THE ECOLOGY OF GYRFALCONS *FALCO RUSTICOLUS* ON THE YUKON-KUSKOKWIM DELTA, ALASKA

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Abstract.—The Yukon-Kuskokwim Delta in western Alaska is dominated by tundra, wetland, and riparian communities in a subarctic landscape characterized by minimal topographic relief. Extensive uplands north of the Yukon River and east of the Kuskokwim River, however, support breeding Gyrfalcons (*Falco rusticolus*). There are also several isolated mountain ranges surrounded by deltaic lowlands that provide habitat oases for cliff-nesting raptors including Gyrfalcons. A few eyries were documented on the Delta prior to the late 20th century, but we now know of 79 nesting territories within this 130,000 km^2 region. Breeding Gyrfalcons occur across the Delta wherever suitable cliff-nesting habitat occurs in, or adjacent to, tundra habitats for foraging. In addition, tree-nesting Gyrfalcons occur regularly at low frequency in at least three geographically separate regions.

Since 1987, we have worked in three primary study areas: the Askinuk Mountains, the Ingakslugwat Hills, and the Kilbuck Mountains. Mean nearest neighbor distances between occupied territories were 5.34 km (N = 10 occupied territories), 3.70 km (N = 11), and 5.49 km (N = 13) in those areas, respectively. Densities (in pairs per 1000 km^2) in years of highest territory occupancy were 24, 16, and 7, in the same three areas, respectively. A fourth area, the Andreafsky Wilderness, was searched less frequently and less comprehensively, but may support even higher local densities than our primary study areas. At the regional level (N = 35 territories monitored), minimum estimates of annual territory occupancy between 2000 and 2004 ranged from 71% to 80%. Among individual study areas, annual variation in territory occupancy was lower among Gyrfalcons than among co-occurring Rough-legged Hawks (*Buteo lagopus*) or Golden Eagles (*Aquila chrysaetos*). Variation in density among study areas was also lower in Gyrfalcons than in the other two species of cliff-nesting raptors.

Gyrfalcon concentrations on the Delta exhibited a wide range of ecologies, varying in breeding landscape, potential and realized diets, the relative abundance of other cliff-nesting raptors, nesting substrate, and reproductive metrics. This variation in ecology within a single subarctic region suggests that a) the Delta may be a natural laboratory for more intensively studying the factors that regulate Gyrfalcon populations, and b) the Delta's Gyrfalcons may be more resilient to the effects of environmental change than is commonly supposed. *Received 18 March 2011, accepted 28 June 2011.*

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The combined deltas of the Yukon and Kuskokwim rivers cover an area of nearly 130,000 km^2 adjacent to the Bering Sea in western Alaska (Thorsteinson et al. 1989). This vast region is dominated by riparian, wetland, and tundra communities in a subarctic landscape characterized by minimal topographic relief. At this regional scale, there is relatively little suitable habitat for nesting Gyrfalcons (*Falco rusticolus;* Swem et al. 1994, Booms et al. 2010a). Potential Gyrfalcon nesting habitat does occur, however, along the periphery of the Yukon-Kuskokwim Delta (henceforth, the Delta) in the southern Nulato Hills (north and east of the Yukon River) and in the Kilbuck Mountains (east of the Kuskokwim River; Figure 1). In addition, there are several isolated ranges, including the Askinuk Mountains, the Ingakslugwat Hills, Nelson Island, and Nunivak Island, that also provide habitat oases for cliff-nesting raptors.

Prior to the late 1970s, very few Gyrfalcon nest sites had been documented on the Delta. Nelson (1887, p. 146) reported that Gyrfalcons were rare breeders on cliffs "along the seacoast in the vicinity of St. Michael" at the northern limit of the Delta, but he did not specify the exact locations. The first confirmed nest in the region was discovered in 1900 at Crater Mountain, 10 km south and inland of St. Michael (McGregor 1902). In 1947 and 1948, H. Kyllingstad and his colleagues spent time in the Askinuk Mountains (Kyllingstad 1948), where they discovered three Gyrfalcon eyries (Gabrielson and Lincoln 1959, Kessel et al. 1964). Cade (1960, Figure 2, p. 159) depicts these four sites (i.e., at Crater Mountain and in the Askinuks), as well as a fifth on Nunivak Island reported by F. Glaser. In the 1960s, Gyrfalcons were reported nesting in the Askinuks in 1963, but not from 1966 through 1969 (Kessel et al. 1964, Holmes and Black 1973).

In 1977, the first formal searches for cliff-nesting raptors on the Delta were conducted (White and Boyce 1978). Gyrfalcons were found along the upper East Fork of the Andreafsky River in the southern Nulato Hills, as well as along the Fog, Kisaralik, and Eek rivers in the Kilbuck Mountains (Figures 2, 3).. Between 1978 and 1984, the Kisaralik and Tuluksak rivers were searched intermittently by helicopter and river-rafting (Weir 1982,

