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DIRECT AND INDIRECT EFFECTS OF NESTING SITE CHARACTERISTICS FOR A CLIFF-NESTING RAPTOR IN WESTERN ALASKA

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ABSTRACT.—Habitat suitability for breeding birds is defined at scales ranging from the landscape to individual nesting sites. Nesting site characteristics that govern exposure to inclement weather may affect breeding success, although attempts to understand this effect for Arctic breeding raptors have yielded ambiguous results. Further, breeding adults incur substantial costs from incubating eggs and brooding nestlings, and it is possible that greater site exposure results in increased nest attendance rates, increasing their cost of breeding. We quantified nesting site characteristics of Gyrfalcons (*Falco rusticolus*) and assessed how breeding parameters and nest attendance rates varied by protective site qualities on Alaska's Seward Peninsula, 2014–2019. The degree of physical exposure in the horizontal plane correlated negatively with the probability of hatching and fledging (provided hatch occurred), as well as overall productivity. The negative effect of horizontal exposure on the probability of fledging and productivity was greatest at nesting sites that were also more exposed in the vertical plane, although this interaction did not affect the probability of hatching. Early breeding pairs had higher productivity and tended to select more protected nesting sites. Additionally, nest attendance rates were higher in more horizontally exposed nesting sites, particularly when nestlings were approximately 2 wk old. The increased nest attendance and concurrent decreased productivity associated with greater nesting site exposure demonstrated that nesting site characteristics can have direct and indirect effects on Arctic breeding raptors and also highlight the importance of small-scale variables when evaluating habitat suitability.

KEY WORDS: *Gyrfalcon*; Falco rusticolus; *Arctic*; *breeding*; *cliff-nesting raptor*; *habitat suitability*; *nest attendance*; *nest site characteristics*; *reproductive rate.*

EFECTOS DIRECTOS E INDIRECTOS DE LAS CARACTERÍSTICAS DEL LUGAR DE CRÍA PARA UNA RAPAZ QUE ANIDA EN ROQUEDOS EN EL OESTE DE ALASKA

RESUMEN.—La conveniencia del hábitat para las aves reproductoras es definida a escalas que van desde el paisaje hasta los sitios de nidificación individuales. Las características del sitio de nidificación que

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determinan la exposición a las inclemencias del tiempo pueden afectar el éxito reproductivo; sin embargo, los intentos por entender estos efectos para las rapaces que se reproducen en el Ártico han dado resultados ambiguos. Más aún, los adultos reproductores incurren en costes sustanciales para incubar los huevos y criar a los polluelos, y es posible que una mayor exposición del sitio resulte en mayores tasas de atención al nido, aumentando su coste reproductivo. Cuantificamos las características de los lugares de cría de *Falco rusticolus* en la Península Seward de Alaska entre 2014 y 2019. Evaluamos cómo los parámetros reproductores y las tasas de atención al nido variaron según la calidad de protección de estos sitios. El grado de exposición física en el plano horizontal se correlacionó negativamente con la probabilidad de eclosión y de que los pollos abandonen el nido, así como con la productividad general. El efecto negativo de la exposición horizontal en la probabilidad de emplumamiento y en la productividad fue mayor en los lugares que también estuvieron más expuestos en el plano vertical, aunque esta interacción no afectó la probabilidad de eclosión. Las parejas de reproducción temprana tuvieron mayor productividad y tendieron a seleccionar lugares más protegidos. Adicionalmente, las tasas de atención al nido fueron mayores en los lugares más expuestos horizontalmente, particularmente cuando los polluelos tuvieron aproximadamente dos semanas de edad. El aumento de la atención al nido y la disminución simultánea de la productividad asociada con una mayor exposición del lugar demostraron que las características del sitio pueden tener efectos directos e indirectos en las rapaces que anidan en el Ártico, y resaltan la importancia de las variables de pequeña escala cuando se evalúa la conveniencia del hábitat.

[Traducción del equipo editorial]

INTRODUCTION

Habitat suitability is determined by numerous abiotic and biotic factors that affect the breeding success and behaviors of wildlife (Sinclair et al. 1985, Menke and Holway 2006). These factors vary in their qualities and density across heterogeneous landscapes and those areas that exhibit a favorable assemblage of these factors promote higher breeding success and tend to have earlier phenology (Newton 1991, Ferrer and Donazar 1996). Breeding success can indicate habitat suitability, thus the identification of habitat variables that affect fecundity is central to our understanding of habitat use and helps to prioritize the conservation of productive habitats (Johnson and Geupel 1996, Anctil et al. 2014). Furthermore, because habitat suitability is determined across various spatial extents, it is necessary to investigate a range of scales, including those that are small (Luck 2002, Frye et al. 2013).

At a relatively small spatial scale, characteristics of nesting sites (including properties of the nest and its immediate surroundings; Franke et al. 2017) can affect the breeding success of birds by influencing the microclimate to which nestlings and adults are exposed during vulnerable life stages (Fast et al. 2007, Anctil et al. 2014). Protective properties of cliff-sites such as overhead protection (overhang) or physical barriers lateral to the nest can shield nestlings from adverse weather, thus providing a microclimate favorable for nestling survival and development (Mearns and Newton 1988, Fast et al. 2007). In contrast, a poor microclimate imposes thermoregulatory costs and can result in the death of nestlings (Polak and Kasprzykowski 2013, de Zwaan 2018). Further, a lack of protection has been correlated with decreased breeding success in Arctic-breeding Rough-legged Hawks (*Buteo lagopus*; Beardsell et al. 2016) and Peregrine Falcons (*Falco peregrinus*; Mearns and Newton 1988, Anctil et al. 2014). However, disparate results and methodology within the literature generate ambiguity in identifying specific nesting site variables that correlate with raptor productivity and occupancy (Mearns and Newton 1988, Barichello and Mossop 2011, Beardsell et al. 2016). Additionally, it is unknown how ubiquitous these effects are for other raptor species breeding in the Arctic (defined collectively as the High Arctic, Low Arctic, and sub-Arctic; Meltofte et al. 2013) or whether there are deleterious behavioral effects associated with nesting site characteristics.

