EFFECTS OF PROTECTIVE NESTING SITE PROPERTIES ON GYRFALCON

BREEDING SUCCESS AND PARENTAL INVESTMENT IN WESTERN ALASKA

by

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The following individuals read and discussed the thesis submitted by student Michael Thomas Henderson, and they evaluated his presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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The final reading approval of the thesis was granted by David Anderson, Ph.D., Chair of the Supervisory Committee. The thesis was approved by the Graduate College.

DEDICATION

To the conservation and better understanding of the Arctic ecosystem and its quintessential falcon. Seeing wild Gyrfalcons fly over the open tundra landscape and gaining an intimate knowledge of their nesting behaviors has had a substantial impact on my life. I hope our efforts, along with those of our collaborators and colleagues, help to preserve their grandeur for many generations to come.

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Abstract

Habitat suitability for wildlife is defined at scales ranging from the landscape to an individual breeding site. Areas that fulfill habitat requirements for birds disproportionally maintain populations, and the identification of variables that distinguish optimal breeding sites helps to prioritize conservation. Nesting site characteristics that protect breeding raptors from harsh weather can promote a more favorable microclimate and increase breeding success, although previous attempts to understand this effect in breeding Gyrfalcons have yielded ambiguous results. Additionally, breeding adults incur substantial costs from the physical shielding of eggs and nestlings, particularly in the Arctic, and it is possible that protective properties can decrease nest attendance rates, thus lowering costs of breeding. My objective was to quantify Gyrfalcon nesting site characteristics and assess how breeding success and nest attendance varies by protective qualities of nesting sites. I studied Gyrfalcons on Alaska's Seward Peninsula from 2016 – 2018 by installing motion-activated cameras to monitor breeding attempts and quantify nest attendance rates. I found that the degree of physical exposure in the horizontal plane was negatively correlated with the probability of hatching and fledging (providing hatch occurred), as well as overall productivity. The negative effect of horizontal exposure on fledging probability and overall productivity was greatest at sites that were also more

exposed in the vertical plane, although this interaction did not affect hatching probability. Productivity more than doubled in nests that provided a refuge in which nestlings could seek shelter, such as a crevice or an overhang. Additionally, nest attendance rates were highest in nests that were maximally exposed in the horizontal plane, particularly when nestlings were two to three weeks old. The increased parental investment and concurrent decreased productivity associated with horizontal nest exposure demonstrated that nesting site characteristics can have both direct and indirect effects on breeding Gyrfalcons. The compounding effects of poor nesting site suitability suggests that breeding sites are a relevant scale for effective conservation of Arctic breeding raptors. As the Arctic continues to see rapid increases in temperature and precipitation, physical protection of nesting sites will likely become increasingly important for the conservation of the world's largest falcon. Understanding factors that dictate habitat suitability, at all spatial scales, will help prioritize the conservation of valuable habitat as the tundra landscape continues to see accelerated climatic changes.

Introduction

Wildlife populations are limited by numerous biotic and abiotic factors that determine habitat suitability (Casado et al. 2008; Heuck et al. 2017; Møller et al. 2018; Murdoch 1994; Sinclair et al. 1985). Because habitat suitability varies across heterogeneous landscapes, wildlife often distribute in a non-random pattern, with areas of high suitability promoting higher fecundity (Ferrer & Donazar 1996; Fretwell & Henry 1970; Newton 1991; Orains & Wittenberger 1991). Breeding productivity is often used as an indicator of habitat suitability and the conservation status of wildlife, because changes in reproductive output can have significant effects on population dynamics (Anctil et al.

2014; Johnson & Geupel 1996). Because highly suitable habitats disproportionally maintain populations, identifying variables that differentiate areas of high suitability helps prioritize the conservation of specific habitats across broad landscapes (Newton 1991). Further, because habitat suitability is determined across multiple spatial scales, it is necessary to investigate as many meaningful spatial scales as possible, from landscape to nesting site (Luck 2002; Morris 1987).

Nesting site characteristics can affect productivity of birds by influencing the microclimate that nestlings and adults are exposed to during vulnerable life stages (Boukhriss & Selmi 2018; Fast et al. 2007; Kim & Monaghan 2005). For the purposes of this study, I defined a nesting site as the area of a cliff that supported and immediately surrounded a nest structure or the location where a breeding attempt occurred (Steenhof et al. 2017; Anderson et al. 2017). Protective properties of nesting sites such as the presence of an overhang, physical protections lateral to the nest, and a southward orientation can shelter nestlings from precipitation, strong winds, and provide increased sunlight, providing a beneficial microclimate for nestling development (Anctil et al., 2014; Fast et al., 2007). Thermoregulation is energetically expensive for nestlings and exposure to inclement weather increases this metabolic cost and may decrease physiological condition (Romero et al. 2000) or can result in the death of young birds (de Zwaan 2018; Polak & Kasprzykowski 2013; Stokes & Boersma 1998). Protective properties of nesting sites have been correlated with increased breeding success in Arctic-nesting Rough-legged Hawks (*Buteo lagopus*; Beardsell et al. 2016) and Peregrine Falcons (*Falco Peregrinus*; Anctil et al. 2014; Mearns & Newton 1988) but it is unclear

if this pattern is present for breeding Gyrfalcons (*Falco rusticolus)*, which are year-round Arctic specialists.

Reproductive attempts impose direct and indirect costs for breeding birds, many of which are precipitated by physically shielding nestlings (Royal et al. 2012; Santos & Nakagawa 2012). Maintaining viable temperatures of eggs and young nestlings when ambient temperatures are low requires consistent incubation and brooding, therefore increasing the daily energy expenditure, decreasing foraging time, and can decrease the body condition of breeding adults (D'Alba, Spencer et al. 2011; Weathers 1985; Williams 1993). Physical shielding of nestlings from the environment is one of the most energetically costly stages of avian life history and the cost is nearly double for Arctic breeding species (Peirsma et al. 2003; Weathers 1985; Williams 1993). Costs of reproduction can carry over to subsequent life history events, making breeding individuals less competitive and less likely to survive, thus reducing future reproductive fitness (Bize et al. 2004; Fokkema et al. 2018; Hanssen et al. 2005). Parental investment, defined as the amount of energy expended to aid current reproduction, may therefore be viewed as a trade-off against future survival and reproductive efforts, particularly for long-lived species like raptors (Golet et al. 1998). Birds increase parental care in response to the thermoregulatory needs of offspring, including shorter and less frequent vacancies from the nest with increased cost to adults (Cresswell et al. 2004; Webb & King 1983). Inclement weather can also increase nest attendance rates of birds and protective properties of nesting sites may ameliorate the need to allocate additional energy to nest attendance, thus reducing parental investment for Arctic, cliff-nesting raptors (Hilde & Christophe 2016; Hilton et al. 2004; Laux et al. 2016; Reid et al. 2000). Further,

passerines can modify their parental investment depending on nesting site accessibility to predators, but it is unclear if this is a concern for cliff-nesting raptors (Fontaine & Martin 2006).

Gyrfalcons are long-lived cliff-nesting raptors that breed in the harsh climate of circumpolar Arctic and sub-Arctic tundra (Booms et al. 2008). Anderson et al. (2019) found a non-random pattern of nesting site occupancy by Gyrfalcons, suggesting heterogeneity in habitat suitability on the Seward Peninsula, Alaska. Their attempts to model Gyrfalcon occupancy patterns as a function of home range-scale habitat variables yielded ambiguous results and raised the suggestion that habitat selection in this system may be directed at smaller spatial scales than the landscape. Gyrfalcons are predicted to be among the most vulnerable bird species to the effects of global climate change because of their narrow ecological niche and the rapid landscape reconfiguration occurring throughout their distribution (Liebezeit 2012; Tape et al. 2016; Tape et al. 2006). Additionally, precipitation can substantially decrease falcon breeding success and as these weather events continue to become more intense and frequent, the importance of physical protection of nesting sites are likely to increase (IPCC 2014; Min et al. 2011; Trenberth et al. 2003). Identifying nesting site characteristics that govern small-scale habitat suitability will strengthen our understanding of factors that influence Gyrfalcon breeding output and help us prioritize the conservation of areas for which they are best suited.

My objective was to quantify characteristics of Gyrfalcon nesting sites and determine the effect of these characteristics on productivity and parental investment. I examined the effect of protective properties to six breeding parameters: overall

productivity, probability that an egg will hatch, the probability a nestling will fledge, hatch date, the length of the brood rearing period, and parental investment. I proposed four generalized hypotheses with specific hypotheses outlined in table 1.2.

(1)   Productivity is higher in nesting sites that provide properties that shield nestlings from the threat of inclement weather. Productivity was defined as the number of nestlings that survived to 80% of fledging age per breeding pair (Steenhof et al. 2017). I also investigated the effects on the probability of hatch and fledging independently from overall productivity because threats and sensitivities vary between these two developmental stages (Polak & Kasprzykowski 2013).

(2)   Eggs in nesting sites with protective properties hatch earlier than those that lack protections potentially due to earlier occupancy of highly suitable habitats (Newton 1991; Tschumi et al. 2014).

(3)   Nestlings reach fledging condition sooner in more protected nesting sites that provide more favorable microclimate.

(4)   Adults reduce nest attendance rates, thus decreasing parental investment, in protected nesting sites.

Methods

Study Area

I studied Gyrfalcon breeding biology on 4,800km^2 of the southern Seward Peninsula (65.37°N, 164.22°W), in western Alaska, a subset of a previous study area (Bente 2011; Anderson et al. 2019; Figure 1.1). The landscape is comprised of rolling hills of Arctic tundra with dispersed rock outcroppings and cliff-lined river systems that provide nesting substrates for approximately 14 Gyrfalcon breeding pairs annually

(Kessel 1989, Anderson unpublished). The predominate vegetation type is upland-tundra comprised of mosses and lichens with dense willows (*Salix* spp.), dwarf birch (*Betula nana*), and alders (*Alnus* spp.) lining riparian areas (Viereck et al. 1992). The climate is characterized by long, cold winters and short cool summers. Early spring conditions, when the Gyrfalcon breeding season begins, can be extremely variable. Average April temperature range -10°C to - 2°C, and snow on the landscape persists until approximately the middle of June, with a high interannual variation. By July, average temperatures range 7°C to 15°C with an average of 9.27 cm of precipitation for the duration of the Gyrfalcon breeding season. Temperature extremes can range from -32°C early in the breeding season to 30°C in latter portion, exposing nestlings and adult Gyrfalcons to dramatic thermoregulatory challenges. The Seward Peninsula is an ideal site in which to study Gyrfalcon ecology because its road system allows relatively easy access to a moderately large breeding population (Bente 2011, Robinson et al. 2019, Anderson et al 2019).

Study Species

The Gyrfalcon is the world's largest falcon and populations breed at the northern limits known for raptors, as far north as 79° N in North America (Cade 1982). Gyrfalcons on the Seward Peninsula study area commonly occupy nests of other species, primarily Common Ravens (*Corvus corax*), Golden Eagles (*Aquila chrysaetos*), and Rough-legged Hawks, but occasionally nest on bare ledges (Bente 2011). Gyrfalcons frequently nest under overhangs in areas where the geologic feature is common, but how this feature affects breeding output is unclear (Cade 1960, Poole and Bromley 1988a, Platt 1977, Kuyt 1980). The incubation period is typically 30 – 35 days and females perform 76% –

83% of incubation (Platt 1977). The brood rearing period is typically ca. 50 days and 75% – 100% of brooding is performed by females (Anderson et al. 2017; Platt 1977, Poole and Bromley 1988a).

