

INFLUENCE OF HABITAT HETEROGENEITY ON DISTRIBUTION, OCCUPANCY PATTERNS, AND PRODUCTIVITY OF BREEDING PEREGRINE FALCONS IN CENTRAL WEST GREENLAND

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Abstract. We used occupancy and productivity data collected at 67 cliffs used for nesting from 1972 to 1999 to assess patterns of distribution and nest-site selection in an increasing population of Peregrine Falcons (*Falco peregrinus*) in central West Greenland. Peregrine Falcons breeding at traditionally occupied cliffs used for nesting had significantly lower variation in productivity and thus these cliffs were better quality sites. This indicates that Peregrine Falcons occupied cliffs according to a pattern of despotic distribution. Falcons breeding at cliffs that were consistently occupied during the breeding season had higher average productivity and lower variation in productivity than falcons at inconsistently occupied cliffs, and thus consistent occupancy also was indicative of cliff quality. Features of high quality habitat included tall cliffs, greater change in elevation from the lowest point within 3 km of the cliff to the cliff top (elevation gain), and protection from weather on the eyrie ledge. Spacing of suitable and occupied cliffs also was an important feature, and the best cliffs generally were more isolated. Increased spacing was likely a mechanism for reducing intraspecific competition. Our results suggest that Peregrine Falcons use a resource defense strategy to compete for better quality habitats and may use spacing and physical features of a nest site to identify good quality breeding habitat.

Key words: arctic, despotic distribution, habitat heterogeneity, nearest neighbor, Peregrine Falcon, productivity.

Influencia de la Heterogeneidad de Hábitat en la Distribución, Patrones de Ocupación y Productividad de Individuos de *Falco peregrinus* durante el Periodo Reproductivo en el Centro Oeste de Groenlandia

Resumen. Usamos datos de ocupación y productividad colectados en 67 acantilados usados para nidificar desde 1972 hasta 1999 para determinar los patrones de distribución y selección de sitio de nidificación en una población creciente de *Falco peregrinus* en el centro oeste de Groenlandia. Los individuos de *F. peregrinus* que criaron en los acantilados tradicionalmente usados para nidificar tuvieron una variación significativamente menor en la productividad, por lo que estos acantilados fueron sitios de mejor calidad. Esto indica que *F. peregrinus* ocupó acantilados de acuerdo a un patrón de distribución despótica. Los halcones que criaron en acantilados ocupados continuamente durante la estación reproductiva tuvieron mayor productividad promedio y menor variación en la productividad que los halcones en los acantilados menos ocupados, y por ende el patrón de ocupación continuo fue también un indicador de la calidad de los acantilados. Las características de un hábitat de alta calidad incluyeron acantilados altos, mayores cambios en elevación desde el punto más bajo dentro de los 3 km del acantilado hasta la punta del acantilado (ganancia en elevación) y protección del clima en los bordes del nido. La distribución espacial de los acantilados adecuados y ocupados fue también un rasgo importante, de modo que los mejores acantilados generalmente fueron los más aislados. El espaciamiento mayor fue probablemente un mecanismo para reducir la competencia intraespecífica. Nuestros resultados sugieren que *F. peregrinus* usa una estrategia de defensa del recurso para competir por ambientes de mejor calidad y puede usar características físicas y de la distribución espacial de los sitios de nidificación para identificar hábitats de cría de buena calidad.

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INTRODUCTION

Comparative reproductive performance can be one measure of habitat quality. Animals often occupy certain habitats from those that are available (Manly et al. 1993, Litvaitis et al. 1994), and if selection of habitats is adaptive, chosen habitats should provide fitness benefits to the occupants (Martin 1998, Garshelis 2000). Habitat selection can be inferred when an animal uses a resource disproportionately to its availability (Johnson 1980) and fitness benefits are typically measured as the reproductive success and survival rates of the occupants (Van Horne 1983, Gende et al. 1997, Clark and Shutler 1999). High quality habitats provide greater fitness benefits than other selected habitats. Thus, natural selection may play a role in an individual's ability to recognize good habitat among gradients of used habitat (Hunt 1988, Clark and Shutler 1999).

Distribution patterns also involve selection by animals among habitat gradients. In an increasing population, animals will distribute themselves among breeding habitats according to one of two distribution patterns. In an *ideal free distribution*, animals exploit the resources of the best habitats. As the population increases, individuals are free to occupy better habitats in higher densities, even when that choice results in increased competition and a subsequent decrease in fitness benefits (Fretwell and Lucas 1970). In theory, in an ideal free distribution, all habitats eventually will provide similar fitness benefits to the animals, but densities will be higher in the better habitats. A decrease in reproductive success throughout all habitats as density increases, with little variation, would indicate an ideal free distribution. In a *despotic distribution*, animals compete for habitats by defending resources. Animals occupy high quality habitats first, and earlier arrivals function as despots, forcing later arrivals into lower quality habitats (Fretwell and Lucas 1970, Krebs and Davies 1993, Newton 1998). As the population increases, high quality habitat continues to provide better fitness benefits to the occupants than low quality habitat. Lower survival or reproductive rates or more variation in reproductive success in the habitats occupied later (i.e., poorer habitat) would indicate a despotic distribution (Ferrer and Donazar 1996).

In addition to intraspecific competition, weather and climate can affect breeding strategies and reproductive success of birds (Newton 1979, Bradley et al. 1997). In the harsh climate of the Arctic, birds may adopt strategies different from those in temperate regions, such as selecting different nest-sites to increase their chances of successful reproduction. For instance, Cade (1960) suggested Peregrine Falcons (*Falco peregrinus*) in Alaska avoid breeding on north-facing cliffs to escape northerly storms. Others have suggested that Peregrine Falcons in Greenland choose eyrie ledges that are a compromise between exploiting solar warmth and protection from weather (Burnham and Mattox 1984, Falk et al. 1986, Wightman and Fuller 2005). Although researchers have suggested biological reasons for observed nest-site choices, no studies have quantitatively compared the fitness benefits associated with different nest-site choices by Peregrine Falcons in the Arctic.

