence and gulls; I did find evidence that incubation activity decreased in the presence of nesting gulls and as gulls increased. In my study, gulls are the main disturbance factor, and these results provide additional evidence that gulls appear to shift parental oystercatcher activities away from the nest.

During chick rearing, vigilance increased significantly when nesting gulls were present and there was a positive relationship between vigilance and the number of gulls (Figure 21). Also, regardless of the number of gulls, vigilance increased significantly when gulls were present (≥ 1). My findings suggest that gulls affected vigilance differently depending on the reproductive period. The findings provide additional

evidence that adults are allocating their time disproportionately as the number of gulls increase. Furthermore, pairs that did not fledge a chick were significantly more vigilant than pairs that did. This suggests that first, increasing vigilance may not be enough to overcome gulls and secondly, other factors including mortality source, chick age, or hatching date may explain these results too. However, considering all my findings, I suggest that high gull densities cause adult oystercatchers to allocate less time towards behaviors that benefit individual fitness and reproductive success.

Based on my results, laughing gulls influenced parental behavior and daily survival more during the chick rearing period. As mentioned before, young chicks are particularly vulnerable to predation. Furthermore, studies have suggested that chick survival is a critical period that affects breeding productivity (Colwell *et al.* 2007; Schulte 2012). During the study, the breeding season was typically over when breeding pairs lost their chicks. Intensifying parental care during the chick rearing period is a reproductive strategy to increase the likelihood of a breeding pair's reproductive success.

Laughing gull predation

Avian predation is very difficult to document because there is usually no evidence and predation occurs very quickly. Gull species are opportunistic feeders and predation typically occurs when eggs and chicks are exposed (Lauro and Burger 1989). Several studies on oystercatchers have documented gull species as predators (Vermeer *et al.* 1992; Hazlitt 2001; Verboven *et al.* 2001). I hypothesized that oystercatcher eggs were extremely vulnerable to gull predation when gulls were nesting or loafing on their breeding territories. In 2013, I employed motion activated game cameras to monitor nests with a high probability of gull predation. Unfortunately, the delay between the motion

sensor and camera prevented us from capturing quick predation events. In 2014, I employed two 24 hour continuous video surveillance systems to record incubating oystercatchers. As a result of frequent camera malfunctions, I only captured one gull predation event; in which a gull cracked open the two eggs and consumed the yolk. In most cases when I attributed nest failures to unknown predation events, I assumed gull predation had occurred evident by eggs with holes and the presence of yolk near the scrape. Typically, predation occurs when oystercatchers flush in response to a disturbance, leaving the nest unattended (Verboven *et al.* 2001; McGowan and Simons 2006; Sabine *et al.* 2006).

In addition to egg predation, I believe that young chicks (< 2 weeks) were predated by gulls even though I was unable to document this visually. Many studies on waterbirds have documented gull species depredating chicks (Kury and Gochfeld 1975; Harris and Wanless 1997; Magella and Brousseau 2001; O'Connell and Beck 2003). Specifically, McGowan (2004) observed a laughing gull depredating an oystercatcher chick in North Carolina. During behavioral observations, I documented several instances of gulls harassing and/or attempting to predate young chicks. These events occurred when the young chick was left in the open unattended. As chicks grew larger, the risk of predation decreased because chicks avoided gulls by running; and I observed little interspecific interactions when older chicks were in the open and near gulls.

Management strategies for laughing gulls

Many Atlantic coast states have implemented mammalian and avian predator control measures in an effort to increase oystercatcher productivity. However, predator control is labor intensive, long-term, and expensive and may not be supported by the

general public. Studies have reported varying results on the efficacy of gull control measures. In an effort to increase a Eurasian oystercatcher population in Scotland, gull control measures were implemented from 1972 to 1988. First, large scale culling of adults occurred from 1972 to 1976, followed by egg destruction from 1984 to 1988. Harris and Wanless (1997) determined that the number of breeding oystercatchers increased immediately after culling, and suggested that gull free areas attracted oystercatcher recruits. Even though gull populations remained low, oystercatcher populations began declining once control measures were relaxed. Furthermore, reproductive success did not significantly improve as a result of culling because gull predation was still occurring. Harris and Wanless (1997) suggested that complete removal instead of a gradual reduction of gulls maybe more effective for improving breeding success.

In a study on common terns, predatory gulls were shot to increase reproductive success. Culling lengthened the life span of broods and increased reproductive success, but it was not a significant improvement (Magella and Brousseau 2001). They suggested reproductive success may have increased considerably if they completely removed gulls earlier in the season. Furthermore, the effects of predator control did not carry over into the subsequent season; and consequently, predation rates were similar to the baseline year (Magella and Brousseau 2001).

Large scale culling is beneficial for rapid and substantial reduction, but influences population dynamics (Wanless *et al.* 1996; Bosch and Sol 1998). Gull fecundity and recruitment is density dependent, and reducing nest density may ultimately attract new recruits to the colony or influence dispersal between colonies (Wanless *et al.* 1996; Bosch

and Sol 1998). Gull control is typically implemented on species like greater black-back and herring gulls. These are large predatory gulls that are highly territorial, in which several dominate males exhibit this feeding behavior (Yorio and Quintana 1997). Selective culling within a high density colony would probably be an ineffective measure, and large scale culling involving egg destruction and/or dispersing poison bait throughout colonies would be more suitable. Long-term logistical and financial support from multiple agencies would be needed to implement laughing gull control. It appears that removal of laughing gulls is not an absolute solution and habitat management could be more feasible.

American oystercatchers and laughing gulls prefer somewhat similar nesting habitat. I propose making habitat less favorable to gulls in an effort to prevent gulls from nesting on oystercatcher breeding sites. Studies have determined that gulls prefer salt marsh islands and higher elevated nest sites surrounded by *Spartina alterniflora* (Bongiorno 1970; Burger and Shisler 1978). Within my study site, gulls tended to nest in two habitat types, 1) within the *S. alterniflora* behind shell hash berms on salt marsh islands and 2) elevated, shrubby areas on dredge spoils. The shrubby areas included vegetation like Carolina wolfberry (*Lycium torreyi*), marsh elder (*Iva annua*), saltwort (*Batis maritima*), and grass species. The shrubby vegetation provided a substrate for nest building and concealment, thus I recommend removing this vegetation from dredge spoil islands. However, monitoring would be needed to determine if vegetation removal increases erosion. Furthermore, there were several islands that gulls nested on in 2013 but did not return to in the subsequent season. I believe this was attributed to vegetation growing too tall and decreasing visibility. Gulls have been found to nest in *S. alterniflora*

that ranged from 0.20 m to 0.80 m (Bongiorno 1970; Burger and Shisler 1978). I also suggest maintaining tall vegetation or low growing vegetation on dredge spoils to provide nest concealment and chick refuge. Munters (2014) found oystercatchers breeding in Texas nested on sites with 30% live vegetative cover that included species like Sea purselane (*Sesuvium portulacastrum*), saltwort, and sea ox eye daisy.

Salt marsh islands are critical coastal ecosystems along the Texas coast and the large islands support many oystercatcher breeding pairs. The salt marsh islands within my study site supported large colonies of nesting gulls. It may be more feasible to implement gull culling on the salt marsh islands. Another strategy could entail increasing the size of existing dredge islands to support more oystercatcher breeding pairs. Implementing habitat manipulation in conjunction with culling at select sites for several seasons may boost reproductive success short term. Research would be needed to determine how management would affect gull dispersal along the upper coast and if management would have long lasting implications on oystercatcher productivity.