Fieldwork

This study is part of a larger, collaborative research program on the population ecology of Arctic raptors performed jointly by The Peregrine Fund, Alaska Department of Fish and Game, and Boise State University (Bente 2011, Anderson et al. 2019, Robinson et al. 2019). I conducted fieldwork May to July 2016 – 2018, corresponding to the late incubation period through fledging for Gyrfalcons on the Seward Peninsula and I increased my sample size by including breeding data collected by Robinson et al. (2019) from 2014-2015. I measured the characteristics of nesting sites that were occupied from 2014-2015 at the end of the 2017 brood rearing period. We identified occupied Gyrfalcon nests by conducting aerial surveys of previously cataloged cliff sites (similar to Anderson et al. 2019; Bente 2011; Robinson et al 2019) from 2 – 15 May from 2015 – 2018 using a Robinson R44 helicopter. In 2014, a smaller subset of historical sites were surveyed from the ground during May to identify occupied sites.

In contrast to nesting site, I define a nest as the location where eggs were laid, which in this study was most often a stick nest and occasionally an empty ledge. I installed Reconyx PC800 and HF2X motion-activated cameras (hereafter referred to as nest cameras) at 53 occupied Gyrfalcon nesting sites to determine hatch date, number of eggs hatched, fledge date, productivity, and to record parental behavior on a subset of nests (Table 1.1). I accessed cliff-nests by rappelling down cliff faces and installed nest cameras during incubation when conditions allowed (n = 38) and installed the remaining

15 cameras within the first two weeks of the brood rearing period. The placement of nest cameras on cliff faces was approximately 1–2 m laterally from nests and 1 m above to capture the entire nesting site while ensuring clear images. To maximize the sample size of nesting behaviors while not exceeding the storage capacity of the memory card (32GB), I programmed camera settings as follows: medium-high motion sensitivity, two rapid-fire photos when motion activated, a 30–second quiet period following motion activation, and a motion-independent photo every half hour.

I measured protective properties of nesting sites and removed nest cameras after nestlings had fledged (>50 days after hatch) or nesting attempts had failed. To measure vertical and horizontal exposure of nesting sites, I established an origin directly behind the location that eggs were laid and used an angle ruler to estimate the degrees of exposure in both planes (Beardsell et al. 2016; Figure 1.2). It is important to note that I measured nesting site exposure but that the protection provided by minimal exposure is more biologically significant, thus I frequently refer to minimal exposure as having greater protection. I measured nest orientation with a handheld compass. I subjectively categorized the presence or absence of available refuge by assessing whether a site contained at least one structure that would provide protections for mobile nestlings, such as an overhang, crevice, or cave. Because there are minimal published values for nesting site and cliff heights for Gyrfalcons, I measured the angle and distance to the top of the structures with a clinometer and range finder and calculated the height with [sin(angle)*distance=height]. Nest substrate can affect conductive heat loss, thus I categorized nesting substrate as stick nest, ledge with mulch (typically a highly decomposed stick nest), or bare ledge (Hilton et al. 2004). Nesting sites size may affect

productivity of Gyrfalcons (Mechnikova et al. 2011) but the size of the nest alone may be incomplete because nestlings commonly perch on ledges that are accessible from the nest. To calculate nesting site size, I measured nest diameter, calculated the area in m^2, and characterized ledge size into one of four categories: no ledge = (0); ledge ≤ 0.1 m^2 = (1); ledge 0.1 $m^2 - 1$ m^2 = (2); ledge > 1 m^2 = (3); nest continuous with the landscape = (4); i.e., nestlings could walk out of the nest directly onto the tundra). I subjectively categorized whether nests were accessible to land predators, particularly red foxes (*Vulpes vulpes*) and wolverines (*Gulo gulo)*, by assessing if there was a clear path that would allow these predators to access nesting sites.

Nest Camera Images Processing

I determined productivity from camera images by counting the number of nestlings observed to have survived to at least 40-days old before leaving the frame of the images (Steenhof et al. 2017; Steenhof & Newton 2007). I considered fledge date as the day the final nestling of a clutch voluntarily left the nest at least once, and the brood rearing period as the length of time between the hatching of the first egg until the last nestling fledged (Steenhof et al. 2017).

To determine nest attendance, I reviewed time-lapsed images taken every half hour and recorded the date, time, whether an adult was present, and the sex and behavior of the adult. I classified adult behavior into five categories: incubating, brooding/shading, feeding, standing, and absent. Incubating and brooding/shading were both characterized by any contact with young or an obvious shading position and were distinguished by pre- or post-hatch, respectively. To account for researcher disturbance, I did not include data immediately following nest visits by researchers until an adult had returned to the nest.

Additionally, nesting sites with large ledges were removed from nest attendance analyses when nestlings became old enough to leave the image frame. Adult sex was determined based on size (females larger than males) and individual markers of each parent, including the brightness of male cere, molting or leucitic feathers, and plumage differences.

Statistical Methods

To examine the effects of nesting site characteristics on breeding Gyrfalcons, I constructed regression model sets for each of my four generalized hypotheses and the probability of hatch and fledge in the statistical platform R in either base R and lme4 (Version 3.4.2). Individual models represented different types of nesting site protections and other variable that may affect breeding parameters of Gyrfalcons (detailed in Table 1.2). For all analyses, I considered minimal horizonal and vertical exposure, inaccessibility to terrestrial predators, presence of a refuge for nestlings, and a southern orientation to be protective properties. I also included the effects of nesting site size (besides for the analysis on the probability of hatch), the nest substrate, and either an intercept only or a control model in all candidate sets.

I used Akaike's Information Criterion corrected for small sample size (AICc) to rank individual models based on their relative likelihood given a set of candidate models, with package MuMIn (Akaike 1973; Barton 2017, Burnham & Anderson 2002). I considered any model with ΔAIC < 2 to have strong statistical support and ΔAIC between 2 – 7 to have relevant but weak statistical support (Burnham et al. 2011). When assessing confidence in parameter estimates, I calculated 85% confidence intervals, to comply with the AIC paradigm (Arnold 2010). Additionally, all parameter estimates and

confidence intervals presented are logit (binomial analyses) or log (Poisson and gamma

analyses) restrained to assess if confidence intervals overlapped 0. I modeled effects only

for those nesting sites for which all measurements were obtained and thus discarded nine

nests lacking any relevant data, and three nests subjected to falconry take (i.e., falconers

legally removed nestlings) for a final sample size of 45 nests. It was not possible to assess

every response variable for all nests due to camera malfunction and other logistical

issues, so samples sizes vary between analyses (Table 1.3). Because orientation is a

directional (circular) variable, I normalized degrees to represent "northness" and

"eastness" by calculating the cosine and sine respectively and included both in the

orientation model for all candidate sets (Pewsey et al. 2013). Because ledge is an ordinal

variable, ranked but with arbitrary intervals, I included linear and polynomial (x^2 and x^3)

relationships in all nesting site size models for all candidate sets, besides the probability

of hatch for which a nesting site size model was not included.

To test the hypothesis that productivity is higher in nesting sites that provide

properties (hypothesis 1), I built Poisson-distributed, generalized linear models to fit

count data that are not over-dispersed (Zuur 2009). I tested for over-dispersion with the

"dispersiontest" function in the AER package, and was unable to find a statistical

difference between the mean and the variance ($p = 0.12$; Kleiber and Zeileis 2008). I

further analyzed if the effects of nesting site characteristics differed by developmental

stage (eggs and nestlings) because survival is not constant throughout development

(Young 1963). I built binomial, logistic regression models to analyze the effects of

nesting site characteristics on the probability of hatch and then on the probability of

fledging, only for those nestlings that successfully hatched. I did not include a nesting site

size model for the probability of hatch because I did not have a biologically relevant, a priori hypothesis to justify how the size of the nesting site could affect an egg's ability to hatch. To test the hypotheses that eggs in nesting sites with protective properties hatch earlier (hypothesis 2) and the hypothesis that nestlings reach fledging condition sooner in more protected nesting sites (hypothesis 3), I built gamma distributed, generalized linear models because neither was normally distributed and were constrained to positive values. Additionally, I built a generalized linear model with a Poisson distribution to test the assumption that early breeders have higher productivity.

To test hypothesis that adults reduce nest attendance rates in protected nesting sites (hypothesis 4), I built 12 models but only included nine in the the AICc analysis. I removed an intercept-only model, an age-only model, and a model containing only a random effect of nesting site (ID) from the analysis because they performed poorly compared to remaining models. I retained a multiple regression model that included nestling age as a fixed effect and a random effect for nesting site (ID) as a control for variables that are not of interest but are likely to effect nest attendance. I included interactions between all model parameters and age because I anticipted nest attendance and the effect of protections to decreases with nestlings age (Zimmerman 1959). I included a random effect for individual nesting site in all models using package "lme4" to account for hierarchical structure and to avoid psudoreplication (Bates et. al 2014). I catorgorized behaviors into those that represent nest attendance (feeding, incubating, and shading/brooding) and those that do not (standing and absent). Nest attendance was used as the binomial response variable for all parental investment analyses. I restricted analysis to the brood rearing period because, prior to hatch, ca. 98% of behaviors were of

incubating adults, with little variation. I scaled horizontal and vertical exposure around their means because the large difference between exposure and age was causing model convergence failure.

Results

Descriptive Statistics of Nesting Sites and Breeding Parameters

I obtained data from 57 breeding attempts by Gyrfalcons 2014 – 2018 on the Seward Peninsula, Alaska. Of these breeding attempts, I performed analyses on 45 nesting sites (Table 1.1). Nesting sites were commonly inaccessible to terrestrial predators (74%), provided available refuge for nestlings (73%), and contained a stick nest (65%; Table 1.3A.). Nesting sites were oriented in all directions, and southern orientation was slightly more common ($\chi^2 = 6.93$, p = 0.07; Figure1.3A). Horizontal exposure varied more than vertical exposure (Table 1.3B) and 88% of nesting sites contained an overhang, applying the overhang definition suggested by Beardsell et al. (2016; vertical exposure <90°). Nest size, cliff height, and nest height varied greatly (ranges: 0.12 m^2 – 5.48 m^2; 5.74 m – 27.62 m; 1.0 m – 19.9 m, respectably). Mean productivity was 1.71 (range 0 – 4) and the mean number of eggs laid and hatched were 3.36 (range: 2 – 5) and 2.62, (range: 0 – 4) respectively (Table 1.3B). The average hatch date was 26 May (range: 16 May – 14 June) and the mean brooding rearing period length was 48 days (range: 35 days – 52 days). For nestlings with confirmed fates, 99 fledged (70% of outcomes) and most mortalities occurred early in the nesting period, either prior to hatch (n = 15, 11% of outcomes, 35% of mortalities) or during the first week of the brood rearing period (n = 14, 10% of outcomes, 33% of mortalities). There was also a notable

spike in nestling mortalities during the fourth week of the brood rearing period (n =10,

7% of outcomes, 23% of mortalities).

I collected 30,849 samples of adult Gyrfalcon nest attendance behavior by adult

Gyrfalcons in 2017 and 2018 (Table 1.1). Nest attendance was nearly constant prior to

egg hatch and during the first week of development, with little variation between nests

(Figure 1.8A). During the second and third weeks of the brood rearing period there was a

noticeable drop in nest attendance and a large increase in the variation among nests

(Figure 1.8A). After week three, nest attendance and variation among nests decreased for

the final four weeks of brood rearing period (Figure 1.8A). Females were

disproportionally responsible for nest attendance. Before eggs hatched, females

performed ca. 65% of the nest attendance and averaged ca. 85% for the remainder of the

brood rearing period (Figure 1.8B). During all stages of the nesting period, female

attendance varied greatly among breeding pairs (Appendix Figure 4).