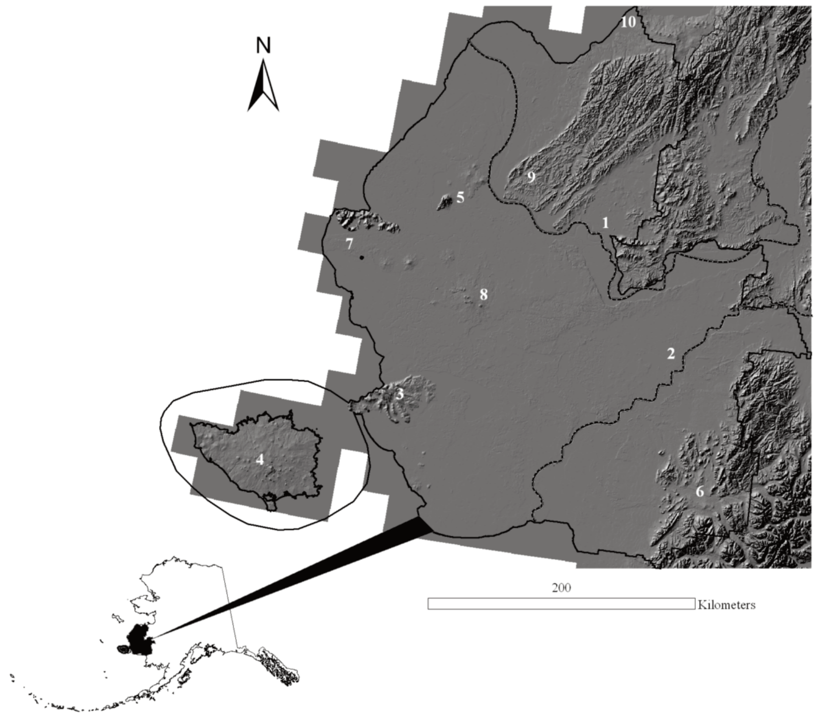

Figure 1. Yukon-Kuskokwim Delta, Alaska. 1) Yukon River (dashed line), 2) Kuskokwim River (dashed line), 3) Nelson Island, 4) Nunivak Island, 5) Kuzilvak Mountain, 6) Kilbuck Mountains, 7) Askinuk Mountains, 8) Ingakslugwat Hills, 9) Nulato Hills, 10) Crater Mountain. Solid black line represents border of Yukon Delta National Wildlife Refuge.

Mindell and Spencer 1982, 1983, Boyce and Fristensky 1984, Petersen et al. 1991). White and Boyce (1978), Mindell (1982), and Boyce and Fristensky (1984) all commented that the Kisaralik River seemed to support unusually high concentrations of both Gyrfalcons and Golden Eagles (*Aquila chrysaetos*).

In 1987, Yukon Delta National Wildlife Refuge (YDNWR) conducted a reconnaissance along the Kisaralik River (McCaffery and Ernst 1989), the first in a series of cliff-nesting raptor investigations conducted under its auspices. In this paper, we summarize the results of the censuses and studies conducted by YDNWR and its cooperators over the last quarter-century. Specifically, we present data on the minimum number, distribution, and densities of Gyrfalcon territories on the Delta; we summarize occupancy and productivity data from three primary study areas (the Askinuk Mountains, the Ingakslugwat Hills, and the Kilbuck Mountains); and we provide preliminary information about the ecological relationships between the falcons, their prey, and several species of co-occurring cliff-nesting raptors.

Methods

Study Areas.—We studied cliff-nesting raptors in four areas—the Andreafsky Wilderness, the Askinuk Mountains, the Ingakslugwat Hills, and the Kilbuck Mountains (Figure 1). Straddling the border of the boreal forest and tundra, the Nulato Hills include the Andreafsky Wilderness and the watersheds of the north and east forks of the Andreafsky River. General descriptions of the area can be found in White and Boyce (1978) and US Fish and Wildlife Service (1988); nesting habitat for Gyrfalcons consists primarily of riparian cliffs. We visited both forks of the Andreafsky River, the Pikmiktalik and Pastolik rivers, and Allen Creek (Figure 2). Along the upper East Fork and its tributaries, we later defined an oval-shaped area of 440 km^2 that included all of the Gyrfalcon nesting areas found to date along that river; only about 50% of this area was actually

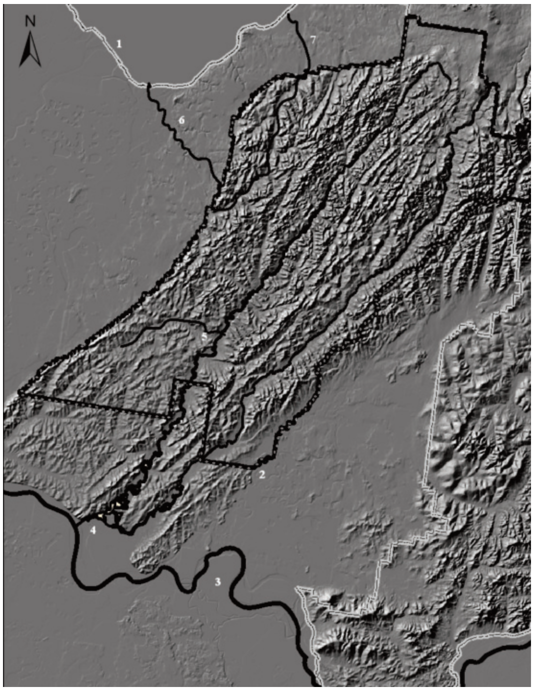

Figure 2. Nulato Hills study area, including the Andreafsky watershed. 1) Yukon Delta National Wildlife Refuge border (white-bordered line), 2) Andreafsky Wilderness border (dotted line), 3) Yukon River, 4) Andreafsky River (confluence of north and east forks), 5) Allen Creek, 6) Pastolik River, 7) Pikmiktalik River.

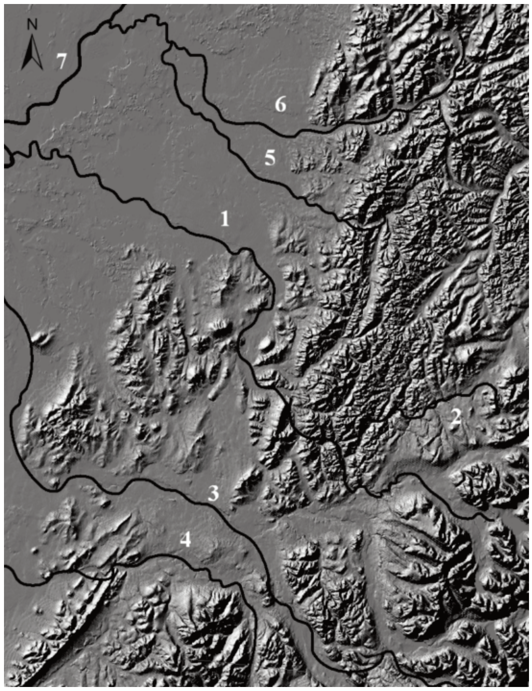

Figure 3. Kilbuck Mountains study area, including the Kuskokwim River and its tributaries. 1) Kisaralik River, 2) Quicksilver Creek, 3) Kwethluk River, 4) Eek River, 5) Fog River, 6) Tuluksak River, 7) Kuskokwim River.

searched, however, so density estimates must be considered a minimum.