Conclusions

The reproductive success of American oystercatchers breeding along the upper Texas coast is dependent on a combination of many intrinsic and extrinsic factors. My study determined that daily survival was primarily influenced by seasonality, nest and brood age, and laughing gulls. I believe that other variables like mate fidelity, vegetation cover, and size and distance to feeding territories not measured during this study potentially influence daily survival. I recommend including these variables in future productivity studies of oystercatchers.

Oystercatcher reproductive success was also influenced by predation and weather. It is apparent that oystercatchers nesting on the mainland or islands connected to the mainland during low tides are vulnerable to mammalian predation. The abundance of mammalian predators within my study sites did not appear to be as severe a problem as reported along the Atlantic coast. Instead, it appears that individual mammals that were able to revisit nest sites were lowering nest survival. I recommend employing live traps near nesting sites where mammalian predation has been documented. Similar to the Atlantic coast, nest survival is also dependent on tide levels and island elevation. I suggest that habitat enhancement that elevates shell mounds on dredge spoil islands above the high tide line would increase American oystercatcher productivity.

In Texas, population growth and high recreational activity along the coast will continue to leave oystercatchers vulnerable to human disturbance. I assisted in putting up conservation signs informing the public to stay a certain distance from breeding birds. Whether it is humans disobeying the signs, recreating on islands, or affecting parental behavior, future research should aim to document the prevalence of human disturbance. Currently, the American Bird Conservancy is partnered with Gulf Coast Bird Observatory in educating fishermen and recreational boaters about nesting birds within the bays.

Based on my findings and other studies, it is apparent that chick survival is a critical period that affects productivity and ultimately population recruitment. As mentioned previously, data is lacking on the survival and dispersal of juvenile oystercatchers along the Gulf coast. In order to better understand the population

dynamics of Texas oystercatchers, future monitoring should focus on band re-sightings along the coasts of Texas, Louisiana, and Mexico.

This was the first study in Texas to quantify American oystercatcher behavior and document the negative effects of laughing gulls. Parental behavior influences nest and brood fate to some extent, but more research on individual characteristics, foraging behaviors, and nest attendance are needed to determine the strength of these potential relationships. Extrinsic factors like conspecifics, other bird species, and abiotic variables are also likely affecting parental behavior. Considering the relationship between foraging and reproductive success, I recommend conducting a future foraging behavioral study that measures foraging rates, prey items, tide levels, feeding area, and time of day.

The results of this study supported my hypothesis that laughing gulls are negatively affecting daily nest and brood survival, parental behavior, and chick body condition; but laughing gulls affected productivity and behavior differently depending on the reproductive period. Laughing gull predation of eggs and young chicks is a predominant threat to oystercatcher reproductive success, but additional documentation of predation events is needed. I recommend continuing twenty-four hour camera surveillance on oystercatcher nests near large gull colonies. Finally, agencies should begin exploring the relationship between laughing gulls and productivity of sensitive waterbird species. I recommend conducting an experimental study to examine if American oystercatcher productivity differs on islands where management for laughing gulls is implemented.

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Table 1. Behavior categories for time-activity budgets for American oystercatchers for the incubation and chick rearing periods based on previous studies by Purdy and Miller 1988; Rave 1989; Peters and Otis 2005; Sabine *et al.* 2008.

Behavior Categories	Primary Behaviors
Reproductive	incubating-vigilant: sitting over nest with no bill tucked incubating-roosting: sitting over nest with bill tucked under wing shading eggs: standing over nest with not bill tucked turning eggs: adult using legs to turn eggs in nest scrape
Foraging	searching: walking along foraging substrate with head and bill directed down probing: using bill to open prey or probe substrate handling: consuming food items or using bill to remove fleshy food items
Self-maintenance	preening: manipulating feathers with bill, bathing, or scratching bill dipping: placing bill in and out of water
Resting	roost: standing or sitting with head turned back and bill tucked under wing standing: standing on one or both legs laying: laying on island substrate
Locomotion	flying, walking, running
Vigilant	standing-vigilant: standing with no bill tucked and neck erect, exhibits head movement lay-vigilant: laying with no bill tucked and neck erect, exhibits head movement
Agonistic	pipng display, head bobbing, chasing or being chased by conspecifics and heterospecifics
Chick care	chick feeding: presenting and breaking food for chicks brooding: sitting or standing over chicks with wings partially extended

Table 2. A predictive model evaluated with Program MARK to determine the effect of site fidelity on constant daily survival for nests' and broods' of American oystercatchers.

Model	Group 1	Group 2
S (.) and site fidelity	1 breeding adult occupied the same nesting territory from 2012-2014	2 breeding adults occupied the same nesting territory from 2012-2014

*S(.) represents constant daily survival

Table 3. Reproductive success of American oystercatchers for Galveston Bay, Drum Bay and Bastrop Bay combined, 2013-2014.

Year	No. of pairs	No. of breeding pairs	No. of clutches	No. of clutches that fledged chicks (%)	No. of chicks fledged	Productivity ^a
2013	45	41	69	23.53	21	0.51
2014	48	39	75	20	23	0.59
Total	93	80	144	43.53	44	

^aProductivity = chicks fledged/breeding pairs

Table 4. Number of American oystercatcher nests found in each bay system surveyed within in the study area from 2013-2014.

Site	# of Nests	%
West Galveston Bay	94	65.28
Galveston Bay East of I-45	19	13.19
Bastrop Bay	9	6.25
Drum Bay	22	15.28
Total	144	

Table 5. The number of American oystercatcher pairs that exhibited first, second, or third re-nesting attempts and the number of nests that hatched per attempt in 2013-2014.

Attempt	# of pairs and (%)	# of nests' hatched and (%)
1	46 (73.0)	14 (73.7)
2	16 (25.4)	5 (26.3)
3	1 (1.6)	0
Total	63	19

Table 6. The reasons for clutch loss for American oystercatcher nests combined, 2013-2014.

	2013-2014
Reasons for clutch loss	<i>n</i> (%)
Predation, unknown source	15 (21.13)
Predation, known source	7 (9.86)
Unknown	30 (42.25)
Human disturbance	4 (5.63)
Overwash/Severe weather	15 (21.13)
Total	71

Table 7. Summary of model selection results from Program MARK for daily nest survival of American oystercatchers, 2013-2014. Models are ranked by ΔAIC_c and W_i represents model weight and K is the number of parameters. Model factors included linear (LT) and quadratic (QT) time trend, nest age (age), territory size (TSz), number of gulls (gulls) and nesting gulls (nesting). S(.) represents model only using constant daily survival.

Model	AIC_c	ΔAIC_c	W_i	K	Deviance
LT + age	459.9068	0 ^a	0.62989	3	453.8973
LT + age + TSz + gulls + nesting	461.4848	1.578	0.28616	6	449.4517
LT	465.8507	5.9439	0.03225	2	461.846
LT + nesting	467.4673	7.5605	0.01437	3	461.4579
LT + gulls	467.6204	7.7136	0.01331	3	461.6109
LT + TSz	467.6204	7.7136	0.01331	3	461.6109
QT	468.0935	8.1867	0.01051	2	464.0888
S(.) constant	476.0657	16.1589	0.0002	1	474.0641

^a Denotes the best competing model

Table 8. Summary of model selection results from Program MARK for daily brood survival of American oystercatchers, 2013-2014. Models are ranked by ΔAIC_c and W_i represents model weight and K is the number of parameters. Model factors included linear (LT) and quadratic (QT) time trend, nest age (age), territory size (TSz), number of gulls (gulls) and nesting gulls (nesting). S(.) represents model using only constant daily survival.