In addition to direct effects that nesting site characteristics can have on breeding birds, indirect effects may be incurred via increased parental investment, defined as the total energy expended to aid in reproduction (Golet et al. 1998, Santos and Nakagawa 2012). In cold temperatures, breeding adults increase their daily energy expenditure to maintain viable tempertures of eggs and young nestlings by physically shielding and transfering heat (Weathers 1985, Williams 1993). Energy investment into incubating and brooding behaviors contribute to the high cost of avian breeding and these costs can carry over to subsequent breeding attempts (Bize et al. 2004). Carryover effects, including decreased

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body condition and survival, can reduce future breeding success and present a trade-off between current and future reproduction, particularly for long-lived species (Hanssen et al. 2005). For example, birds increase nest attendance, and thus parental investment, in response to the thermoregulatory needs of their offspring, shielding eggs and nestlings more often when temperatures are low (Webb and King 1983, Cresswell et al. 2004). Nesting sites that do not minimize the thermoregulatory needs of eggs and nestlings may impose energetic costs on breeding adults that carry over and indirectly decrease lifetime reproductive success, particularly in harsh environments (Piersma et al. 2003, Hilton et al. 2004, Hilde et al. 2016).

The Gyrfalcon (*Falco rusticolus*) is a long-lived, cliff-nesting raptor of the circumpolar Arctic tundra (Booms et al. 2020) and an ideal species for investigating the effects of protective characteristics on breeding birds in a harsh environment. Unfavorable weather is known to impact breeding success of Arctic-breeding falcons, typically because strong winds and heavy precipitation negatively affect nestling survival (Poole and Bromley 1988a, Anctil et al. 2014). Nesting site characteristics that provide protection from unfavorable weather conditions vary greatly for Alaskan Gyrfalcons, which frequently occupy nesting sites with stick nests built by other species (e.g., Common Raven [*Corvus corax*], Golden Eagle [*Aquila chrysaetos*], and Rough-legged Hawk) or nest on bare ledges (Bente 2011). These Gyrfalcon habits provide a gradient by which to test the effect of protective properties on raptor breeding parameters. Identifying Gyrfalcon nesting site characteristics that govern small-scale habitat suitability will strengthen our understanding of factors that influence breeding raptors in the Arctic, as they continue to experience rapid climatic changes including disruptions to precipitation profiles (Christensen et al. 2013).

Our objective was to quantify the effects of nesting site characteristics on Gyrfalcon breeding parameters in Alaska. We examined the effect of protective characteristics at Gyrfalcon nesting sites on five breeding parameters: overall productivity, probability of an egg hatching, probability of a nestling fledging, hatch date (phenology), and nest attendance rates. To identify variation in the effects of nesting site characteristics on the different breeding stages, we analyzed the probability of hatching and the probability of fledging independently from overall productivity because threats and sensitivities vary between these two developmental stages (Polak and Kasprzykowski 2013). We proposed five generalized hypotheses describing how nesting site characteristics affect breeding Gyrfalcons (Table 1). In nesting sites that provide more protection from inclement weather as compared to less protected nesting sites: (1) productivity will be higher; (2) probability of hatching will be higher; (3) probability of fledging will be higher; (4) eggs will hatch earlier; (5) adult nest attendance will be lower. We speculated that less horizontal and vertical exposure, presence of a refuge for nestlings, a stick nest structure, a southern orientation, inaccessibility (to terrestrial predators), and larger size are nesting site properties that may benefit breeding Gyrfalcons.

METHODS

Study Area. We studied Gyrfalcon breeding biology on 4800 km^2 of the southern Seward Peninsula (64°–65°N, 164°–166°W) in western Alaska. Although the study area is below the Arctic Circle (66.5°N), the climate is best characterized as Low Arctic (Meltofte et al. 2013). Dispersed rock outcroppings and cliff-lined river systems provide nesting platforms for Gyrfalcons (Kessel 1989, Bente 2011). The predominant vegetation type is upland tundra consisting of mosses and lichens with dense willows (*Salix* spp.), dwarf birch (*Betula nana*), and alders (*Alnus* spp.) lining riparian areas (Viereck et al. 1992). Average daily temperatures on the study area vary between and within months (May: high = 7° ± 6° C, low = –1° ± 4° C; July: high = 16° ± 5° C, low = 7° ± 3° C) with an average of 55 ± 18 mm of precipitation from May to July; these conditions expose nestlings and adults to substantial thermoregulatory challenges (National Oceanic and Atmospheric Administration 2020; date range: 2000–2020). The historical weather trends on the Seward Peninsula may be changing due to increased southerly winds and the unusually high water temperatures of the Bering Sea, resulting in warmer surface temperatures for terrestrial systems (Cornwall 2019).

Field Work. We conducted fieldwork May to July 2014–2019, which corresponded to the mid-incubation period through fledging for Gyrfalcons on the Seward Peninsula. From 2 to 15 May, 2015–2019, we located nesting sites in which Gyrfalcons were attempting to breed (i.e., indicated by eggs in nest or an incubating adult; hereafter referred to as nests with eggs) by conducting annual helicopter surveys (Robinson R44 helicopter; Robinson Helicopter

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Table 1. Overview of hypotheses, model distributions, predictions, and sample sizes regarding the effects of nesting site characteristics for Gyrfalcons on the Seward Peninsula, Alaska, 2014–2019. All model types are generalized linear mixed models (GLMM). All models contain year as a random effect and nesting site characteristics as fixed effects. Nest attendance models contain an additional random effect for the breeding pair and fixed effect for brood age. Models for the probability of hatching were based on the proportion of eggs that hatched (relative to those that did not), whereas models for the probability of fledging were based on the proportion of nestlings that successfully fledged (relative to those that did not).

HYPOTHESIS NAME	MODEL DISTRIBUTION	PREDICTIONS AND PROTECTIVE NESTING SITE CHARACTERISTICS INCLUDED IN MODELS	NUMBER OF NESTS
1. Productivity	Poisson	Productivity is higher at more protected sites. Characteristics of more protected sites for this hypothesis include: has minimal site exposure, provides a refuge for nestlings, contains a stick nest, is oriented away from the north, is inaccessible to terrestrial predators, and is larger.	46
2. Probability of Hatching	Binomial	Eggs are more likely to hatch at more protected sites. Characteristics of more protected sites for this hypothesis include: has minimal site exposure, contains a stick nest, is oriented away from the north, and is inaccessible to terrestrial predators.	40
3. Probability of fledging	Binomial	Nestlings are more likely to fledge from more protected sites. Characteristics of more protected sites for this hypothesis include: has minimal site exposure, provides a refuge for nestlings, contains a stick nest, is oriented away from the north, is inaccessible to terrestrial predators, and is larger.	40
4. Phenology	Gamma	Clutches hatch early at more protected sites. Characteristics of more protected sites for this hypothesis include: has minimal site exposure, provides a refuge for nestlings, contains a stick nest, is oriented away from the north, is inaccessible to terrestrial predators, and is larger.	37
5. Nest Attendance	Binomial	Nest attendance is lower in more protected sites. Characteristics of more protected sites for this hypothesis include: has minimal site exposure, provides a refuge for nestlings, contains a stick nest, is oriented away from the north, and is inaccessible to terrestrial predators.	14

Company, Torrence, CA, USA). In May 2014, we surveyed a small subset of historical nesting sites from the ground to identify nests with eggs.