The Askinuk Mountains rise along the coast of the Bering Sea and extend 50 km inland (Figure 1); they are the westernmost uplands along the Alaska coast south of the Seward Peninsula. Their geology and avian habitats are summarized in Hoare and Condon (1968) and Holmes and Black (1973), respectively. The 414 km^2 study area was defined by the abrupt lowland border of the mountains along their southeastern and northeastern flanks, by Scammon Bay and Kokechik Bay to the northwest and southwest respectively, and along the southern Askinuks by straight-line chords across the mouth of the Lithkealik River (connecting to the southwest tip of Kikuktok Mountain, an isolated spur of the Askinuks), across the Kolomak River basin from the eastern tip of Kikuktok Mountain 6 km to the southernmost extension of the Askinuks, and from the latter point across the Kuttak River basin another 5 km to the next southern extension of the main mountains. Isolated tors and outcroppings on both inland and sea-facing slopes are used by cliff-nesting raptors (Figures 4, 5).

The Ingakslugwat Hills are a complex of small volcanoes and lava flows located in the central Delta (Hoare and Condon 1971, Booms et al. 2010b; Figure 1); the vegetation is described in Tande and Jennings (1986; Figure 6). The

Figure 4. Gyrfalcon nesting habitat in the central Askinuk Mountains. Outcroppings used for nesting by Gyrfalcons overlook complex wetlands that support dense and diverse assemblages of breeding waterbirds.

Figure 5. Gyrfalcon nesting habitat overlooking the Bering Sea in the western Askinuk Mountains. Adjacent waters support sea ducks, kittiwakes, puffins, and other potential Gyrfalcon prey.

Figure 6. The northern Ingakslugwat Hills. This volcanic landscape is dominated by tundra and tall shrub communities; wetlands are much less abundant than elsewhere on the Yukon-Kuskokwim Delta. Willow Ptarmigan are the primary prey taken by both Gyrfalcons and Golden Eagles in the Ingakslugwat Hills.

Figure 7. Volcanic habitat used by Gyrfalcons in the Ingakslugwat Hills. Cliff-nesting raptors, including Gyrfalcons, nest on crater walls, crater rims, and on isolated outcroppings inside of, and on the flanks of, these extinct volcanoes.

707 km^2 study area was defined by the spatial extent of the basaltic flows that provide the majority of cliff-nesting habitat in the region (Hoare and Condon 1971), which includes the inner walls of craters, crater rims, isolated volcanic outcroppings on both the inner and outer slopes of volcanic cones, and the steep jumbled slopes at the edge of lava flows (Figure 7). Due to the accessibility and proximity of the Ingakslugwat Hills to YNDWR headquarters in Bethel, this study area was not only searched by aircraft, but was also the site of a multi-year focused study of Gyrfalcon breeding biology by ground crews (Booms 2010).

The Kilbuck Mountains rise east of the lower Kuskokwim River at the nexus of three of Alaska's six biogeographic regions (Kessel

Figure 8. The Kisaralik Corridor in the Kilbuck Mountains. The tundra and shrub habitats in these mountain valleys support populations of ptarmigan, squirrels, and hares exploited by breeding Gyrfalcons.

Figure 9. Gyrfalcon nesting habitat in the Kilbuck Mountains. Breeding Gyrfalcons nest on riparian cliffs (as shown here), as well as on rocky outcroppings up to 8 km from the nearest major streams with riparian cliffs.

and Gibson 1978); for the purpose of this study, the Kilbucks also include the headwaters and upper valleys of the Kisaralik, Eek, and Kwethluk rivers east and south of the Kilbucks (Figure 3). In this landscape dominated by tundra, shrublands, and boreal forest (Figure 8), cliff-nesting raptor habitat includes riparian cliffs and upland outcroppings in the surrounding mountains (White and Boyce 1978, Petersen et al. 1991, Booms et al. 2010b; Figure 9). Our field work was concentrated within a 339 km^2 corridor (the Kisaralik corridor) along the Kisaralik River from Clear Creek upriver to the last riparian bluff (2 km downstream of the mouth of North Fork) and along its tributary, Quicksilver Creek, from its confluence with the Kisaralik upstream to the last suitable riparian bluff (4.5 km upstream of the mouth of Anvil Creek). This area is the same 3.22-km wide corridor that was searched by helicopter from 1977 to 1979 (White and Boyce 1978, Weir 1982), although the corridor length is 105 km, rather than the 79 km reported by Weir (1982). In several years, we expanded our census area to a 1,833-km^2 region of the central Kilbuck Mountains which included the Kisaralik corridor, as well as additional habitat east of the summit of Greenstone Ridge and south of the Kisaralik River as far as Fork Creek canyon.

Data collected in these four study areas were supplemented by opportunistic observations of Gyrfalcons on Nunivak Island, Nelson Island, and Kuzilvak Mountain (Figure 1). Among the areas we worked, the Askinuk Mountains, Ingakslugwat Hills, and Kilbuck Mountains were our primary study areas (i.e., areas in which funding and logistics allowed us to collect both occupancy and productivity data over multiple years).

