

EVALUATING BRANDT'S CORMORANT (*Phalacrocorax penicillatus*)
REPRODUCTIVE SUCCESS: EFFECTS OF PARENTAL CARE BEHAVIORS AND
ESTIMATING INDIVIDUAL CHICK SURVIVAL

By

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ABSTRACT

EVALUATING BRANDT'S CORMORANT (*Phalacrocorax penicillatus*) REPRODUCTIVE SUCCESS: EFFECTS OF PARENTAL CARE BEHAVIORS AND ESTIMATING INDIVIDUAL CHICK SURVIVAL

Shannon Eileen Murphy

Variation in reproductive success is widely measured in seabird biology in an effort to indicate changes in the marine environment, or understand basic questions about ecology or conservation of seabirds. When variation in seabird reproductive success is suggested to indicate changes in the marine environment without identifying the proximate causes of such variation, inference is limited to association, and the proximate causes themselves could prove more effective as indicators. My study informs this problem by examining and quantifying proximate causes of variation in reproductive success, at the level of nests and individual chicks.

I used video of Brandt's Cormorant (*Phalacrocorax penicillatus*) nests on Castle Rock National Wildlife Refuge (NWR) to monitor parental care behaviors and test their influence on reproductive success in 2015. I also estimated annual variation in survival of both nests and individual eggs and chicks from 2011-2015 on Castle Rock NWR. Lastly, I compared nest survival to individual egg and chick survival to evaluate and improve upon how seabird reproductive success is traditionally measured.

Parental care behaviors had no statistical influence on survival in 2015, but nest and individual egg and chick survival varied dramatically from 2011-2015 (nest survival range: 0.083-0.942; individual survival range: 0.037-0.719). Derived estimates of nest survival from egg and chick survival demonstrated validity of measuring individual survival. My results demonstrated that inclusion of proximate causal factors that influence reproductive success and contemporary parameter estimation methods help inform seabird biology and current monitoring techniques.

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INTRODUCTION

The population sizes, diets, vital rates, and behaviors of seabirds – bird species that depend on the marine environment for food resources – are often used as indicators of change in the marine environment (Boekelheide and Ainley 1989; Diamond and Devlin 2003; Einoder 2009; Pichegru et al. 2010; Ronconi et al. 2012; Velarde et al. 2013; Elliott et al. 2015). Methods for sampling and estimation of these metrics in seabirds are thus a key part of their application as indicators. Seabird interactions with the marine environment, largely through sensitivity to variable food resources, is thought to influence the expression of seabird life histories as vital rates (Weimerskirch 2002). Therefore, seabird vital rates are often measured to help assess biological and physical parameters of the marine environment (Boekelheide and Ainley 1989; Einoder 2009; Ronconi et al. 2012; Velarde et al. 2013; Elliott et al. 2015). Reproductive success, and variation in reproductive success, is one vital rate that is widely measured in seabird biology, in an effort to indicate changes in the marine environment, or understand basic questions about ecology or conservation of seabirds (Diamond and Devlin 2003; Mallory et al. 2010; Ronconi et al. 2012; Velarde et al. 2013; Elliott et al. 2015). Thus, methods for measurement and estimation of seabird vital rates, their variation, and relationship to predictor variables play an important role in seabird ecology and the use of seabirds as indicators.

One such vital rate, seabird reproductive success, is often measured at the level of the colony by grouping individuals of the same species to measure colony reproductive

success, or indexed by estimates of breeding productivity or nest success (Carter et al. 1984; Cam et al. 2002). Breeding productivity is generally defined as the number of fledglings produced per adult breeding pair or the percentage total of eggs laid that hatched and successfully fledged (Elliott et al. 2015). Nest success is typically defined as at least one chick from an individual nest successfully fledging (Mayfield 1975; Jones and Geupel 2007). Such quantities are frequently estimated to either relate seabird reproductive success to variation in the marine environment, or to relate seabird reproductive success to the general ecology or conservation of populations.

Relatively few studies have examined the proximate causal factors that influence individual seabird reproductive success, or attempted to apply contemporary parameter estimation methods to seabird reproductive success (Wanless et al. 2007; Einoder 2009; Cook et al. 2014). When variation in seabird reproductive success is suggested to indicate changes in the marine environment without identifying the proximate causes of such variation, inference is limited to association, and the proximate causes themselves (such as parental care or diet) could prove more effective as indicators (Mallory et al. 2010). My study informs this problem by examining and quantifying techniques for improving parameter estimation of reproductive success and associating individual variation in reproductive success with parental care behaviors.

I conducted an observational experiment on Brandt's Cormorants (*Phalacrocorax penicillatus*) on Castle Rock National Wildlife Refuge, in northern California. I evaluated: 1) parental care behaviors and their influence on reproductive success within a year, 2) variation in reproductive success between years, and 3) compared nest success to

individual egg and chick success between years. Cormorants are different from most other seabirds in that they have relatively large clutch sizes and variable adult survival, which is thought to be a result of changing marine conditions and food availability because they rely on the same nearshore marine ecosystem year-round (Boekelheide and Ainley 1989; Ainley 1990a; Ainley 1990b; Wallace and Wallace 1998; Weimerskirch 2002).

Variability in seabird reproductive success often relates strongly to variability in foraging success, and foraging success depends on current marine conditions (Cairns 1987; Hipfner et al. 2007). Inshore and offshore upwelling along the California coast, coupled with strong northwesterly winds during spring and early summer, brings an influx of nutrient-rich water from the north and increases phytoplankton abundance (Ainley 1990a). Conversely, during El Niño-Southern Oscillation (ENSO) years, and in non-ENSO years as well, warm water conditions can decrease phytoplankton abundance (Ainley 1990a). Such differences in phytoplankton abundance ultimately lead to variability in seabird food supplies and the result is temporal variation in seabird foraging success (Cairns 1987; Ainley 1990a; Hipfner et al. 2007).

When the marine environment is productive, seabirds are more successful foragers, which can positively influence their reproductive success through high levels of parental care (Cairns 1987; Martin 1987; Boekelheide et al. 1990; Schreiber and Burger 2002; Hipfner et al. 2007; Schwagmeyer and Mock 2008; Elliott et al. 2015). Therefore, improvement to methods for monitoring parental care behaviors and relating them to individual or inter-annual variation in reproductive success could help explain how

reproductive success relates back to variation in the marine environment (Cairns 1987; Clutton-Brock 1991; Parker 2005; Hipfner et al. 2007).

Seabird parental care behaviors include nest attendance and chick provisioning (Cairns 1987; Clutton-Brock 1991; Hipfner et al. 2007). Nest attendance can be divided into attendance, co-attendance and no-attendance. Attendance is when one or both parents are present at the nest site and co-attendance is when two adults are present at the nest site at the same time, a behavior that is most common during incubation (Parker 2005). Also, high rates of co-attendance suggests that both parents are at the nest because they are more efficient at obtaining resources and therefore can spend more time attending the nest (Parker 2005). No-attendance occurs when no adults are present at the nest site. Chick provisioning is defined as the provisioning of chicks with food resources after they hatch (Clutton-Brock 1991). For altricial nestlings that require parental care and feeding, provisioning strongly influences individual growth (Martin 1987).

Seabirds are top consumers in marine food webs, which may make their foraging success, and thus reproductive success, informative about changes at lower trophic levels (Diamond and Devlin 2003; Bergamino et al. 2012; Velarde et al. 2013; Elliott et al. 2015). Changes in fish abundance can appear strongly related to seabird reproductive success and seabird responses can even provide early warnings for fisheries about changes in the abundance of harvested species (Boekelheide and Ainley 1989; Velarde et al. 2013; Elliott et al. 2015). However, possible changes in marine processes are better recognized when reproductive success is measured for multiple years, and therefore improving techniques for estimating annual variation in seabird reproductive success and

the possible changes within or between breeding seasons could help identify possible changes in the marine environment (Boekelheide and Ainley 1989; Gremillet and Charmantier 2010; Elliott et al. 2015).

While monitoring breeding productivity or nest success can be effective, monitoring individual behaviors and their variation may also be effective and more informative when attempting to explain variation in reproductive success. Individual variation within a colony represents an individual birds' quality and their response to variable food supplies (Carter et al. 1984; Boekelheide and Ainley 1989; Boekelheide et al. 1990). How individual seabirds respond to fluctuating food supplies not only has the potential to impact their parental care behaviors, but could impact individual eggs or chicks within a brood, causing individual egg and chick failures within a breeding season or across breeding seasons due to diminished resources (O'Connor 1978; Boekelheide and Ainley 1989; Boekelheide et al. 1990; Stenning 1996). The causes and timing of these individual failures are ignored when summarizing breeding productivity or nest success by colony, a common practice (Carter et al. 1984). Therefore, comparing nest success to individual success might highlight individual failures that could be informative when trying to explain variation in seabird reproductive success. This also has the potential to allow for a deeper understanding of their population biology (Saether and Bakke 2000; Cam et al. 2002).

It is important to have a deeper understanding of the causal associations which help influence seabird reproductive success for several reasons. The first is the marine environment has large value for human societies. Humans rely on the marine

environment for food, jobs, trade, and ocean-related industries, including fishing, recreation, and transportation (Ronconi et al. 2012; CDFW 2016). Secondly, having a deeper understanding of the mechanistic basis for seabird reproductive success could identify parental care behaviors and demographic parameters important to seabird population biology and conservation (Saether and Bakke 2000; Cam et al. 2002). Third, many seabird monitoring programs, such as those designed to monitor effectiveness of Marine Protected Areas (MPAs), often measure reproductive success as an indicator of marine processes that may change as a result of MPA establishment or other management actions (Pichegru et al. 2010; Ronconi et al. 2012; CDFW 2016). Increased seabird reproductive success can also be a target of MPA establishment (Pichegru et al. 2010; Ronconi et al. 2012; CDFW 2016). Ultimately, because seabird reproductive success is sometimes a primary metric used as an indicator of the marine environment or management, it is imperative to improve estimation of reproductive success and be able to more effectively relate individual or annual variation to possible proximate causes of such variation.

Study Species

Brandt's Cormorants are endemic to the Pacific coast of North America where individuals reside year-round in the California Current System, with the exception of Brandt's Cormorants in Alaska (Boekelheide and Ainley 1989; Wallace and Wallace 1998). Brandt's Cormorants forage by diving and pursuing prey underwater, seeking out inhabitants on, or just above rocky reefs, using their feet for propulsion (Ainley et al.

1981; Ainley et al. 1990). In California, their diet is dominated by midwater schooling rockfish (*Sebastes sp.*), northern anchovy (*Engraulis mordax*), and flatfish (*Pleuronectes sp.*) species (Ainley et al. 1981; Wallace and Wallace 1998; Elliott et al. 2015). Brandt's Cormorants forage alone in nearshore habitats, or in foraging flocks that range in size and are composed of multiple species (Ainley et al. 1990).