In central West Greenland (Berthelsen et al. 1993), the Greenland Peregrine Falcon Survey has routinely surveyed for breeding Peregrine Falcons since 1972. On their initial search they found only nine pairs of Peregrine Falcons occupying cliffs (Mattox and Seegar 1988). By 1999, there were 133 cliffs known to be occupied by Peregrine Falcons in the study area (W. G. Mattox, Conservation Research Foundation, unpubl. data). Because of the long-term monitoring of the Greenland Peregrine Falcon Survey after the DDT-caused population decline, the pattern of reoccupancy and productivity in this recovering population can be relatively well described. We took advantage of the Greenland Peregrine Falcon Survey data to evaluate patterns of distribution and habitat selection and to determine whether there are physical characteristics of cliffs that Peregrine Falcons may use as indicators of high quality breeding habitat.

METHODS

STUDY AREA

We conducted this study in the Kangerlussuaq region of central West Greenland, which encompasses one of the widest portions of ice-free land on the island. The study area, delineated by W. G. Mattox and colleagues in 1972, is approximately 2500 km² and located

just above the Arctic Circle from 66°45'N to 67°15'N (Mattox and Seegar 1988). Søndre Strømfjord divides this area from the western coast almost to the inland ice cap. Elevation ranges from sea level to 1120 m and this treeless, mountainous area is interspersed with many small lakes. Located in a low arctic vegetation belt, willow scrub (*Salix* spp.), dwarf birch (*Betula nana*), lichens, mosses, sedges, and grasses are the dominant vegetation (Böcher et al. 1968). Summer temperatures are generally above freezing and usually range from 0–15°C.

DEFINITIONS

An eyrie is the place on a ledge on which a falcon lays her eggs (Ratcliffe 1993). We used the term “nesting cliff” to define a topographic feature containing one or more eyries or potential eyries. Alternative nesting cliffs are possible within the range of one mated pair of birds. We classified a nesting cliff as occupied if a pair was observed at the nesting cliff during the breeding season (June–August) in any year from 1972 to 1999. The majority of observations represent egg-laying attempts, but there are a few examples in the study area of an adult pair occupying a nesting cliff for several seasons but not producing eggs (W. G. Mattox, pers. comm.).

The pattern in which Peregrine Falcons reoccupied nesting cliffs should represent their distributional behavior. Thus, we categorized each nesting cliff based on its year of first occupancy. Hickey (1942) and Ratcliffe (1993) also suggested that Peregrine Falcons occupy the best habitats most consistently. Therefore, we also categorized each nesting cliff based on consistency of occupancy. We treated reoccupancy and consistency patterns independently and placed each nesting cliff in a reoccupancy and consistency category. We used a categorical rather than a linear approach because our survey effort varied among years and the more remote nesting cliffs were not visited in every year, however our data were sufficient to allow us to assign nesting cliffs accurately to categories. We classified nesting cliffs as traditionally occupied if a falcon pair was first resident at a cliff for two or more years between 1972 and 1985 and as recently occupied if residency was first recorded between 1986 and 1999. At a few recently occupied nesting cliffs a pair occupied the nesting cliff once before 1986 but

occupied it more regularly after 1986. We defined consistently occupied sites as all nesting cliffs occupied by any pair with fewer than three years of continuous vacancy after the year of first occupancy. Inconsistently occupied sites were nesting cliffs with three or more years of continuous vacancy after the year of first occupancy. Our consistency categories are irrespective of the year a nesting cliff was first occupied. We compared habitat measures and productivity between traditionally and recently occupied nesting cliffs and between consistently and inconsistently occupied nesting cliffs. We did not evaluate interactions between year of first reoccupancy and consistency of occupancy (e.g., all traditionally and consistently occupied sites compared with all recently and inconsistently occupied sites) because of sample size constraints.

PRODUCTIVITY AND HABITAT MEASURES

Along with members of the Greenland Peregrine Falcon Survey, we collected data on the occupancy and productivity of breeding Peregrine Falcons in the study area between 1972 and 1999 (Mattox and Seegar 1988, Geissler et al. 1990, Gould and Fuller 1995). We surveyed cliffs along established backpacking or kayaking routes (1–21 day trips) and located each pair of falcons by observing adult behavior. If a pair was present but did not have an eyrie, we considered it a failed breeding attempt. After we located an eyrie, we climbed to the ledge and banded nestlings. We used the number of nestlings in the eyrie at the time of banding (age 18–30 days old) as our estimate of productivity. For a complete description of survey methods, see Burnham and Mattox (1984).

In 1998–1999, we measured physical features of nesting cliffs at the three spatial levels of eyrie, cliff, and surrounding topography. We chose 29 characteristics to measure based on results from previous studies and knowledge of Peregrine Falcon biology (Wightman and Fuller 2005). A team of two persons hiked to cliffs to measure and record data. The team also climbed to eyries to collect ledge measurements. We calculated height and slope measures from clinometer and rangefinder readings taken at the site. We summarized habitat features by reoccupancy and consistency patterns (Table 1, 2).

TABLE 1. Physical characteristics of occupied cliffs used for nesting measured to evaluate features associated with good quality Peregrine Falcon habitat in central West Greenland. Each cliff was categorized as traditionally or recently occupied and consistently or inconsistently occupied. Measurements were made in 1998–1999; however, cliffs were categorized based on their occupancy history from 1972–1999. Data are presented as mean \pm SE (r^2 , range).