Field Protocols.—The majority of our searches for cliff-nesting raptors were helicopter-based and timed to assess either occupancy (usually early May; rarely, late May) or productivity (mid- to late July). June and early July flights yielded data on the occupancy of specific nesting areas and contents of specific nests, but these data were not used to generate occupancy or productivity metrics (e.g., proportion of occupied territories, young fledged per nest) because of the possibility of nest failures both prior to and after these summer flights. Because we attempted to locate all cliff-nesting raptors within our study areas, our efforts were censuses rather than sample surveys. We recorded all observations of cliff-nesting raptors, including Gyrfalcons, Golden Eagles, and Rough-legged Hawks (*Buteo lagopus*). For the purposes of our study, we also considered Common Ravens (*Corvus corax*) to be members of the cliff-nesting "raptor" guild. We use the term "territory" (in the sense of "nesting territory" in Nielsen 1999 and Steenhof and Newton 2007) to refer to areas 1) within which nesting was confirmed in at least one year, and 2) within which no more than one pair of Gyrfalcons ever nested in the same year. As so defined, territories could include multiple nest sites used in different years. If we observed either a pair in a territory or a bird on a nest, we considered the territory occupied. We did not consider other observations of single Gyrfalcons within a territory to be sufficient evidence for occupancy. Because such "lone" individuals were almost certainly members of territorial pairs in at least some instances, however, our metric of occupancy underestimates true occupancy and overestimates productivity when expressed as fledged young per occupied territory. For each of our three primary study areas, we report two metrics of occupancy: annual territory occupancy (i.e., the proportion of territories occupied in a year) and individual territory occupancy (i.e., the proportion of years in which individual territories were occupied). The ranges for these two metrics will differ, but the mean values should be the same; rounding errors and incomplete coverage of territorial arrays in some years, however, result in some slight differences.

We provide two indices of abundance: territory density (i.e., territories per 1000 km^2) and mean nearest neighbor distances (NND). We calculated mean NND by simply averaging the distances between each nest (or territory center) and its nearest neighbor. Therefore, a sample of 10 nests yields 10 data points. For example, if nests A and B were closer to one another than to any other nests in the study area, the distance between them was entered into the series twice, once for each nest. We report territory density and NND for the years of maximum occupancy (i.e., the year with the highest proportion of known territories occupied), as well as for all known territories in each study area. NND distances for all known territories were generated by measuring distances between territory centroids. For territories with one, two, and three known nest sites, territory centroids were the one known nest site, the midpoint connecting a straight-line chord between two nests sites, or the approximate center of the triangle formed by three nest sites, respectively.

During occupancy censuses conducted by helicopter, nests were generally approached only as closely as necessary to determine if an adult Gyrfalcon was present. Incubating adults were not intentionally flushed to reveal nest contents; as a result, clutch size data were collected only opportunistically. The sole exception to this protocol occurred in 2003, when laying seemed conspicuously later than in previous years; on 5 May, we attempted to revisit nests first visited on 1–2 May to determine if more eggs had been produced. During July productivity assessments, nests were visited either on foot or via helicopter. Flying young, fully-feathered young outside the nest, and nestlings that appeared to have reached 80% of the minimum fledging age were all considered to have fledged (Steenhof and Newton 2007). Because the number of pairs occupying territories and the number of pairs actually laying eggs can vary (Steenhof and Newton 2007), we report two metrics of nest success, the proportion of territorial pairs and the proportion of laying pairs that raised > 1 young to 80% of fledging. For each of our three main study areas, we report five metrics of productivity: total young fledged, young fledged per occupied territory, young fledged per laying pair, young fledged per successful pair, and young fledged per 1000 km^2.

Study History.—In 1991, 1992, and 1997, we conducted occupancy censuses along the Upper East Fork of the Andreafsky from the upstream limit of spruce north to the last suitable cliff habitat along the flanks of Iprugalet Mountain. During the 1992 effort, we also searched a few tributaries of the upper East Fork, the North Fork of the Andreafsky, the Pikmiktalik and Pastolik rivers, and Allen Creek.

From 2001 to 2002 and 2003 to 2004, we conducted occupancy censuses in the Askinuk Mountains; all potential cliff-nesting sites were searched on all flights. In 2003 and 2004, we returned in the third week of July to determine productivity at all Gyrfalcon nests that were active during the occupancy censuses. In 2006, 2007, and 2008, we did not conduct occupancy censuses, but visited all potential nest sites in the last week of June to determine nest contents. As of this date, nestlings had not reached 80% of their fledging age, and so were not old enough to be considered "fledged" (Steenhof and Newton 2007). In 2006, however, we did revisit all the nests from 22 to 24 July that were initially found active on 24 June. At the five nests where nest contents were determined on both visits, all of the young present on the first visit had survived the intervening four weeks, suggesting that the late June data in 2007 and 2008 might also at least approximate fledging success.

Refuge personnel first visited the Ingakslugwat Hills from 10 to 16 June 1988 for a preliminary ground-based inventory of cliff-nesting raptors and their habitats. Occupancy censuses were conducted by helicopter in 1992, 1997, and each year from 2000 to 2004; productivity assessments were conducted by helicopter from 2001 to 2004. Ground crews conducted occupancy censuses from 2005 to 2007. Examinations of nest contents were conducted in the last week of June or first week of July each year between 2004 and 2010.

In the Kilbuck Mountains in 1987 and 1988, YDNWR personnel inventoried cliff-nesting raptors and empty stick nests during June floats down the Kisaralik River from just upstream of Upper Falls to the mouth of Quartz Creek. From 1991 to 2004, we conducted annual occupancy censuses by helicopter in the entire Kisaralik corridor. Three additional contiguous Gyrfalcon territories occurred between the corridor and our fuel cache; we refer to the area including the Kisaralik corridor plus these 3 additional territories as the extended Kisaralik corridor. Occupancy and productivity flights were conducted in the extended Kisaralik corridor each year from 2000 to 2004 and from 2002 to 2004, respectively. In 2001, 2003, and 2004, we also conducted occupancy censuses throughout the expanded Kilbuck Mountains study area. Finally, on 2 May 2001, we conducted an occupancy census along the main fork of the Eek River from 14 km below the Great Ridge upstream to the Eek's headwaters on the north face of Mount Oratia, and along the Kwethluk River from where it exits the high mountains near Boundary Lake upstream to the head of its glacial headwater valley.