Brandt's Cormorants nest in colonies on gentle slopes or cliff ledges, often sharing a colony with multiple other seabird species (Boekelheide et al. 1990; Wallace and Wallace 1998). Nests are typically saucer-shaped, and nest site locations can be used in successive years. Nests from previous years decompose over winter but leave a small platform on which a nest can be rebuilt (Boekelheide et al. 1990; Wallace and Wallace 1998). Males and females participate in nest building, constructing their nest with grasses, seaweed, sticks and feathers; guano solidifies the nest material and nest building generally begins in mid-April to early May (Williams 1942; Ainley 1984; Boekelheide and Ainley 1989; Wallace and Wallace 1998).

Brandt's Cormorants typically return to a breeding colony at two years old and begin breeding at three and four years old (Schreiber and Burger 2002; Boekelheide and Ainley 1989). They often change mates between years but remain monogamous within a season, except when laying replacement clutches, when mate-switching can occur (Boekelheide et al. 1990; Wallace and Wallace 1998). They lay their clutch between May and July, and their clutch size ranges from two to five eggs (Boekelheide et al. 1990; Wallace and Wallace 1998; Schreiber and Burger 2002). Eggs are laid in intervals of two

days, and incubation averages 30 days including egg laying and is shared by both the male and female (Boekelheide et al. 1990; Wallace and Wallace 1998; Elliott et al. 2015).

Brandt's Cormorant parents share both brooding and chick provisioning duties (Wallace and Wallace 1998; Schreiber and Burger 2002). The parents brood the chicks continuously for five to ten days after hatch because the chicks are unable to thermoregulate until growth of their natal down is complete (Boekelheide et al. 1990; Wallace and Wallace 1998). Brooding and co-attendance by the parents are also important for protection, nests left unattended are almost always preyed upon by gulls (*Larus sp.*) (Osborne 1972; Willett 1910). The parents feed their young by regurgitation, which softens food and adds digestive enzymes and symbionts (Ainley et al. 1981; Clutton-Brock 1991). Chicks fledge at 25-40 days and variation in fledge date is most likely due to variation in prey abundance, and thus could be a result of variation in provisioning rates (Boekelheide et al. 1990; Schreiber and Burger 2002; Elliott et al. 2015).

Study Site

Castle Rock National Wildlife Refuge (NWR) is the largest single-island seabird colony in California (Cunha et al. 2008; Golightly and Schneider 2016). Castle Rock NWR is 6.82 hectares in size and its highest point rises 335 feet above sea level (Osborne 1972; Golightly and Schneider 2016). The island is located 0.5 miles offshore of Crescent City, California (Figure 1, Cunha et al. 2008; Golightly and Schneider 2016). The island is managed by Humboldt Bay National Wildlife Refuge Complex and was

purchased from The Nature Conservancy in 1979 (USFWS 2015). The National Wildlife Refuge System, within the U.S. Fish and Wildlife Service, manages the island not only for seabirds but terrestrial birds, marine mammals, fish, insects, and their habitats (USFWS 2015).



Figure 1. Castle Rock National Wildlife Refuge, 0.5 miles offshore of Crescent City, located in Del Norte County, California.

Castle Rock NWR is made up of several different habitat types, including sheer rock cliffs, talus slopes, vegetated terraces and rocky reefs (Osborne 1972). The location of the island within the California Current System and the continental shelf bathymetry north of Castle Rock NWR creates atypical patterns of highly productive waters (USFWS 2015; Golightly and Schneider 2016). Upwelling along the California coast typically creates a nearshore productive area throughout the upwelling period (Hickey 1998; Huyer et al. 2005). However, the bathymetric features surrounding Castle Rock NWR cause upwelling to divide into two separate upwelling jets, with one upwelling jet 40km offshore that is typically weak, and a second upwelling jet that creates productive waters 100km offshore (Barth et al. 2000; Huyer et al. 2005; Golightly and Schneider 2016). The divide typically occurs in late July or early August (Golightly and Schneider 2016).

Three Brandt's Cormorant specimens were collected in 1912 and are the earliest record of Brandt's Cormorants on Castle Rock NWR (Golightly and Schneider 2016). In 1970, the first breeding survey was conducted over four days on the island and estimated 1,800 Brandt's Cormorants breeding (Osborne 1972). A second breeding survey that included Brandt's Cormorants was conducted in 1989 and the colony estimate was 2,500 individuals (Carter et al. 1992). After 1989, surveys were no longer conducted by visiting the island. Instead colony sizes were estimated by aerial photographs, the collection of which began in 1996 (Capitolo et al. 2006). The most recent estimate of Brandt's Cormorant on Castle Rock NWR was conducted in 2004, with 3,100 individuals and 1,561 nests (Capitolo et al. 2006).

To minimize disturbance to nesting seabirds, Castle Rock NWR has been closed to the public since 1979, when it was designated as a National Wildlife Refuge (USFWS 2015). However, in 2006, the U.S. Fish and Wildlife Service allowed limited access to biologists prior to the seabird nesting season to install an audiovisual monitoring system (Golightly and Schneider 2016). From 2006 to 2016, the audiovisual monitoring system has been maintained by the U.S. Fish and Wildlife Service and Humboldt State University and allows for intensive behavioral and biological monitoring of multiple species over a large area on Castle Rock NWR with very little disturbance to the colony.

METHODS

Field Methods

The audiovisual monitoring system on Castle Rock NWR was located on a rocky slope on the north side of the island. From this location, the higher elevation areas on the island are visible (Appendix A). The system, which includes three waterproof remotely controlled video cameras and one microphone, is operated 24-hours a day throughout each seabird breeding season, usually beginning in March and continuing until the end of the breeding season. Two of the cameras are operable for visible light, zooming and auto-focusing, while the third camera is operable as a thermal imaging camera that senses temperatures and is used for monitoring the colony at night. All three cameras are capable of real-time panoramic scanning (360°) and tilting (120°), and power for the entire system is provided by solar panels that are used to charge 12-volt batteries. Video and audio are transmitted via microwave from Castle Rock NWR to a receiving station on the mainland and the signal is recorded as high resolution (29 frames per second at a resolution of 720x480 pixels) digital video onto hard drives. This system allows the videos to be viewed both in real time via the internet or at a later time via playback from hard drives; all digital video recordings are backed up and archived at Humboldt State University.

Video of nests were recorded for Brandt's Cormorants from 2011 to 2015 on Castle Rock NWR with the use of the audiovisual monitoring system. Data recorded

during the nest checks included the date the nest was checked and the number of eggs or chicks present. The camera was remotely moved to focus on each nest and, when necessary, zoomed in to record the data required. Nests visible from the monitoring system varied annually, and the number of Brandt's Cormorant nests monitored ranged from 13 to 29 nests each year. Dates the nests were checked varied between years and within years depending on other research being conducted on the island and the need to move the camera position to view different locations or to monitor different species.

In addition to the nest check data, I obtained video from the 2015 breeding season on Castle Rock NWR to monitor and record parental care behaviors of Brandt's Cormorants. Due to the high demand of the camera for other research being conducted on Castle Rock NWR, it was not efficient to have the camera focused on a single nest. However, to record detailed parental care behaviors, it likewise was not efficient to zoom out and record the entire visible colony. Therefore, I compromised camera zoom to two different fixed camera angles to monitor a total of 18 Brandt's Cormorant nests (Figure 2). The sample of nests I monitored were not randomly determined and were only a subset of the colony. In 2015, nest checks were performed on 26 nests, but eight of those nests were not visible from the camera position used to record parental care behaviors.

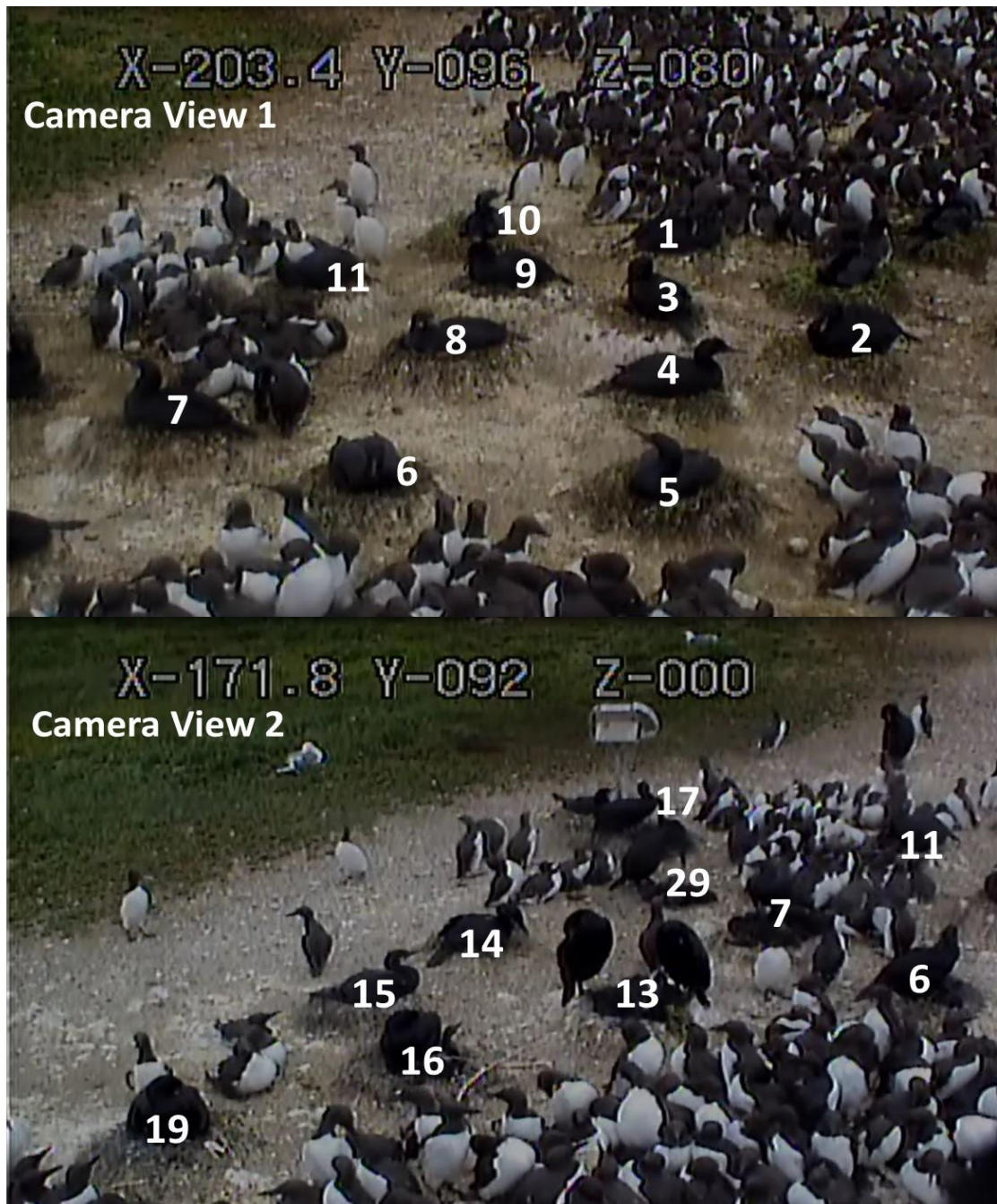


Figure 2. Still images from recorded video of the Brandt's Cormorant colony on Castle Rock National Wildlife Refuge in June 2015. The camera was moved to a fixed angle to monitor a total of 18 Brandt's Cormorant nests and record their parental care behaviors. From camera view one I monitored 11 nests and from camera view two I monitored 10 nests, with three nests (6, 7, and 11) visible from both camera angles.