Model	AICc	ΔAIC_c	W_i	K	Deviance
QT + gulls	171.7211	0 ^a	0.49586	3	165.7039
QT + nesting	174.0411	2.32	0.15545	3	168.0239
QT + gulls + TSz + nesting + age	174.7293	3.0082	0.11019	6	162.669
QT + age	175.5541	3.8330	0.07295	3	169.5369
QT	175.8318	4.1107	0.06349	2	171.8232
QT + TSz	176.1367	4.4156	0.05452	3	170.1195
LT	176.4824	4.7613	0.04586	2	172.4738
S(.) Constant	183.0931	11.372	0.00168	1	181.0903

^a Denotes the best competing model

Table 9. Time activity budgets for American oystercatchers in relation to reproductive stage (egg or chick). Raw frequency of behaviors is also provided as proportion of time spent per behavior category for 2013-2014 combined.

Behavior Category	Reproductive Stage			
	Incubation		Chick rearing	
	<i>n</i>	%	<i>n</i>	%
Incubation	9598	52	-	-
Foraging	1434	8	1309	9
Self-maintenance	1854	10	2144	15
Resting	3001	16	4898	35
Locomotion	894	5	711	5
Vigilant	1561	8	3976	29
Agonistic	187	1	360	3
Chick care		-	578	4
Total	18540		13976	

Table 10. Attributes of American oystercatcher nests identified by cluster analysis. Nests were distinguished into three groups. The median and interquartile range of each variable are given.

Variable	Group					
	1		2		3	
	<i>n</i> = 33		<i>n</i> = 17		<i>n</i> = 7	
	Med	IQR	Med	IQR	Med	IQR
Incubation	33.5	11.25	39	9.25	80	0
Roosting	5	8.25	10	23.5	0	0
Vigilance	5	7.25	2	4.75	0	0
Locomotion	3	4.75	3	2.25	0	0
Agonistic	0	0.25	0	0.75	0	0
Lay date	80	55	126	33.5	102	63
Island size	0.12	0.18	0.09	0.08	0.2	0.23
Gull #	25	83.5	80.5	121.8	0	3
Nesting gulls	Absent		Present		Absent	

Table 11. The results from the principle component analysis for the incubation period. The eigenvalue, cumulative proportion of variance explained, and principle component loading score are listed for each variable. Principle component loadings > 0.40 were considered significant.

	Incubation				
	PC1	PC2	PC3	PC4	PC5
Eigenvalue	2.032	1.794	1.452	1.262	1.015
Cumulative Prop Var	0.203	0.383	0.528	0.654	0.756
Lay date	-0.07	0.592	-0.19	-0.371	-0.014
Incubation	-0.514	-0.194	0.026	-0.385	-0.061
Locomotion	0.425	-0.131	-0.43	-0.192	0.239
Roosting	0.085	0.499	0.006	0.375	0.078
Vigilance	0.446	-0.127	-0.403	0.113	0.065
Agonistic	0.348	-0.126	0.449	-0.355	-0.105
Foraging	0.307	-0.094	0.449	-0.258	0.429
Island size	0.152	-0.136	-0.291	-0.334	-0.636
Gull #	0.282	0.282	0.065	0.307	-0.571
Nesting gulls	0.163	0.531	0.531	-0.354	-0.047

Table 12. Attributes of American oystercatcher broods identified by cluster analysis. Broods were distinguished into two groups. The median and interquartile range of each variable are given.

Variable	Group			
	1		2	
	<i>n</i> = 21		<i>n</i> = 17	
	Med	IQR	Med	IQR
Chick care	0.00	0.50	0.00	4.13
Vigilance	6.75	21.75	26.75	17.63
Roosting	28.25	22.63	16.75	17.25
Forage	1.25	8.00	1.75	4.00
Locomotion	1.00	3.13	4.00	3.88
Agonistic	0.00	0.00	0.50	1.75
Self-maintenance	4.75	5.38	3.50	6.50
Chick age	14.50	15.50	13.00	15.13
Island size	0.10	0.20	0.10	0.12
Gull #	0.00	6.25	86.00	144.00
Nesting gulls	Absent		Present	

Table 13. The results from the principle component analysis for the chick rearing period. The eigenvalue, cumulative proportion variance explained, and principle component loading scores are listed for each variable. Principle component loadings > 0.40 were considered significant.

Chick Rearing					
	PC1	PC2	PC3	PC4	PC5
Eigenvalue	2.988	1.677	1.354	0.993	0.790
Cumulative Prop Var	0.299	0.467	0.602	0.701	0.780
Chick age	-0.158	-0.425	0.537	0.196	-0.080
Vigilant	0.403	-0.006	0.262	-0.008	0.549
Resting	-0.406	-0.228	-0.039	-0.181	-0.381
Foraging	-0.142	0.402	-0.171	0.708	-0.155
Chick care	0.357	0.142	-0.426	-0.274	-0.273
Locomotion	0.156	0.522	0.305	0.124	0.001
Agonistic	0.093	0.338	0.496	-0.209	-0.542
Gull #	0.476	-0.174	-0.125	-0.066	-0.237
Nesting gulls	0.421	0.266	0.228	0.141	-0.229
Other species	0.252	-0.343	-0.155	0.518	-0.213

Table 14. The Mann Whitney results for comparing the median proportion of time spent per behavior category between successful and unsuccessful oystercatcher nests and broods. Significant difference ($P < 0.05$) was detected in roosting by nest fate category. Significant differences were also detected in roosting and vigilance by brood fate category.

Behavior	Incubation		Chick Rearing	
	U	P	U	P
Incubation	6879.5	0.15		
Chick care			3400.5	0.267
Roosting	6476.5	0.042	3016.5	0.031
Vigilance	5059	0.108	4449.5	0.009
Self maintenance	5096.5	0.275	3622	0.884
Foraging	1310.5	0.132	3424	0.399

Table 15. The median proportion of time spent per behavior category during the incubation period versus the absence or presence of gulls, number of gulls, absence or presence of nesting gulls, and nest fate. Significant differences were only detected in roosting by nest fate category.

	Gulls present		# of gulls		Gulls nesting		Nest fate	
	No	Yes	Low (0-75)	High (76-300)	No	Yes	Hatch	Fail
Incubation	93.7	95	95.6	92.5	96.8	90	97.5	91.5
Self-Maintenance	10.6	11.7	12.5	10	11.7	10	13.8	10
Roosting	11.8	19.4	15	17.5	17.7	17.5	12.5	37.5

Table 16. The Mann Whitney results for comparing the total proportion of time spent per behavior category between the presence or absence of nesting gulls. No significant differences were detected for the incubation period. Significant differences were detected for chick care, roosting, and vigilant behaviors during the chick rearing period.

Behavior	Incubation		Chick Rearing	
	U	P	U	P
Incubation	9371.5	0.388		
Chick care			12576	0.022
Roosting	6863.5	0.854	4872.5	0.013
Vigilance	5662.5	0.435	10601.5	0.000
Self maintenance	6327	0.351	12084.5	0.487
Foraging	1924.5	0.602	12440.5	0.071

Table 17. The median proportion of time spent in roosting, vigilant, and chick care behaviors during the chick rearing period versus brood fate and the presence or absence of nesting gulls. Significant differences were detected in vigilance and roosting by brood fate category

	Brood fate		Gulls nesting	
	Fledge	Fail	No	Yes
Roosting	29.3	16.3	31.3	18.8
Vigilance	13.6	36.3	12.5	32.5
Chick care			4.1	4.5

Table 18. The results of the T-test analysis of scaled mass index versus the density of gulls and presence or absence of other nesting species. Scaled mass index differed significantly for all laughing gull variables.