Camera Installation and Operational Definitions. To determine how many eggs hatched, the number of nestlings fledged, hatch date (phenology), and to record nest attendance behaviors at nests with eggs and nestlings, we installed Reconyx PC800 and HF2X motion-activated cameras (hereafter referred to as nest cameras) at 68 nests with eggs or nestlings; on average we installed 10.5 cameras per year (2014–2019). To determine how many eggs were laid, we counted eggs during camera installation or during helicopter surveys. We mounted 49 cameras during incubation and 19 within the first 2 wk of the brood-rearing period. Additionally, we included measurements of five nesting sites for which we were able to confirm nest failure prior to our first nest visit, for a total of 73 nests with eggs or nestlings. We standardized nest camera placement and programing following Robinson et al. (2017) such that the nest and some of the surrounding cliff were visible on images. Nest cameras captured images when triggered by motion and every half hour regardless of motion (one image every 30 min; hereafter timed images). We defined productivity as the number of nestlings successfully fledged per egg-laying pair (observed from images) based on the minimal acceptable age for assessing success (80% of fledging age: 36 d old; Franke et al. 2017). We considered individual eggs successfully hatched (i.e., hatching success) when nestlings were observed (on images) fully out of the shell and we recorded hatch date as the date the first egg hatched in a clutch. For cases when mobile nestlings moved beyond the view of cameras, they were categorized as fledged only if photos clearly showed them older than 36 d old. When nestlings left camera view before 36 d without a confirmed mortality, they were removed from analyses. We defined a nest as the physical location where the scrape (depression where eggs were laid) was made, in contrast to a nesting site, which was

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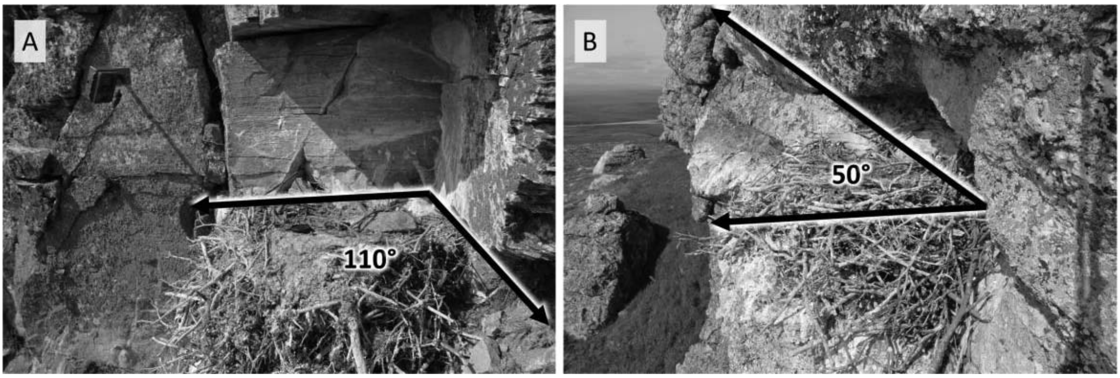

Figure 1. Representation of (A) horizontal exposure and (B) vertical exposure at Gyrfalcon nesting sites, Seward Peninsula, Alaska, 2014–2019. To measure these angles, we established an origin directly behind the scrape and used an angle ruler to determine the degrees of exposure in both planes. Also note the placement of the nest camera on the left of panel A.

defined to include the nest and surrounding features accessible to nestlings (Franke et al. 2017). Because Gyrfalcon nestlings become increasingly mobile with age, it was important to consider how properties surrounding nests influenced the survival of eggs and nestlings.

Processing Images for Nest Attendance. To determine nest attendance rates, we reviewed all timed images (24 hr/d) for a subset of 14 breeding pairs between 2017 and 2018. We did not review nest attendance for all nesting sites because clear trends had become evident based on our sample size, and considerable time is required to process images for adult behaviors. Motion-activated photos were also recorded, but were used only to verify hatching and fledging, not to characterize behaviors. From timed images, we recorded adult nest behaviors that we classified into one of four categories: brooding/shading, feeding nestlings, standing, and absent. Brooding/shading was characterized by any contact with nestlings or an obvious shading position. Standing was characterized by the adult being present in the image but not tending to nestlings. To account for researcher disturbance, we did not include data immediately following researcher nest visits until an adult had returned to the nest and resumed typical parental behavior (return times ranged from 0.25–4.5 hr).

Nesting Site Measurements. We characterized nesting sites on the basis of six physical variables: nesting site exposure, available refuge, nest substrate, orientation, accessibility to terrestrial predators, and nesting site size. We measured all nesting site characteristics after nestlings had fledged or nesting attempts had failed. We measured degrees of exposure (i.e., how open a nesting site was to the elements) separately for the vertical and horizontal planes. To measure these angles, we established an origin directly behind the scrape and used an angle ruler to determine the degrees of exposure in both planes (Fig. 1). To help models converge, we scaled horizontal and vertical exposure around their means. We subjectively categorized presence or absence of available refuge by assessing whether a nesting site included a feature, such as an overhang, crevice, or cave that would provide protection for mobile nestlings. Because substrate can affect conductive heat loss (Hilton et al. 2004), we categorized the nest substrate as (1) a stick nest, (2) a ledge with mulch (typically a highly decomposed stick nest), or (3) a bare ledge. We measured nest orientation with a handheld compass and normalized degrees to represent "northness" and "eastness" by calculating the cosine and sine, respectively (Pewsey et al. 2013). Nesting site northness likely dictates the daily duration of direct sunlight whereas the eastness likely affects the sunlight intensity, as an afternoon sun would provide additional warmth relative to the morning. We categorized whether nesting sites were accessible to terrestrial predators, particularly red foxes (*Vulpes vulpes*) and wolverines (*Gulo gulo)*, by subjectively assessing whether nest placement and cliff arrangement would allow access by these predators from the ground (binomial variable: allows access or does not allow access; Beardsell et al. 2016). Finally, because

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nesting site size can affect productivity of Gyrfalcons (Mechnikova et al. 2011) and may affect other breeding parameters, we quantified nest and ledge sizes and included both in relevant models. For nesting sites that contained a stick nest, nest size (surface area) was calculated from the diameter of the nests. For nesting sites without stick nests, nest size was the surface area of the structure on which the scrape was made (e.g., a rock ledge). To help models converge, nest size was categorized as either below average size or above average size. We classified ledge size (areas distinct from nest but accessible to nestlings) into one of four categories: (1) = ledge 0–0.1 m^2; (2) ledge 0.1–1 m^2; (3) ledge > 1 m^2; (4) nest continuous with the landscape (i.e., nestlings could walk out of the nest directly onto the tundra).