From camera view one I monitored 11 nests and from camera view two I monitored 10 nests, with three nests visible from both camera angles (Figure 2). Videos for parental care behaviors began on June 15, 2015 and ended on August 6, 2015. I reviewed eight days of video from camera view one (15, 21, 29 June, and 3, 8, 14, 21, 28 July), and reviewed eight days of video from camera view two (19, 27 June, 6, 12, 16, 22, 29 July, and 6 August). Each day I recorded parental care behaviors for 13 hours from 0800 to 2000, for a total of 208 hours for the season, including both camera views.

I measured nest attendance in Brandt's Cormorant by recording the arrival and departure times of a second adult at individual nests to determine the total time of co-attendance. I summed the total time to determine co-attendance of an individual nest for one observation day. I also recorded the arrival and departure times of a single adult to determine no-attendance and again summed the total time to determine no-attendance of adults for one observation day per individual nest.

I measured chick provisioning in Brandt's Cormorants by recording the number of times a parent delivered a meal to a chick. If multiple feedings occurred back to back, I recorded each individual feeding with a separate time. I then divided chick provisioning per observation day by the brood size of each individual nest and used provisioning per chick as the explanatory variable. Within the scope of my study it was not possible to determine which chick within a nest received each meal, therefore I assumed meals were equally divided among the brood.

Brandt's Cormorants fed their chicks by regurgitation, therefore I could not measure the amount of food delivered by the parents. However, feeding frequency is

directly correlated to meal mass in Manx Shearwaters (*Puffinus puffinus*), who also provision by regurgitation (Shoji et al. 2015). Also, in both Manx Shearwaters and White-tailed Tropicbirds (*Phaethon lepturus*) feeding frequency has a positive relationship with daily chick growth rate and survival (Ramos and Pacheco 2003; Shoji et al. 2015).

Twice I observed an adult attempting to feed a chick but the regurgitated meal was intercepted and taken by a Western Gull (*Larus occidentalis*). Once I observed an adult attempting to feed a chick but the meal was not received by the chick and later taken by a Western Gull. These observations were not included in the frequency of chick provisioning per individual nest.

While reviewing the video from 2015, I also recorded the status of each Brandt's Cormorant nest, the total number of eggs or chicks, and the failure of an egg or chick for each individual nest. I updated the information if the status of a nest changed while reviewing film of one observation day to ensure all obtainable information for each nest was current. I recorded when chicks left the nest and either moved to a neighboring nest, or out of sight, to ensure I did not incorrectly record the status of any nest. Lastly, the data set was based only on nest checks after each nest had hatched, therefore the incubation stage of parental care was not included.

All research was conducted under Institutional Animal Care and Use Committee (IACUC) protocols: 08/09.W.54.A (2008-2011), 11/12.W.88-E (2012-2014), 15/16.W.01-E (2015-2016).

Analytical Methods

To estimate Brandt's Cormorant daily survival probabilities of nests and chicks at Castle Rock NWR, I used the logistic exposure model (Shaffer 2004). The logistic exposure model is a generalized linear model (GLM) with a binomial response variable and a custom link function (Shaffer 2004). The link function used (Appendix B) is similar to the logit link function but reflects variation in exposure time, thus modeling how variation in exposure days affects risk of failure for individual Brandt's Cormorant nests. Exposure days are defined as the number of days between checks; for example, if a nest was checked on Julian date 172 and checked again on Julian date 180, the number of exposure days was eight (Shaffer 2004; Appendix C). This is an important factor to consider because the interval between nest checks in the videos was variable for my research and failure risk increases with exposure when mortality is time-dependent (Shaffer 2004).

The model estimates were on the logit-scale. Reported β coefficients from logit-scale linear models are thus log-odds ratios. I transformed all the logit-scale estimates to the probability scale to report survival as daily survival probabilities. I used Program R to estimate daily survival probabilities as a function of explanatory variables and reported 95% confidence intervals for all estimates (Shaffer 2004; Grant et al. 2005; R Core Team 2014). I compared candidate models using Akaike's Information Criterion (AICc) corrected for small-sample bias, Delta AICc (Δ_i) which is the difference in AICc value from top-ranked model, and Akaike weight (w_i) which is the probability the model is the

best model in the candidate set, given the data and the candidate set (Burnham and Anderson 2002).

Analytical Methods: Parental Care Behaviors

I used the logistic exposure model to estimate daily survival probabilities of individual chicks as a function of Brandt's Cormorant parental care explanatory variables recorded on Castle Rock NWR in 2015. Each trial in the logistic exposure model represented an individual chick (Appendix C).

I examined the distribution of the covariates a priori and no-attendance was extremely right-skewed and confounded with age, therefore it was not included in the analysis. Both co-attendance and provisioning were correlated with age of the chick, therefore I standardized co-attendance and provisioning to chick age. To standardize co-attendance and provisioning I fit a linear model with a quadratic effect of age, and co-attendance and provisioning transformed to the log scale. I then plotted the predicted values from the linear model versus my observed values from the videos for co-attendance and provisioning, and used the residuals to create two new explanatory variables: standardized co-attendance and standardized provisioning.

I considered eight candidate models to evaluate the effect of parental care behaviors in estimating daily survival probabilities of individual chicks (Table 1). The explanatory variables I included were co-attendance, standardized co-attendance, provisioning, standardized provisioning and age of the individual chicks. When estimating daily survival probabilities for individual chicks I could not consider chicks from the same nest independent. Therefore, all models of individual chick survival were

mixed effect models with nest as a random effect (Bennington and Thayne 1994; Bolker et al. 2008; Dingemanse and Dochtermann 2013). In addition, the predict function, used in Program R, does not have an efficient method to compute standard error for the predicted values of a mixed effect model, therefore confidence intervals reported in my figures are likely underestimates (Bolker et al. 2008).

Table 1. Candidate model set to evaluate the effect of Brandt's Cormorant parental care behaviors on daily survival probabilities of individual chicks. Explanatory variables included chick age, provisioning and co-attendance, and all models included nest as a random effect. Parental care behaviors were recorded on Castle Rock National Wildlife Refuge in 2015.

Candidate Model ^a	K ^b
NULL	2
CO-ATTENDANCE	3
CO-ATTENDANCE (standardized)	3
PROVISIONING	3
PROVISIONING (standardized)	3
AGE	3
AGE + CO-ATTENDANCE (standardized)	4
AGE + PROVISIONING (standardized)	4

a: Model name including covariates used.

b: Number of parameters.

Analytical Methods: Annual Variation

To examine annual variation in survival probabilities at Castle Rock NWR, I used the Brandt's Cormorant nest monitoring data from 2011 to 2015 to estimate daily survival probabilities of nests and individual eggs and chicks. The logistic exposure

model allowed easy modification depending on my specific research objective, as one trial could be defined as an individual nest or an individual chick (Appendix C).

I included year as an explanatory variable to estimate annual variation, and additional variables; age, stage, and clutch size, were included to test if they helped explain annual variation. I defined the first day eggs were identified in a nest via the video as day one. The interval between nest checks in the videos was variable, therefore I could not be certain of the exact start date. I chose to be consistent in how I defined day one as opposed to back-dating the start date, and because of this assumption age should be considered an estimate and not exact. I also examined both methods and the results revealed back-dating the start date did not change the qualitative model results or interpretation.

I defined stage by either incubation stage or nestling stage. I identified the incubation stage by eggs only in the nest, and identified the nestling stage by a minimum of one chick in the nest. I also considered the interaction of age and stage, because stage is confounded with age and survival could vary by age within a stage. Lastly, I included clutch size, to test if clutch size influences chick survival or nest success (Boekelheide and Ainley 1989). Cormorants can have large variability in their clutch size depending on current marine conditions (Boekelheide and Ainley 1989; Ainley 1990a; Ainley 1990b; Wallace and Wallace 1998; Weimerskirch 2002).

The models I considered were (1) a null model, (2) a year effect, (3) an interacting year and age effect, (4) an interacting year and stage effect, (5) an interacting year, age and stage effect, and (6) an interacting year and clutch size effect. As before, when

estimating daily survival probabilities for individual eggs and chicks, my models were mixed effect models with nest as a random effect (Bennington and Thayne 1994; Bolker et al. 2008; Dingemanse and Dochtermann 2013).

Analytical Methods: Comparison of Egg and Chick Success to Nest Success

I used nest monitoring data from 2011 to 2015 at Castle Rock NWR to compare egg and chick success to nest success. I could not make model comparisons using AICc because models based on different dependent data sets cannot be compared (Burnham and Anderson 2002). However, I could make comparisons between the estimated coefficients for the two models. I used total survival probability, as opposed to daily survival probability, to compare between results of the two modeling approaches. Brandt's Cormorants incubate their eggs for 30 days, which includes egg laying as Brandt's Cormorants begin incomplete incubation after laying their first egg (Boekelheide et al. 1990; Elliott et al. 2015). Chicks fledge between 25 and 40 days after hatch, but typically 25 days after hatch is used as a minimum estimate because chicks can first leave the nest at 25 days after hatch (Boekelheide et al. 1990; Elliott et al. 2015). Therefore, to calculate total survival probability, I exponentiated daily survival probability to 55, the number of days included in the incubation (30 days) and fledging period (25 days).

I derived the total survival rate, or total survival probability of nests, from the daily survival rate (DSR) of individual eggs and chicks to make further comparisons of egg and chick success to nest success using the following expression:

$$1 - (1 - (\textit{individual DSR}^{55}))^{\textit{average clutch size}} = \textit{nest total survival rate}$$

I used the Delta method to compute 95% confidence intervals for the derived parameter estimates (Powell 2007; Cooch and White 2015).