T-test	Mean scaled mass index	SD	t _a	P
Gulls absent or present				
Absent	407.6	48.8	2.62	0.012
Present	364.3	60.4		
Nesting gulls (Y/N)				
Yes	357.2	65	-2.2	0.033
No	398	52		
Number of gulls				
0-20	400.8	50.6	2.82	0.007
21-140	350.3	62.4		
Other species nesting (Y/N)				
Yes	372.1	74.7	-1.07	0.289
No	392.1	49.4		



Figure 1. A year one hatchling and adult American oystercatcher. The hatchling is on the left and the adult on the right. Also pictured are the maroon color leg bands used during the study.



Figure 2. Galveston Bay study area where breeding American oystercatchers were monitored.



Figure 3. Bastrop and Drum Bay study areas where breeding American oystercatchers were monitored



Figure 4. An American oystercatcher nest with a full clutch of eggs.



Figure 5. Conducting a time activity budget estimate on a breeding pair of American oystercatchers from an adjacent reef.



Figure 6. A setup of a whoosh net and oystercatcher decoys employed to capture American oystercatcher breeding pairs.



Figure 7. A box trap used to capture incubating American oystercatchers.

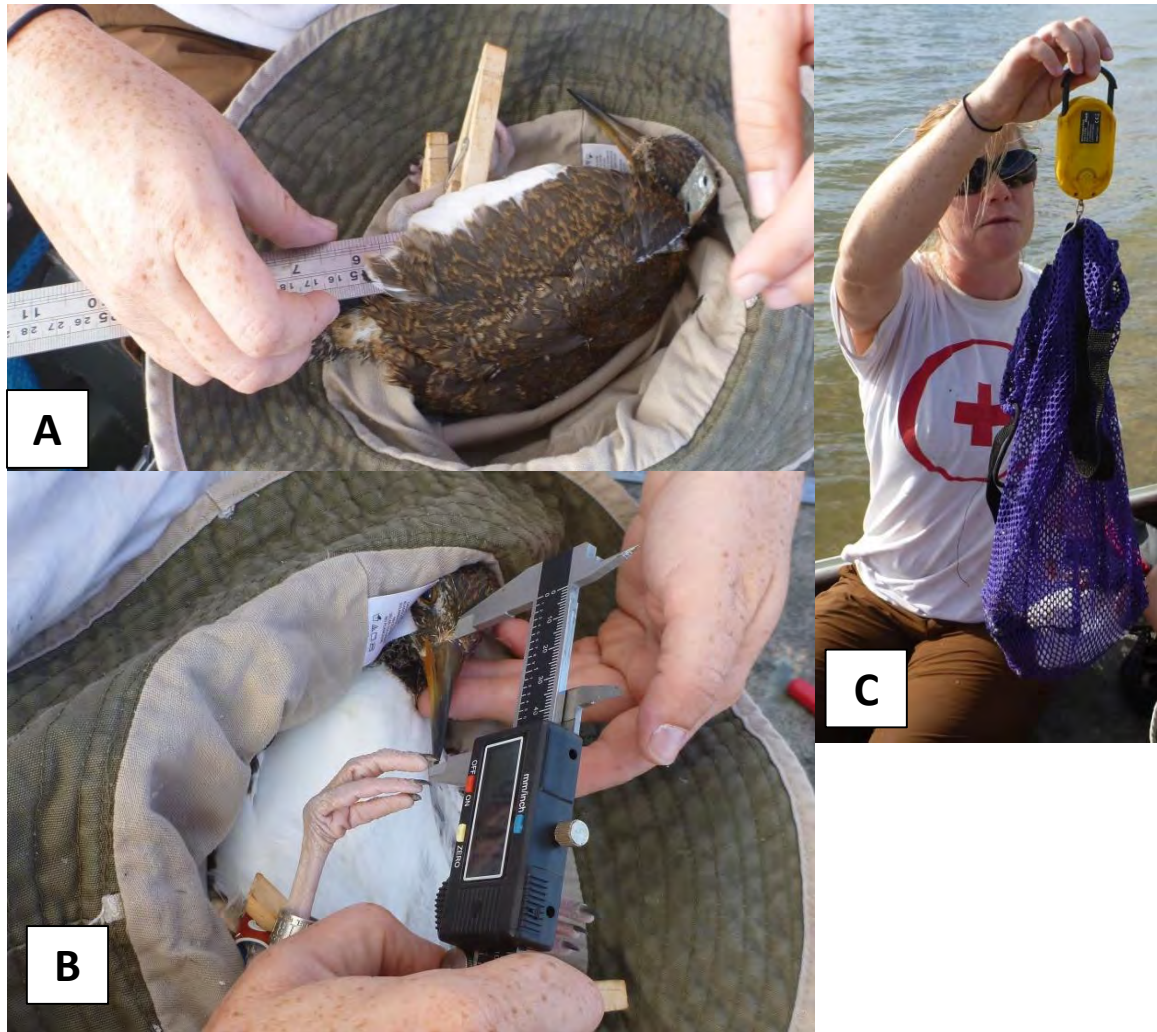


Figure 8a-c. Morphometric measurements taken on American oystercatcher chicks 2013-2014. (a). unflattened wing chord length using a metal ruler. (b). culmen length using digital calipers. (c). weight measured using a digital spring scale



Figure 9. Physical estimation of subcutaneous fat within the furculum region of American oystercatcher chicks.



Figure 10. Two American oystercatcher chick carcasses found in West Galveston Bay in 2014.