Prey Resources.—The relative abundance of potential Gyrfalcon prey in our three main study areas was estimated qualitatively, based on observations during our flights as well as during ground field work of at least eight weeks over at least two years in each study area. We have quantitative estimates of potential prey abundance and Gyrfalcon diet from both the Ingakslugwat Hills and the Askinuk Mountains. In the Ingakslugwat Hills, the density of Willow Ptarmigan (*Lagopus lagopus*) was estimated in spring 2005. During the period of peak territorial male ptarmigan activity, we surveyed ptarmigan along seven randomly-selected 3.5-km line transects which had starting points within 5 km of Gyrfalcon nests. Perpendicular distances between observed ptarmigan and the transect line were recorded; data were analyzed with Program Distance (Thomas et al. 2010) to generate an estimate of density. Prey remains and pellets were collected from nest sites and plucking stations within falcon and eagle territories in 2003 and 2004. All prey remains and, if available, up to 20 pellets per nest were analyzed.

Analyses were completed by Wildlife Dynamics Consulting.

In 1997, we determined Willow Ptarmigan and Rock Ptarmigan (*L. muta*) densities in the western Askinuks in two ways (McCaffery et al. 1998). First, we randomly selected seven plots (totaling 95 ha) in tundra habitats, visited each plot five times from late May to mid-June 1997, recorded all ptarmigan observations on each plot, and estimated densities by taking the average number detected on the five visits and expanding that value to the number per km^2. We also conducted standardized breeding bird censuses (Hall 1964, Robbins 1970) in riparian shrub-tundra habitat on two plots of 15.4 and 17.5 ha, respectively. Ptarmigan densities derived from these two breeding bird plots are expressed as territorial males per km^2. We collected prey remains at and around Gyrfalcon eyries in the Askinuks during the middle of the brood-rearing stage in 2006 (5 sites) and 2007 (9 sites).

Statistics.—Because our data are derived from censuses, rather than survey sampling, we do not invoke statistical inference for comparing results among years or study areas; instead, we simply present the census results summarized as means ± SD. The major exception to that approach is our statistical comparison of clutch sizes among years and study areas. Although our opportunistic collection of data did not represent true sampling (e.g., no random selection of nests for determining clutch size), we have treated the data as if they were samples. We acknowledge that, if the number of eggs in a clutch is correlated with the likelihood that a bird will flush from its nest, our estimates of clutch size will be biased. Statistical tests are identified in Results; the *alpha* level for all tests is 0.05.

Results

Numbers, Distribution, and Densities of Breeding Gyrfalcons.—Prior to 1987, 23 Gyrfalcon territories had been located within the Yukon-Kuskokwim Delta (Cade 1960, Ritchie 1978, White and Boyce 1978, Mindell 1983, YDNWR files); we have discovered another 56 since that time. Nesting Gyrfalcons have been found across the Delta in almost all areas of potential cliff-nesting habitat, to include the Kilbuck Mountains (34 known territories), Andreafsky Wilderness (16), the Askinuk Mountains (11), the Ingakslugwat Hills (11), Nunivak Island (5), Nelson Island (1), and Kuzilvak Mountain (1). Among those regions, only the Askinuk Mountains and Ingakslugwat Hills have been thoroughly inventoried for breeding Gyrfalcons, so it is probable that the Delta supports more than the 79 territories documented to date.

At maximum occupancy, the density of occupied territories in our four study areas ranged from 7 per 1000 km^2 in the Kilbuck Mountains to 24 per 1000 km^2 in the Askinuk Mountains. Mean NND ranged from 3.70 ± 1.87 km in the Ingakslugwat Hills to 5.49 ± 1.44 km in the Kilbuck Mountains (Table 1). The density of total Gyrfalcon territories ranged from 10 per 1000 km^2 in the expanded Kilbuck Mountains study area to 29 per 1000 km^2 in the Kisaralik corridor. Mean nearest neighbor distances among all territories in a territorial array ranged from 3.21 ± 1.28 km along the East Fork of the Andreafsky to 6.20 ± 5.46 km in the Kisaralik corridor (Table 1).

Territory Occupancy.—We derived annual estimates of territory occupancy in the Askinuk Mountains (4 years), the Ingakslugwat Hills (10 years), and the Kisaralik corridor (14 years). In the Askinuk Mountains, we identified 11 territories which were checked every year (2000, 2001, 2003, and 2004); annual territory occupancy ranged from 73% to 91%, and averaged 79.8 ± 8.62%. Individual territory occupancy (i.e., the proportion of years in

Table 1. Density (territories per 1000 km^2) and mean nearest neighbor distance (km) of Gyrfalcon territories (at maximum occupancy and for the total territorial arrays) in four study areas on the Yukon-Kuskokwim Delta, Alaska. Number of territories in parentheses follow density estimates.

Study Area	Maximum Occupancy Density	NND[a]	Total Territories Density	NND[a]
E. Fork Andreafsky (440 km^2)	13.6 (6)	4.00	20.5 (9)	3.21
Askinuks (414 km^2)	24.2 (10)	5.34	26.6 (11)	6.12
Ingakslugwat Hills (707 km^2)	15.6 (11)	3.70	15.6 (11)	3.91
Kilbucks (1833 km^2)	7.1 (13)	5.49	9.8 (18)	6.15
Kisaralik corridor[b] (339 km^2)	20.6 (7)	5.31	29.5 (10)	6.20

[a] NND = Nearest Neighbor Distance

[b] The Kisaralik corridor is within the Kilbucks study area.

which individual territories were occupied) across the four years ranged from 25% (one territory) to 100% (six territories), and averaged 79.5 ± 26.97%.

In the Ingakslugwat Hills, we identified 11 territories, but the number checked annually for occupancy (1992, 1997, 2000–2007) varied from 7 to 11. Expressed as a proportion of the territories checked, annual territory occupancy ranged from 43% (7 checked) to 100% (11 checked); the mean of 10 annual estimates was 84.7 ± 16.62%. Over the five consecutive years in which all 11 territories were checked annually (2000 to 2004), annual territory occupancy ranged from 73% to 100%, and averaged 87.4 ± 10.26%. During the 10 years when occupancy was determined, the 11 individual territories were checked between 5 years (one territory) and 10 years (four territories). Expressed as a proportion of years checked, individual territory occupancy ranged from 43% (one territory) to 100% (four territories); the mean of annual estimates was 85.4 ± 21.84%.