RESULTS

Parental Care Behaviors

Out of 49 individual chicks monitored via the recorded videos in 2015, 39 chicks survived to fledge and 10 chicks died (Table 2), and all the chick failures occurred before they were 15 days old (Figure 3, 4). To standardize co-attendance and provisioning to the age of the chick I fit a linear model with a quadratic effect of age, and co-attendance and provisioning transformed to the log scale (Figure 3, 4). The relationship between co-attendance and the age of the chick revealed co-attendance by the parents decreased as the age of chick increased (Adjusted $R^2 = 0.0537$, $\beta_0 = 0.747$, $\beta_1 = -0.018$, $\beta_2 = 0.0002$, Figure 3). The relationship between provisioning and the age of the chick revealed a negative quadratic relationship of provisioning per chick in response to the age of the chick (Adjusted $R^2 = 0.4506$, $\beta_0 = 0.954$, $\beta_1 = 0.110$, $\beta_2 = -0.003$, Figure 4).

Table 2. Data table of the Brandt's Cormorant nests and individuals that were monitored on Castle Rock National Wildlife Refuge (NWR) from 2011-2015. Individuals were defined as the eggs and chicks monitored within each nest. All nests and individuals were monitored with the audiovisual monitoring system on Castle Rock NWR from 2011-2015.

Year	Nests ^a	Nest Failures	Individuals	Individual Failures	Re-nest Attempts
2011	28	21	88	74	9
2012 ^c	13	10 ^b	35	28 ^b	0
2013 ^c	29	10	107	57	1
2014	23	9	78	49	0
2015	26	2	85	31	0
2015 ^d	17	0	49	10	0

a: The total number of nests includes number of re-nests.

b: In 2012 all documented failures were during the egg stage/individual egg failures.

c: In 2012 and 2013 the audiovisual monitoring system on Castle Rock NWR failed prior to the end of the breeding season.

d: Subset of nests and individuals monitored to record parental care behaviors.

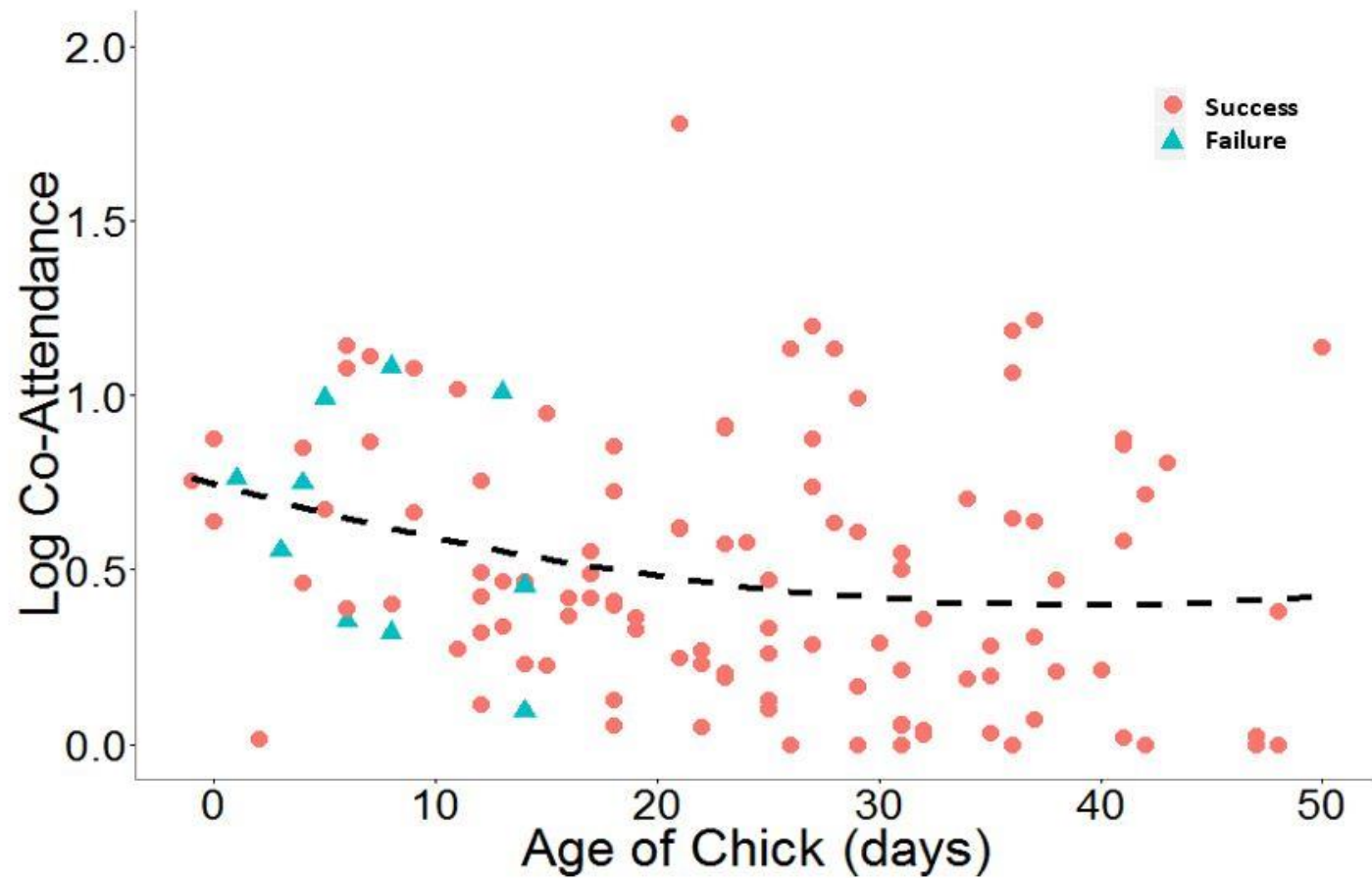


Figure 3. Brandt's Cormorant co-attendance decreased as the age of chicks increased on Castle Rock National Wildlife Refuge in 2015. Co-attendance was monitored via the audiovisual monitoring system, and the relationship between co-attendance and age of the chick is shown with the regression equation: $\log(\text{CO-ATTENDANCE}+1) = \beta_0 + \beta_1 * \text{CHICK-AGE} + \beta_2 * \text{CHICK-AGE}^2$.

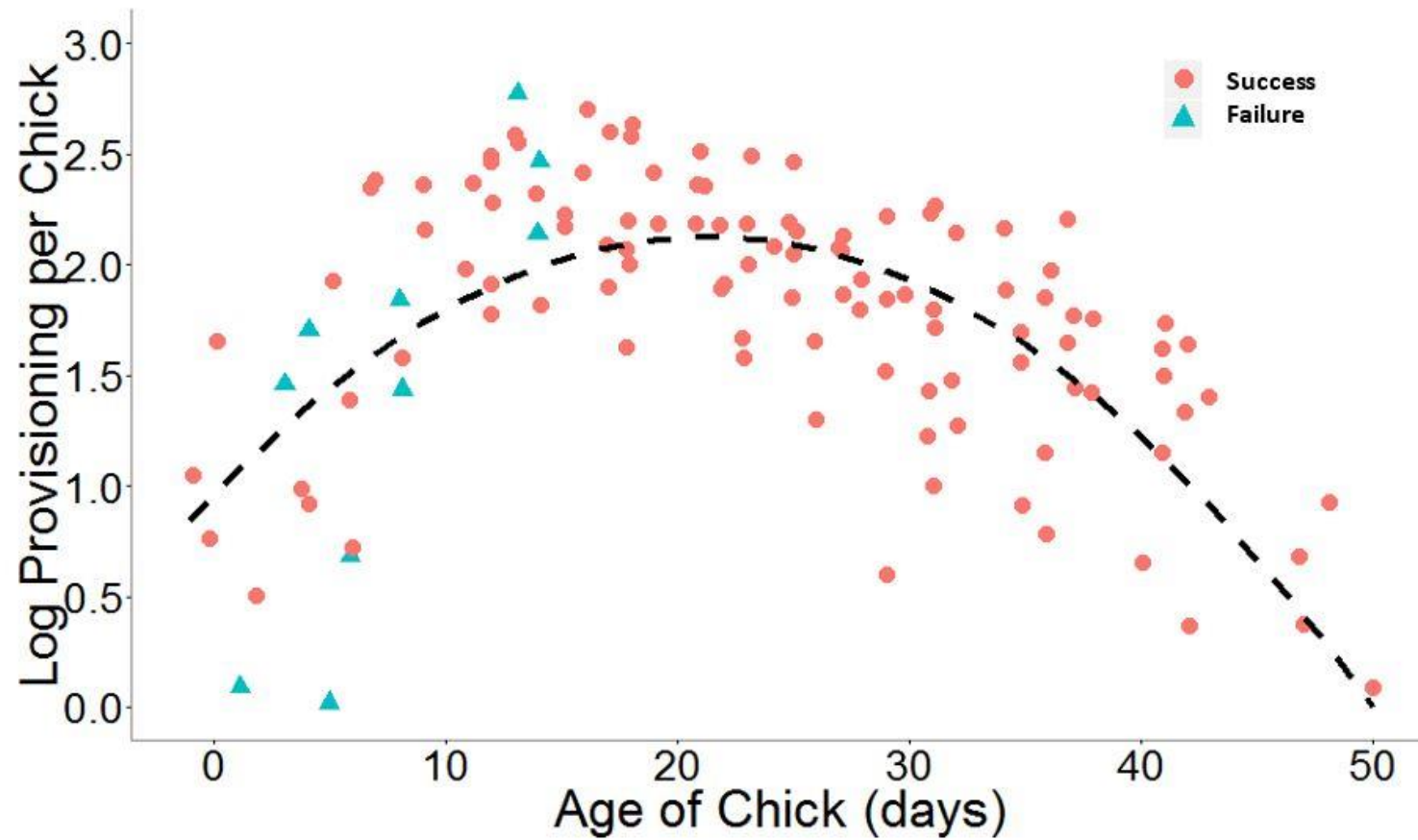


Figure 4. Brandt's Cormorant provisioning revealed a negative quadratic relationship of provisioning per chick in response to the age of the chick. Provisioning was recorded on Castle Rock National Wildlife Refuge in 2015 via the audiovisual monitoring system, and the relationship between provisioning and age of the chick is represented by the regression equation:
 $\log(\text{PROVISIONING}+1) = \beta_0 + \beta_1 * \text{CHICK-AGE} + \beta_2 * \text{CHICK-AGE}^2$.

Parental Care Behaviors: Chick Success

I monitored a total of 18 Brandt's Cormorant nests in 2015, but one nest was removed from analysis because it failed before hatch, and I did not include the incubation stage of parental care behaviors in my analysis. Therefore, I evaluated 8 models based on 17 nests and 49 individual chicks, with AGE, CO-ATTENDANCE, and PROVISIONING as covariates and nest as a random effect (Table 2).