Analysis of Hypotheses

Productivity was predominantly affected by the interaction of horizontal and

vertical exposure, such that the effect of horizontal exposure was greatest (most negative)

in nesting sites with more vertical exposure (Table 1.4; Figure 1.3A). The confidence

interval for the interaction did not overlap 0, suggesting high confidence in the direction

of the relationship (Table 1.6; β = -0.004; C.I. = -0.0007 – -0.0002). It is worth noting

that the confidence interval and predicted value of the high vertical exposure trend line in

figure 1.3A exceeded the maximum clutch size of Gyrfalcons (five). I did not interpret

the coefficients for the Horizontal Exposure or Exposure models, though the AICc

analysis suggested strong and weak support (respectively), because the detected

interaction deemed them uninformative. There was also weak evidence for nesting sites

with an available refuge having more than double the productivity compared to those that

lacked a refuge (2 fledgling and 0.8 fledglings respectably), and the confidence interval

did not overlap 0 (Figure 1.3B; $\beta = 1.16$; C.I. $= 0.69 - 1.71$). Although ΔAICc for the

Accessibility to Predators model was > 7, it is worth noting that inaccessible nests

fledged one additional nesting on average compared to accessible nests, and the

confidence interval does not overlap 0 ($\beta = -0.72$; C.I. $= -1.38 - -0.16$).

The probability of hatch was higher in nesting sites with minimal horizontal

exposure and maximum vertical exposure, with no interaction (Table 1.4). The effect of

horizontal exposure was much stronger than vertical exposure, and neither confidence

interval overlapped 0 (Table 1.6; Figure 1.4; horizontal $\beta = -0.026$; C.I. $= -0.033 - -$

0.018; vertical $\beta = 0.019$; C.I. $= 0.005 - 0.034$). An increase of two standard deviations in

horizontal exposure (centered around the mean), correlated with a 58% decrease in the

probability of an egg hatching, whereas the same increase in vertical exposure correlated

with only a 1% increase. Similar to the productivity analysis, I did not examine the

coefficients from the Exposure Horizontal and the Exposure Interaction models, even

though the AICc analysis suggested they were informative. The parameter estimate for

horizontal exposure is more accurate within the Exposure model because the effect of

vertical exposure is accounted for, although the effect size is similar in both models. I

also did not interpret the Exposure Interaction model because it failed to overcome the

penalty applied when adding an additional parameter in an AICc analysis (Arnold 2010).

The probability of fledging was affected by a suite of nesting site characteristics,

but predominately by the interaction of horizontal and vertical exposure, consistent with

results for productivity analysis (Table 1.4). The negative effect of the horizontal exposure of nesting site was intensified (more negative) by increased vertical exposure (Figure 1.5A; interaction β = -0.001; C.I. = -0.002 – -0.0006). Nestlings were unlikely to fledge from nesting sites that were more exposed in both planes (Figure 1.5A). There was weak evidence for a 27% and 24% increase in probability of fledge for nesting sites that contained a refuge (Figure 1.5B; β = 1.16; C.I = 0.426 – 1.908) and were not accessible to predators (Figure 1.5C; β = -1.01; C.I. = -1.799 – -0.231), respectively (Table 1.6). Although the Size of Nesting Site model's ΔAICc was < 7, all confidence intervals within the model overlapped 0. Because this overlap suggests low confidence in the direction of the parameter estimates, I did not interpret them.

The length of the brood rearing period was affected exclusively by horizontal exposure, with more exposure correlating with shorter brood rearing periods (Table 1.5 & Table 1.7). An increase of two standard deviations (centered around the mean) correlated with a 4.7-day reduction in the length of the brood rearing period (Figure 1.6; β = -0.001; C.I. = -0.001 – -0.0003). All other nesting site models ranked below the intercept only model, thus I did not interpret their coefficients.

Hatch date was 7.9 days earlier for nesting sites that contained a refuge (Figure 1.7A; β = -0.053; C.I. = -0.078 – -0.29) and 8.6 days later for nesting sites that contained a stick nest (Figure 1.7B; β = 0.06; C.I. = 0.031 – 0.088), compared to bare ledges and ledges with mulch (Table 1.5 & Table 1.7). There was also weak evidence for more horizontally exposed nesting sites having later hatch dates than less exposed nests (Figure 1.7C; β = 0.0005; C.I. = 0.0002 – 0.007), and interactive effects of ledge and nest size (Table 1.5 & Table 1.7). The positive effect of nest size was greatest when the ledge was

small with no effect on hatch date when the ledge was large (Figure 1.7D; Table 1.7). Additionally, early breeders had much higher productivity than late breeders, consistent with high quality site being occupied earlier (Appendix Figure 1).

Nest attendance was more frequent in nesting sites with greater horizontal exposure, but the effect decreased greatly and eventually disappeared as nestlings approach fledging age (Figure 1.9; Table 1.5). High vertical exposure slightly increased the effect of horizontal exposure early in the brood rearing period and slightly decreases the effect in the middle (Appendix figure 2; Table 1.7). There was also weak evidence for nests that were accessible to terrestrial predators having decreased nest attendance during the middle of the season, but not early or late (Appendix figure 3; Table 1.7).

Discussion

Protective nesting site characteristics were associated with increased breeding success, early phenology, and decreased parental investment for breeding Gyrfalcons. Additionally, protective properties were also associated with a greater probability of hatching and fledging as well. In particular, protections gained from minimal horizontal exposure seemed to be the most biologically significant property for Gyrfalcon nesting sites throughout my research on Alaska's Seward Peninsula.

Analysis of productivity and nesting site characteristics supported the hypothesis that nesting site exposure was negatively correlated with the breeding success of nesting Gyrfalcons in western Alaska. Importantly, I found the strongest effects of exposure when examining the interaction between vertical and horizontal exposure. The negative effect of horizontal exposure on productivity was greater (more severe) in sites with greater vertical exposure. Mortalities of altricial birds, such as Gyrfalcons, early in

development coincide with a period of complete dependence on parental care for thermoregulation and protection from the elements (Gill 2007). Thermoregulatory ability of nestlings increases as the physiological mechanisms mature, mass increases, and feathers develop (Fortin et al. 2000). Previous research suggested that half of Gyrfalcon young die prior to fledging and that the majority of mortality occurs during egg and early nestling stages, consistent with my findings (Cade 1960; Nielsen 1986; Poole & Bromley 1988a). These early-life mortalities occurred during a life history stage when nestlings were particularly vulnerable to inclement environmental conditions. Gyrfalcon hatchlings have scarce primary down feathering and require two to three weeks to develop secondary down, leaving nestlings with a minimal thermal envelope during harsh early spring conditions of the low Arctic (Anderson et al. 2017; Chappell 1980; Kirkley & Gessaman 1990).

Before reaching thermoregulatory independence, nestlings are particularly vulnerable to the microclimate of their nesting site, which is governed primarily by wind convection, solar radiation, and moisture (Heenan 2013; Heenan & Seymour 2012; Webb & King 1983). Convective heat loss can be reduced by protective nesting site properties, such as minimal horizontal exposure, creating a more favorable microclimate for nestlings (With & Webb 1993). Vertical exposure of nesting sites likely imposes trade-offs because an overhang reduces the amount of direct sunlight, and thus solar radiation received, but also exposes nestlings to more precipitation and excessive heat later in the brood rearing period (Anctil et al. 2014; Poole & Bromley 1988a). The wetting of downy feathers significantly decreases thermal properties, and convective cooling increases dramatically when nestlings or nesting materials are wet, suggesting a greater cost of

convection for wet nestlings compared to dry ones (Nye 1964; Reid et al. 2002). This suggests that nesting sites with greater vertical exposure benefited slightly from additional radiation only if protected from convective heat loss by minimal horizontal exposure. Nesting sites that lacked a large degree of protection from wind and were exposed vertically experienced the compounding costs of moisture and convection and had exceptionally low breeding success. It has also been suggested that the ability to visually assess predation risks presents trade-offs with protection from the elements, such that protected nests reduce the ability of an incubating adult to detect approaching predators (Gotmark 1995; Fast et al. 2007). This trade-off seems unlikely for Gyrfalcons because during five years of nest image observations, I observed only one instance of nestling predation and there are minimal observations of nestling predation in the literature (reviewed in Booms et al. 2008).

Nesting site exposure affected eggs and nestlings differently, suggesting temporal variation in the environmental threats to offspring. Horizontal exposure correlated negatively with the probability of egg hatching, whereas more vertically exposed sites were slightly more likely to hatch and no interactive effects, in contrast with productivity analysis. The positive correlation between vertical exposure and the probability of hatching was not consistent with my predicted directionality, but the minimal effect size and lack of confidence in the coefficient estimate suggest that this effect is likely biological inconsequential. Unlike nestlings, wet eggs do not experience a dramatic increase in heat loss due to convective cooling compared to dry eggs, which may explain the lack of interaction between vertical and horizontal exposure on eggs (Webb & King 1983). Additionally, prior to hatch, adults incubated almost continuously which would

help keep eggs dry and likely reduced the negative impact of vertical exposure while promoting the positive effects of solar radiation. More horizontally exposed nesting sites, regardless of vertical exposure, had a much lower probability of hatching, likely due to convective heat loss during the coldest portion of the breeding season. Further, the thermal environment of eggs can affect nestling condition after hatch, suggesting that incubation conditions can have moderately long-term effects on young birds (Naas et al. 2009; Webb 1987).

For young that hatched, a suite of nesting site properties affected their ability to fledge. The negative effect of horizontal exposure was much stronger for nesting sites with greater vertical exposure, which likely drove the interacting effects on overall productivity. Nesting sites that contained a refuge for nestlings had a greater probability of fledging young compared to those that lacked this protective property. Refuges in nesting sites allow mobile nestlings to seek shelter from precipitation or unfavorable temperatures because refuges typically have a more consistent temperature than exposed areas (Fast et al. 2007; Glassey & Amos 2009). Nest camera images demonstrated that refuges were commonly occupied by nestlings, predominantly the larger and more developed nestlings, suggesting it may be an important resource for which nestlings compete. Nesting sites that were accessible to terrestrial predators were less likely to fledge young, but I observed no mortalities attributable to nest predation, so it is unlikely predation had a direct effect on Gyrfalcon reproduction in our study area. It is possible that Gyrfalcons interpreted inaccessible nests as higher quality, thus high-quality individuals occupied them, indirectly increasing the probability of fledging. The effect of nesting site size, although identified as informative by AICc analysis, had low confidence

in parameter estimates and direction of the relationships, so results cannot be interpreted with any certainty, suggesting that more research is warranted.

Studies investigating nest exposure in circumpolar breeding raptors are few, and their support for the effects of protective properties on productivity are ambiguous or weak. In previous literature, nesting site exposure had no detectable effect on the productivity of Rough-legged Hawks (Beardsell et al. 2016), was negatively correlated with productivity of Peregrine Falcons, but only in the vertical plane (Mearns and Newton 1988), and had no detectable effect on Gyrfalcons (Barichello and Mossop 2011). I offer two explanations why findings in previous research offered only weak support for a correlation between protective nest properties and breeding productivity of Arctic raptors. First, horizontal and vertical exposure were combined in previous work into a single variable for exposure (Barichello and Mossop 2011; Beardsell et al. 2016), thus overlooking the interaction that I found to be statistically and biologically significant. Second, in some studies exposure was categorized subjectively, obviating analysis at more precise scales (Mearns and Newton 1988). My research is the first to investigate nesting site characteristics with use of precise measurements and to investigate the interacting effects of the two planes of exposure, which, if ignored, can mask effects of individual predictor variables (Jaccard & Turrisi 2003). Surprisingly, I found no effect of orientation on breeding productivity, although southern facing nests were most common. Nesting sites with a southern orientation receive more direct sunlight, which likely leaves them clear of snow in March and April when nest selection is occurring (Booms et al. 2008). The disproportionate number of south-facing nesting sites may be a consequence of availability during the sub-Arctic spring, rather than a

characteristic chosen to maximize breeding success. Additionally, the benefit of orientation may differ temporally such that early in the breeding season the increased temperature increases survival but later in the season can cause heat stress in nestlings.