Habitat feature ^b	Traditional			Recent			Consistent			Inconsistent		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Eyrie characteristics												
Length of eyrie ledge (cm)	827 \pm 257	(27, 50–6098)	568 \pm 181	(29, 61–5000)	734 \pm 200	(36, 50–6098)	803 \pm 375	(13, 130–5000)				
Depth of eyrie ledge (cm)	235 \pm 66	(27, 40–1500)	101 \pm 11	(29, 17–240)	195 \pm 51	(36, 17–1500)	109 \pm 16	(13, 52–240)				
Eyrie aspect ($^{\circ}$)	199 \pm 1	(28, 15–337)	173 \pm 2	(30, 28–345)	192 \pm 1	(37, 15–337)	194 \pm 3	(13, 28–345)				
Vertical angle of exposure ($^{\circ}$)	70 \pm 4	(24, 30–110)	60 \pm 4	(24, 25–95)	69 \pm 4	(30, 30–110)	62 \pm 6	(10, 35–95)				
Horizontal angle of exposure ($^{\circ}$)	139 \pm 7	(24, 54–197)	149 \pm 6	(25, 100–205)	146 \pm 6	(31, 54–201)	137 \pm 11	(10, 100–205)				
Cliff characteristics												
Elevation of cliff (m)	315 \pm 18	(29, 200–550)	264 \pm 21	(37, 100–550)	297 \pm 17	(40, 100–550)	289 \pm 26	(18, 100–480)				
Cliff height (m)	129 \pm 14	(29, 32–365)	77 \pm 8	(37, 14–220)	113 \pm 11	(40, 23–365)	81 \pm 13	(18, 14–220)				
Height of hill below cliff (m)	47 \pm 7	(29, 0–120)	35 \pm 5	(37, 0–138)	45 \pm 5	(40, 0–120)	26 \pm 4	(18, 0–55)				
Slope (m)	1.7 \pm 0.1	(21, 0.9–2.8)	1.7 \pm 0.2	(36, 0.7–5.1)	1.7 \pm 0.1	(31, 0.7–4.0)	1.7 \pm 0.3	(17, 0.8–5.1)				
Cliff aspect ($^{\circ}$)	199 \pm 1	(29, 104–326)	179 \pm 1	(37, 21–345)	196 \pm 1	(40, 21–360)	196 \pm 2	(18, 82–345)				
Height of eyrie (m)	66 \pm 9	(29, 8–201)	40 \pm 7	(35, 5–224)	57 \pm 7	(40, 5–201)	42 \pm 12	(17, 7–224)				
Cliff height at eyrie (m)	123 \pm 13	(29, 17–365)	73 \pm 9	(35, 14–260)	106 \pm 11	(40, 25–365)	78 \pm 15	(17, 14–260)				
Topographical characteristics												
Distance to permanent water (m)	449 \pm 93	(29, 0–2750)	463 \pm 69	(37, 0–1500)	475 \pm 58	(40, 0–1500)	448 \pm 152	(18, 0–2750)				
Elevation gain within 3-km radius (m)	228 \pm 16	(29, 75–400)	187 \pm 15	(37, 50–475)	221 \pm 14	(40, 100–400)	179 \pm 17	(18, 50–300)				
Elevation of cliff above drainage (m)	192 \pm 15	(29, 75–400)	139 \pm 16	(37, 26–450)	183 \pm 13	(40, 50–400)	107 \pm 12	(18, 26–200)				
Distance to drainage (m)	570 \pm 98	(29, 0–2200)	578 \pm 107	(37, 0–2250)	668 \pm 102	(40, 0–2250)	387 \pm 77	(18, 0–1000)				
Elevation of hill across valley (m)	371 \pm 21	(29, 200–600)	331 \pm 19	(37, 125–600)	360 \pm 18	(40, 125–600)	326 \pm 25	(18, 125–600)				
Distance to hill across valley (km)	2.3 \pm 0.2	(29, 0.8–4.8)	2.1 \pm 0.2	(37, 0.3–5.0)	2.4 \pm 0.2	(40, 0.5–5.0)	1.7 \pm 0.2	(18, 0.3–4.0)				
Distance to nearest cliff (km)	2.4 \pm 0.2	(29, 0.3–4.8)	2.1 \pm 0.2	(37, 0.3–5.0)	2.4 \pm 0.2	(40, 0.3–5.0)	1.8 \pm 0.3	(18, 0.2–5.0)				
Distance to nearest historical cliff (km)	3.0 \pm 0.2	(29, 0.3–4.8)	2.5 \pm 0.2	(37, 0.3–5.1)	2.9 \pm 0.2	(40, 0.3–5.1)	2.5 \pm 0.3	(18, 0.3–5.0)				
Distance to nearest neighbor (km)	3.4 \pm 0.3	(29, 1.6–11.2)	3.1 \pm 0.2	(37, 1.3–5.2)	3.0 \pm 0.2	(40, 1.6–5.0)	4.0 \pm 0.6	(18, 1.3–11.2)				

^a At a few nesting cliffs, we were unable to access the eyrie ledge. Thus, our sample size for eyrie characteristics or location varies within an occupancy category. We also could not calculate the slope of the cliff if we could not measure accurately the distance from the observer to the top of the cliff.

^b See Wightman and Fuller (2005) for definition of habitat features.

TABLE 2. Categorical habitat features at cliffs occupied by Peregrine Falcons measured to evaluate features associated with high quality breeding habitat in central West Greenland. Each cliff used for nesting was categorized as traditionally or recently occupied and consistently or inconsistently occupied. Cliffs were categorized based on their occupancy history from 1972–1999 and habitat features were measured in 1998–1999. Data are presented as % (n^a).