AGE was the most informative explanatory variable for daily survival probabilities of individual chicks based on the associated AICc scores (Table 3). AGE was included in the top three models, the second-ranked model included AGE and CO-ATTENDANCE (standardized) and the third-ranked model included AGE and PROVISIONING (standardized). The NULL model had a ΔAICc of 12.1 suggesting explanatory variables were related to Brandt's Cormorant chick survival (Table 3).

Table 3. Model selection table for the effect of Brandt's Cormorant parental care behaviors on daily survival probabilities of individual chicks. Explanatory variables included chick age, provisioning and co-attendance, and all models included nest as a random effect.

Model ^a	K ^b	AICc ^c	Δ AICc ^d	AICc Weight ^e
AGE	3	74.7774	0.0000	0.6175
AGE + CO-ATTENDANCE (standardized)	4	77.1296	2.3522	0.1905
AGE + PROVISIONING (standardized)	4	77.1531	2.3758	0.1883
NULL	2	86.8794	12.1020	0.0015
CO-ATTENDANCE	3	88.4655	13.6881	0.0007
CO-ATTENDANCE (standardized)	3	88.5393	13.7619	0.0006
PROVISIONING (standardized)	3	88.8946	14.1172	0.0005
PROVISIONING	3	89.0133	14.2359	0.0005

a: Model name including covariates used.

b: Number of parameters.

c: Calculated AICc value for each model.

d: Difference in AICc value from top-ranked model.

e: Proportion of total weight calculated for each model.

The parameter estimate of the effect of AGE from the top model ($\beta = 0.13$, CI = [0.04, 0.21]) revealed that chick age had a positive effect on Brandt's Cormorant chick survival, and daily survival probabilities for a chick increased with age. Specifically, the estimated daily survival probabilities linearly increased from 0.962 (CI = [0.906, 0.985]) at age 0 days to 0.990 (CI = [0.982, 0.995]) at age 11 days and 1.000 (CI = [0.996, 1]) at age 35 days (Figure 5).

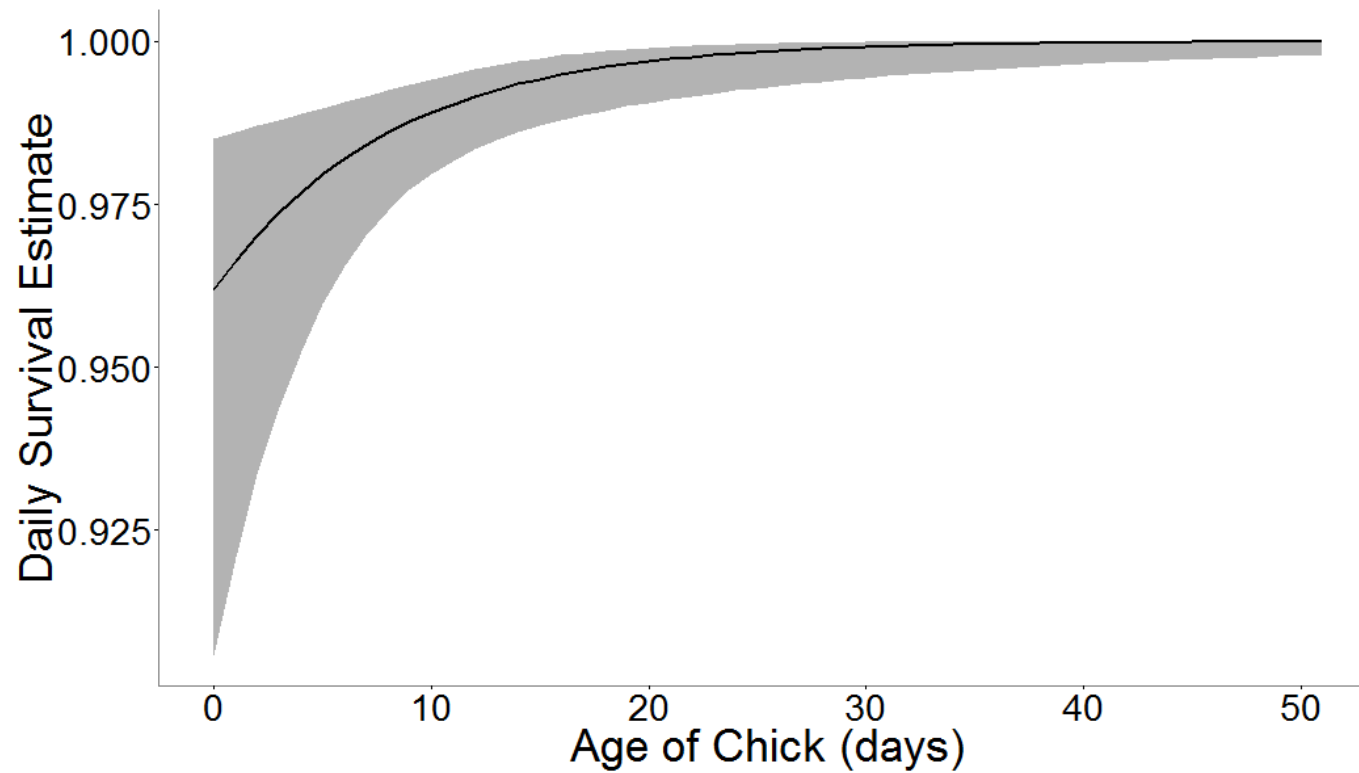


Figure 5. Daily survival estimates for Brandt's Cormorant chicks based on their age during the nestling period on Castle Rock National Wildlife Refuge in 2015. Chick age had a positive effect on Brandt's Cormorant chick survival, and daily survival probabilities linearly increased with age. The shaded region represents the 95% Confidence Intervals of the daily survival estimates.

Parental care behaviors, CO-ATTENDANCE (standardized) and PROVISIONING (standardized), were included in the second and third-ranked model respectively (Table 3). Based on their AICc scores, these models indicated that parental care behaviors could be also be informative when estimating daily survival probabilities of chicks. However, both explanatory variables did not increase log-likelihood or reduce deviance.

Model parameter estimates of the second-ranked model, CO-ATTENDANCE (standardized) suggested a negative effect on daily survival probabilities (Table 3). With inclusion of CO-ATTENDANCE (standardized) the daily survival probability decreased ($\beta = -0.07$, CI = [-1.04, 0.89]). Based on the model parameter estimates of the third-ranked model, PROVISIONING (standardized) had no influence on daily survival probabilities (Table 3). The estimated constant daily survival probability was 0.382 ($\beta = -0.48$, CI = [-3.75, 2.79]) and with PROVISIONING (standardized) included, the daily survival probability was still 0.382 ($\beta = -0.0002$, CI = [-0.96, 0.96]).

While recording parental care behaviors, no complete nest failures or predation events were observed, and only one chick was observed to have failed in the nest cup at 14 days old (Table 2). Correspondingly, the variance of the random effect, nest, was estimated as zero, suggesting little correlation in fates of chicks within nests in 2015.

Annual Variation: Egg and Chick Success

Nest checks were performed on a total of 119 nests, including 393 individual eggs and chicks from 2011 to 2015 on Castle Rock NWR (Table 2). Two one-egg clutches

observed on only one occasion during the course of nest checks, one in 2011 and one in 2012, were removed from the data set before analysis. These outlying individual failures caused convergence issues when attempting to run some of the survival models and examining the results revealed the outlying failures did not change the qualitative model results or interpretation. Therefore I evaluated 6 models to examine annual variation in daily survival probabilities of individual eggs and chicks based on 391 individual eggs and chicks from 2011 to 2015, with the covariates YEAR, AGE, STAGE, and CLUTCH and nest as a random effect.

The top-ranked model included the interacting covariates YEAR, AGE and STAGE, and had a ΔAICc value >100 from the second model (Table 4). The second-ranked model included the interacting covariates YEAR and AGE (Table 4), and based on model parameter estimates the daily survival probabilities of eggs and chicks varied by their age between years. In 2011, estimated daily survival probability was 0.987 ($\beta = 4.36$, $\text{CI} = [3.63, 5.09]$), with survival linearly decreasing with AGE ($\beta = -0.05$, $\text{CI} = [-0.07, -0.03]$), and in 2015 the daily survival probability was 0.997 ($\beta = 1.39$, $\text{CI} = [0.24, 2.54]$), with survival linearly increasing with AGE ($\beta = 0.04$, $\text{CI} = [0.01, 0.06]$). Also, the NULL model had a ΔAICc value >200 indicating that inclusion of explanatory variables was informative (Table 4).

Table 4. Model selection table for individual egg and chick survival of Brandt's Cormorants between 2011 and 2015 at Castle Rock National Wildlife Refuge. Explanatory variables included year, clutch size, age and stage, and all models included nest as a random effect.

Model ^a	K ^b	AICc ^c	Δ AICc ^d	AICc Weight ^e
AGE * STAGE * YEAR	19	1551.974	0.0000	1
AGE * YEAR	11	1680.536	128.5623	0
STAGE * YEAR	10	1728.508	176.5336	0
YEAR	6	1731.228	179.2536	0
CLUTCH * YEAR	15	1741.791	189.8172	0
NULL	2	1776.088	224.1139	0

a: Model name including covariates used.

b: Number of parameters.

c: Calculated AICc value for each model.

d: Difference in AICc value from top-ranked model.

e: Proportion of total weight calculated for each model.

The top-ranked model suggested that not only did egg and chick success vary annually, but egg and chick success varied by age within each stage (Figure 6). For example, in 2011 estimated daily survival probability during the incubation stage was 0.997 ($\beta = 5.79$, CI = [4.70, 6.87]), with survival linearly decreasing with age ($\beta = -0.14$, CI = [-0.19, -0.10]), and estimated daily survival probability during the nestling stage was 0.830 ($\beta = -5.57$, CI = [-8.53, -2.61]), with survival linearly increasing with age ($\beta = 0.20$, CI = [0.12, 0.28]). The variance of the random effect (Var. = 2.32, CI = [2.17, 2.47]), which represents the correlation of egg and chick fates within a nest, suggested that the fates of individual egg and chicks were not independent within nests.