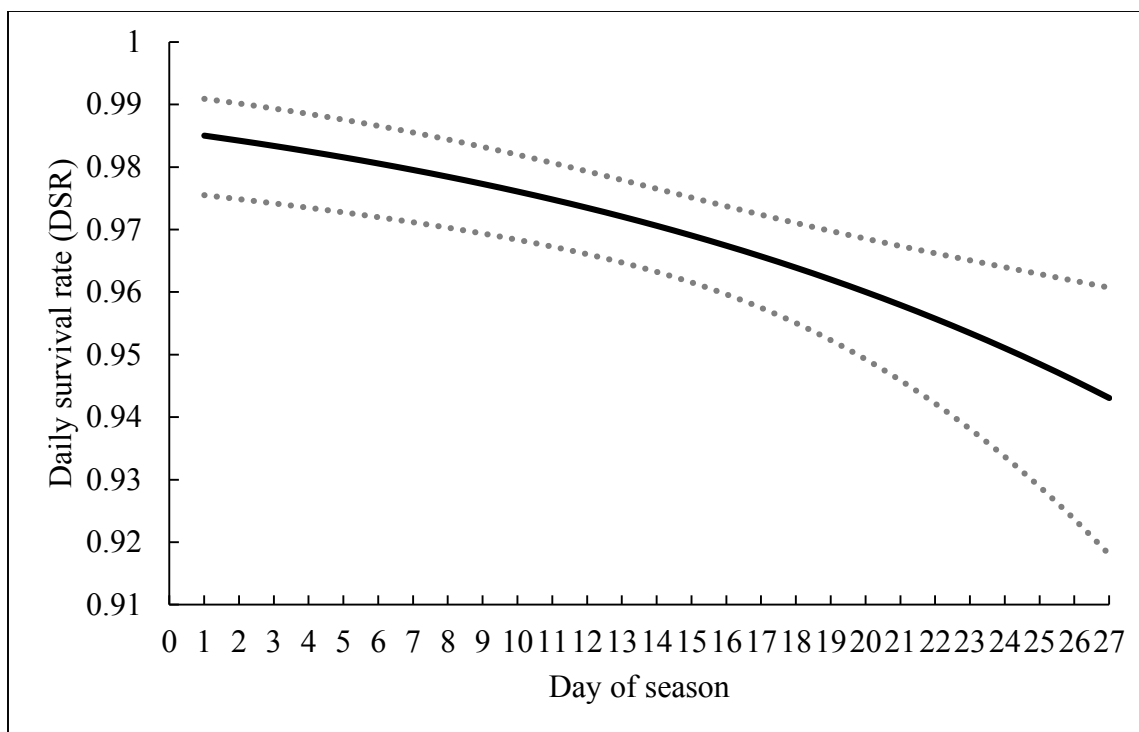


Figure 11. Nest survival of American oystercatchers using Program Mark. Daily survival rates and 95% confidence intervals were estimated from the model with the lowest ΔAIC_c value which incorporated a linear time trend and nest age. Day 1 of the season corresponds to 10 February.

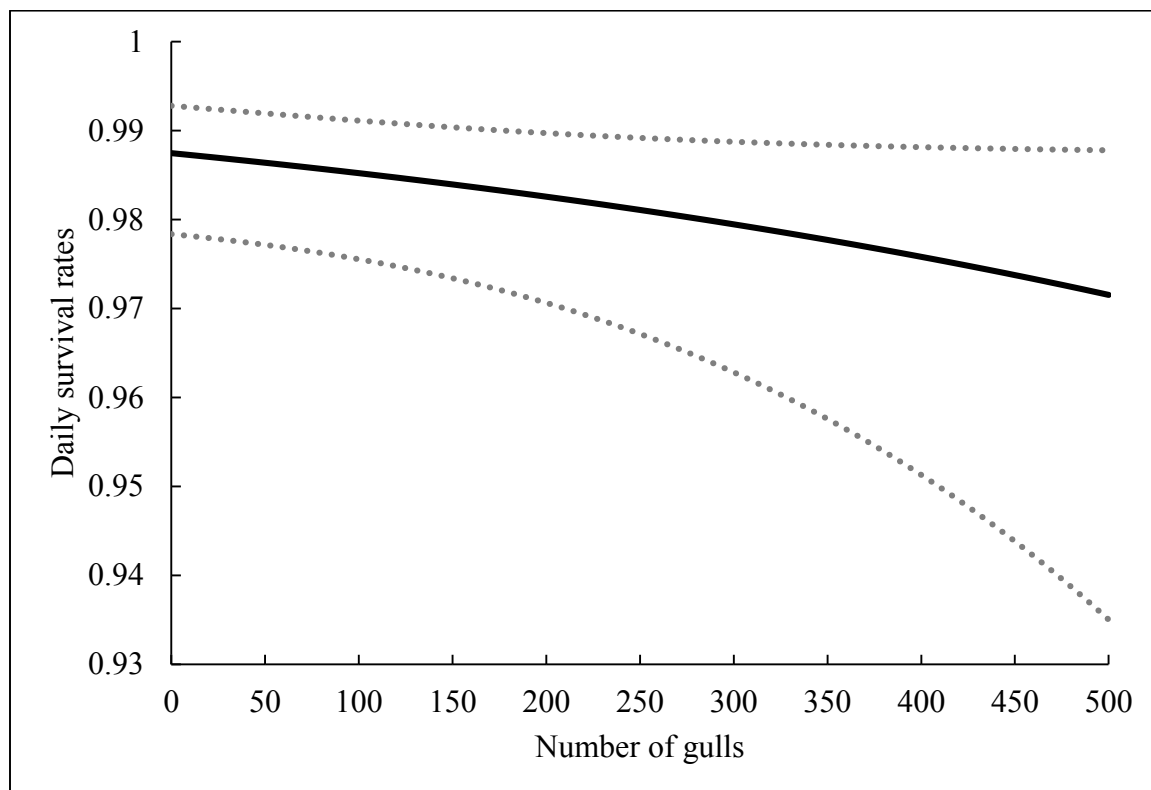


Figure 12. Daily survival rates and 95% confidence intervals for nest survival of American oystercatchers predicted from the model incorporating the number of gulls.

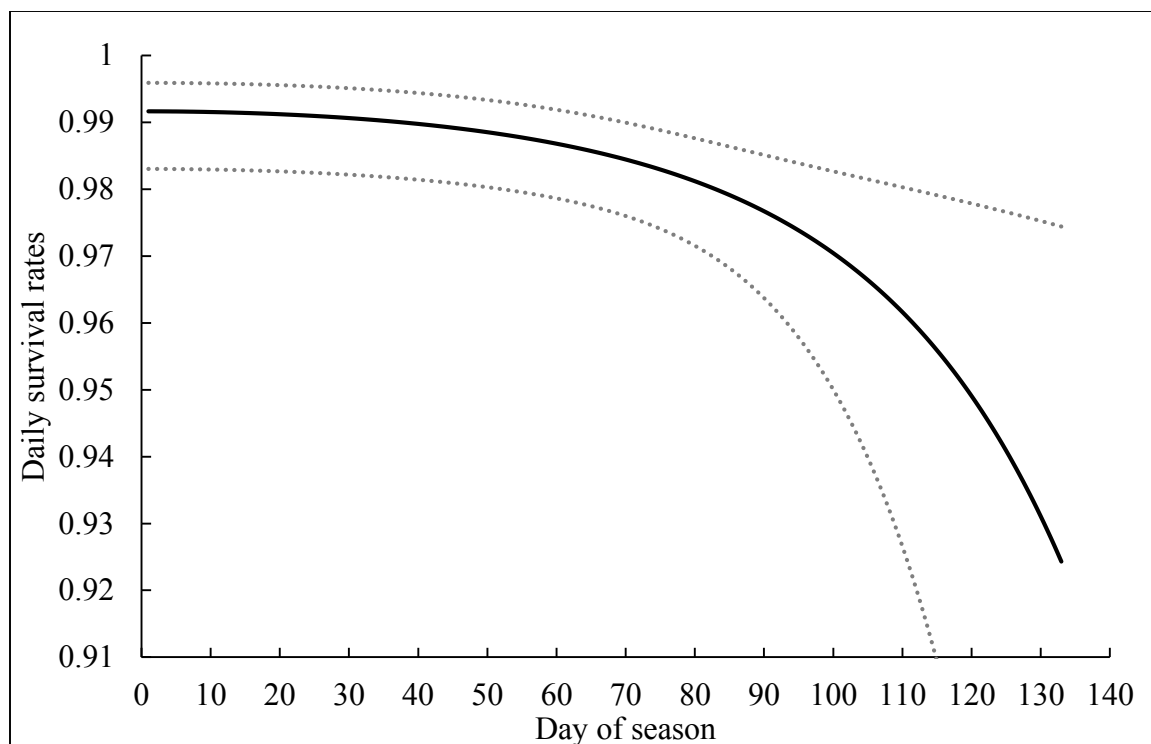


Figure 13. Brood survival of American oystercatchers using Program Mark. Daily survival rates and 95% confidence intervals were estimated from the model with the lowest ΔAIC_c value which incorporated a quadratic time trend and the number of laughing gulls. Day 1 of the season corresponds to 10 March.