Hatch dates were earlier for nesting sites that contained a refuge for nestlings and that had minimum horizontal exposure, suggesting that Gyrfalcons may preferentially select for nesting sites with these properties (Newton 1991). The effect of refuge should be interpreted with caution because of the small sample size of sites that lacked a refuge (n = 9). Surprisingly, nesting sites with stick nests were occupied later than bare ledges or ledges with mulch, in contrast to my stated hypothesis. Gyrfalcons do not construct stick nests and must compete for available stick nests with those species that do, namely Golden Eagles and Common Ravens, which can delay lay date and breeding phenology of raptors (Booms et al. 2008; Hakkarainen & Korpimäki 1996). Larger nesting sites, which typically included a stick nest built by Golden Eagles, were occupied later than smaller nests, possibly because eagles outcompete Gyrfalcons for nesting sites (Poole and Bromley 1988a). Competition for nesting sites among the raptor assemblage may disrupt selection for some nesting site properties, like those that contain a large stick nest, but not other properties such as horizontal exposure and refuge, which are less common in Golden Eagle nests (Poole and Bromley 1988b).

The length of the brood rearing period was shorter for nests that were more exposed horizontally, in contrast to my predicted direction. I can think of several explanations for this finding. First, nest departure by juvenile birds is initiated by increasing levels of circulating stress hormones (e.g., corticosterone), often facilitated by food restriction by the parents (Corbel & Groscolas 2008; Heath 1997). Release of stress

hormones is also facilitated by exposure to inclement weather and can possibly cause

nestlings to depart the nest prematurely, suggesting that not all juveniles fledge with ideal

body condition (Romero et al. 2000). Nestlings that depart from nesting sites with high

body mass are more likely to survive their first year, but we did not obtain pre-fledging

mass, thus we do not know if birds that departed early reached a healthy mass prior to

fledging (Mumme et al. 2015). Ultimately, there may not be value in staying in a nest that

does not provide protections, because fledglings can search for more protected locations

while still receiving parental care away from the nesting site (Platt 1976; Fletcher and

Webby 1977; Bente 1981). Conversely, nesting sites with more horizontal exposure

tended to have few nestlings, so it is possible that the reduction in sibling competition

allowed for a faster growth rate and a shorter brood rearing period.

Nest attendance was highest in nesting sites that were more exposed, particularly

in the horizontal plane, potentially increasing the cost of reproduction for breeders in

nesting sites that lacked protection from the harsh Arctic climate (Cresswell et al., 2004).

Precipitation and convective cooling also interact to maximize parental heat loss to the

cold environment (Weimerskirch et al. 2002). Exposure to inclement weather has

correlated consistently with significantly more weight loss in Arctic-breeding seabirds,

indicating a direct benefit of protective properties for incubating adults (D'Alba et al.

2009; Fast et al. 2007; Hilde & Christophe 2016; Kilpi & Lindström 1996). Costs

incurred during reproduction can decrease survival and life-time reproductive fitness in

long-lived species, such as Gyrfalcons, and are driven primarily by decreased body

condition (Golet et al., 1998; Hanssen et al. 2005; Stearns 1992). In the current study,

fitness costs incurred during reproduction in more exposed nesting sites were twofold

because not only did parental investment increase, but the additional effort was unable to offset the decrease in productivity.

Understanding habitat suitability and factors that affect breeding productivity are important components of effective conservation (Gaillard et al. 1998; Johnson & Geupel 1996; Luck et al. 2002; Newton 1991). My findings suggest that protective properties of nesting sites increase productivity and decrease the cost of reproduction for breeding Gyrfalcons by mitigating the negative effects of inclement weather. My results further highlight the importance of breeding site suitability when evaluating habitat quality. Precipitation is increasingly regarded as a primary factor reducing breeding output of circumpolar-breeding falcons and my results suggest that these effects are likely magnified by exposure to wind (Anctil et al. 2014; Mearns & Newton 1988; Nielsen 1986; Poole & Bromley 1988a). As severe weather events increase due to global climate change, properties that shield adult birds and nestlings from inclement weather will likely become increasingly important for Arctic breeding raptors (Min et al. 2011). Climatic changes in the Arctic are unfolding rapidly compared to lower latitudes, and Gyrfalcons are among the most threatened bird species to the negative effects of climate change (Buechley et al. 2019; Liebezeit et al. 2012; Thomas et al. 2004). Gyrfalcons and conservation efforts will continue to face novel challenges, but by understanding the contemporary effects of habitat characteristics and prioritizing areas that meet all scales of habitat requirements, we can ensure our readiness to preserve the world's largest falcon.

Tables

Table 1.1.   **Annual summary of data collected at Gyrfalcon nesting sites on the Seward Penninsula, Alaska from 2014 – 2018. Successful nests are based on nesting sites that were measured, not neccisarily encompassing all breeding attemps in the study area.**

Year	Cameras Installed	Nests Measured	Successful Nests	Quantified Parental Investment?	Parental Investment Samples
2014	10	5	3 (60%)	No	-
2015	13	10	8 (80%)	No	-
2016	6	13	11 (85%)	No	-
2017	13	15	7 (47%)	Yes	17,932
2018	11	14	9 (64%)	Yes	12,919
Total	53	57	38 (67%)		30,849

Table 1.2.   Overview of models. Model names are consistent between all analyses. Predictions were based on observed effects in other species or common features of Gyrfalcon nesting sites.

Model Name	Hypotheses
Accessibility to preds	Terrestrial predators, such as foxes, bears, and wolverines depredate accessible nests reducing productivity, probability of hatch and fledging, increase parental investment and the length of the brooding period. Accessible nests are also occupied later, suggesting they are lower quality. (Crabtree et al. 1989; Velando & Márquez 2002; Beardsell et al. 2016)
Exposure	Nests with greater horizontal and vertical exposure subject nestlings to a harsher microclimate, thus negatively correlate with productivity, probability of hatch, and probability of fledging. Exposure is negatively correlated with parental investment, brooding season length, and hatch date. (Anctil et al. 2014)
Exposure Interaction	Similar to Exposure model but the effect of horizontal exposure is dependent on the level of vertical exposure. As vertical exposure increases the effect of horizontal exposure will become stronger (more negative).
Exposure Horizontal	Nests with greater horizontal exposure subject nestlings to metabolic costs associated with wind, and therefore reduce productivity, probability of hatch, and probability of fledge. Horizontal exposure negatively correlates with parental investment, brooding season length, and hatch date (Anctil et al. 2014; Cade 1960).
Exposure Vertical	Nests with greater vertical exposure subject nestlings to metabolic costs associated with precipitation, and therefore reduce productivity, probability of hatch, and probability of fledge. Vertical exposure is negatively correlated with parental investment, brooding season length, and hatch date (Anctil et al. 2014; Cade 1960).
Nesting Site Size	Nestlings are more likely to accidentally fall from small nests, thus smaller nests have decreased productivity and probability of fledging, unless available ledge can compensate. Nestlings from smaller nests will fledge at a younger age. Additionally, smaller nests are occupied later. Effects are dependent on the level of ledge, which can compensate for small nest area (Mechnikova et al. 2012).
Orientation	Southern facing nests receive more sun, create a more favorable microclimate in early spring, and have higher productivity, probability of hatch, and probability of fledge. Southern facing nests also have decreased parental investment, shorter brooding season, and hatch earlier (Beardsell et al. 2016; Cade 1960).
Refuge	Nesting sites that contain a refuge for nestlings provide shelter from harsh weather and increase productivity, probability of hatch, and probability of fledging. Also, in nesting sites with refuge have\ shorter brood rearing periods, hatch earlier, and adults reduce parental investment due to reduced thermoregulatory needs (Anctil et al. 2014).
Substrate	Bare ledges do not offer insulating properties, and thus have lower productively, probability of hatch, and probability of fledging, compared to nesting sites that have nest structures. Breeding attempts on bare ledges have longer brood rearing periods, later hatch dates, and increased parental investment (Akreshetal et al. 2017).
Intercept Only / Control	Nesting site characteristics do not affect productivity, probability of hatch, probability of fledging, brooding season length, hatch date, or parental investment.

Table 1.3. **Descriptive statistics of discrete (A) and continuous variables (B).**

(A) Discrete variables

Variable	Category	Num. of Nests
Accessible to preds	Yes	41 (74%)
	No	15 (26%)
Refuge	Yes	41 (73%)
	No	15 (27%)
Ledge	0	1 (2%)
	1	13 (23%)
	2	17 (30%)
	3	10 (18%)
	4	16 (28%)
Orientation	North	11 (19%)
	East	15 (26%)
	South	22 (39%)
	West	9 (16%)
Substrate	Bare Ledge	8 (14%)
	Mulch Ledge	12 (21%)
	Stick Nest	37 (65%)

(B) Continuous Variables

Variable	Mean ± SD	Range	Num. of Nests
Predictor variables			
Vertical Exposure	69° ± 27.84°	36° – 160°	56
Horizontal Exposure	129° ± 51.65°	65° – 360°	56
Area	$1.09 \text{ m}^2 \pm 1.06 \text{ m}^2$	$0.12 \text{ m}^2 – 5.48 \text{ m}^2$	51
Cliff Height	13.5 m ± 6.58 m	5.74 m – 27.62 m	45
Nest Height	8.1 m ± 4.22 m	1.0 m – 19.9 m	47
Response Variables			
Productivity	1.71 ± 1.50	0 – 4	55
Proportion fledged	0.69 ± 0.40	0 – 1	38
Eggs Laid	3.63 ± 0.67	2 – 5	49
Eggs Hatched	2.62 ± 2.28	0 – 4	48
Proportion hatched	0.71 ± 0.39	0 – 1	48
Julian Hatch date	146 ± 7.14 days	136 – 165	47
Length of Brooding season	48 days ± 3.5 days	35 days – 52 days	27

Table 1.4. AICc table for hypothesis one. Includes productivity, probability of egg hatch, and probability of fledge, given that hatch had occurred. Coefficients for informative models (ΔAICc < 7) are examined in Table 1.6.

Model	k	logLik	AICc	ΔAICc	Weight	Cum. Wt
Productivity						
Exposure Interaction	4	-71.24	151.40	**0.00**	0.55	0.55
Exposure Horizontal	2	-74.55	153.36	**1.96**	0.21	0.76
Refuge	2	-74.96	154.18	**2.78**	0.14	0.90
Exposure	3	-74.31	155.16	**3.76**	0.08	0.98
Accessibility to preds	2	-77.80	159.87	8.47	0.01	0.99
Exposure Vertical	2	-77.98	160.23	8.82	0.01	1.00
Nesting Site Size	8	-71.29	162.27	10.87	0.00	1.00
Substrate	3	-79.75	166.05	14.64	0.00	1.00
Intercept Only	1	-82.17	166.43	15.02	0.00	1.00
Orientation	3	-81.46	169.47	18.07	0.00	1.00
Hatch Probability						
Exposure	3	-61.19	128.99	**0.00**	0.53	0.53
Exposure Horizontal	2	-63.06	130.42	**1.43**	0.26	0.79
Exposure Interaction	4	-60.91	130.88	**1.88**	0.21	1.00
Refuge	2	-68.63	141.55	12.56	0.00	1.00
Accessibility to preds	2	-76.45	157.19	28.20	0.00	1.00
Substrate	3	-75.32	157.25	28.26	0.00	1.00
Exposure Vertical	2	-76.69	157.67	28.68	0.00	1.00
Orientation	3	-76.02	158.65	29.66	0.00	1.00
Intercept Only	1	-78.62	159.33	30.34	0.00	1.00
Fledge Probability						
Exposure Interaction	4	-42.50	94.11	**0.00**	0.78	0.78
Refuge	2	-47.15	98.61	**4.50**	0.08	0.86
Accessibility to preds	2	-47.99	100.30	**6.19**	0.04	0.89
Exposure Vertical	2	-48.24	100.79	**6.68**	0.03	0.92
Nesting Site Size	8	-40.20	100.89	**6.78**	0.03	0.95
Intercept Only	1	-49.72	101.55	7.44	0.02	0.97
Exposure Horizontal	2	-48.82	101.97	7.86	0.02	0.98
Exposure	3	-48.11	102.87	8.76	0.01	0.99
Substrate	3	-48.95	104.56	10.45	0.00	1.00
Orientation	3	-49.20	105.04	10.93	0.00	1.00