Statistical Analysis. To examine the effects of nesting site characteristics on breeding Gyrfalcons, we constructed generalized linear mixed model sets for each of our five generalized hypotheses in the statistical platform R 3.2.4 with package *lme4* (Bates et al. 2014). Probability of fledging analysis only included eggs that hatched, which in conjunction with the probability of hatching separated survival into distinct nestling and egg stages. Statistical models represented individual nesting site characteristics, except for models designed to test for the interaction between the two planes of exposure and nesting site size. For parameters present in multiple models, we examined coefficients from models that were deemed most informative by Akaike's Information Criterion corrected for small sample size (AIC_c) analyses.

We used AIC_c to rank individual models based on their relative likelihood given a set of candidate models, with package *MuMIn* (Akaike 1973, Burnham et al. 2011, Barton 2017). For productivity, probability of hatching, probability of fledging, and phenology analyses, candidate model sets included six univariate regression models for individual nesting site characteristics: vertical exposure, horizontal exposure, available refuge (excluding analysis of probability of hatching), substrate, orientation, and accessibility to predators. We also built multivariate regressions for exposure (both planes), the interaction between the two planes of exposure, and nesting site size (Table 1). We considered any model with $\Delta AIC_c < 2$ to have strong statistical support. When assessing confidence in parameter estimates, we 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 whether confidence intervals contained 0. A random effect of year was included in all analyses to account for inter-year variation. We were unable to add additional random effects to models because their addition caused model convergence issues and overparameterization. To avoid the potential for pseudoreplication, we included in our analyses only the first time egg-laying pairs used a nesting site during our study and removed subsequent nesting attempts, which reduced our sample size from 73 to 46. Due to missing data for particular variables, final sample sizes varied by analysis (Table 1). We also built a Poisson-distributed generalized linear model to test the assumption for the phenology hypothesis, i.e., that early breeders (as indicated by hatch date) have higher productivity. Finally, we built univariate models with nest substrate and size predicting the variation in horizontal and vertical exposure, to determine whether these variables covary.

To test the nest attendence hypothesis (i.e., that adults in nesting sites that provide less protection have greater nest attendance rates) we categorized behaviors as either indicative of nest attendance (shading/brooding and feeding nestlings) or not (standing and absent) and used these categories as a binomial response variable for analysis. We combined standing and absent into a single factor, because for images not containing an adult (and thus categorized as absent), we could not eliminate the possibility that adults were just outside of the camera's field of view. Although we recognize that most researchers classify standing near nestlings as nest attendance (e.g., predator defense), we were only interested in attendence behaviors that specifically described care of the nestlings. We restricted analysis of behaviors to the brood-rearing period (spanning from the hatching of the first egg to the fledging of the last nestling) because most (approximately 98%) of the adult behavior prior to the hatching of the first egg was incubation. For the nest attendance hypothesis, we built nine generalized linear mixed models and compared them with AIC_c. Individual nesting site characteristics and brood age were included as fixed effects and allowed to interact, because we expected nest attendance rates and the effect size of nesting site characterisitics would decrease with nestling age (Zimmerman 1959). We included in all nest attendance models, including the control model, random effects for the

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Table 2. Descriptive statistics of discrete and continuous variables at Gyrfalcon nesting sites on Seward Peninsula, Alaska, 2014–2019. Productivity, eggs laid, and eggs hatched are the number of fledglings, eggs present during helicopter survey or during camera installation, and eggs observed to have hatched (respectively) via nest camera images per egg-laying pair.

DISCRETE VARIABLES			CONTINUOUS VARIABLES		
VARIABLE	CATEGORY	SAMPLE SIZE	VARIABLE	MEAN ± SD	SAMPLE SIZE
Refuge	Yes	22 (31%)	Vertical exp.	70° ± 26.68°	72
	No	50 (69%)	Horizontal exp.	127° ± 48.00°	72
Substrate	Bare ledge	10 (14%)	Nest area	0.95 ± 0.99 m^2	66
	Mulch ledge	15 (20%)	Orientation	147° ± 85.96°	73
	Stick nest	48 (66%)	Productivity	1.75 ± 1.52	71
Predator accessibility	Yes	21 (29%)	Prop. fledged	0.65 ± 0.75	51
	No	51 (71%)	Eggs laid	3.55 ± 0.67	64
Ledge size	1	18 (25%)	Eggs hatched	2.70 ± 1.48	63
	2	19 (26%)	Prop. hatched	0.75 ± 0.39	63
	3	17 (23%)	Hatch date	146 ± 7.2 days	61
	4	19 (26%)			

territory and year to account for hierarchical structure and to avoid pseudoreplication. No territories or nesting sites were recorded in both years of the analysis of nest attendence.

RESULTS

We obtained data from 73 Gyrfalcon nesting attempts and 46 unique nesting sites (descriptive statistics: Table 2). From nest camera photos and direct observations, we determined that 215 eggs were laid, of which 162 hatched, and 108 nestlings fledged. We confirmed the age at mortality for 58 eggs and nestlings that perished. Most mortalities occurred early in the nesting period, during incubation (i.e., the eggs did not hatch; 21, 36%) or during the first week of the brood-rearing period (16, 28%). The remaining mortalities (21, 36%) occurred throughout the rest of the brood-rearing period.

Nesting site exposure negatively influenced productivity (Tables 3, 4). Specifically, horizontal and vertical exposure interacted such that the negative

Table 3. AIC_c table for all hypotheses at Gyrfalcon nesting sites on the Seward Peninsula, Alaska, 2014–2019. Informative models ($\Delta AIC_c < 2$) and intercept only/control models are displayed and parameter estimates are displayed in Table 4. All models contain year as a random effect and nesting site characteristics as fixed effects. Nest attendance models contain an additional random effect for the territory and fixed effect for brood age.