Physical features ^b	Traditional	Recent	Consistent	Inconsistent
Eyrie characteristics				
Overhang protection on ledge				
none	18 (5)	7 (2)	11 (4)	15 (2)
slight	18 (5)	17 (5)	22 (8)	15 (2)
partial	53 (15)	48 (14)	51 (19)	39 (5)
complete	11 (3)	28 (8)	16 (6)	31 (4)
Accessible to predation				
yes	32 (9)	25 (8)	26 (10)	33 (5)
no	68 (19)	75 (24)	74 (28)	67 (10)
Substrate on ledge				
sand or dirt	89 (25)	76 (22)	89 (33)	62 (8)
moss	0 (0)	0 (0)	0 (0)	0 (0)
vegetation	11 (3)	11 (3)	8 (3)	15 (2)
gravel	0 (0)	3 (1)	0 (0)	15 (2)
stick nest	0 (0)	7 (2)	3 (1)	8 (1)
bare rock	0 (0)	3 (1)	0 (0)	0 (0)
Vegetation near scrape				
yes	79 (22)	69 (22)	71 (27)	80 (12)
no	21 (6)	31 (10)	29 (11)	20 (3)
Cliff characteristics				
Vegetation at base of cliff				
willow-steppe mix	17 (5)	43 (16)	35 (14)	22 (4)
heath-willow mix	41 (12)	16 (6)	27 (11)	27 (5)
heath-steppe mix	14 (4)	14 (5)	8 (3)	33 (6)
herb slope	3 (1)	8 (3)	8 (3)	6 (1)
water	11 (3)	5 (2)	8 (3)	6 (1)
willow copse	14 (4)	14 (5)	15 (6)	6 (1)
Boulders at base of cliff				
yes	93 (27)	84 (31)	95 (38)	78 (14)
no	7 (2)	16 (6)	5 (2)	22 (4)
Position of eyrie on cliff				
lower	31 (9)	16 (6)	28 (11)	17 (3)
middle	52 (15)	49 (18)	50 (20)	50 (9)
upper	17 (5)	35 (13)	23 (9)	33 (6)
Human disturbance				
minimal	86 (25)	84 (31)	85 (34)	83 (15)
moderate	14 (4)	13 (5)	13 (5)	17 (3)
severe	0 (0)	3 (1)	2 (1)	0 (0)

^a At a few cliffs, we were unable to access the eyrie ledge. Thus, our sample size for eyrie characteristics or placement varies from our total set of cliffs used for nesting.

^b See Wightman and Fuller (2005) for definition of habitat features.

Three of the 29 physical characteristics were measures of spatial distribution. The nearest cliff was the closest cliff to the nesting cliff irrespective of whether Peregrine Falcons ever occupied it. The nearest nesting cliff was the nearest cliff ever occupied by Peregrine Falcons, irrespective of whether Pere-

grine Falcons occupied the sample cliff and the nearest nesting cliff simultaneously. The third spatial measure, distance to nearest neighbor, we defined as the nearest nesting cliff that other Peregrine Falcons occupied simultaneously with the occupied sample cliff.

STATISTICAL ANALYSES

We calculated average productivity at each nesting cliff as the mean number of young produced per pair per year occupied between 1972 and 1999 (Appendix). Total productivity was the total number of young produced from each nesting cliff over the same 28-year period. We used a *Z* test to compare the variation in productivity among cliff categories (Zar 1996). Because the productivity data tended to deviate from normality and homoscedasticity, we used the Kruskal-Wallis test to examine differences in mean productivity among nesting cliff categories (Zar 1996).

We analyzed cliff and eyrie aspect independently because the data were circular. We conducted Rayleigh's test of circular uniformity on aspect data for each nesting cliff category to determine whether aspect data were significantly oriented (Zar 1996). Parametric tests for circular data assume the data are from a von Mises distribution, which is the circular equivalent to a normal distribution. Our data did not necessarily meet this assumption. Therefore, we used a nonparametric procedure for unimodal data to compare the mean direction of traditionally and recently occupied nesting cliffs against a chi-square distribution (Fisher 1993:116, Method P). Chi-square distributions often are not appropriate for data with small sample sizes, such as our sample of 18 inconsistently occupied sites. Therefore, we compared the mean direction of consistently and inconsistently occupied cliffs and eyries against a bootstrap distribution to determine differences of aspect between these two categories (Fisher 1993:118). The test statistic for both of these comparisons (Y_r) evaluates whether there is a common mean direction underlying the samples (r).

Before using habitat features to predict occupancy patterns we eliminated some habitat variables based on correlation with another measurement, inadequate sample size, or circular data (Mosher et al. 1986, Grebence and White 1989). When deciding which of a pair of correlated variables to eliminate ($r \geq 0.60$), we retained those variables that were easier to measure or have been found to be important features of Peregrine Falcon biology. We eliminated six variables (height of eyrie, cliff height above eyrie, length of ledge, cliff elevation, elevation of cliff above the

drainage, and nearest cliff distance) because they were correlated with one or more variables. We eliminated slope because of low sample size ($n = 57$). Cliff and eyrie aspect data were circular and therefore also eliminated.

To determine which of the remaining 20 habitat variables to include in our modeling of occupancy patterns, we used the best subset variable selection technique, which provides model statistics for each possible combination of variables. We included interactions of certain habitat features in this variable selection step. We chose the one set of habitat variables that produced the best C_p Mallow statistic. Then, we used these habitat variables in a logistic regression to predict occupancy patterns (Hosmer and Lemeshow 2000, Allison 1999). We produced two independent models using habitat features, one predicting reoccupancy patterns and one predicting consistency patterns. We evaluated the fit and predictive power of the model using the Hosmer-Lemeshow goodness of fit test (\hat{C} ; Hosmer and Lemeshow 2000:147–151) and the maximum-rescaled R^2 value, respectively.

We used multiple regression to examine associations between habitat features and productivity without the constraint of the occupancy categories (Hatcher and Stepanski 1994, Zar 1996). We could not use all habitat variables because of low sample size, so we tested for associations using only the variables identified as being important for predicting reoccupancy or consistency patterns. We log-transformed variables that failed to meet the assumptions of homogeneity of variance or normality. We used SAS v. 6.0 (SAS Institute 1990) to conduct analyses. We report means \pm SE and used an alpha of 0.05 for significance.