In the Kisaralik corridor, we identified 10 territories that were checked annually (1991–2004). Annual territory occupancy ranged from 20% to 70%, and averaged 52.9 ± 15.41%. Individual territory occupancy over the 14-year study period ranged from 21% (one territory) to 93% (one territory), and averaged 52.9 ± 22.66%.

Because both the timing of censuses and the number of study years varied among our study areas, comparisons of overall occupancy rates among these areas may be misleading. To control for this, we also present occupancy rates for 2000, 2001, 2003 and 2004 (Table 2), years during which we conducted standardized censuses in all three areas. Because all 13 territories in the extended Kisaralik corridor were also checked in those four years, we have included that area in this analysis. This comparison indicates that a) high and low values for occupancy were not synchronous across the three study areas, and b) occupancy rates in the Kisaralik study area were 14% to 19% lower than in the Askinuks and Ingakslugwat Hills, respectively. If only the 10 territories in the Kisaralik corridor are considered, the difference is even larger (17% to 22%). A consideration of 2002, when the Askinuks were not censused, further highlights the degree of variation among sites within the same year. In 2002, all 11 territories were occupied in the

Table 2. Gyrfalcon territory occupancy rates in three study areas on the Yukon-Kuskokwim Delta, Alaska. Values are percentages of total territories occupied. For each study area, numbers of total territories are in parentheses.

Study Area	2000	2001	2003	2004	Mean
Askinuks (11)	91	73	82	73	79.8
Ingakslugwat Hills (11)	73	91	82	91	84.3
Extended Kisaralik corridor (13)	69	54	77	62	65.5

Ingakslugwat Hills, but only 4 of 13 were occupied in the extended Kisaralik corridor (and only 2 of 10 in the Kisaralik corridor itself).

At the regional level, when we consider the entire suite of territories within our three primary study areas (32) for the four years of comprehensive censusing (2000, 2001, 2003, and 2004), the total occupied varied between 23 and 25 (mean=24.25 ± 0.96), ranging from 72% to 78%. Including the extended Kisaralik corridor (i.e., N=35), the total number occupied annually varied between 25 and 28 (mean = 26.5 ± 1.29), ranging from 71% to 80%.

In addition to providing information about spatial variation in occupancy among study areas, our data also allow us to consider temporal variation. In the Askinuks, we can compare our four years of data with accounts from ornithologists who worked there between 1924 and 1989 in order to assess changes in occupancy rates and, perhaps, population size. These earlier ornithological visitors to the Askinuk Mountains camped at and conducted most of their field work on, and in the vicinity of, Kikuktok Mountain, an isolated spur detached to the south of the west-central Askinuks. Their accounts indicate that they searched for and noted the presence of cliff-nesting raptors during their field efforts (Brandt 1948, Kessel et al. 1964, White and Springer 1965, Holmes and Black 1973, Gerhardt 1989). Their observations suggest that Gyrfalcon nesting on or near Kikuktok Mountain was sporadic at best over the years of their visits (Table 3). In contrast, during our study, Kikuktok Mountain was at the heart of the core falcon nesting area in the Askinuks. Seven territories occur on or within 7 km of Kikuktok Mountain, three of which are on the mountain itself. During the four years of our occupancy study, those seven territories were occupied in 23 of 28 site-years (82%). Considering just the three territories on Kikuktok Mountain reveals a similar pattern. In addition to the 4 years with occupancy censuses (2000, 2001, 2003, and 2004), we also made June visits to those three territories from 2006 to 2008. Because pairs that failed early in the season would not be detected during our June visits, including June data in our analysis may underestimate the true occupancy rates. Even with this conservative assessment of annual occupancy, the three Kikuktok territories were occupied in ≥ 15 of 21 site-years (71%), with an average of 2.14 Kikuktok territories active each year (range = 1–3). Late June and/or July visits to those sites in five of the years found an average of 1.2 nests with young (range = 0–3). In summary, Kikuktok Mountain was occupied by one to three pairs of Gyrfalcons every year during our study, and one to three nests containing young in late June were present in four of five years (Table 3). These findings suggest that in recent years, Gyrfalcon numbers and/or the frequency of breeding in the Askinuk Mountains may be higher than in previous decades, but we lack sufficient data beyond the immediate vicinity of Kikuktok Mountain to provide for confident inference.

In the Ingakslugwat Hills, six territories were searched at some point during the breeding season in each of the 14 study years between 1988

Table 3. Historical (1924–1989) and recent (2000–2008) Gyrfalcon observations at Kikuktok Mountain, Askinuk Mountains, Alaska. "—" denotes none observed.

Year	Gyrfalcons Observed	Occupied Territories	Active Nests[a]	Successful Nests[b]
1924[c]	one observation	no data	—	no
1948[d]	yes	≥ 2	2	no data
1963[d]	yes	≥ 1	1	no data
1966[e]	one observation	—	—	—
1967[e]	—	—	—	—
1968[e]	—	—	—	—
1969[e]	—	—	—	—
1989[f]	—	no data	—	—
2000[g]	yes	2	2	no data
2001[g]	yes	2	2	no data
2003[g]	yes	2	2	1
2004[g]	yes	3	1	0
2006[g]	yes	3	3	3
2007[g]	yes	1	1	1
2008[g]	yes	2	1	1

[a] Nests with either eggs seen or an adult in incubation posture.
[b] For this analysis, defined as nests with young in late July in 2003, 2004, and 2006, or the last week of June in 2007 and 2008.
[c] Brant 1943.
[d] Kessel et al. 1964.
[e] Holmes and Black 1973.
[f] Gerhardt 1989.
[g] This study.

and 2010. These territories were occupied in 76 of the 84 site-years (90%). Five of the eight apparent vacancies occurred either early or late in the time series, in years with only June searches (1988, 2008, and 2010), by which time some pairs may have already failed. Considering only the 10 years with occupancy (i.e., May) censuses (1992 to 2007), these six territories were occupied in 57 of 60 site-years (95%) with the only three vacancies all occurring in 1997. Among all territories monitored over that 16-year period, there was no trend in the proportion of territories occupied or the proportion of territories with laying pairs (we used proportions because not all territories were checked annually). Overall, therefore, there is no evidence for changes in the rate of territory occupancy in the Ingakslugwat Hills over the last two decades.