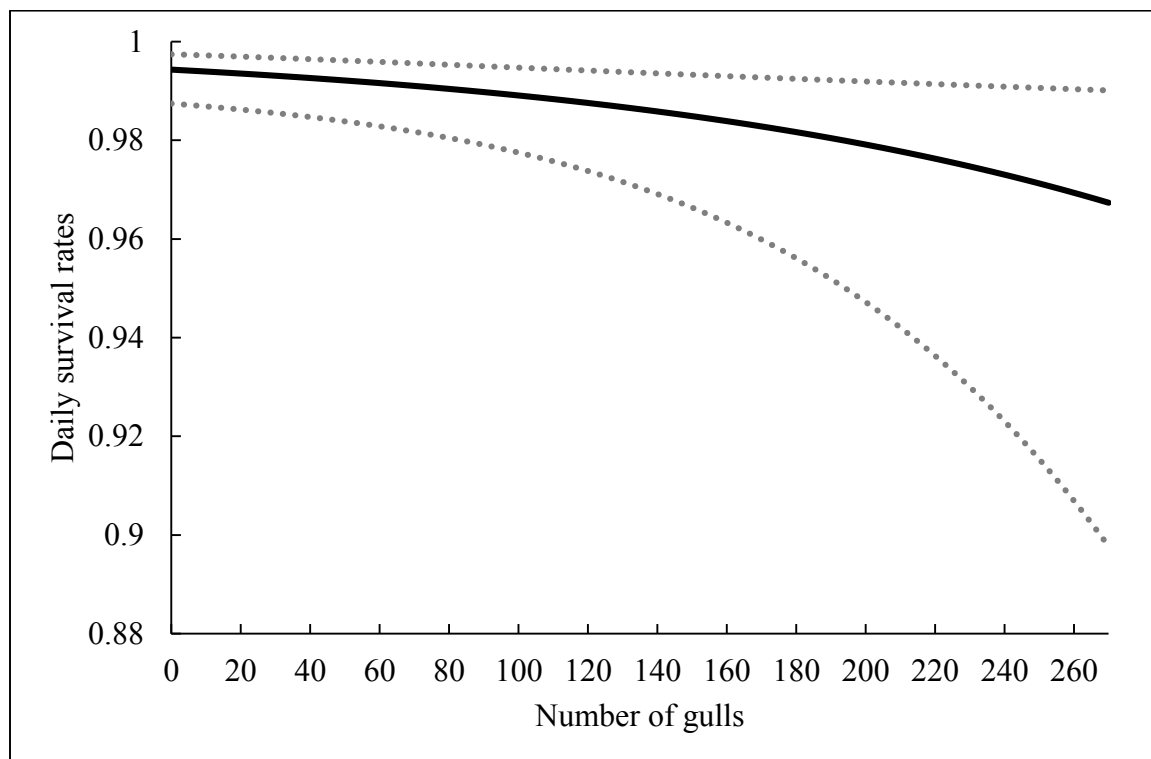


Figure 14. Daily survival rates and 95% confidence intervals of brood survival for American oystercatchers predicted from the model incorporating the number of gulls.

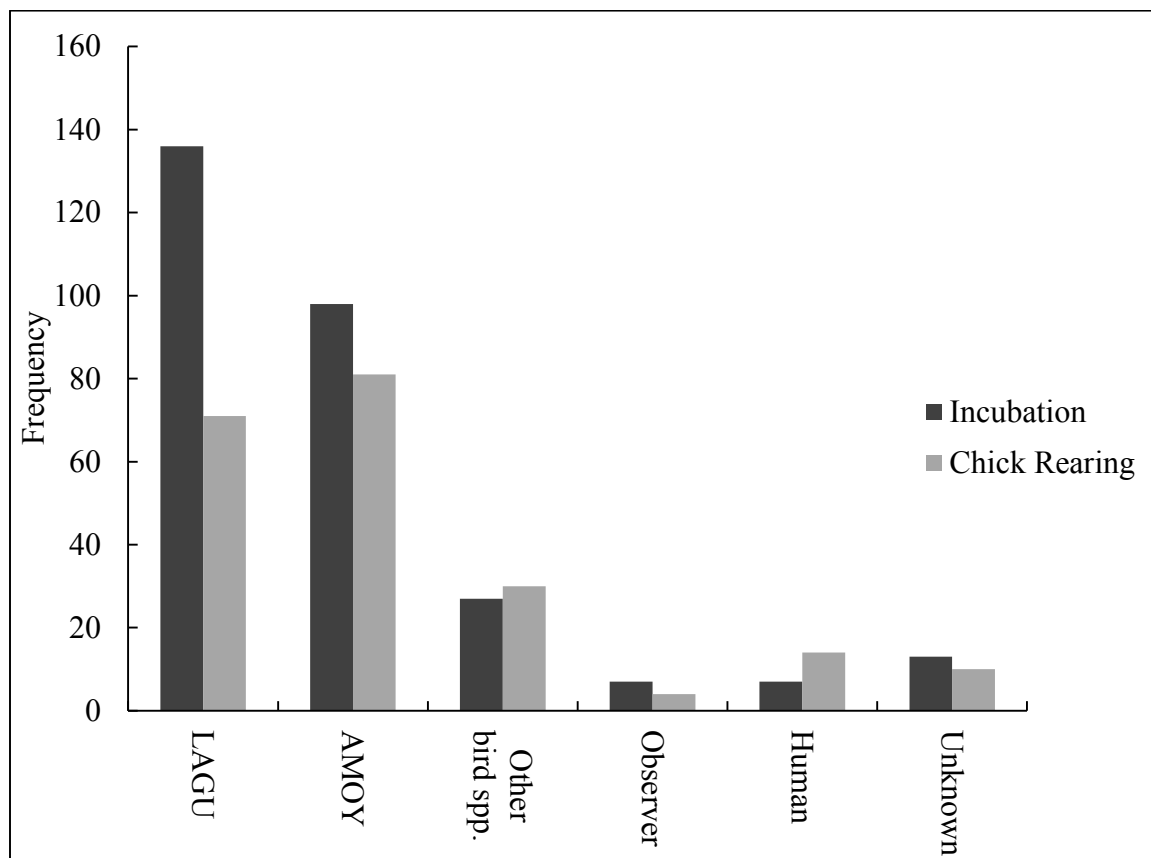


Figure 15. The frequency of various causes for agonistic behaviors exhibited by American oystercatchers during the incubation and chick rearing periods for 2013-2014.