RESULTS

REOCCUPANCY PATTERNS

We evaluated 67 occupied Peregrine Falcon nesting cliffs. We eliminated one cliff from reoccupancy comparisons because it did not fit the definition for either category. For productivity comparisons, we eliminated a second nesting cliff for which we had occupancy data but no productivity data. This latter cliff was included in subsequent habitat analyses. We found no difference in average productivity

TABLE 3. Traditionally occupied cliffs used for nesting by Peregrine Falcons were characterized by tall cliffs with eyrie ledges that provided protection from weather and were farther from other nesting cliffs and neighbors in central West Greenland. Our logistic regression model predicts the probability of initial occupation of a cliff by Peregrine Falcons between 1972 and 1985 using habitat features measured at 24 traditionally occupied (1) and 25 recently occupied (0) cliffs^a. Negative coefficients (β) indicate a negative association between that variable and traditional occupancy. Habitat variables included in our model were selected using the best subset variable selection technique.

Variable ^b	$\beta \pm SE$	Wald χ^2_1	P^c	exp(β) ^d	95% Wald CL
Intercept	-5.38 ± 3.33	2.6	0.11	—	—
Cliff height	0.03 ± 0.01	6.0	0.01	1.03	1.01–1.05
Ledge depth	0.01 ± 0.01	2.1	0.14	1.02	1.00–1.03
Horizontal angle of exposure	-0.05 ± 0.02	5.7	0.02	0.96	0.92–0.99
Nearest nesting cliff	2.15 ± 0.77	7.8	0.01	8.55	1.90–38.41
Nearest neighbor	0.56 ± 0.36	2.5	0.12	1.75	0.87–3.50

^a We were unable to measure eyrie characteristics at some cliffs with inaccessible ledges. Our sample for the logistic regression model is lower than our complete sample of 29 traditionally and 37 recently occupied cliffs because it includes only those cliffs where all eyrie variables were measured.

^b See Wightman and Fuller (2005) for definition of terms.

^c P -values based on Wald χ^2 statistic.

^d Odds ratios indicate the change in odds of occupancy for each unit change of the variable. For example, the odds ratio for cliff height is 1.03. This means that for each 1 m increase in cliff height the odds of occupancy increases by 3%.

between traditionally ($n = 29$) and recently ($n = 36$) occupied nesting cliffs (2.5 ± 0.1 and 2.3 ± 0.2 young per year occupied, respectively, $H_1 = 0.3$, $P = 0.61$). However, variation in productivity at traditionally occupied sites was significantly lower than at recently occupied sites ($CV = 20\%$, $CV = 48\%$, respectively, $Z_2 = 4.0$, $P < 0.001$).

Traditionally occupied cliffs were significantly oriented to the southwest ($Z_{29} = 13.8$, $P < 0.001$) and recently occupied cliffs were significantly oriented to the south ($Z_{37} = 12.9$, $P < 0.001$). The difference in mean direction between these categories was not significant ($Y_{66} = 2.8$, $P = 0.09$). Mean direction of eyrie aspect was also significantly oriented to the southwest and south for traditionally and recently occupied sites, respectively ($Z_{28} = 14.2$ and $P < 0.001$, $Z_{30} = 5.3$, $P < 0.001$, respectively). We found no significant difference in eyrie aspect between these categories ($Y_{58} = 3.2$, $P = 0.08$).

Five habitat features were important for predicting traditional occupancy of a nesting cliff by Peregrine Falcons (Table 3; $G_5 = 36.5$, $n = 49$, $P < 0.001$). Our logistic regression model was effective for describing traditionally occupied cliffs ($\hat{C}_8 = 8.2$, $P = 0.41$) and had relatively strong predictive power (rescaled $R^2 = 0.71$). The odds ratio for each variable in the model indicated the effect of each variable on the probability of traditional occupancy of

a nesting cliff. For example, an odds ratio of 1.03 for cliff height indicated that there was a 3% increase in odds of traditional occupancy with every 1-meter increase in cliff height. Odds ratios less than one represent a negative association with traditional occupancy. Therefore, the odds ratio of 0.96 for the horizontal angle of exposure on the eyrie ledge indicated there was a 4% increase in odds of traditional occupancy with every 1-degree decrease in exposure. The confidence limits around the odds ratio for nearest nesting cliff are wide, which indicates the odds ratio for this feature should be evaluated with caution.

CONSISTENCY OF OCCUPANCY PATTERNS

We eliminated nine of 67 nesting cliffs from consistency of occupancy comparisons because of insufficient information about their pattern of occupancy. Productivity at consistently occupied sites ($n = 40$) was significantly greater than at inconsistently ($n = 18$) occupied nesting cliffs (2.5 ± 0.1 and 2.0 ± 0.2 young per year occupied, respectively, $H_1 = 4.8$, $P = 0.03$). Variation in productivity was lower at consistently occupied than at inconsistently occupied nesting cliffs ($CV = 29\%$, $CV = 51\%$, respectively, $Z_2 = 2.7$, $P < 0.01$).

Consistently and inconsistently occupied cliffs were both significantly oriented to the south-southwest ($Z_{40} = 14.8$, $P < 0.001$ and

TABLE 4. Consistently occupied Peregrine Falcon cliffs were characterized as prominent cliffs that were farther from the nearest cliff used by Peregrine Falcons in any year between 1972 and 1999, but closer to the nearest neighbor (i.e., Peregrine Falcon cliffs used in the same year) than inconsistently occupied cliffs in central West Greenland. Our logistic regression model predicts the probability of a cliff being consistently occupied by peregrines using habitat features measured at 40 consistently occupied (1) and 18 inconsistently occupied (0) nesting cliffs. Negative coefficients (β) indicate a negative association between that variable and consistent occupancy. Habitat variables included in our model were selected using the best subset variable selection technique.

Variable ^a	$\beta \pm SE$	Wald χ^2_1	P^b	$\exp(\beta)^c$	95% Wald CL
Intercept	-0.39 ± 1.39	0.1	0.78	—	—
Elevation gain within a 3-km radius	1.01 ± 0.01	4.7	0.03	1.01	1.00–1.02
Nearest nesting cliff	0.62 ± 0.37	2.9	0.09	1.87	0.90–3.85
Nearest neighbor	-0.77 ± 0.40	3.7	0.06	0.46	0.21–1.02

^a See Wightman and Fuller (2005) for definition of terms.