Table 1.5. AICc table for hypothesis two, three, and four regarding phenology and parental investment. Includes hatch date, breeding season length, and nest attendance. Coefficients for informative models (ΔAICc < 7) are examined in Table 1.7.

| Model	k	logLik	AICc	ΔAICc	Weight	Cum. WT
Hatch Date						
Refuge	3	-137.04	280.72	**0.00**	0.36	0.36
Substrate	4	-135.97	281.01	**0.30**	0.31	0.66
Exposure Horizontal	3	-138.22	283.08	**2.36**	0.11	0.77
Exposure	4	-137.10	283.28	**2.56**	0.10	0.87
Exposure Vertical	3	-138.71	284.05	**3.33**	0.07	0.94
Exposure Interaction	5	-136.96	285.58	**4.86**	0.03	0.97
Nesting Site Size	9	-131.48	286.58	**5.87**	0.02	0.99
Intercept Only	2	-141.85	288.01	7.29	0.01	1.00
Orientation	4	-140.94	290.97	10.25	0.00	1.00
Brood Rearing Period Length						
Exposure Horizontal	3	-63.09	133.38	**0.00**	0.36	0.36
Intercept Only	2	-65.21	134.99	1.61	0.16	0.53
Exposure	4	-62.60	135.30	1.92	0.14	0.67
Exposure Vertical	3	-64.24	135.68	2.29	0.12	0.78
Accessibility to preds	3	-64.38	135.96	2.57	0.10	0.88
Refuge	3	-65.11	137.42	4.04	0.05	0.93
Exposure Interaction	5	-62.53	138.40	5.02	0.03	0.96
Substrate	4	-64.45	139.00	5.62	0.02	0.98
Orientation	4	-64.75	139.60	6.22	0.02	1.00
Nesting Site Size	9	-62.81	156.47	23.09	0.00	1.00
Parental Investment						
Exposure Interaction	9	-6180.70	12379.41	**0.00**	0.77	0.77
Accessibility to preds	5	-6185.93	12381.87	**2.46**	0.23	1.00
Exposure	7	-6213.55	12441.11	61.70	0.00	1.00
Exposure Horizontal	5	-6218.67	12447.34	67.93	0.00	1.00
Refuge	5	-6221.01	12452.02	72.61	0.00	1.00
Substrate	7	-6221.68	12457.36	77.95	0.00	1.00
Exposure Vertical	5	-6233.55	12477.11	97.70	0.00	1.00
Control	3	-6237.77	12481.54	102.13	0.00	1.00
Orientation	7	-6234.68	12483.37	103.96	0.00	1.00

Table 1.6.   Coefficient estimates from analysis of hypothesis one models. Includes overall productivity, hatch probability, and fledge probability. Confidence intervals (85%) that do not overlap 0 are bolded. Parameter estimates of productivity models are log restricted and both hatch and fledge probabilities are logit restricted.

| Model	Variable	Estimate	Std. Error	z-value	Confidence Level 7.500	92.500
Productivity						
Exposure Interaction	(Intercept)	-1.211	1.321	-0.92	-3.142	0.666
	Horizontal exposure	0.015	0.011	1.42	**2.57E-05**	**0.031**
	Vertical exposure	0.048	0.023	2.15	**0.016**	**0.081**
	Exposure interaction	-4.05E-04	1.72E-04	-2.35	**-6.60E-04**	**-1.63E-04**
Exposure Horizontal	(Intercept)	1.719	0.336	5.12	1.237	2.203
	Horizontal exposure	-0.010	0.003	-3.56	-0.015	-0.006
Refuge	(Intercept)	-0.442	0.333	-1.33	-0.963	0.002
	Refuge	1.164	0.354	3.29	**0.685**	**1.711**
Exposure	(Intercept)	1.822	0.369	4.93	1.294	2.358
	Horizontal exposure	-0.009	0.004	-2.58	-0.014	-0.004
	Vertical exposure	-0.004	0.006	-0.68	-0.013	0.004
Hatch Probability						
Exposure	(Intercept)	3.043	0.713	4.27	2.071	4.126
	Horizontal exposure	-0.026	0.005	-4.91	**-0.033**	**-0.018**
	Vertical exposure	0.019	0.010	1.85	**0.005**	**0.034**
Exposure Horizontal	(Intercept)	3.669	0.657	5.59	2.776	4.670
	Horizontal exposure	-0.021	0.005	-4.58	-0.028	-0.015
Exposure Interaction	(Intercept)	1.665	2.235	0.74	-1.816	4.332
	Horizontal exposure	-0.016	0.015	-1.05	-0.034	0.008
	Vertical exposure	0.041	0.037	1.09	0.001	0.102
	Exposure interaction	-1.43E-04	2.36E-04	-0.60	-0.001	0.000
Fledge Probability						
Exposure Interaction	(Intercept)	-6.266	2.652	-2.36	-10.228	-2.548
	Horizontal exposure	0.057	0.020	2.80	**0.029**	**0.088**
	Vertical exposure	0.130	0.047	2.74	**0.064**	**0.202**
	Exposure interaction	-0.001	0.000	-3.06	**-1.50E-03**	**-5.52E-04**
Refuge	(Intercept)	-0.201	0.449	-0.45	-0.860	0.445
	Refuge	1.160	0.512	2.26	**0.426**	**1.908**
Assessible to preds	(Intercept)	0.892	0.237	3.76	0.557	1.243
	Accessible to preds	-1.010	0.541	-1.87	**-1.799**	**-0.231**
Exposure Vertical	(Intercept)	1.674	0.609	2.75	0.811	2.573
	Vertical exposure	-0.015	0.009	-1.71	-0.027	-0.002
Nesting Site Size	(Intercept)	1.254	0.535	2.35	0.530	2.111
	Area	-0.647	0.496	-1.30	-1.413	0.044
	Ledge	1.035	0.937	1.10	-0.306	2.427
	Ledge (x^2)	-0.256	1.070	-0.24	-1.951	1.227
	Ledge (x^3)	-0.405	1.187	-0.34	-2.421	1.156
	Area:ledge	-0.867	0.862	-1.01	-2.139	0.400
	Area:ledge (x^2)	-0.766	0.992	-0.77	-2.194	0.733
	Area:ledge (x^3)	1.166	1.107	1.05	-0.333	2.949

Table 1.7. **Coefficient estimates from analysis of hypothesis two, three, and four regarding phenology and parental investment. Confidence intervals that do not include 0 are bolded. Models ranked below the intercept only model were omitted. Parameter estimates of both brood rearing period and hatch date models are logit restricted and parental investment is log restricted to display whether confidence intervals include 0.**

Model	Variable	Estimate	SEM	z-value	Confidence Level 7.5	92.5
Hatch Date						
Refuge	(Intercept)	5.027	0.015	335.12	5.005	5.048
	Refuge	-0.053	0.017	-3.14	**-0.078**	**-0.029**
Substrate	(Intercept, Bare ledge)	4.943	0.018	274.05	4.917	4.969
	Ledge with mulch	0.018	0.023	0.76	-0.016	0.051
	Stick nest	0.060	0.020	2.99	**0.031**	**0.088**
Exposure Horizontal	(Intercept)	4.927	0.022	220.60	**4.895**	**4.960**
	Horizontal Exposure	4.88E-4	1.8E-4	2.726	**2.30E-4**	**7.47E-4**
Size	(Intercept)	4.97	0.01	444.90	4.96	4.99
	Area	0.02	0.01	2.06	**0.01**	**0.03**
	Ledge	0.06	0.02	2.64	**0.03**	**0.10**
	Ledge (x^2)	0.00	0.02	0.11	-0.03	0.03
	Ledge (x^3)	-0.04	0.02	-2.01	**-0.07**	**-0.01**
	Area: Ledge	-0.04	0.02	-1.88	**-0.07**	**-0.01**
	Area: Ledge (x^2)	0.02	0.02	0.97	-0.01	0.04
	Area: Ledge (x^3)	0.02	0.01	1.32	0.00	0.03
Brood Rearing Period length						
Exposure Horizontal	(Intercept)	3.945	0.047	84.52	3.877	4.012
	Horizontal exposure	-0.001	0.000	-2.11	**-0.001**	**-2.65E-04**
Parental Investment						
Exposure Interaction	(Intercept)	4.085	0.169	24.14	3.835	4.339
	Age	-0.26	0.004	-68.83	**-0.265**	**-0.254**
	Horizontal exposure	0.794	0.167	4.75	**0.551**	**1.046**
	Vertical exposure	-0.661	0.174	-3.8	**-0.922**	**-0.404**
	Age: Horizontal exp	-0.026	0.004	-6.19	**-0.032**	**-0.02**
	Age: Vertical exp	-0.003	0.004	-0.67	-0.009	0.003
	Exposure interaction	0.133	0.128	1.04	-0.055	0.326
	Age:Horizontal:Vertical	-0.028	0.004	-7.29	**-0.033**	**-0.022**
Assessible to Preds	(Intercept)	4.106	0.244	16.83	3.744	4.474
	Age	-0.252	0.004	-67.99	**-0.258**	**-0.247**
	Accessible to preds	0.888	0.572	1.55	**0.065**	**1.773**
	age: accessible to preds	-0.151	0.017	-8.82	**-0.176**	**-0.127**