Figure 16. A dendrogram showing the classification of nests into three groups based on similarities in lay date, behavior, number of gulls, nesting gulls, and territory size. The cluster analysis method employed Euclidean distance metric and Wards linkage. All variables were standardized standardized prior to cluster analysis

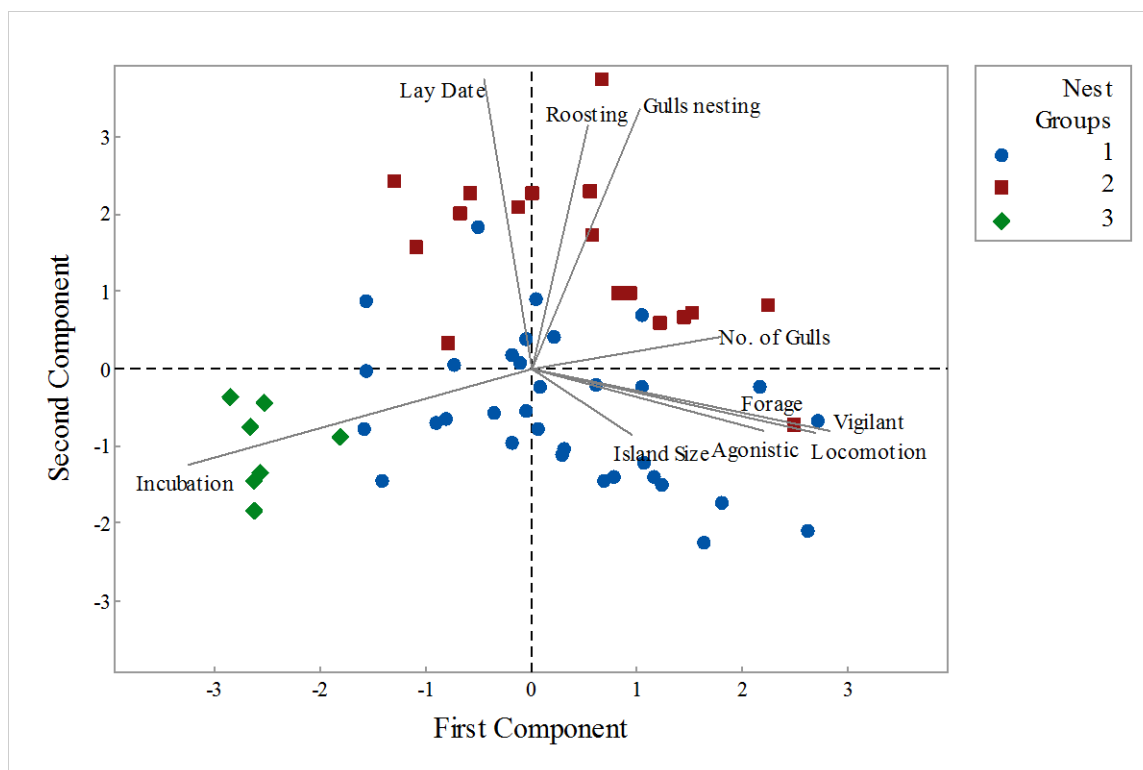


Figure 17. A biplot depicting nest scores and rescaled loading factors of the variables incorporated into the PCA analysis for the incubation period.¹

¹ Biplot macro function used in Minitab 17 was provided by Keith Jewell. Tel: +44 (0) 1386 842055. Email: keith.jewell@campdenBRI.co.uk

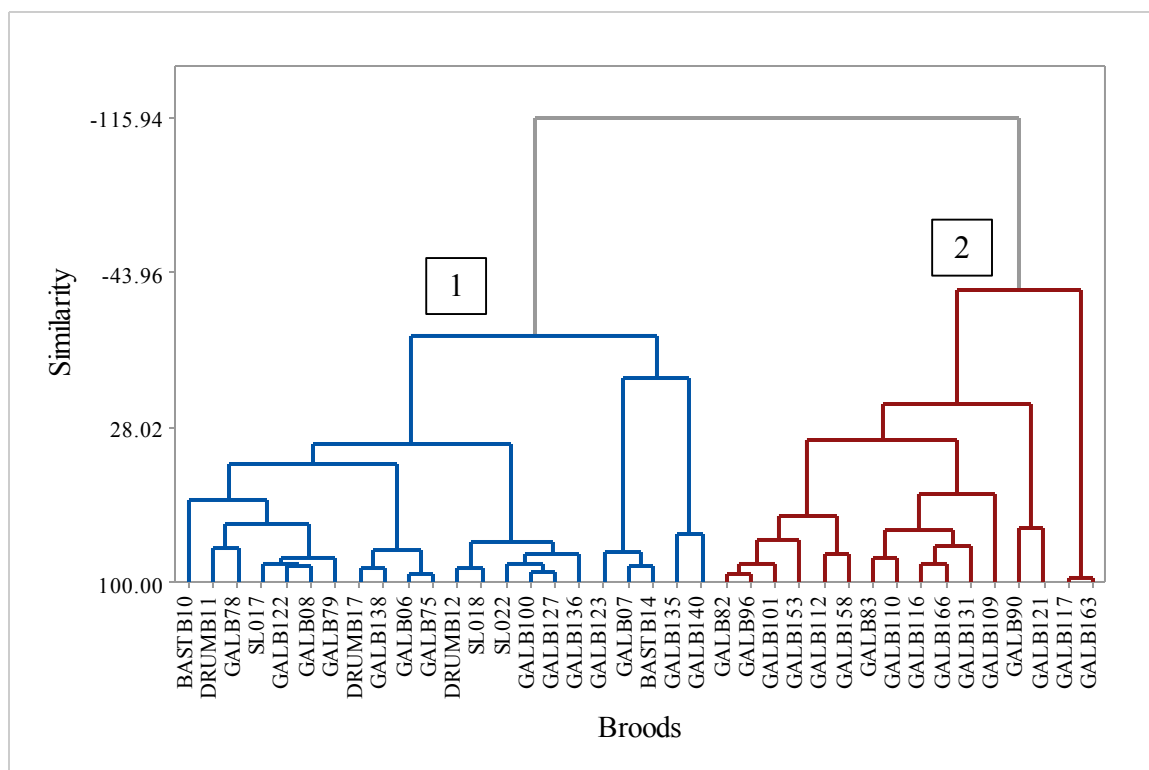


Figure 18. A dendrogram showing the classification of broods into two groups based on similarities in chick age, behavior, number of gulls, nesting gulls, and territory size. The cluster analysis method employed the Euclidean distance metric and Wards linkage. All variables were standardized prior to cluster analysis.