^b P -values based on Wald χ^2 statistic.

^c Odds ratios indicate the change in odds of occupancy for each unit change of the variable. For example, the odds ratio for nearest neighbor is 0.46, which means that for every 1 km decrease in nearest neighbor distance, there is a 54% increase in the odds of a cliff being consistently occupied.

$Z_{18} = 6.5$, $P = 0.001$, respectively). We found no significant difference in cliff orientation based on consistency of occupancy ($Y_{58} < 0.01$, $P = 0.97$). Eyries were also significantly oriented to the south-southwest at consistently occupied cliffs ($Z_{37} = 13.5$, $P < 0.001$). We failed to find a significant eyrie orientation at inconsistently occupied nesting cliffs ($Z_{13} = 2.5$, $P < 0.10$), probably because of low sample size for this category. We found no differences in eyrie aspect between these categories ($Y_{55} < 0.01$, $P = 0.97$).

We identified three habitat features that were important for modeling the probability of consistent occupancy at a cliff site (Table 4; $G_3 = 13.0$, $n = 58$, $P < 0.01$). Our model effectively described consistent occupancy ($\hat{C}_7 = 8.1$, $P = 0.33$), but the predictive power of our model was relatively low (rescaled $R^2 = 0.28$). Odds ratios should be interpreted as previously described.

HABITAT FEATURES AND PRODUCTIVITY

We found no significant associations between average productivity and the six habitat features important in the logistic regression models ($F_{6,41} = 1.1$, $P = 0.41$). In a multiple regression of these habitat features and total productivity ($F_{6,41} = 3.3$, $P < 0.01$), we found distance to the nearest nesting cliff increased with increasing total productivity at each nesting cliff ($t_{1,41} = 4.1$, $P < 0.001$). However, the variables in this multiple regression accounted for only one-

third of the variation in total productivity ($R^2 = 0.33$). We found no associations between the five other habitat variables and total productivity.

DISCUSSION

REOCCUPANCY PATTERNS

We interpreted the distribution pattern of an increasing population (Gould and Fuller 1995) of Peregrine Falcons in central West Greenland by evaluating reoccupancy of habitat and reproductive performance. The lower variation in productivity at traditionally occupied nesting cliffs indicated that these cliffs offered greater fitness benefits and thus were better quality nesting cliffs than those occupied recently. Peregrine Falcons tended to occupy the poorer quality nesting cliffs in later years only when the better quality habitats were saturated. The reduced fitness benefits associated with nesting cliffs occupied in later years, when the population was larger, indicate that Peregrine Falcons were competing for breeding sites by resource defense and occupied the study area in a pattern of despotic distribution. This pattern may be common in raptors; Spanish Imperial Eagles (*Aquila adalberti*, Ferrer and Donazar 1996) and Northern Spotted Owls (*Strix occidentalis caurina*, Franklin et al. 2000) also distribute themselves despotically.

Features offering protection from weather were some of the primary habitat descriptors of high quality, traditionally occupied nesting

cliffs. Eyrie ledges at traditionally occupied cliffs were deeper with a smaller horizontal angle of exposure than eyrie ledges at recently occupied cliffs. The eyrie ledge structure at traditionally occupied cliffs likely provides better protection from weather and consequently less variation in productivity than at the less protected, recently occupied cliffs. Bradley et al. (1997) found that mean clutch size of Peregrine Falcons decreased with increases in precipitation in subarctic Canada. They also found a positive relationship between nestling mortality and annual precipitation during storms. More variable productivity at recently occupied nesting cliffs might be associated with a greater sensitivity to arctic weather at these cliffs because of poorer protection.

Taller cliffs also characterized higher quality habitats. Taller cliffs probably provide better perches for hunting or defense (Mearns and Newton 1988, Ratcliffe 1993, Jenkins 2000), energetic advantages by providing better updrafts for flights (Jenkins 1995), and better protection from predators and human disturbance (Mearns and Newton 1988). Although there is relatively little human disturbance in central West Greenland, Peregrine Falcons might select taller cliffs as lookouts for potential intrusions from conspecifics, other cliff-nesting species (e.g., Common Ravens [*Corvus corax*] and Gyrfalcons [*Falco rusticolus*]), and predators (e.g., arctic foxes [*Alopex lagopus*]).

Traditionally occupied cliffs were more likely to be farther from the nearest nesting cliff and nearest neighbor, implying that high quality cliffs generally were more isolated. Distance to the nearest nesting cliff was also the only habitat characteristic we found to be positively associated with total productivity. Peregrine Falcons likely select for greater isolation as a means of reducing interference competition during the breeding season.

CONSISTENCY OF OCCUPANCY PATTERNS

Birds tend to show greater site fidelity in good habitats than in poor habitats, and they tend to abandon nesting sites more frequently after a failed breeding attempt (Newton 1998). Consistent use of sites where breeding rates are high would have obvious fitness benefits and therefore adaptive importance (Martin

1998). We found higher and less variable reproductive rates at consistently occupied nesting cliffs, suggesting that consistently occupied nesting cliffs do provide fitness benefits for the occupants.

One measured difference between consistently and inconsistently occupied nesting cliffs was a greater change in elevation from the lowest point within a 3 km radius around the cliff and the cliff top (elevation gain) associated with consistently occupied nesting cliffs. The higher position of the cliff over the surrounding landscape likely creates stronger updrafts, which may provide Peregrine Falcons with an advantage in hunting and site defense.