MODEL	k	logLIK	AIC_C	ΔAIC_C	WEIGHT
Productivity					
Exposure interaction	5	−66.31	144.11	0.00	0.66
Intercept only	2	−78.64	161.55	17.44	0.00
Probability of Hatching					
Exposure Horizontal	3	−54.47	115.61	0.00	0.69
Intercept Only	2	−65.78	135.88	20.28	0.00
Probability of Fledging					
Exposure interaction	5	−34.67	81.10	0.00	0.95
Intercept only	2	−45.88	96.08	14.98	0.00
Phenology					
Refuge	4	−121.59	252.43	0.00	0.45
Exposure vertical	4	−121.96	253.18	0.75	0.31
Intercept only	3	−125.32	257.37	4.94	0.04
Nest attendance					
Exposure interaction	10	−6179	12,379	0.00	0.83
Control	4	−6237	12,482	102.7	0.00

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Table 4. Coefficient estimates from Gyrfalcon nesting site analysis on the Seward Peninsula, Alaska, 2014–2019. Confidence intervals that do not contain 0 are bolded. Estimates of productivity and phenology models are log restricted; probability of hatching and probability of fledging, as well as nest attendance models, are logit restricted. Horizontal and vertical exposure are scaled around their means by their standard deviations. All models contain year as a random effect and nesting site characteristics as fixed effects. Nest attendance models contain an additional random effect for the breeding pair and fixed effect for brood age.

Model	Variable	Estimate	Confidence Level	
			7.500	92.500
Productivity				
Exposure interaction	(Intercept)	0.36	0.09	0.57
	Horizontal exposure	−0.67	**−0.97**	**−0.39**
	Vertical exposure	−0.47	**−0.78**	**−0.18**
	Exposure interaction	−0.63	**−1.01**	**−0.27**
Probability of hatching				
Exposure horizontal	(Intercept)	1.14	0.61	1.80
	Horizontal exposure	−1.26	**−1.75**	**−0.82**
Probability of fledging				
Exposure interaction	(Intercept)	1.09	0.64	1.56
	Horizontal exposure	−0.93	**−1.67**	**−0.25**
	Vertical exposure	−0.59	**−1.19**	**−0.04**
	Exposure interaction	−1.84	**−2.72**	**−1.09**
Phenology				
Refuge	(Intercept)	5.03	5.00	5.05
	Refuge	−0.05	**−0.07**	**−0.02**
Exposure vertical	(Intercept)	5.00	4.97	5.02
	Vertical Exposure	0.02	**0.01**	**0.03**
Nest attendance				
Exposure interaction	(Intercept)	4.07	3.79	4.35
	Age	−0.26	**−0.27**	**−0.25**
	Horizontal exposure	0.84	**0.59**	**1.08**
	Vertical exposure	−0.67	**−0.92**	**−0.42**
	Age: Horizontal exp	−0.03	**−0.03**	**−0.02**
	Age: Vertical exp	0.00	−0.01	0.00
	Exposure interaction	0.13	−0.05	0.32
	Age:Horizontal:Vertical	0.03	**−0.03**	**−0.02**

effect of horizontal exposure was strongest (most negative) when nesting sites were more vertically exposed (Fig. 2A). We deemed the main effects of horizontal and vertical exposure uninformative because they did not consider the interaction of the parameters. We did not find support for effects of refuge, substrate, orientation, accessibility to predators, or nesting site size on productivity.

The probability of hatching and the probability of fledging were both affected negatively by nesting site exposure, although the probability of fledging was influenced by the interactive effect of horizontal and vertical exposure and the probability of hatching was not (Table 3). Eggs were more likely to hatch in nesting sites with less horizontal exposure (Table 4, Fig. 2B). The probability of fledging was greatest in nesting sites that were more protected in both planes of exposure and the negative effect of horizontal exposure was greatest in nesting sites that were more vertically exposed (Table 4, Fig. 2C). Nestlings in nesting sites with greater exposure in both planes were substantially less likely to fledge. We found no evidence for the effect of an available refuge on the probability of fledging and no evidence that substrate, orientation, accessibility to predators, or nesting site size affected probabilities of hatching or fledging.

Our phenology analysis revealed that hatch dates were earlier at nesting sites with less vertical exposure and those with a nestling refuge (Fig. 3, Tables 3, 4). We did not find effects of horizontal exposure, orientation, or accessibility to terrestrial

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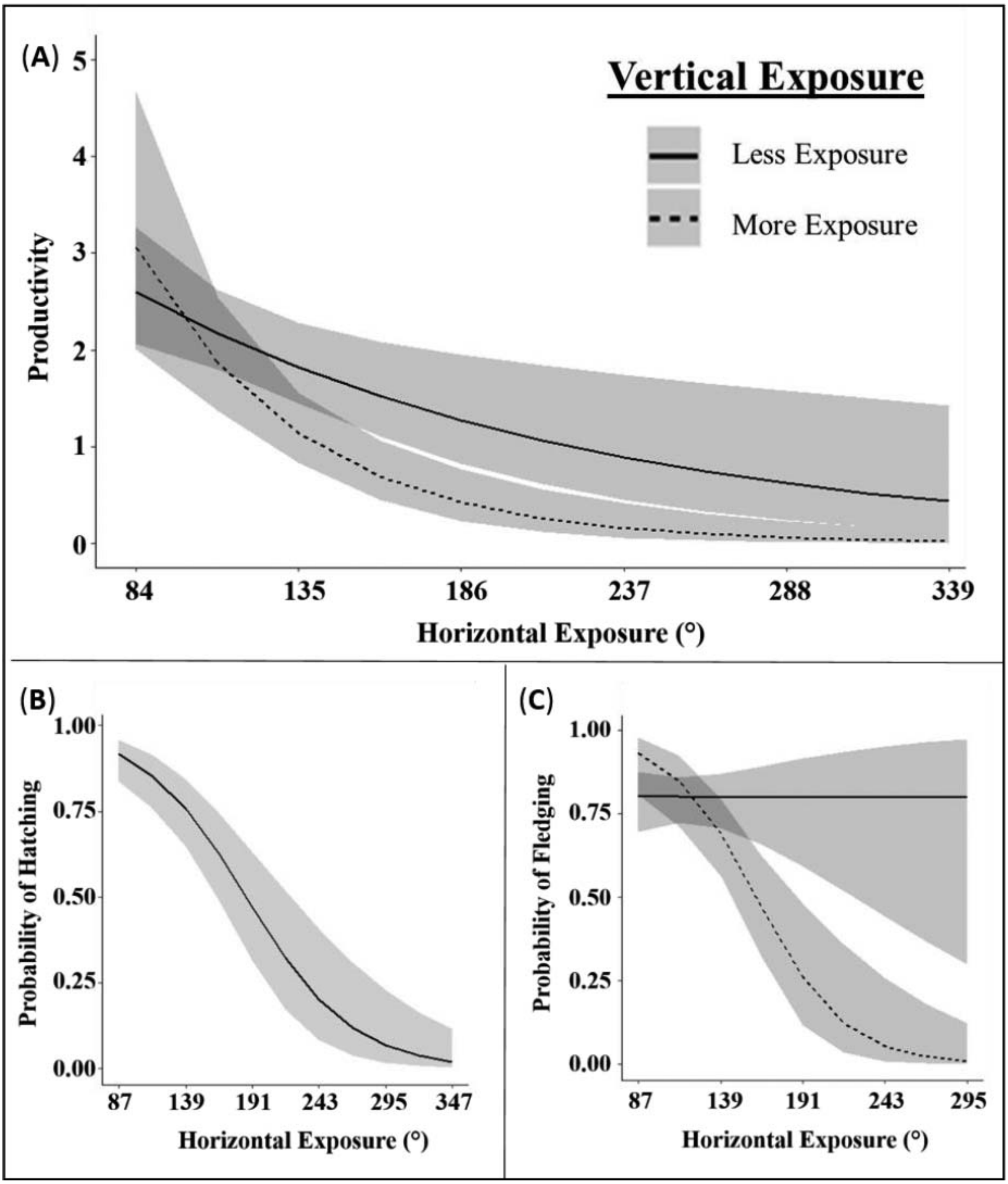