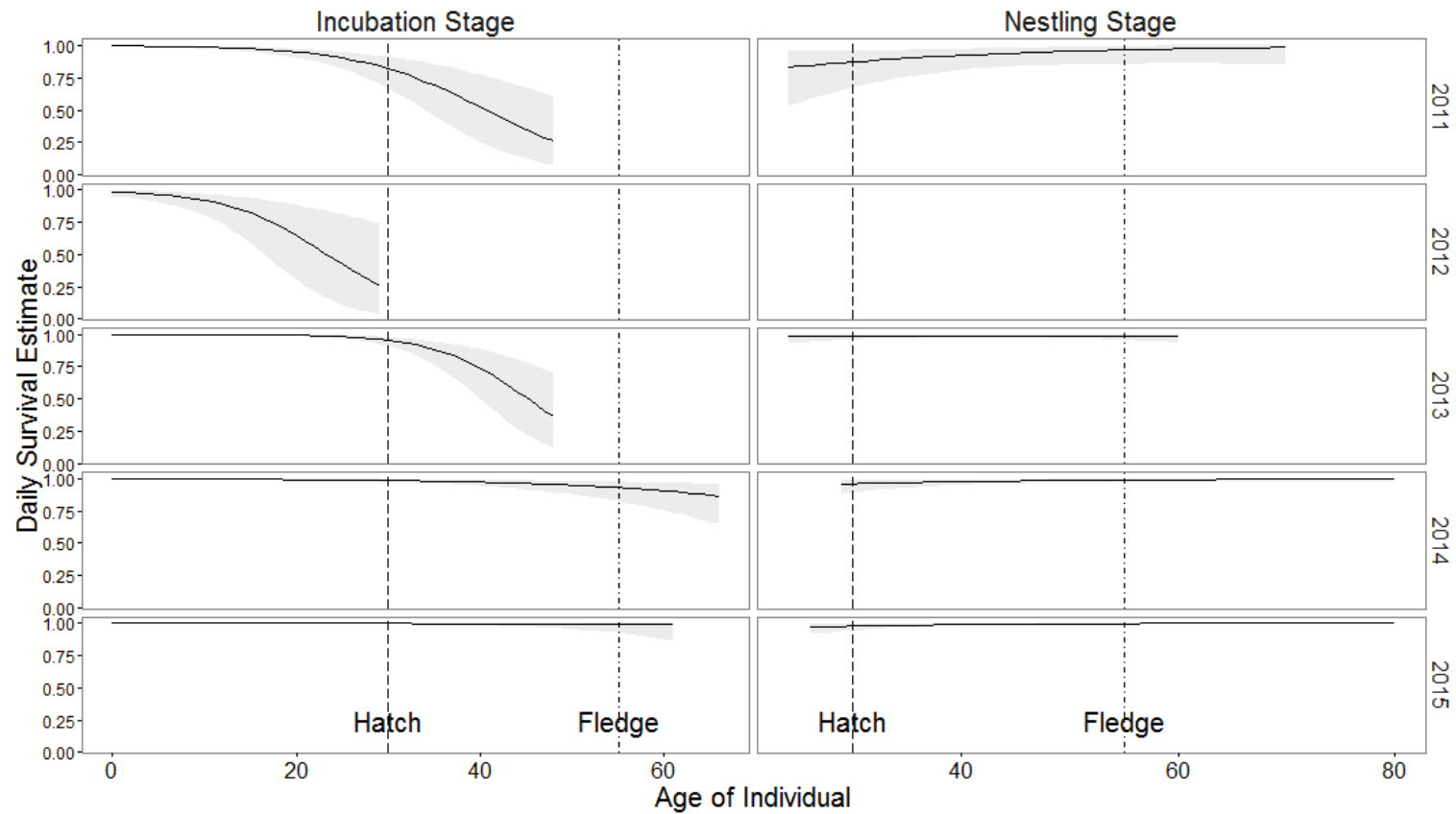


Figure 6. Daily survival estimates for individual Brandt's Cormorant eggs and chicks from 2011 to 2015 at Castle Rock National Wildlife Refuge. The lines represent daily survival estimates that varied annually and varied between the incubation and nestling stage by age. The shaded region represents the 95% Confidence Intervals of the daily survival estimates. Hatch is normally at 30 days and minimum fledge is at 55 days, or 25 days after hatch, and both are average estimates based on local observations of Brandt's Cormorant natural history.

Annual Variation: Nest Success

Using the same data set (Table 2), I evaluated 6 models to examine annual variation in daily survival probabilities of nests from 2011 to 2015, with YEAR, AGE, STAGE, and CLUTCH as covariates. The top-ranked model included the interacting covariates YEAR, AGE and STAGE, and had a $\Delta AICc$ value >45 from the second model (Table 5).

The second-ranked model included the interacting covariates YEAR and STAGE (Table 5), and model parameter estimates revealed that nest success varied by stage between years. For instance, in 2011, the incubation stage daily survival probability was 0.974 ($\beta = 3.61$, $CI = [3.16, 4.06]$), and during the nestling stage the daily survival probability increased to 0.996 ($\beta = 1.98$, $CI = [-0.01, 3.98]$), while in 2013, the incubation stage daily survival probability was 0.994 ($\beta = 1.51$, $CI = [0.59, 2.44]$), and during the nestling stage the daily survival probability decreased to 0.989 ($\beta = -2.60$, $CI = [-4.97, -0.23]$). The NULL model had a $\Delta AICc$ value >85 indicating that inclusion of explanatory variables was informative (Table 5).

Table 5. Model selection table for nest survival of Brandt's Cormorants between 2011 and 2015 at Castle Rock National Wildlife Refuge. Explanatory variables included year, clutch size, age and stage.

Model ^a	K ^b	AICc ^c	Δ AICc ^d	AICc Weight ^e
AGE * STAGE * YEAR	18	349.2193	0.0000	1
STAGE * YEAR	9	397.4935	48.2743	0
YEAR	5	399.6781	50.4589	0
AGE * YEAR	10	401.8617	52.6424	0
CLUTCH * YEAR	14	405.8781	56.6588	0
NULL	1	439.1644	89.9452	0

a: Model name including covariates used.

b: Number of parameters.

c: Calculated AICc value for each model.

d: Difference in AICc value from top-ranked model.

e: Proportion of total weight calculated for each model.

The top-ranked model suggested that not only did nest success vary annually, but nest success varied by age within each stage (Figure 7). In 2014, nine nest failures occurred, eight during the incubation stage and only one during the nestling stage (Table 2). Based on the parameter estimates, in 2014, the daily survival probability during the incubation stage was 0.999 ($\beta = 1.98$, CI = [-1.86, 5.82]), with survival slightly decreasing with age ($\beta = -0.02$, CI = [-0.12, 0.07]), while the daily survival probability during the nestling stage was 0.985 ($\beta = -5.13$, CI = [-21.74, 11.48]), and survival increased with age ($\beta = 0.14$, CI = [-0.33, 0.62]) (Figure 7).

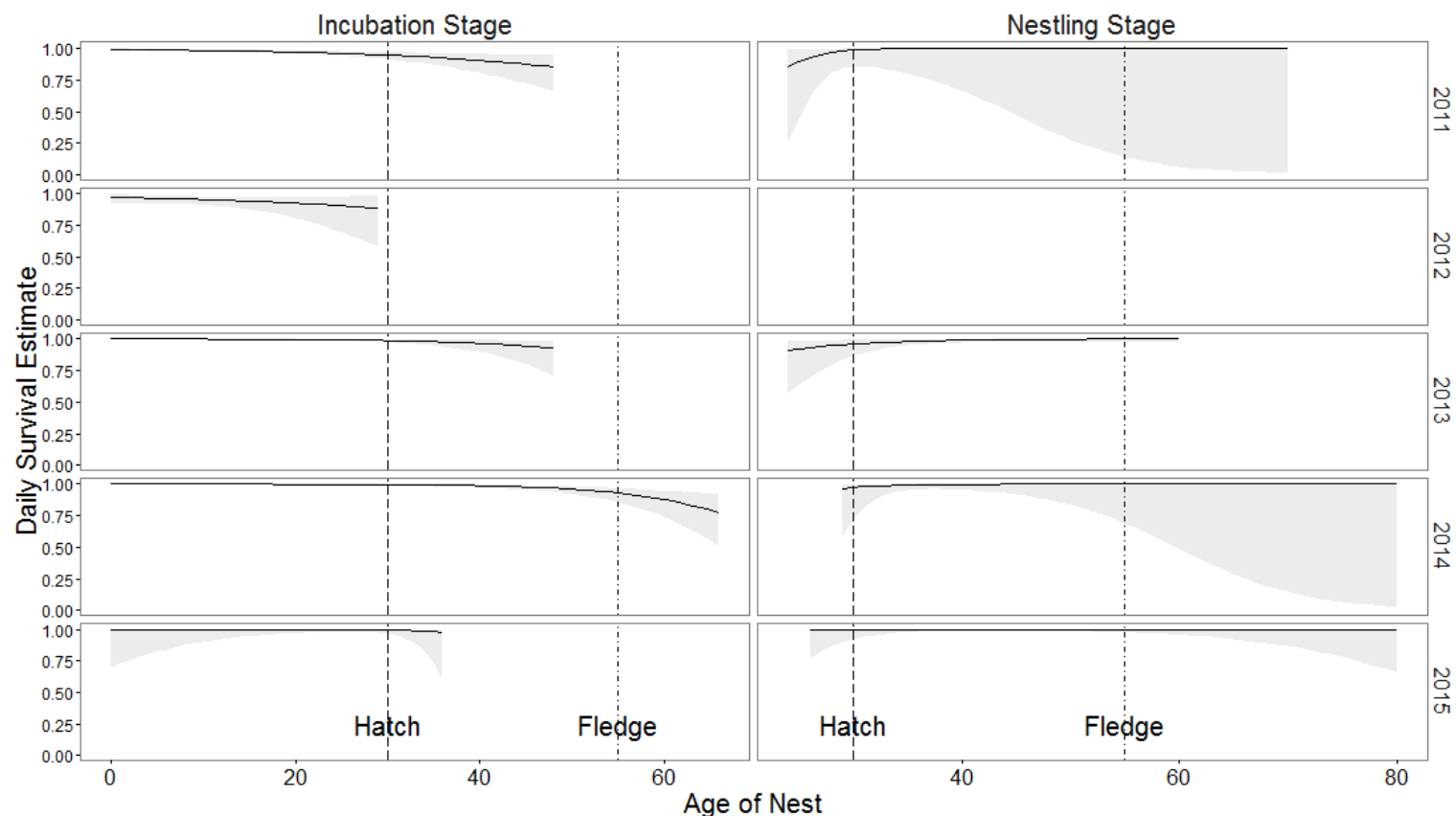


Figure 7. Daily survival estimates for Brandt's Cormorant nests from 2011 to 2015 at Castle Rock National Wildlife Refuge. The lines represent daily survival estimates that varied annually and varied between the incubation and nestling stage by age. The shaded region represents the 95% Confidence Intervals of the daily survival estimates. Hatch is normally at 30 days and minimum fledge is at 55 days, or 25 days after hatch, and both are average estimates based on local observations of Brandt's Cormorant natural history.