Along the Kisaralik River, four territories were checked regularly between 1977 and 2004 (three in all 21 years with field work, one for 18 years). Individual territory occupancy rates for the four territories were 11%, 24%, 39%, and 86%, respectively, with the most recent year of nesting being 1979, 2001, 1995, and 2004 for the same four territories, respectively. A comparison of the first six and the most recent six years of the time series data reveals a striking difference. During the four years with field data from 1977–1982 (i.e., 16 site-years), these four territories supported 11 laying pairs (69% of site-years) and three lone birds. During the six years from 1999–2004, however, there were only six laying pairs among 24 site-years (25%), and five of them were on the same territory. The picture that

Table 4. Gyrfalcon clutch sizes on the Yukon-Kuskokwim Delta.

Clutch size:	1	2	3	4	5	n	Mean
Primary Study Areas, 2000–2004	2	7	15	39	1	64	3.47 ± 0.84 SD
All other sites and years, 1992–2008	0	4	15	17	0	36	3.36 ± 0.68 SD
Totals	2	11	30	56	1	100	3.43 ± 0.78 SD

emerges from these data is one of gradual attrition of active nesting territories.

Such a conclusion seems unwarranted, however, if we consider the overall pattern of occupancy for the 10 territories known along the Kisaralik corridor. Only one of the four long-term territories was not occupied during our 14-year series of consecutive annual censuses (1991–2004); the other three were all occupied in at least two years. Over that interval, there was no trend in either the total number of occupied territories (linear regression, ANOVA F=0.007, P=0.94) or the number of laying pairs (F=0.21, P=0.66) within the Kisaralik corridor. In summary, over the late 20th and early 21st Century, there is no compelling evidence for change in any of our three primary study areas.

Productivity.–Our data allow us to generate summary statistics for four elements of Gyrfalcon productivity—laying frequency (i.e., the proportion of total territories in which laying occurred), clutch size, nest success, and number of young fledged. During the four years with comprehensive occupancy censuses in the Askinuk Mountains, laying frequency was 70.5%. If the years with only June field work (2006 to 2008) are included in the analysis with the four comprehensive years, laying frequency was still ≥ 67.5%. During the 10 years with occupancy censuses in the Ingakslugwat Hills, the number of territories checked annually varied (see preceding section). The mean of annual laying frequencies, expressed as a proportion of territories checked, was 67.4 ± 16.13%. During the five years when all 11 territories were checked in May (2000 to 2004), the laying frequency was 70.9%. Along the Kisaralik corridor, the laying frequency among 10 territories during the 14 consecutive annual occupancy censuses was 47.1%. Over the same 5-year interval when comprehensive censuses were conducted in the Askinuks and the Ingakslugwat Hills, laying frequency along the Kisaralik corridor was 48%. Considering the extended Kisaralik corridor, the laying frequency during that 5-year interval is still virtually identical at 47.7%. Finally, during the three years in which all 18 Kilbuck study area territories were monitored (2000, 2003, and 2004), laying frequency overall was 63%, with frequencies of 56.7% and 70.8% within and outside of the Kisaralik corridor, respectively. These data suggest that Gyrfalcon productivity within the Kisaralik corridor was consistently lower than in our other two primary study areas, and may have even been low relative to average production elsewhere in the Kilbuck Mountains.

The mean size of 100 clutches from the Delta was 3.43 ± 0.78. Clutch sizes ranged from one to five, with both the median and mode (N=56) being four (Table 4). During the comprehensive censuses in the Askinuk Mountains, Ingakslugwat Hills, and Kilbuck Mountains from 2000 to 2004, 64 clutch sizes were determined. Because clutch size data were not normally distributed, we used the non-parametric Mann-Whitney U-test to see if the mean clutch size derived from these data (3.47 ± 0.84, n=64) differed from the mean size of clutches recorded in other years and at other sites (3.36 ± 0.68, n=36); no difference was found (Mann-Whitney U= 1,295, P=0.25). We also compared clutch sizes among years (2000 to 2004) and among our three main study areas in years of comparable field work. Mean clutch sizes

Table 5. Comparison of Gyrfalcon reproductive metrics among primary study areas on the Yukon-Kuskokwim Delta, Alaska, 2003 and 2004.

	Total Fledged	Fledged/ Occupied Territory	Fledged/ Laying Pair	Fledged/ Successful Pair	Fledged/ 1000 km²/ year
Askinuks	24	1.41	1.50	2.67	29
Ingakslugwat Hills	28	1.47	1.75	2.00	20
Extended Kisaralik corridor	8	0.44	0.50	1.60	[a]
Kisaralik corridor	3	0.25	0.27	1.50	4

[a] We did not define borders around the additional three territories in the extended Kisaralik corridor because their placement would be arbitrary; therefore we have not calculated densities for that area.

were 3.46 ± 0.78 (n=13), 3.55 ± 0.93 (n=11), 2.60 ± 1.14 (n=5), 3.44 ± 0.92 (n=18), and 3.71 ± 0.47 (n=17), respectively, from 2000 to 2004. Mean clutch sizes in the Askinuk Mountains, Ingakslugwat Hills, and Kilbuck Mountains were 3.71 ± 0.69 (n =17), 3.72 ± 0.58 (n =18), and 3.29 ± 0.91 (n=24), respectively. Although the point estimates for clutch size were conspicuously lower in 2002 and in the Kilbuck Mountains relative to other years and sites, respectively, we found no statistical differences among years (Kruskal-Wallis test statistic=5.66, P=0.23) or study areas (Kruskal-Wallis test statistic=3.67, P=0.16).

We determined nest success in the Askinuk Mountains (2003, 2004), in the Ingakslugwat Hills (2001 to 2004), and in the extended Kisaralik corridor (2002 to 2004). Nest success values (per territorial pair) in the three study areas were 53%, 58%, and 23%, respectively. Among laying pairs, nest success was 56%, 74%, and 29% in the three study areas, respectively. The year 2002 was particularly unproductive in both the Ingakslugwat Hills and the extended Kisaralik corridor, with only two of 15 occupied territories (13%) producing young in the two study areas combined; both successful nests were in the Ingakslugwat Hills.