Figures
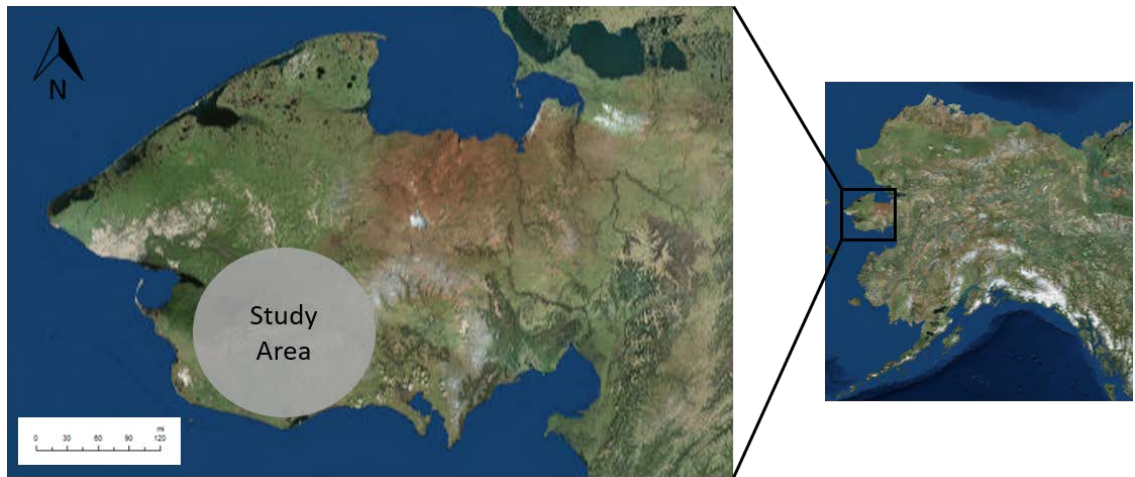
Figure 1.1. Map of Study Site. I studied breeding Gyrfalcons within a ca. 4,800 km2 study site on the southern portion the Seward Peninsula (65°N, 164°W), in western Alaska, 2014 – 2018. The Gray circle is a rough estimation of the study site to avoid divulging confidential nesting sites of raptors.
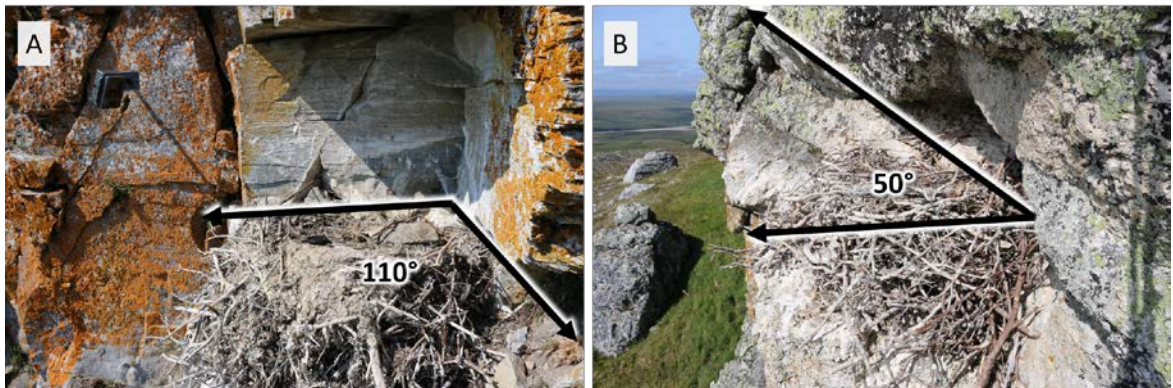
Figure 1.2. Representation of (A) horizontal exposure and (B) vertical exposure. To measure these angles, I established an origin directly behind the location where eggs were laid and used an angle ruler to determine the degrees of exposure in both planes. Also note the placement of the camera on the left of panel A.
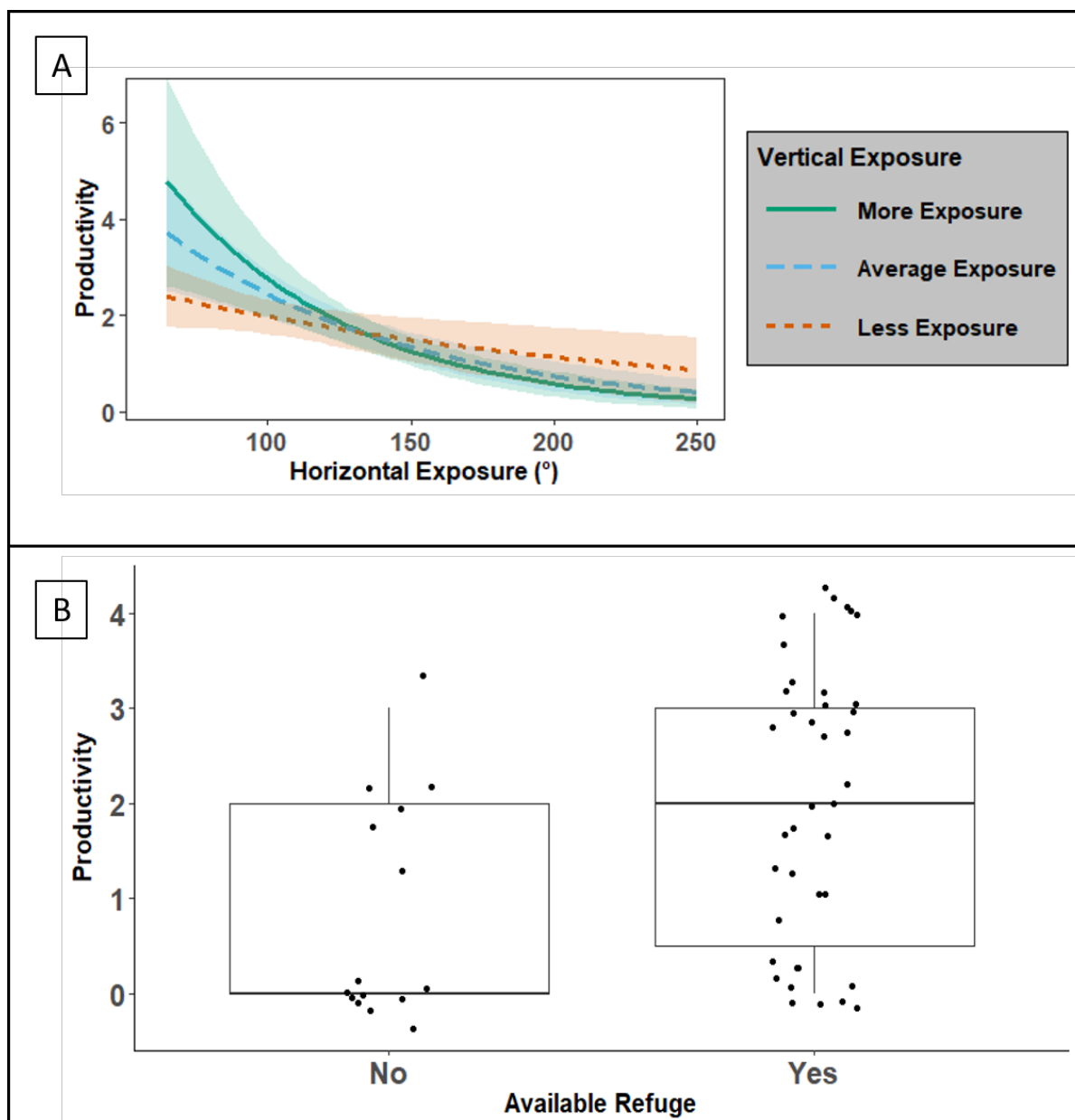
Figure 1.3. Effects of nesting site characteristics on Gyrfalcon productivity, Seward Peninsula, Alaska, 2014 - 2018. Productivity was defined as the number of nestlings to reach 80% of fledging age ($\geq$ 40-days) per breeding pair. (A) Interactive effects of horizontal and vertical exposure on productivity. The negative effect of horizontal exposure was greatest in nests that were more exposed vertically. Levels of vertical exposure are: 50°, 69°, and 80°. Note that although confidence intervals reached above 6 fledglings, the maximum clutch size for Gyrfalcons is five, and average clutch size is 3.63. (B) Effect of an available refuge on Gyrfalcon productivity. On average, productive was roughly double in nesting sites that provided refuge for nestlings to escape the harsh Arctic climate.
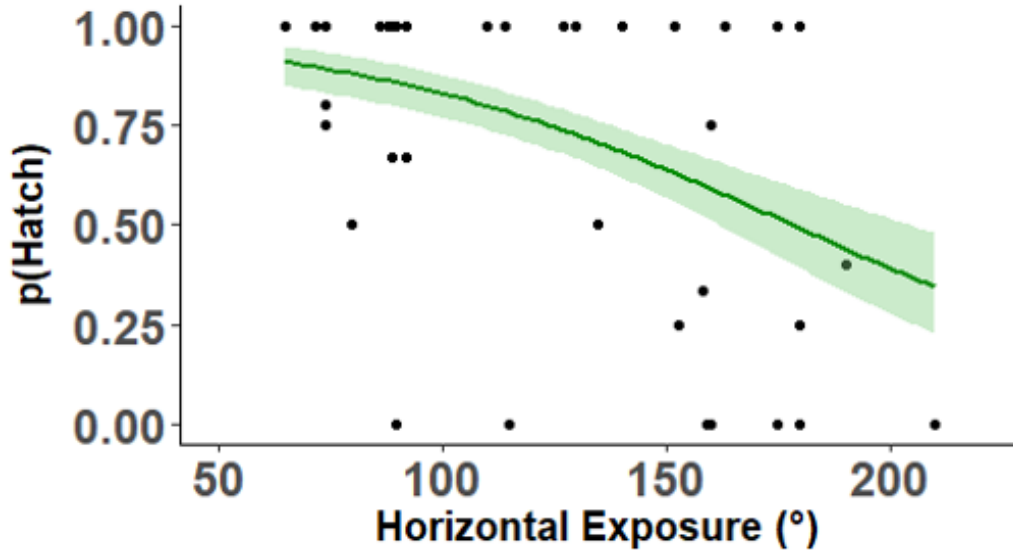
Figure 1.4. **Effects of the horizontal exposure of nesting sites on the probability of Gyrfalcon eggs hatching, Seward Peninsula, Alaska, 2014 - 2018. Eggs in sites with minimal horizontal exposure were more likely to hatch than eggs in more exposed sites. Vertical exposure was slightly, positively correlated with the probably of eggs hatching, but the effects had a large degree of uncertainty is likely biologically insignificant. Proportions are weighted by the number of eggs that were laid by individual pairs.**
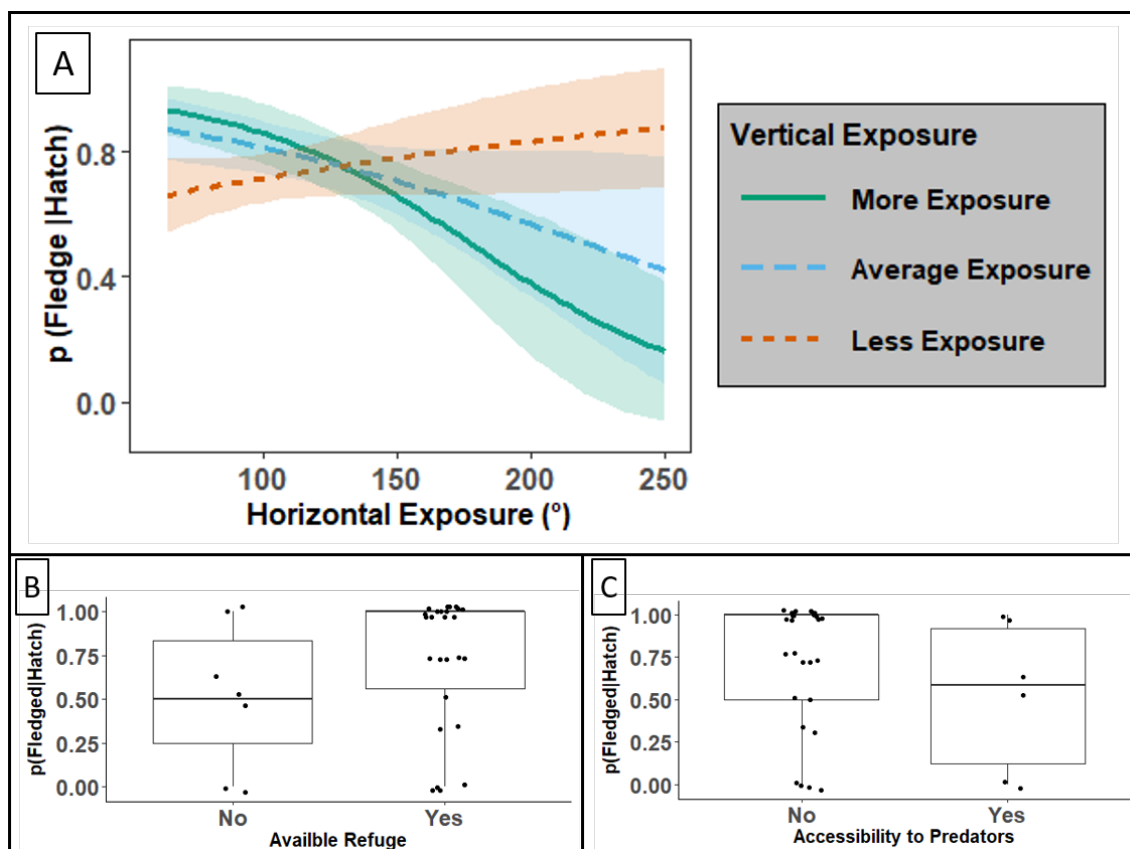
Figure 1.5. Effects of nesting site characteristics on probability of Gyrfalcon nestlings fledging, Seward Peninsula, Alaska, 2014 - 2018. **(A)** Interactive effects of nesting site exposure on the probability of an individual Gyrfalcon nestling surviving to fledge. Horizontal exposure was negatively correlated with the probability of fledging in nesting sites with an average level of vertical exposure and the effect becomes increased (became more negative) as vertical exposure increases. In nests with less vertical exposure, there was no relationship between horizontal exposure and the probability of fledging. Levels of vertical exposure are: 50°, 69°, and 80°. **(B)** Effect of an available refuge on the probability