However, the difference in spacing among cliffs may better explain the lower average and higher variation in productivity at inconsistently occupied nesting cliffs than cliff elevation gain. Inconsistently occupied cliffs tended to have closer nearest nesting cliffs, but farther neighbors. These results may seem contradictory; however, at 12 of the 18 inconsistently occupied cliffs the nearest nesting cliff was an alternative nesting cliff. Alternative nesting cliffs lie within the same range or territory as the occupied cliff and the resident pair switches occupancy between the original and alternative nesting cliff in different years (Ratcliffe 1993). We know from banded adults that these nesting cliffs are true alternatives and not occupied by a new pair of birds (W. S. Seegar and W. G. Mattox, unpubl. data). Therefore, although Peregrine Falcons occupied some nesting cliffs inconsistently, they occupied the territory or range consistently. Alternative cliffs can be up to 3 km apart and Peregrine Falcons that use areas with alternative cliffs would need to dominate a large area to preclude potential close neighbors. We have observed resident males defending one cliff while breeding at another. This behavior would lead to farther nearest neighbor distances, and it could contribute to lower productivity at inconsistently occupied sites because the pair would expend more energy for resource defense and less for other aspects of reproduction.

HABITAT SELECTION AND QUALITY

Previously, we compared occupied nesting cliffs and unused cliffs, and found Peregrine Falcons were more likely to occupy tall nesting cliffs with open views, and a suitable ledge that provided

some protection from weather and predators (Wightman and Fuller 2005). In this study, we found that among occupied nesting cliffs the taller, more elevated cliffs and ledges with better protection from weather provided increased fitness benefits to the occupants. From this similarity between features important in habitat suitability and quality, we conclude that unused nesting cliffs are unsuitable because of low fitness benefits associated with the habitat features at these sites. Peregrine Falcons will select other nesting cliffs or forego breeding rather than occupy sites without an adequate combination of habitat characteristics. Because of the importance of spacing to habitat quality, the location of other nesting Peregrine Falcons apparently influences a Peregrine Falcon's final decision on whether to occupy a cliff site, even if the cliff is otherwise suitable. These nesting cliff choices suggest that habitat selection by Peregrine Falcons in central West Greenland is adaptive and influenced by the process of natural selection.

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LITERATURE CITED

- ALLISON, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Inc., Cary, NC.
- BERTHELSEN, C., I. H. MORTENSEN, AND E. MORTENSEN [EDS.]. 1993. Kalaallit Nunaat Greenland Atlas. 2nd ed. Atuakkiortfik, Copenhagen.
- BÖCHER, T. W., K. HOLMEN, AND K. JAKOBSEN. 1968. The flora of Greenland. P. Haase and Son, Copenhagen.
- BRADLEY, M., R. JOHNSTONE, G. COURT, AND T. DUNCAN. 1997. Influence of weather on breeding success of Peregrine Falcons in the Arctic. *Auk* 114:786–791.
- BURNHAM, W. A., AND W. G. MATTOX. 1984. Biology of the Peregrine and Gyrfalcon in Greenland. Meddelelser om Grønland, BioScience 14:1–28.
- CADE, T. J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. University of California Publications in Zoology 63:151–290.
- CLARK, R. G., AND D. SHUTLER. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80:272–287.
- FALK, K., S. MØLLER, AND W. A. BURNHAM. 1986. The Peregrine Falcon *Falco peregrinus* in south Greenland: nesting requirements, phenology and prey selection. *Dansk Ornitologisk Forenings Tidsskrifter* 80:113–120.
- FERRER, M., AND J. A. DONAZAR. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology* 77:69–74.
- FISHER, N. I. 1993. Statistical analysis of circular data. Cambridge University Press, Cambridge, UK.
- FRANKLIN, A. B., D. R. ANDERSON, F. J. GUTIÉRREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70:529–590.
- FRETWELL, S. D., AND H. L. LUCAS. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- GARSHELIS, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance, p. 111–163. *In* L. Boitani and T. K. Fuller [EDS.], Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.
- GEISSLER, P. H., L. MCALLISTER, AND M. R. FULLER. 1990. A trend analysis for raptor nest surveys: an example with peregrine falcon data, p. 139–143. *In* J. R. Sauer and S. Droege [EDS.], Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish and Wildlife Service Biological Report 90(1).
- GENDE, S. M., M. F. WILSON, AND M. JACOBSEN. 1997. Reproductive success of Bald Eagles (*Haliaeetus leucocephalus*) and its association with habitat or landscape features and weather in southeast Alaska. *Canadian Journal of Zoology* 75:1595–1604.
- GOULD, W. R., AND M. R. FULLER. 1995. Survival and population size estimation in raptor studies: a comparison of two methods. *Journal of Raptor Research* 29:256–264.
- GREBENCE, B. L., AND C. M. WHITE. 1989. Physiographic characteristics of Peregrine Falcon nesting habitat along the Colorado River system in Utah. *Great Basin Naturalist* 49:408–418.
- HATCHER, L., AND E. J. STEPANSKI. 1994. A step-by-step approach to using the SAS system for univariate and multivariate statistics. SAS Institute, Inc., Cary, NC.
- HICKEY, J. J. 1942. Eastern population of the Duck Hawk. *Auk* 59:176–204.
- HOSMER, D. W., AND S. LEMESHOW. 2000. Applied logistic regression. 2nd ed. John Wiley and Sons, Inc., New York.