Figure 2. Effects of nesting site characteristics on Gyrfalcon breeding parameters, Seward Peninsula, Alaska, 2014–2019. To display the effect of horizontal exposure at different levels of vertical exposure, vertical exposure is held constant at ± 1 SD of the mean (44° [less exposure] and 98° [more exposure]). Gray shading represents the 85% confidence interval and all models contained a random effect for year. (A) Interactive effects of horizontal and vertical exposure on productivity (the number of fledglings per egg-laying pair). The negative effect of horizontal exposure was greatest in nesting sites that were more exposed vertically (pseudo $r^2 = 0.88$). (B) Eggs in nesting sites with minimal horizontal exposure were more likely to hatch than eggs in more exposed sites (pseudo $r^2 = 0.39$). (C) Nestlings were more likely to fledge from less horizontally exposed nesting sites, particularly for sites that were more vertically exposed (pseudo $r^2 = 0.89$).

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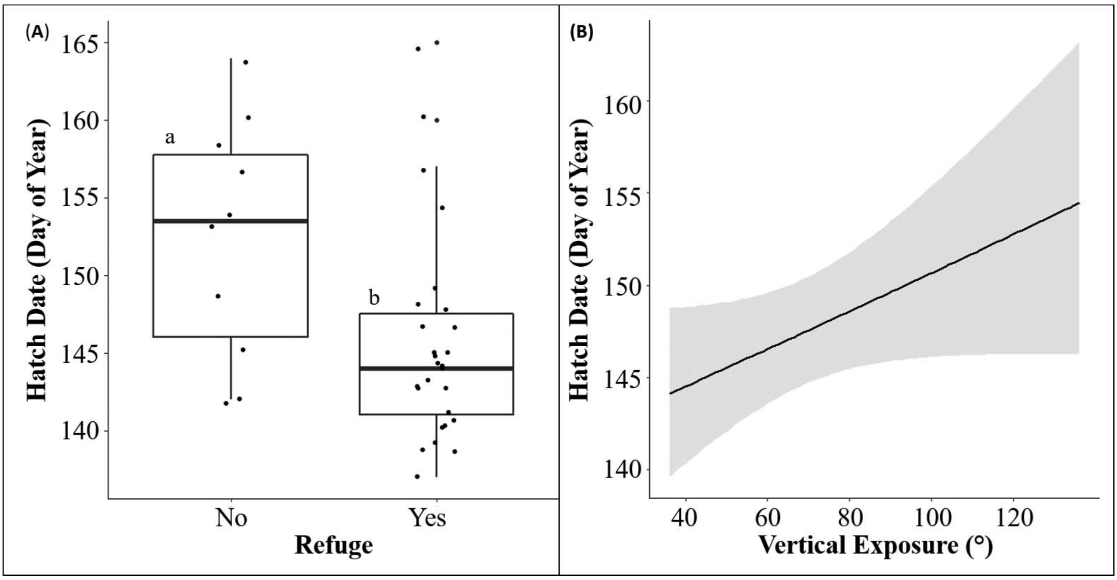

Figure 3. Effects of nesting site characteristics on Gyrfalcon phenology, measured by hatch date, Seward Peninsula, Alaska, 2014–2019. Lower case letters denote statistically different groups, gray shading represents the 85% confidence interval, and all models contained random effect for year. (A) Hatch date was earlier in nesting sites that contained a protective refuge for nestlings (pseudo $r^2 = 0.28$) and (B) in those nesting sites with less vertical exposure (pseudo $r^2 = 0.28$).

predators on Gyrfalcon phenology. Additionally, early breeders had higher productivity than late breeders, which was consistent with the principle that high-quality nesting sites correlate with earlier phenology (Fig. 4). Further, nesting sites containing stick nests were more exposed horizontally compared to ledges with mulch and bare ledges (ledge with mulch: β = 0.23, CI = –0.35, 0.82; stick nest: β = 0.63, CI = 0.13, 1.13) but nest substrate did not vary with vertical exposure (ledge with mulch: β = 0.15, CI = –0.44, 0.75; stick nest: β = 0.44, CI = –0.06, 0.95). There was also no evidence that nest size varied with horizontal (β = 0.30, CI = –0.09, 0.69) or vertical exposure (β = –0.002, CI = –0.39, 0.39).

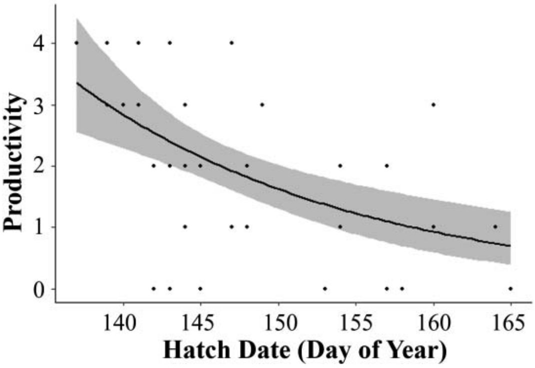

Figure 4. Negative correlation between hatch date and Gyrfalcon productivity, Seward Peninsula, Alaska, 2014–2019. Productivity was defined as the number of nestlings successfully fledged per egg-laying pair. Gray shading represents the 85% confidence interval and the model contains a random effect for year. Earlier breeding pairs had higher productivity than later breeders (pseudo $r^2 = 0.22$).

We collected 30,849 samples (i.e., timed images) of adult Gyrfalcon nest attendance behaviors from 14 nests between 2017 and 2018. Nest attendance was nearly constant through the first week of development and decreased substantially in the second and third weeks, with a corresponding increase in variation among nests (Fig. 5). After week three, nest attendance and the variation among nests decreased for the remainder of brood rearing.