of nestlings fledging. On average, nestlings reared in a nesting site with an available refuge were 27% more likely to fledge, but the sample size of nestlings in sites lacking a refuge was small. **(C)** Effects of the accessibility of nesting sites to terrestrial predators on the probability of nestlings fledging. On average, nestlings reared in nesting sites that were not assessible to land predators were 24% more likely to fledge, though I observed only one nest depredation by a terrestrial predator in five years of nest camera photos.
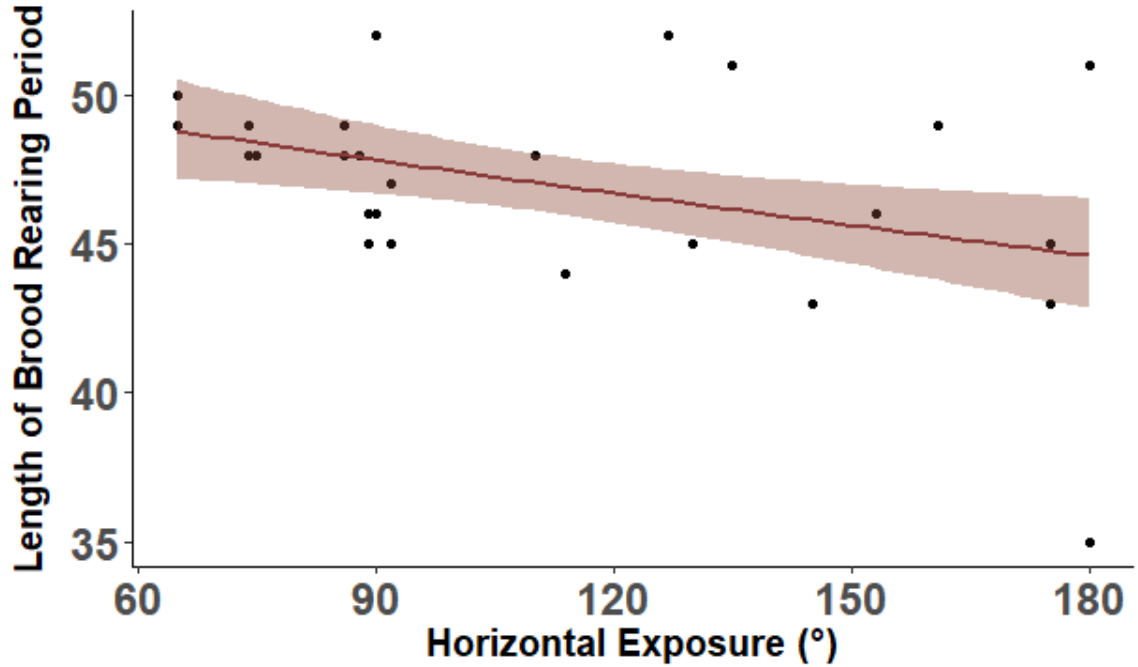
Figure 1.6.   **Negative correlation between horizontal exposure of nesting site and the length of the brooding period, Seward Peninsula, 2014 – 2018. 26 nesting sites were included in the analysis of the length of the brood rearing period and the confidence interval did not include 0.**
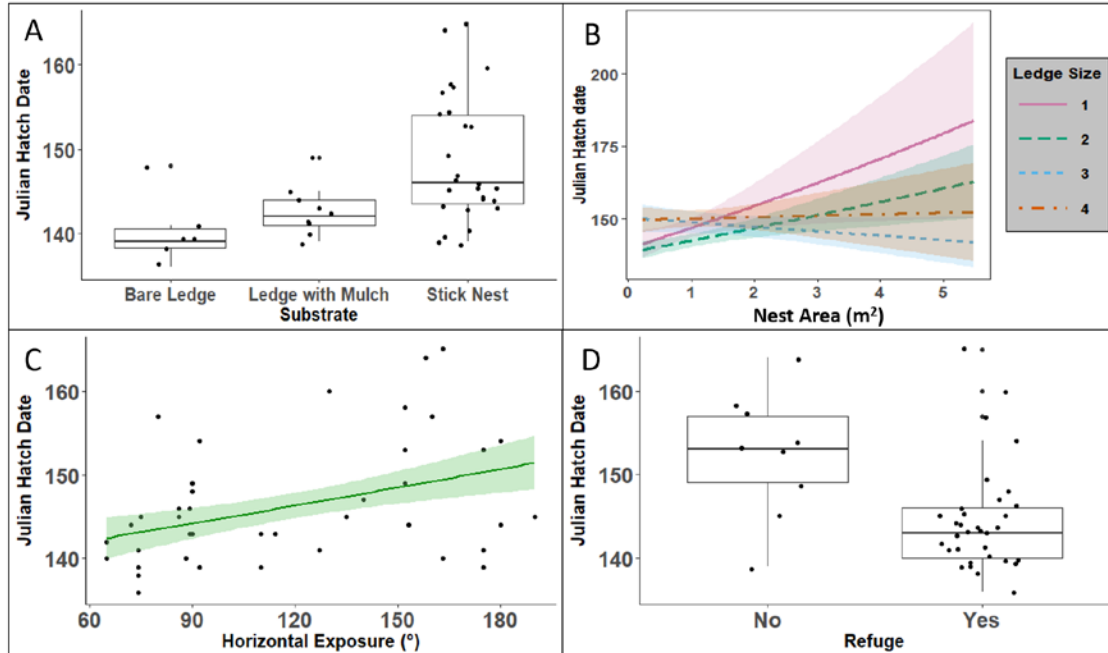
Figure 1.7. **Effects of nesting site characteristics on the hatch date for Gyrfalcons on the Seward Peninsula, 2014 – 2018. (A) Clutches in nesting sites classified as bare ledges and ledges with mulch hatched at similar dates, whereas sites containing a stick nests hatched later, on average. (B) The effect of nest area was greatest when the ledge was small, but results are ambiguous. (C) Nesting sites that are less exposed in the horizontal plane hatch earlier than more exposed sites. (D) Nesting sites that contained a protective refuge for nestlings hatched earlier than sites that lack such protections, but again the sample size of nestlings in sites lacking a refuge was small.**
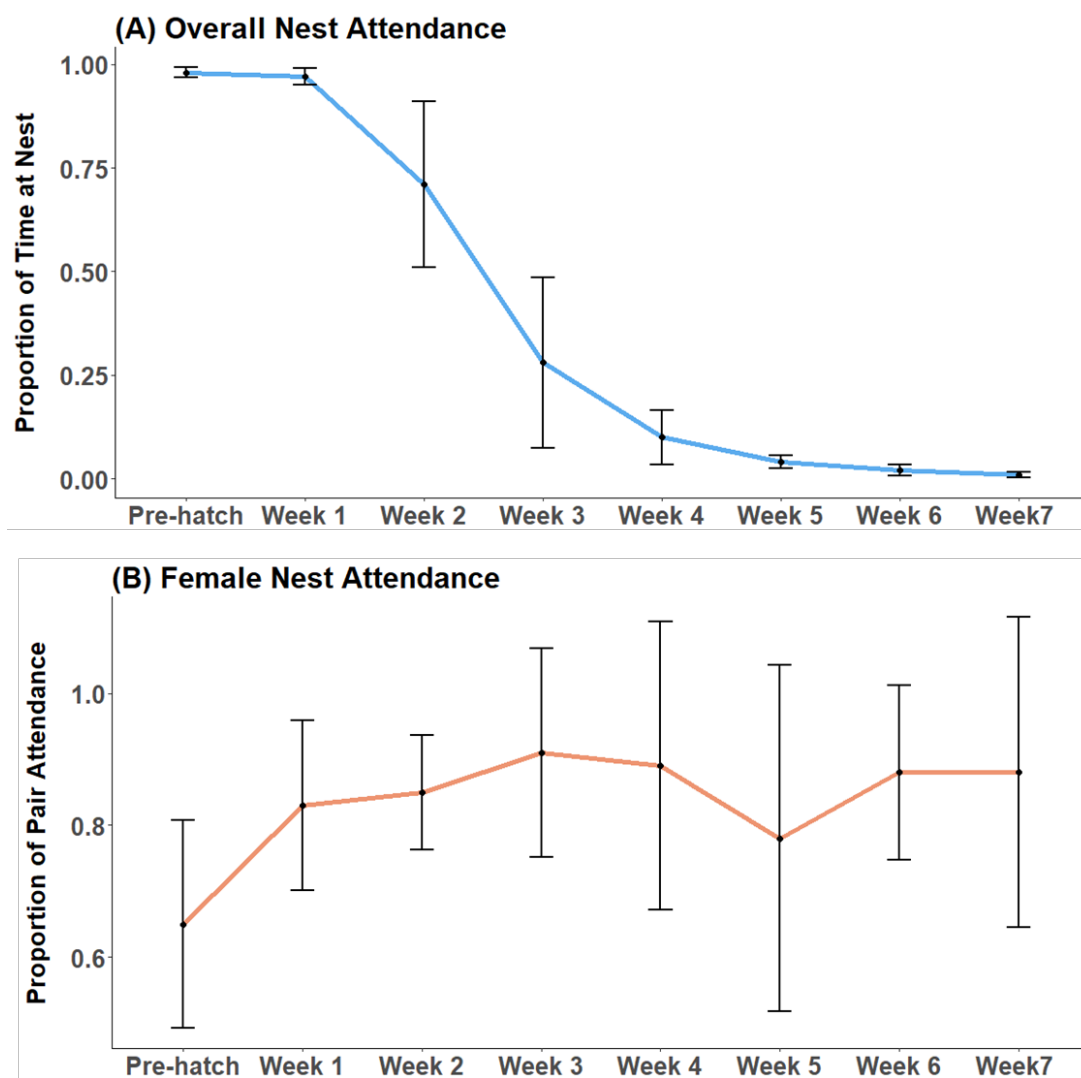
Figure 1.8. Nest attendance by adult Gyrfalcons during the brood rearing period, Seward Peninsula, Alaska, 2014 - 2018. (A) The proportion of time either adult tended to nestlings (incubating, brooding, shading, or feeding). Error bars are the standard deviation of the proportion of attendance of individual breeding pairs during each week of the breeding season, indicating variation between nests. Variation in attendance was minimal between nests early and late in the season, and highest during weeks two and three. (B) Proportion of overall nest attendance completed by female Gyrfalcons. Note the high variation in female attendance between nests throughout the breeding season. Individual female proportions are graphed in Appendix Figure 1.3.
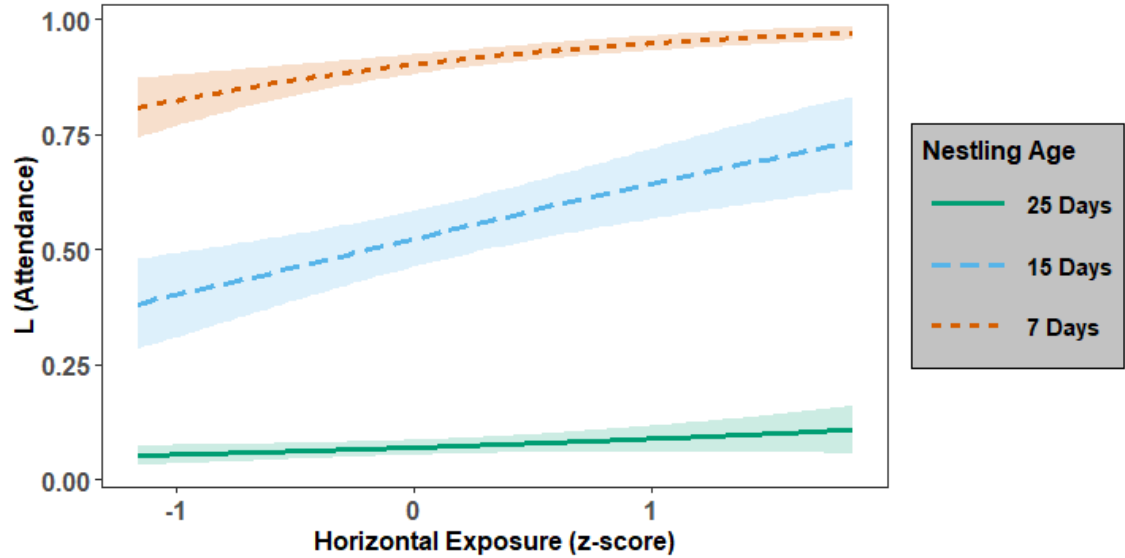
Figure 1.9. Interactive effects of horizontal exposure of nesting site and nestling age on adult attendance by Gyrfalcons, Seward Peninsula, Alaska, 2014 - 2018. Horizontal exposure correlated positively with adult attendance for nestlings at ages seven and 15 days and the effect decrease as nestlings approach fledging age. The observed effects differed slightly at different levels of vertical exposure (see Appendix figure 1.4)