- HUNT, W. G. 1988. The natural regulation of Peregrine Falcon populations, p. 667–676. *In* T. J. Cade, J. E. Enderson, C. G. Thelander, and C. M. White [EDS.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Inc., Boise, ID.
- JENKINS, A. R. 1995. Morphometrics and flight performance of southern African Peregrine and Lanner Falcons. *Journal of Avian Biology* 26: 49–58.
- JENKINS, A. R. 2000. Hunting mode and success of African Peregrines *Falco peregrinus minor*: does nesting habitat quality affect foraging efficiency? *Ibis* 142:235–246.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- KREBS, J. R., AND N. B. DAVIES. 1993. *An introduction to behavioral ecology*. 3rd ed. Blackwell Science Ltd, Oxford, UK.
- LITVAITIS, J. A., K. TITUS, AND E. M. ANDERSON. 1994. Measuring vertebrate use of terrestrial habitats and foods, p. 254–274. *In* T. A. Bookhout [ED.], *Research and management techniques for wildlife and habitats*. The Wildlife Society, Bethesda, MD.
- MANLY, B. F. J., L. L. McDONALD, AND D. L. THOMAS. 1993. *Resource selection by animals: statistical design and analysis for field studies*. Chapman and Hall, London.
- MARTIN, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79:656–670.
- MATTOX, W. G., AND W. S. SEEGAR. 1988. *The Greenland Peregrine Falcon Survey, 1972–1985*, with emphasis on recent population status, p. 27–36. *In* T. J. Cade, J. E. Enderson, C. G. Thelander, and C. M. White [EDS.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund, Inc., Boise, ID.
- MEARNS, R., AND I. NEWTON. 1988. Factors affecting breeding success of Peregrines in south Scotland. *Journal of Animal Ecology* 57:903–913.
- MOSHER, J. A., K. TITUS, AND M. R. FULLER. 1986. Developing a practical model to predict nesting habitat of woodland hawks, p. 31–35. *In* J. Verner, M. L. Morrison, and C. J. Ralph [EDS.], *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, WI.
- NEWTON, I. 1979. *Population ecology of raptors*. T. and A. D. Poyser, London.
- NEWTON, I. 1998. *Population limitation in birds*. Academic Press, London.
- RATCLIFFE, D. A. 1993. *The Peregrine Falcon*. 2nd ed. Buteo Books, Vermillion, SD.
- SAS INSTITUTE. 1990. *SAS/STAT user's guide*. Version 6.0. 4th ed. SAS Institute, Inc., Cary, NC.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- WIGHTMAN, C. S., AND M. R. FULLER. 2005. Spacing and physical habitat selection patterns of Peregrine Falcons in central West Greenland. *Wilson Bulletin* 117:226–236.
- ZAR, J. H. 1996. *Biostatistical analysis*. 3rd ed. Prentice-Hall Inc., Englewood Cliffs, NJ.

APPENDIX. Average and total productivity of Peregrine Falcons breeding at cliffs in central West Greenland, 1972–1999. Each cliff was categorized as recently or traditionally occupied (reoccupancy pattern) and consistently or inconsistently occupied (consistency pattern). Sample sizes (n) for productivity measures were the number of breeding seasons a cliff was occupied by Peregrine Falcons out of the years a cliff was visited by Greenland Peregrine Falcon Survey members. All cliffs were not visited in all years between 1972 and 1999.

Cliff	Reoccupancy pattern	Consistency pattern	Mean productivity ^a	Total productivity ^b	n
1	Traditional	Consistent	2.7	43	16
2	Traditional	Consistent	3.3	30	9
3	Recent	Consistent	4.0	12	3
4	Recent	Inconsistent	0.0	0	7
5	Recent	Consistent	2.8	22	8
6	Recent	Inconsistent	0.0	0	1
7	Traditional	Consistent	2.4	31	13
8	Traditional	Consistent	2.5	65	26
9	Traditional	Consistent	1.7	22	13
10	Recent	.	3.0	6	2
11	.	Inconsistent	3.0	3	1
12	Traditional	Inconsistent	2.2	20	9
13	Recent	Inconsistent	2.6	21	8
14	Recent	Inconsistent	1.6	8	5
15	Recent	Consistent	0.0	0	1
16	Recent	Consistent	2.9	26	9
17	Recent	Consistent	2.6	13	5
18	Traditional	Consistent	2.8	44	16

APPENDIX. Continued.

Cliff	Reoccupancy pattern	Consistency pattern	Mean productivity ^a	Total productivity ^b	<i>n</i>
19	Traditional	Consistent	2.3	21	9
20	Recent	Inconsistent	2.6	29	11
21	Recent	Consistent	1.0	3	3
22	Recent	Inconsistent	2.6	18	7
23	Recent	Consistent	3.1	37	12
24	Recent	Inconsistent	2.0	4	2
25	Recent	Consistent	2.9	20	7
26	Traditional	Consistent	2.7	64	24
27	Traditional	Consistent	2.3	56	24
28	Traditional	Consistent	2.9	29	10
29	Traditional	Consistent	2.2	29	13
30	Traditional	Consistent	2.4	33	14
31	Recent	Inconsistent	1.0	1	1
32	Recent	Consistent	2.5	15	6
33	Recent	Consistent	3.3	33	10
34	Recent	Inconsistent	1.0	1	1
35	Traditional	Consistent	1.5	19	13
36	Recent	Inconsistent	1.5	3	2
37	Traditional	Inconsistent	2.7	43	16
38	Recent	.	2.0	6	3
39	Recent	Inconsistent	4.0	4	1
40	Traditional	Consistent	3.3	23	7
41	Recent	.	n/a	n/a	n/a
42	Recent	.	2.0	4	2
43	Traditional	Consistent	2.4	26	11
44	Recent	.	3.0	3	1
45	Recent	Consistent	1.6	8	5
46	Traditional	Consistent	2.2	20	9
47	Recent	.	4.0	4	1
48	Traditional	Consistent	3.0	39	13
49	Traditional	Inconsistent	2.0	12	6
50	Traditional	Consistent	2.8	55	20
51	Traditional	Consistent	2.6	29	11
52	Recent	Consistent	3.2	29	9
53	Recent	Consistent	3.3	10	3
54	Recent	.	3.7	11	3
55	Recent	.	2.3	9	4
56	Traditional	Inconsistent	2.5	32	13
57	Recent	.	1.0	2	2
58	Recent	Consistent	2.0	12	6
59	Traditional	Consistent	1.8	16	9
60	Traditional	Consistent	2.8	17	6
61	Recent	Consistent	2.3	7	3
62	Traditional	Consistent	1.6	23	14
63	Traditional	Consistent	2.4	33	14
64	Recent	Inconsistent	2.3	14	6
65	Traditional	Consistent	3.3	30	9
66	Traditional	Consistent	2.3	27	12
67	Recent	Inconsistent	2.2	13	6

^a Mean number of young produced per pair per year occupied.

^b Total number of young produced at each nesting cliff.