Comparison of Egg and Chick Success to Nest Success

Using the same data set (Table 2), I compared survival probabilities for egg and chick success to nest success. I used total survival probabilities, and as a result interpretation could be made at the level of a nesting season on Castle Rock NWR.

Comparing total survival probabilities of egg and chick success to nest success found similar annual trends in survival probabilities between 2011 and 2015 (Figure 8). For example, 2012 had the lowest survival probabilities: egg and chick total survival probability was 0.037 ($\beta = -0.64$, CI = [-1.29, -0.001]) and nest total survival probability was 0.083 ($\beta = -0.81$, CI = [-1.62, -0.01]). In contrast, 2015 had the highest survival probabilities: egg and chick total survival probability was 0.719 ($\beta = 1.69$, CI = [1.14, 2.24]) and nest total survival probability was 0.942 ($\beta = 2.94$, CI = [1.49, 4.40]).

Overall nest total survival probabilities were estimated to be higher than individual egg and chick total survival probabilities. The odds of a nest surviving in 2015 (OR = 0.16) was greater than an individual egg or chick surviving. In addition, based on model parameter estimates, nest total survival probability in 2012 was 0.083 (CI = [0.008, 0.276]), while the derived total survival probability of nest success was 0.106 (CI = [0.013, 0.522]). In 2015, nest total survival probability was 0.942 (CI = [0.788, 0.985]), while the derived total survival probability of nest success was 0.985 (CI = [0.933, 0.997]).

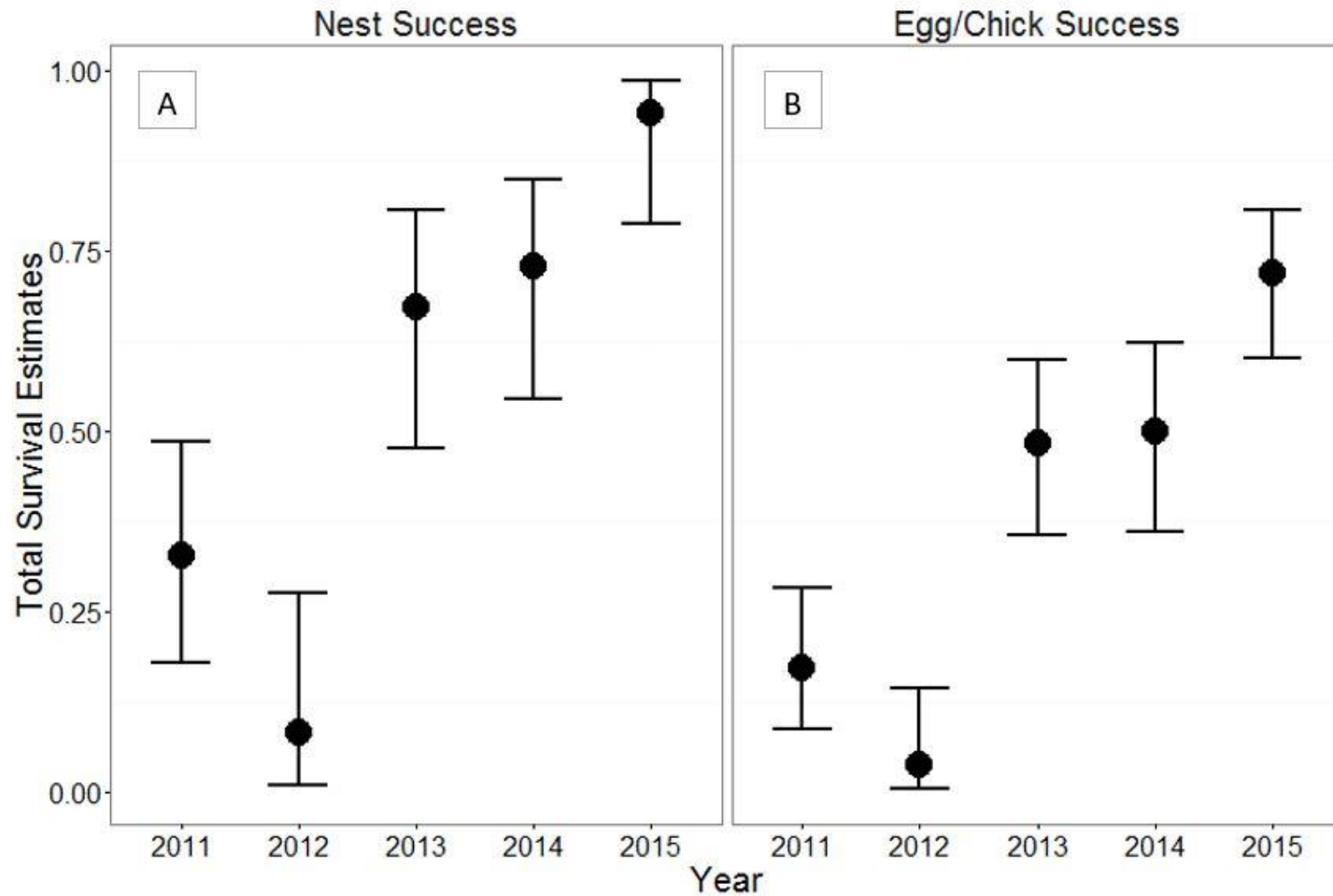


Figure 8. Total survival estimates for Brandt's Cormorant nests (A) and individual eggs and chicks (B) on Castle Rock National Wildlife Refuge from 2011 to 2015. Brandt's Cormorant survival, both nest survival and individual survival, varied dramatically between 2011 and 2015 at Castle Rock National Wildlife Refuge.

DISCUSSION

Parental Care Behaviors

The expression of parental care behaviors in Brandt's Cormorants varied with chick age. Co-attendance decreased as the age of the chick increased (Figure 3). This pattern was expected as Brandt's Cormorant chicks are brooded almost continuously for five to ten days after hatch, and once they can thermoregulate on their own brooding bouts decrease (Carter and Hobson 1988; Boekelheide et al. 1990). However, all observed chick failures in 2015 occurred before the chicks were 15 days old, when recorded rates of co-attendance were the highest (Figure 3). These results were potentially counter-intuitive because seabird natural history indicates that higher levels of co-attendance should increase a chicks' probability of survival, and thus correcting for chick age is important (Carter and Hobson 1988; Boekelheide et al 1990; Clutton-Brock 1991).

The relationship between Brandt's Cormorant provisioning and age of the chick revealed a negative quadratic relationship of provisioning per chick with the age of the chick (Figure 4). The observed provisioning rate more than twenty days after hatch is likely biased low due to chicks being fed out of view at crèche sites (Carter and Hobson 1988). Also, individual chick failures occurred with both relatively high rates of provisioning and low rates of provisioning (Figure 4), which was unexpected as Brandt's Cormorant chicks are altricial and therefore dependent on their parents for food, and

provisioning is often associated with offspring survival (Clutton-Brock 1991; Wallace and Wallace 1998).

Brandt's Cormorant nests hatch asynchronously, and the first chick that hatches is different in size than the last chick to hatch, therefore the first chick may outcompete nest-mates for food (Boekelheide et al. 1990; Stenning 1996). In my study, I measured chick provisioning by recording the number of times a parent delivered a meal to a chick and divided the frequency by the clutch size to determine provisioning per chick per individual nest. However, I could not identify individual chicks and therefore had to assume that meals were equally divided between the chicks within a nest. Therefore, the chick failures observed via the recorded videos in 2015 could be due to within-nest competition, and individual failures could still occur within nests with high provisioning rates and high co-attendance (Stenning 1996).

The individual failures observed in 2015 could also be the result of predation, weather, adult mortality or adult quality (Carter and Hobson 1988; Boekelheide and Ainley 1989; Boekelheide et al. 1990; Wallace and Wallace 1998). While recording parental care behaviors, no predation events were observed and only one chick was observed to have failed in the nest cup at 14 days old. Therefore, the remaining nine failures occurred between checks and their causes are unknown. Within the scope of my study I cannot determine the causes of the individual failures but it is important to identify these alternatives to further understand individual chick survival.

Brandt's Cormorant chicks are naked when they first hatch and completely dependent on their parents for thermoregulation until five to ten days after hatch (Carter

and Hobson 1988; Boekelheide et al. 1990; Wallace and Wallace 1998). Therefore, up to five to ten days of age and in the absence of parents, chicks are extremely vulnerable to current weather conditions. Also, the adult breeding population of Brandt's Cormorants on Castle Rock NWR are not individually marked, therefore the identity of parents was unknown. Individual parent identity may influence chick survival in terms of age, experience or simply poor quality parents that provide poor parental care (Boekelheide and Ainley 1989).

Parental Care Behaviors: Chick Success

Age of individual Brandt's Cormorant chicks at Castle Rock NWR had a positive influence on their survival in 2015. Age is directly related to development, and within ten to twenty days after hatch, growth of their natal down is complete, they thermoregulate, become mobile and gain enough strength to orient their begging toward the parent and insert their entire head inside their parent's mouth for food, and all these traits contribute to an increased probability in survival (Van Tets 1965; Boekelheide et al. 1990; Clutton-Brock 1991; Wallace and Wallace 1998).

In 2015, based on the 17 nests monitored, no complete nest failures occurred, no nests were preyed upon, and chick failures occurred individually. Across all the parental care models (Table 3), the random effect, nest, had an estimated variance of zero, suggesting that individual chick failures across nests were independent in 2015.

Results from the parameter estimates revealed that both standardized co-attendance and standardized provisioning per chick covariates were “pretending

variables”, meaning that from an information-theoretic perspective they were non-informative variables (Anderson 2008). Based on the AICc scores (Table 3) the variables appeared to be informative, however they did not increase the log-likelihood or reduce the deviance (Anderson 2008). While effects of parental care behaviors on individual chick survival were not detectable in my results, larger sample sizes or examining more than one year might produce expected results.

Quantifying survival between 2011 and 2015 at Castle Rock NWR revealed 2015 had the highest survival probabilities for both nest success and individual egg and chick success (Figure 8). Therefore 2015 could have been a very productive year in terms of food resources for Brandt’s Cormorants, resulting in high nest and individual egg and chick survival. In years with lower resource availability, there is evidence for increased differences in individual variation in seabirds (Boekelheide and Ainley 1989). Therefore, individual variation in parental care behaviors simply may have been more difficult to detect in 2015, as opposed to other years at Castle Rock NWR. Further, nest and individual egg and chick survival varied dramatically between 2011 and 2015 (Figure 8), which demonstrates the need to measure this relationship across multiple years, potentially indicating variation in food resources between years (van Noordwijk and de Jong 1986). My methods and results demonstrate how parental care behaviors can be effectively included in a survival model and measured quantitatively, and could be used in future studies attempting to test the influence of seabird parental care on reproductive success.