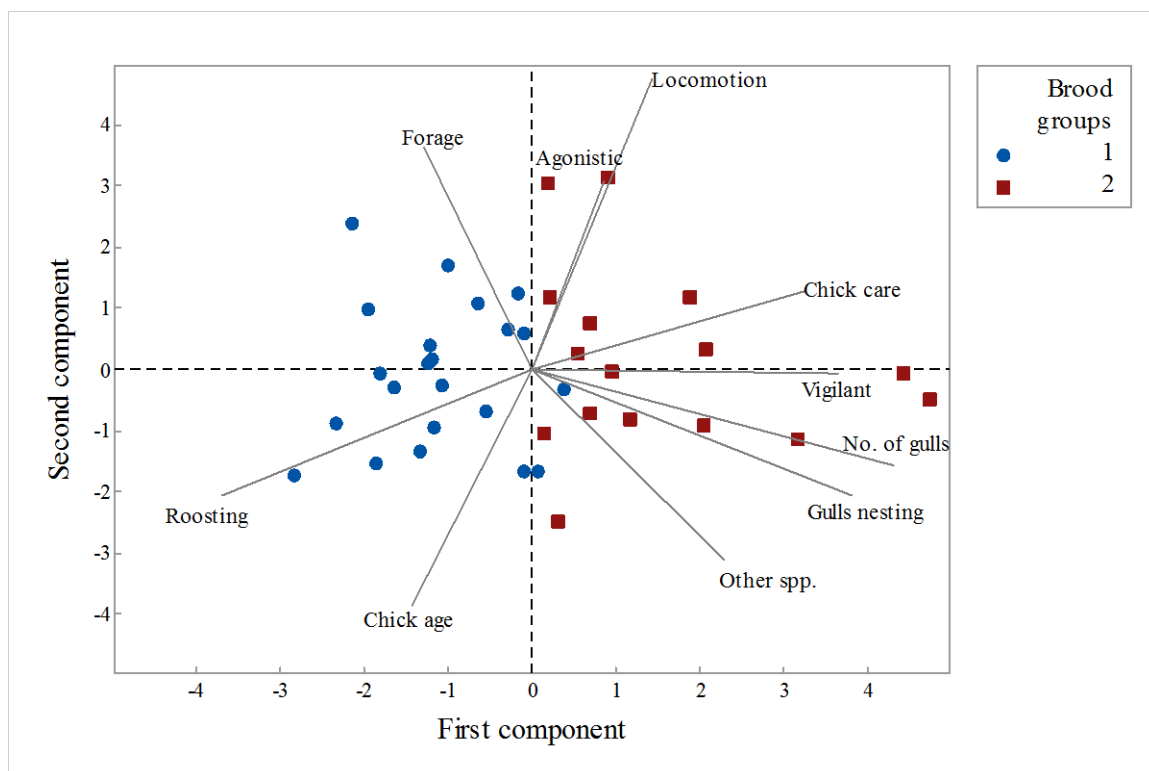


Figure 19. A biplot depicting brood scores and rescaled factor loadings for variables incorporated into the PCA analysis for the chick rearing period.

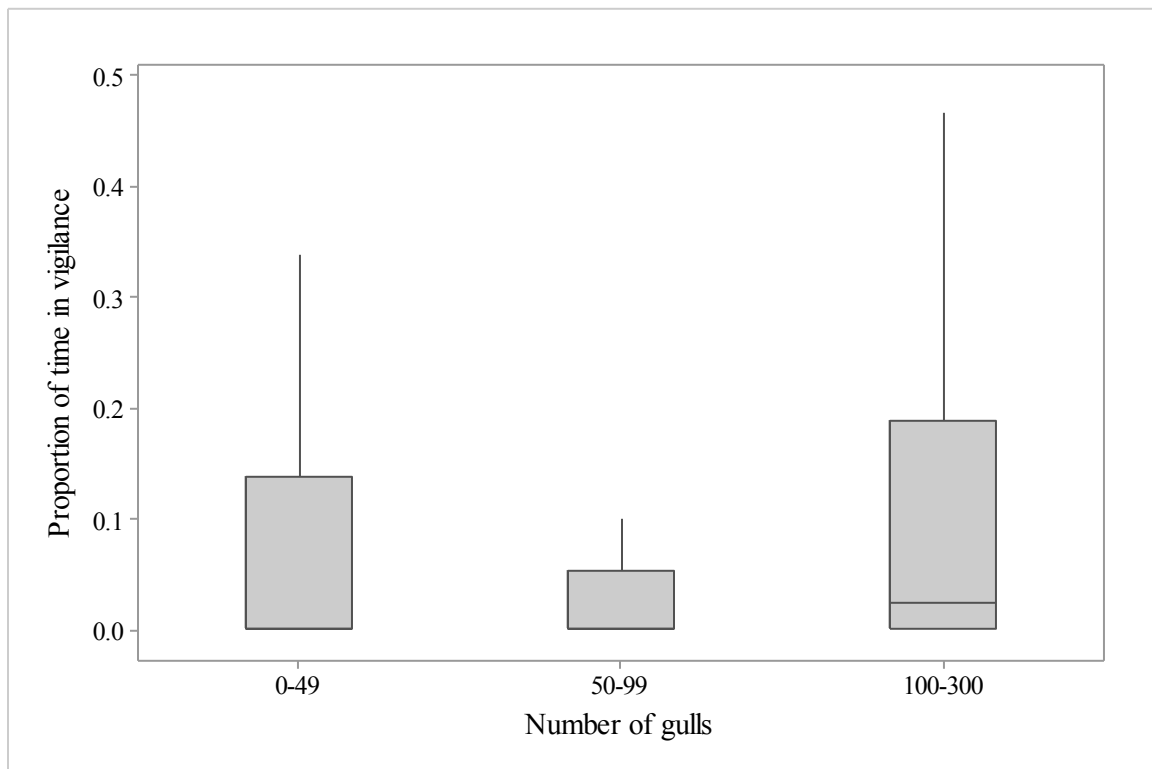


Figure 20. Boxplot displaying the median proportion of time spent in vigilance versus three categories of gull abundance during the nest rearing period. No significant differences were detected at the lower two gull abundances. Vigilance increased significantly when there was 100-300 gulls ($H_2 = 6.86$, $P = 0.032$).

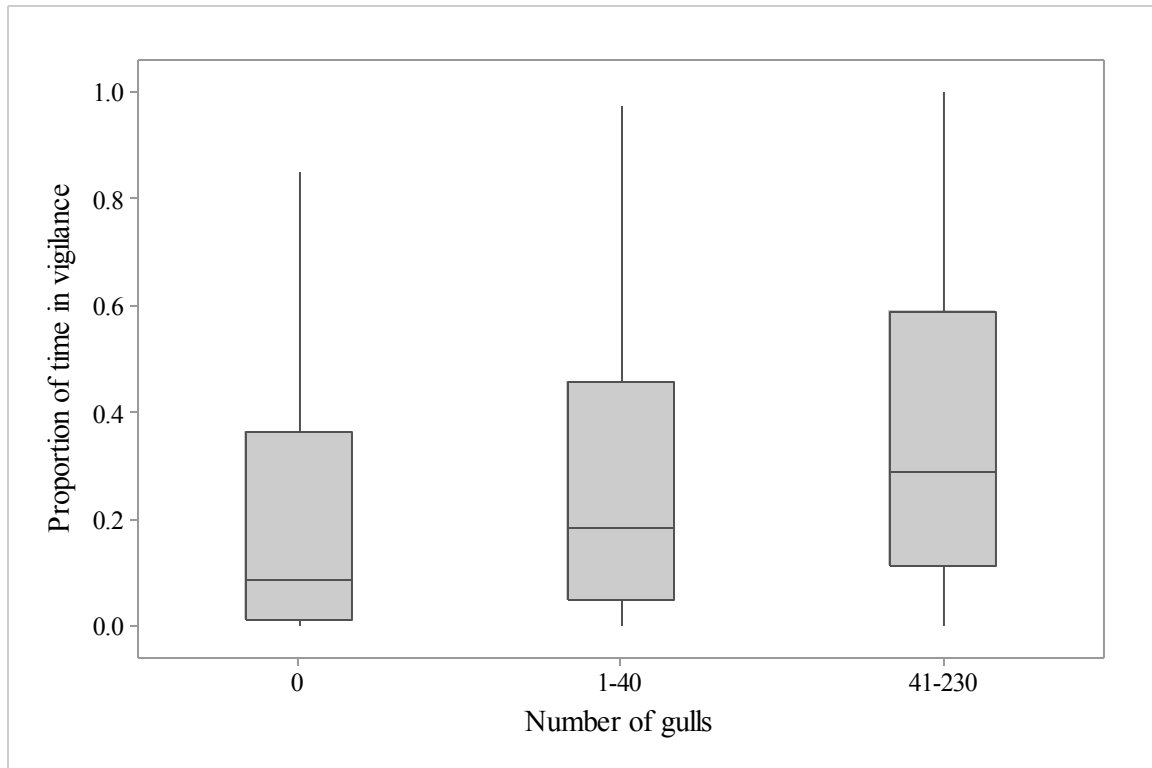


Figure 21. Boxplot displaying the median proportion of time spent in vigilance versus three categories of gull abundance during the chick rearing period. Vigilance increased significantly between broods from all gull abundance categories ($H_2 = 11.11$, $P = 0.004$).