Appendix Figures
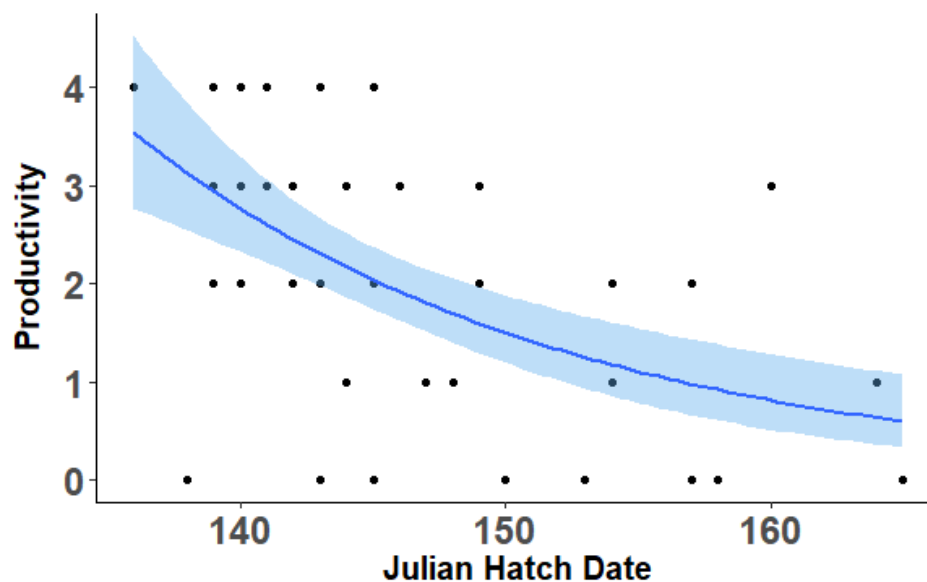
Appendix Figure 1. Negative correlation between hatch date and the productivity on Gyrfalcons, Seward Peninsula, 2014 – 2018. Breeding early correlated with an increase in the number of young successfully fledged.
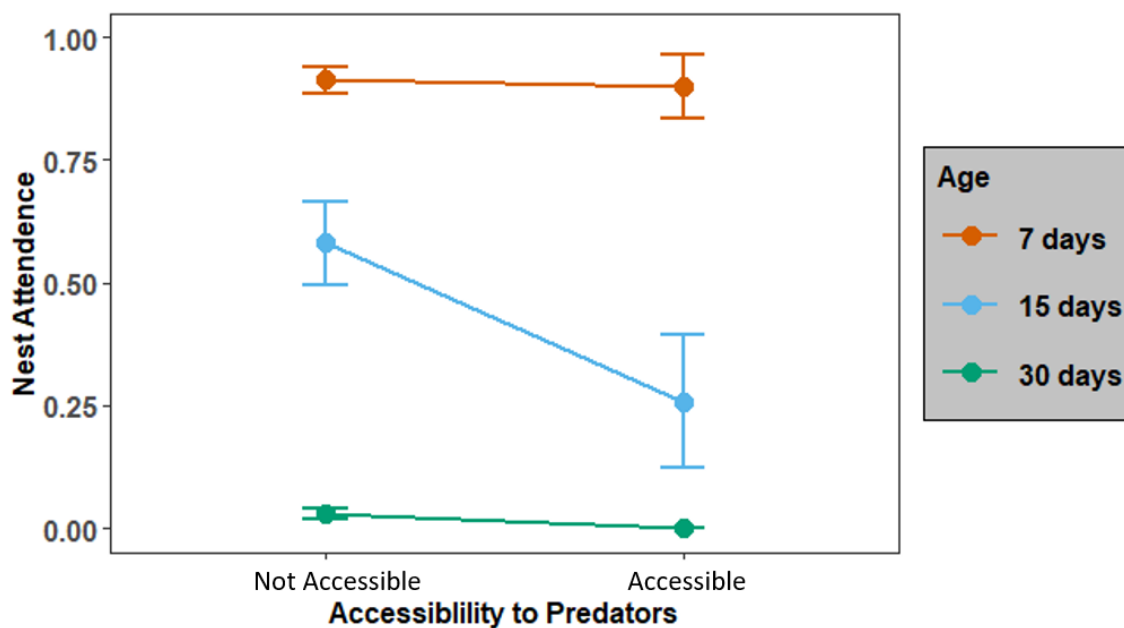
Appendix Figure 2 Effect of nesting sites being accessible to terrestrial predators on nest attendance. There was no effect at seven or 30 days old, but at 15 days assessible nests had a lower likelihood of nest attendance.
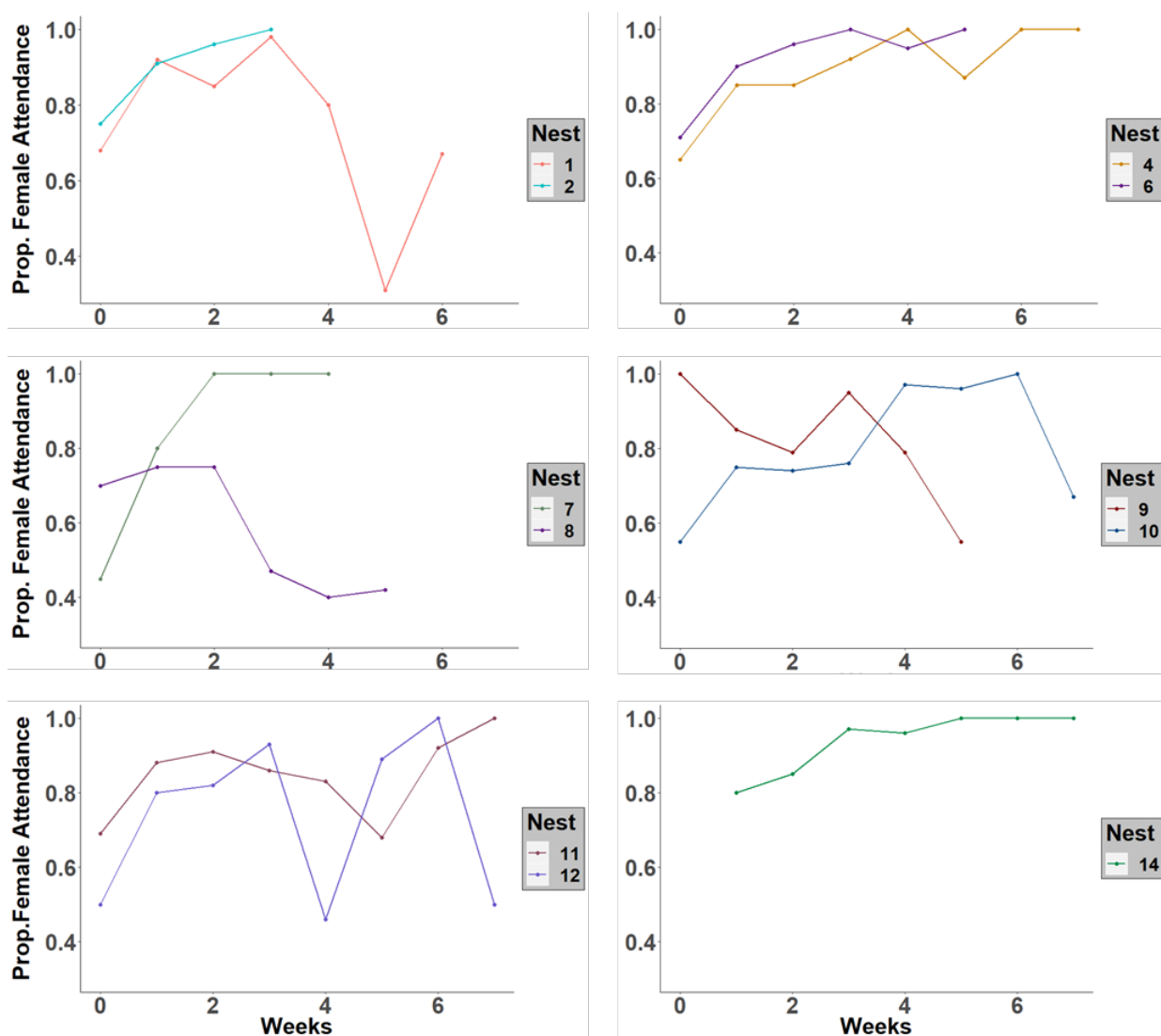
Appendix Figure 3. Proportion of female attendance for individual pairs, throughout the brood rearing period. There was a high degree of individual differences evident, but the increase in female attendance after hatch is still apparent. Each "nest" represents an individual breeding pair. Breeding pairs that failed prior to week 3 were omitted from figure (nests 3,5, and 13). Incomplete data resulted from nestlings consistently residing out of the frame of the camera (nest 2), relatively early fledge (nests 6, 8, and 9), nest failure (nest 7), and the camera being installed after hatch (nest 14).
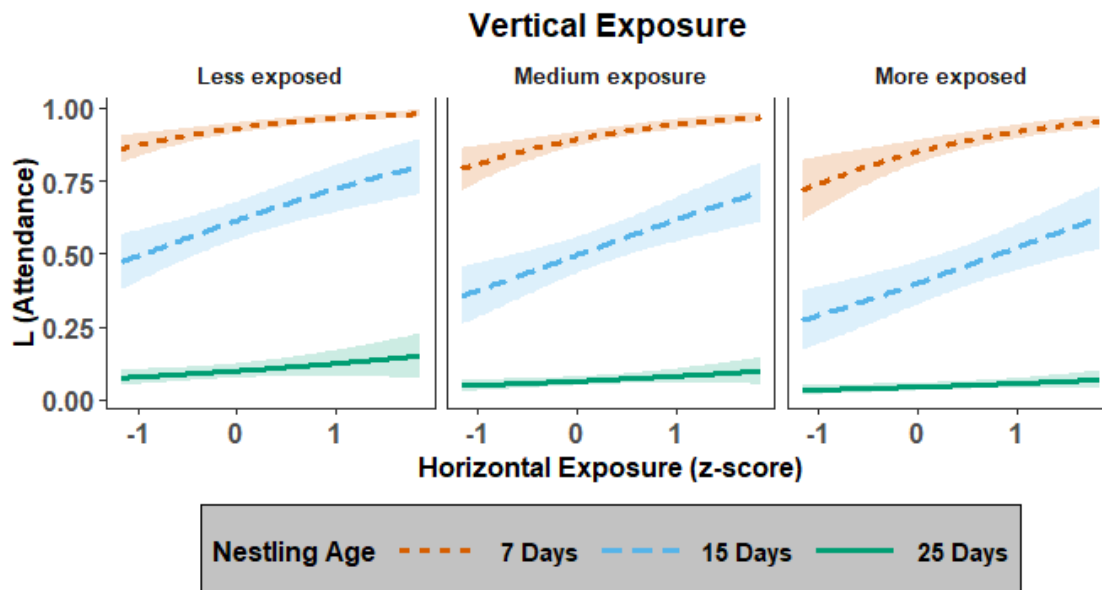
Appendix Figure 4. Three-way interaction between vertical exposure, horizontal exposure, and nestlings age.

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