Annual Variation

In both the individual egg and chick analysis and the nest analysis, the covariate YEAR was informative, suggesting survival probabilities varied inter-annually. In addition, inclusion of explanatory variables helped to inform intra-annual variation. The top model from both analyses demonstrated that survival not only varied annually, but also varied by age within stage (Table 4, 5). Parental effort and strategy varies between stages, meaning parental care behaviors are different between the incubation stage and the nestling stage (Clutton-Brock 1991). Age in both stages is related to development, which is likely to have a positive influence on survival (Clutton-Brock 1991; Wallace and Wallace 1998). Therefore inclusion of YEAR, STAGE and AGE identified variation in survival rates within a season and how that variation can change annually at the same colony.

The interaction between YEAR and CLUTCH in both the individual egg and chick analysis and the nest analysis was the second to lowest-ranked model (Table 4, 5). Cormorants rely all year long on the same marine systems, with widely fluctuating food availability, therefore they can have large variability in their clutch size depending on current marine conditions (Boekelheide and Ainley 1989; Ainley 1990a; Ainley 1990b; Wallace and Wallace 1998; Weimerskirch 2002). I included clutch size to test the prediction that larger clutch sizes would yield higher nest survival estimates, and be an indicator of food availability (Boekelheide and Ainley 1989). However, Brandt's Cormorants could be using a different strategy in which clutch size is determined before

they lay, based on current conditions (Lack 1968; Boekelheide and Ainley 1989). Thus, if Brandt's Cormorant clutch size is adjusted to varying environmental conditions, it would be unlikely for clutch size to be related to survival probability of chicks. Quantifying annual variation in clutch size might be more informative, as opposed to estimating survival as a function of clutch size.

Comparison of Egg and Chick Success to Nest Success

All nest survival estimates were higher than individual egg and chick survival estimates because nest success was defined as one or more individuals successfully fledging from a nest (Mayfield 1975; Jones and Geupel 2007). Derived estimates of nest success from individual egg and chick success were apparently biased high, because the derived estimates assumed all failures within a nest were independent. However, this approach is only biased when estimated nest success is low and there is high correlation of individual fates within nests, meaning a high estimated variance of the random effect. When estimated nest success is high and there is low correlation of individual fates within nests, the derived estimate is less likely to be biased or violate its assumption. The similarity between the nest-based model estimates for nest success, and the derived estimates for nest success from individual egg and chick success demonstrated the validity of quantifying individual survival and suggested that both approaches have value in different situations.

Both individual egg and chick survival and nest survival were highly variable between 2011 and 2015 at Castle Rock NWR. Brandt's Cormorants rely all year long on

the same marine system, and thus they can have variable survival (Boekelheide and Ainley 1989; Ainley 1990a; Ainley 1990b; Wallace and Wallace 1998; Weimerskirch 2002). The annual productivity estimates on Southeast Farallon Island were also highly variable over time, and Southeast Farallon Island hosts the largest Brandt's Cormorant colony in the world and has been monitored for over 40 years (Elliott et al. 2015).

Seabird Biology and Monitoring Implications

Model-based, rather than ad hoc, approaches to estimating nest and chick survival are a potentially valuable tool for seabird monitoring and seabird ecology. The logistic exposure model is not only an effective way to estimate survival using commonly available seabird monitoring data, but it is flexible in a way that can support different experimental designs, and allows for estimation and comparison of nest or chick survival rates, even when observations vary in interval (Shaffer 2004; Grant et al. 2005). One trial could easily be defined as a nest or an individual egg and chick, and allows for the easy incorporation of explanatory variables (Appendix C; Shaffer 2004; Grant et al. 2005). The logistic exposure model also allows estimation of survival with incomplete nest check data. On Castle Rock NWR in 2012 and 2013, the audiovisual monitoring system failed before the Brandt's Cormorant nesting season was complete, but the model allowed me to successfully estimate survival based on exposure days and known fates of nests that were complete before the camera failure.

Improving available methods for estimating within – and between – year variance in nest survival or individual egg and chick survival is a valuable tool for seabird

ecology. A common goal in ecology is to predict population dynamics based on demographic information (Saether and Bakke 2000). For seabirds with a clutch size greater than one, efficiently quantifying individual survival of eggs and chicks and estimating variance, shown by my results, helps contribute to accurate estimates of species vital rates and their variances. Estimates of vital rates and their variances is key when building demographic models and ultimately helps inform seabird population biology (Saether and Bakke 2000).

The effect of year identified in my results was important for both individual egg and chick survival and nest survival, suggesting Brandt's Cormorant reproductive success varied annually. Biologists and managers cannot assign possible changes in the marine environment to annual changes in survival, without first being able to effectively quantify annual variation in survival. My results provide a framework for quantifying annual variation in seabird reproductive success, specifically seabird reproductive success with clutch sizes greater than one. My results also have important implications for MPA monitoring, as variation in seabird reproductive success is often used as an indicator for current management practices and marine processes that may change as a result of MPA establishment (Pichegru et al. 2010; Ronconi et al. 2012).

Quantifying the variation occurring within a season, and more specifically quantifying the timing of failures of individual eggs and chicks within a season, could also allow biologists and managers to recognize known environmental changes or events as the cause of observed failures. For example, seabird colonies could experience brief

atypical weather conditions, or a large disturbance event, which could impact individual egg and chick survival (Willett 1910; Osborne 1972; Wallace and Wallace 1998).

Brandt's Cormorants are sensitive to disturbance during incubation and brooding, and flushes from their nest increase the chance of predation of their eggs and chicks, breaking their own eggs, and repeated disturbance could cause colony abandonment (Willett 1910; Osborne 1972; Wallace and Wallace 1998). Therefore MPAs, which are often designed to not only protect the marine ecosystem but protect the seabirds using that ecosystem, are very interested in disturbance events and how they could impact breeding seabirds. Impacts of disturbance to breeding seabirds is also a very important issue concerning seabird conservation (Rodway et al. 1996; Albores-Barajas et al. 2009; Carey 2011; Soldatini et al. 2015). Disturbance, particularly human disturbance, affects a suite of seabird species and can have detrimental effects on seabird breeding activities and reproductive success (Rodway et al. 1996; Albores-Barajas et al. 2009; Carey 2011; Soldatini et al. 2015). Quantifying temporal variation in individual failures could provide MPA monitors and seabird biologist with the tool to assign known disturbance events to observed failures.

Colony productivity of Brandt's Cormorants on the Southeast Farallon Island has been measured for over 40 years (Elliott et al. 2015). Colony productivity was defined as the number of fledglings produced per adult breeding pair (Elliott et al. 2015). Even with over 40 years of data, managers found it difficult to relate fluctuations in colony productivity to changes in the marine environment (Elliott et al. 2015). Only El Niño or warm water events were related to some years of low productivity, which are a well-

studied phenomenon known to impact seabird food supplies (Cairns 1987; Ainley 1990a; Hipfner et al. 2007; Elliott et al. 2015). When only colony productivity is suggested to indicate changes in the marine environment without identifying the proximate causes of such variation, inference is limited to association (Mallory et al. 2010). Based on my results, inclusion of explanatory variables were helpful to inform both within – breeding season and between – breeding season variation in survival. Therefore, the logistic exposure model, along with inclusion of parental care behaviors or other informatory explanatory variables, could potentially help managers better understand annual variation and how it relates to the marine environment (O'Connor 1978; Boekelheide and Ainley 1989; Boekelheide et al. 1990; Stenning 1996).

While seabird reproductive success is often measured at the level of the colony, indexed by colony productivity or nest success, measuring parental care behaviors or individual egg and chick success simply allows biologists and managers to use all of the information from the same set of nests (Carter et al. 1984; Cam et al. 2002). If nest success or colony productivity is already being monitored, inclusion of individual egg and chick success of seabirds with clutch sizes greater than one could easily be included; or likely already is, since the data collected is often the same. Ultimately a greater understanding and inclusion of proximate causal factors that influence seabird reproductive success and contemporary parameter estimation methods helps inform seabird biology and current monitoring techniques, potentially leading to more informed science-based management and a better understanding of seabird colonies monitored.

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APPENDIX A

Appendix A: The audiovisual monitoring system on Castle Rock National Wildlife Refuge was located on a rocky slope on the north side of the island and from this location the higher elevation areas on the island are visible, including the Brandt's Cormorant colony I monitored for my research.



APPENDIX B

Appendix B: R-code for the logistic exposure function used in all the logistic exposure models to estimate survival. The code is modified from Point Blue Conservation Science (PRBO), specifically Nest Survival.chat code, adapted from Shaffer 2004.

```
logitexp <- function(exposure = 1)
  #Function allowing exposure to be one or greater
{
linkfun <- function(mu) qlogis(mu^(1/exposure))
  #The link function (Shaffer, 2004)
linkinv <- function(eta) plogis(eta)^exposure
  #Inverse of the link function
logit_mu_eta <- function(eta) {
  ifelse(abs(eta)>30,.Machine$double.eps, exp(eta)/(1+exp(eta))^2)
  #Function added to fix an error, when a value is close to one or zero it will no longer be
  divided by zero
}
mu.eta <- function(eta) {
  exposure * plogis(eta)^(exposure-1) * logit_mu_eta(eta)
  #Function that allows estimates to be back-transformed
}
valideta <- function(eta) TRUE
link <- paste("logexp(", deparse(substitute(exposure)),
  ") ", sep="")
  #Double checks the previous function
structure(list(linkfun = linkfun, linkinv = linkinv, mu.eta =
mu.eta, valideta = valideta, name = link), class = "link-glm")
  #Structure required for the generalized linear model (GLM) to use the logistic exposure
  function
```

APPENDIX C

Appendix C: R data table used to estimate Brandt's Cormorant chick survival, the data table includes trials representing individual chicks, exposure days and explanatory variables used in the analysis.

YEAR	NEST	DATE	JULIAN DATE	EXPOSURE	PROVISION/ CHICK	CO-ATTEND	STATUS	TRIALS	SURVIVE	SUCCESS	FAILURE
2015	1	6-15	166	6	2.00	1.13	3E/1C	4	1	4	0
2015	1	6-21	172	8	0.00	1.69	3E/1C	3	1	3	0
2015	1	6-21	172	8	0.00	1.69	3E/1C	1	0	0	1
2015	1	6-29	180	4	11.33	0.59	3C	3	1	3	0
2015	1	7-03	184	5	13.00	0.52	3C	3	1	3	0
2015	1	7-08	189	6	6.33	0.31	3C	3	1	3	0

A subset of data from 2015, Brandt's Cormorant Nest #1.