Nest attendance rates were higher in nesting sites with greater horizontal exposure (Tables 3, 4). This effect was strongest during the second and third week of the brood-rearing period, with a three-way interaction between horizontal exposure, vertical exposure, and brood age (Fig. 6). More vertical

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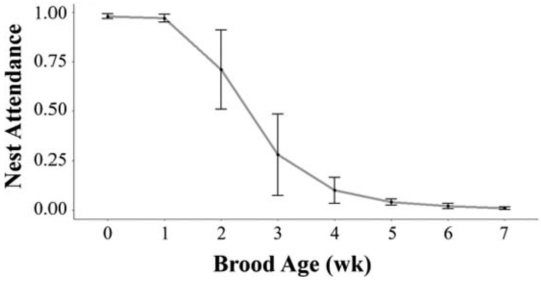

Figure 5. Nest attendance by adult Gyrfalcons during incubation and the brood-rearing period, Seward Peninsula, Alaska, 2017–2018 ($n = 14$ nests and 30,849 behaviors). The proportion of adult nest attendance (brooding/shading, or feeding nestlings, but not including standing at the nest) based on behaviors recorded every 30 min by nest cameras. Error bars are the standard deviation of the proportion of attendance for individual breeding pairs, indicating variation among nests. Nest attendance decreased with brood age, with a large degree of variation in week two and three.

exposure was associated with a decreased effect size of horizontal exposure, and nest attendance decreased with brood age.

DISCUSSION

We found nesting site characteristics affect Gyrfalcon breeding directly via numeric responses in multiple breeding parameters, and indirectly through adult behavioral responses. Birds at nesting sites that provided less protection had lower productivity resulting from decreases in the probability of hatching and the probability of fledging. Additionally, nesting sites with less protection were associated with later breeding and increased parental attendance, which suggests that such nesting sites were lower quality and increased the cost of breeding. Among the measured properties, nesting site exposure was the most influential characteristic for breeding Gyrfalcons and our results underscored

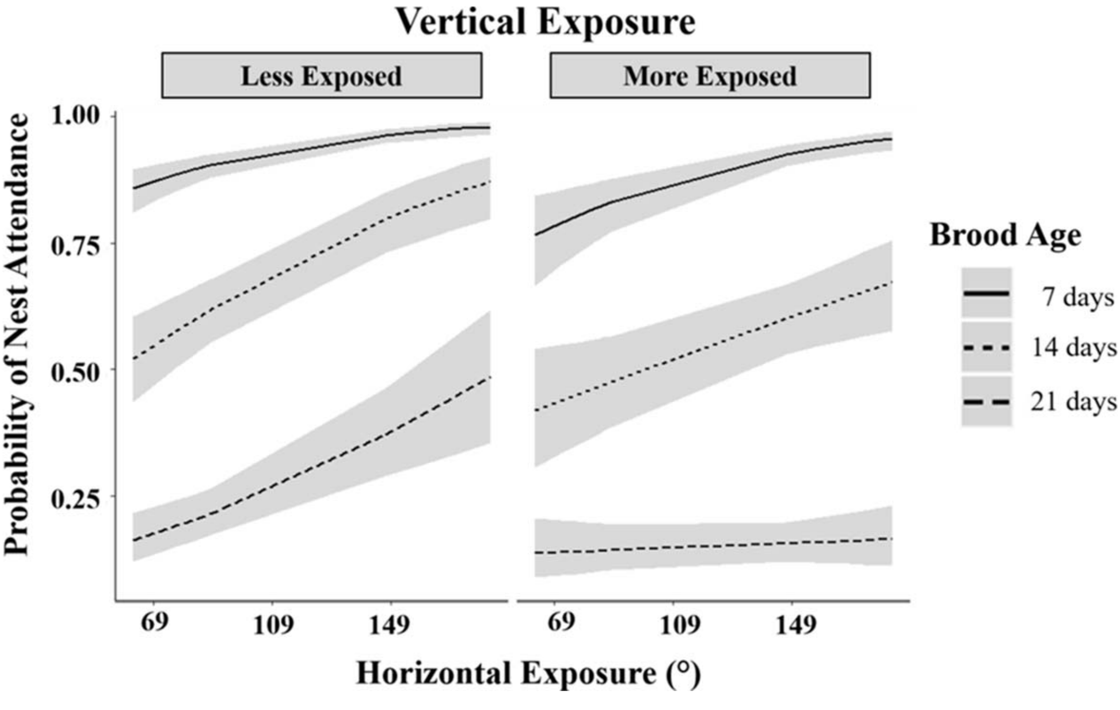

Figure 6. Interactive effects of nesting site horizontal and vertical exposure and brood age on adult Gyrfalcon nest attendance, Seward Peninsula, Alaska, 2017–2018. To display the effect of horizontal exposure, at different levels of vertical exposure and throughout the brood-rearing period, vertical exposure is held constant at 61° (less exposure) and 150° (more exposure) and age was held constant at brood ages 7 d, 14 d, and 21 d. Horizontal exposure correlated positively with adult nest attendance, nest attendance decreased with brood age, and vertical exposure modified the effect of horizontal exposure differently for different brood ages. There was a three-way interaction between horizontal exposure, vertical exposure, and brood age (pseudo $r^2 = 0.80$). Bottom dotted line in both panes represents 21-d-old broods.

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the need to consider the interactive effects of exposure in the horizontal and vertical planes.

The compounded cooling from wind, entering the nest laterally, and precipitation from above may explain why horizontal exposure was more influential on productivity when nesting sites were more vertically exposed. Internal heat loss due to convection increases substantially when downy feathers are wet, suggesting a greater cost of convection for wet nestlings (Nye 1964, Reid et al. 2002); such heat loss may reduce nestling survival during inclement weather, particularly storm events. This effect is likely amplified when nestlings are young, due to scarce down feathering, low body mass, and absence of physiological mechanisms required for thermoregulation (Fortin et al. 2000, Anderson et al. 2017). This period of vulnerability coincides with the Arctic spring, which is characterized by sporadic cold temperatures and precipitation that can result in the death of young nestlings (Anctil et al. 2014). The early-life mortality observed here and in other studies may suggest that vulnerabilities of young nestlings can have substantial effects on Gyrfalcon productivity (Cade 1960, Poole and Bromley 1988a). It is likely that physical properties minimizing nest exposure promote a beneficial microclimate (Webb and King 1983, With and Webb 1993, Heenan and Seymour 2012) and help protect nestlings from the negative effects of inclement weather.

Notably, the effects of nesting site exposure varied with offspring developmental stage, suggesting temporal variation in the sensitivity to environmental threats. In contrast to nestlings, convective cooling of eggs is not substantially increased due to wetting because the shell prevents moisture penetration (Webb and King 1983). Additionally, nearly constant incubation by adults may help ameliorate negative effects of vertical exposure, but may fail to prevent strong winds from cooling the eggs, as evidenced by the negative effect of horizontal exposure on probability of hatching. Together, egg shells and consistent incubation may help explain the lack of interactive effects of exposure on the probability of hatching, whereas there was a pronounced effect on the probability of fledging and productivity.

In contrast to our findings, previous research has provided ambiguous evidence for the effects of nesting site protection on several species of cliff-nesting raptors in the Arctic. Nesting site exposure was found to have no detectable effect on the productivity of Rough-legged Hawks (Beardsell et al. 2016) or Gyrfalcons (Barichello and Mossop 2011), but Mearns and Newton (1988) found that vertical protection (presence of overhang over nest) increased productivity of Peregrine Falcons. We offer two explanations for the disparate results. First, combining horizontal and vertical exposure into a single exposure variable (Barichello and Mossop 2011, Beardsell et al. 2016), overlooks the interaction that we found to be statistically and biologically significant. Second, the subjective categorization of nesting site exposure (Mearns and Newton 1988) can overlook effects detectable by more quantitative analyses.

Our results also differed from previous research in that we found no effect of substrate (Mearns and Newton 1988), orientation (Beardsell et al. 2016), accessibility to predators, or nesting site size (Mechnikova et al. 2012) on breeding parameters. Mearns and Newton (1988) found Peregrine Falcons in Scotland were more productive in stick nests, and the authors attributed the higher productivity of stick nests, most of which were built by Common Ravens, to the fact that these were more recessed into cliffs than nesting sites without stick nests. Our disparate results for nest substrate may result from differences in the assemblage of nest builders, specifically the addition of Rough-legged Hawks and Golden Eagles in our study area, which may build more exposed nests. There may also be other differences between the breeding ecologies of Peregrine Falcons and Gyrfalcons, which may promote differences in the importance of stick nests (Poole and Bromley 1988a). Species differences may also explain variation in the effect of nesting site orientation. Beardsell et al. (2016) found south-facing nests of Rough-legged Hawks correlated with higher hatching success and productivity, whereas Barichello and Mossop (2011) found no effect for Gyrfalcons. Further, Poole and Bromley (1988b) reported no orientation preference for Gyrfalcons, which contrasts with the propensity for a southern orientation by Rough-legged Hawks, Golden Eagles, and Peregrine Falcons. This lack of preference for orientation may result from Gyrfalcons, as well as ravens, selecting nesting sites with greater overhead protection, relative to the other species (Poole and Bromley 1988b). Although southern-facing nests were more common in our current research, we found no evidence that orientation affected breeding Gyrfalcons. We speculate that snow melts earlier from nesting sites facing south, rendering them more available to Gyrfalcons beginning to breed in

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March and April, but does not provide a reproductive advantage. Alternatively, the value of increased sunlight due to southern orientation may vary temporally, such that direct sunlight warms eggs and young nestlings early in the season when temperatures are low, but excessive heat stresses nestlings in the summer. It is unclear why we found no effect of accessibility to predators; however, Beardsell et al. (2016) found accessibility affects Rough-legged Hawks on Bylot Island, Canada. Interspecific differences in nest defense behaviors or ecological differences between study sites could play a role. Lastly, conflicting findings for the effect of nesting site size on Gyrfalcon productivity may result from nesting platform differences, as Mechnikova et al. (2011) sampled mostly nesting sites in trees. Smaller nests may fall more easily from trees during breeding attempts (Mechnikova et al. 2011), effectively ending reproductive attempts, but this effect may be less severe for cliff-nesting sites due to more stable platforms and relative protection from wind compared to nesting sites in trees.

Hatch date was earlier for nesting sites that offered greater protection, specifically minimal vertical exposure, and that contained a nestling refuge, which suggests that Gyrfalcons may preferentially select for nesting sites with these properties (Newton 1991). Explanatory value of phenology models was limited and analysis did not reveal a clear top model, suggesting that other factors, likely snow melt, weather, prey availability, and nest competition, may have more substantial effects on Gyrfalcon phenology. Further, although Gyrfalcons reside on our study site year-round, whether they maintain territories during winter or how this might affect their phenology is not well understood.

Nest attendance rates were highest at more exposed nesting sites, potentially increasing the cost of reproduction for breeders at those nesting sites (Cresswell et al. 2004). While tending to nestlings, adults are unable to forage and are exposed to harsh weather which can increase energetic demands, decrease body condition, and may facilitate carry-over effects (Golet et al. 1998, Hanssen et al. 2005, Fast et al 2007, Hilde et al. 2016). The indirect cost of more nest attendance was compounded by a simultaneous reduction in productivity, suggesting that the increased parental investment was not adequate compensation for greater nesting site exposure. For all analyses, we did not manipulate nest protection, thus we were unable to disassociate individual and habitat quality. High-quality individuals tend to occupy high-quality habitats and contribute disproportionate numbers of young to the population; thus, functional conservation should aim to identify characteristics that maximize productivity, regardless of individual quality (Newton 1991, Kim and Monaghan 2005).

The importance of nesting site characteristics for breeding raptors is highlighted by their effects on critical breeding parameters and demonstrates that small-scale habitat variables are important components of habitat suitability. This small-scale suitability is likely most important for species breeding in habitats that present thermoregulatory challenges including hot (Beecham and Kochert 1975) or cold (Eeva et al. 2002) temperatures. Meaningful nesting site characteristics likely vary by breeding habits (e.g., nesting in cavities [Alabrudzińska et al. 2003], on the ground [With and Webb 1993], in open-cup nests [Burton 2006], or on artificial structures [Møller et al. 2004]). The importance of nest protection to habitat suitability highlights the value of prioritizing landscapes that provide highly suitable nesting sites in addition to important large-scale habitat characteristics. Understanding habitat suitability within Arctic ecosystems is pivotal for designing and implementing effective conservation measures because climate change is rapidly altering northern habitats and subjecting Arctic specialists to alarming threats (Johnson and Geupel 1996, Gaillard et al. 1998, Thomas et al. 2004, Tape et al. 2006). Inclement Arctic weather can substantially reduce reproductive success of mammals (Vors and Boyce 2009), birds (Anctil et al. 2014), and entire ecosystems (Schmidt et al. 2019). As severe weather increases, including greater wind speeds and precipitation (Trenberth et al. 2003, Min et al. 2011, Mioduszewski et al. 2018), nesting site characteristics that shield nesting raptors will likely become more important. Rapid Arctic transformation, driven by climate change, precipitates the need to understand habitat suitability of Arctic species, including characteristics at relatively small spatial scales.

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