During the two years (2003, 2004) with comparable productivity data across all three primary study areas, fledging success varied dramatically (Table 5). Fledging success was moderate in both years in the Askinuks and Ingakslugwat Hills, but very poor in the Kisaralik region. The poor production in 2003–2004 in the Kisaralik area followed 2002 when no young were fledged either in the corridor or the extended Kisaralik corridor; in fact, only three total young fledged in the main Kisaralik corridor from 2002 to 2004.

Tree-nesting.–Tree-nesting by Gyrfalcons is relatively rare in North America (Booms et al. 2008a), but has been documented previously in western Alaska (Kessel 1989). We found Gyrfalcons using old Common Raven nests in Balsam Poplars (*Populus balsamifera*) in three of our four study areas; there are no trees in the Askinuk Mountains. In the Andreafsky Wilderness, we found tree-nesting Gyrfalcons in two of 16 territories, one on the upper East Fork and one on the Pikmiktalik River. In the Kilbuck Mountains, tree nests occurred in two of 34 territories, one each on the Kisaralik and Eek rivers. In the Ingakslugwat Hills, tree-nesting was more prevalent, occurring at six sites in five of the 11 territories. In the 14 years of field work in the Ingakslugwat Hills, 15 of 84 known nesting attempts (18%) were in poplars. During the five years in which all 11 territories were checked annually, eight of 39 (21%) nests were in trees. During those same years, six of eight tree nests (75%) and 17 of 31 nests on rocky volcanic substrates (55%) were successful. Among successful nests, mean fledged brood sizes were 1.83 ± 0.75 and 2.00 ± 0.94 in trees and rocks, respectively. Overall, 1.38 ± 1.06 and 1.10 ± 1.22 young fledged per nesting attempt in trees and rocks, respectively. From 2005–2010, we made late June visits to five tree nests and 30 rock nests known to have been active in those years. Overall, we found 2.20 ± 1.64 young per tree-nesting attempt, and 2.33 ± 1.27 young per rock-nesting attempt. Among nests still active at the time of our late June visits, there were 2.75 ± 1.26 and 2.69 ± 0.93 young present per tree and rock nest, respectively.

Prey Resources.–In the Ingakslugwat Hills in 2005, the density of Willow Ptarmigan was 16.1 ± 10.9 birds per km^2. In the Askinuk Mountains, the estimated densities of Willow and Rock Ptarmigan in tundra habitats were 4.00 ± 0.88 per km^2 and 4.21 ± 2.47 per km^2, respectively. On the two riparian shrub-tundra breeding bird plots, the densities of territorial male Willow Ptarmigan were 6.5 per km^2 and 28.6 per km^2, respectively; Rock Ptarmigan were not detected on those plots.

The relative abundance of potential Gyrfalcon prey varied among our three primary study areas. In the extensive and diverse mountainous landscape of the Kilbucks, all three species of North American ptarmigan occurred (although White-tailed Ptarmigan [*L. leucura*] were very rare). The Kilbucks also supported several species of medium-sized mammals, including Snowshoe Hare (*Lepus americanus*), Alaskan Hare (*L. othus*), Arctic Ground Squirrel (*Spermophilus parryii*), and Hoary Marmot (*Marmota caligata*); both the Snowshoe Hare and Arctic Ground Squirrel could be quite common. Waterfowl and shorebirds were present, but primarily limited to the riparian corridors of major streams. In the Askinuk Mountains, the only medium-sized mammal was the rare Alaskan Hare, but both Willow and Rock Ptarmigan were quite common. In addition, because the Askinuks are adjacent to the Bering Sea and surrounded by extraordinarily rich wetlands, waterfowl, shorebirds, seabirds (including gulls, terns, jaegers, and puffins), and tundra songbirds were all fairly common to abundant. Not surprisingly given their position between the mountains and the coast, the Ingakslugwat Hills had the least diverse assemblage of potential Gyrfalcon prey. Willow Ptarmigan were common, but were the only ptarmigan species present, and the only medium-sized mammal detected was the Alaskan Hare, which was rarely observed. Because of the mild topographic relief and increased drainage resulting from the volcanic history of the area, wetlands were relatively scarce in the Ingakslugwat Hills, when compared to the surrounding deltaic plain. As a result, waterbird density and diversity were much lower than in the Askinuks, and roughly comparable to the Kilbuck Mountains. Overall, therefore, the Kilbuck Mountains had the highest diversity of both ptarmigan and potential mammalian prey, while the Askinuk Mountains had the highest diversity and abundance of potential avian prey (other than ptarmigan).

Table 6 summarizes data on Gyrfalcon diets on the Yukon-Kuskokwim Delta, including published sources as well as those collected during our study. In addition to ptarmigan, Gyrfalcon prey on the Delta includes more than 30 species of birds and five species of mammals. Although variation in the types of data (remains vs. pellets) and sample sizes preclude quantitative comparisons, the dietary data are consistent with our assessments of relative prey abundance. Ptarmigan dominated the diet in the Ingakslugwat Hills, where Willow Ptarmigan are common, while other avian prey and mammalian prey are relatively scarce. Although still dominated by ptarmigan (57%), remains from Gyrfalcon nests in the Kilbuck Mountains and Nulato Hills (Mindell 1983, Petersen et al. 1991) had the highest frequency of mammals (36%). Ptarmigan made up a comparable percentage (58%) of the prey items among the 15 nest sites sampled in the Askinuks (14 in this study, 1 by White and Springer 1965), but the balance of the diet in that coastal range was primarily made up of migratory waterbirds (32%). The unusual prevalence of boreal songbirds in the remains at the Anvik River eyrie (6 of 13 items) reflects

Table 6. Gyrfalcon diet from locations on and adjacent to the Yukon-Kuskokwim Delta, Alaska.

	Anvik River[a]	Tuluksak River[b]	Kilbucks and Nulato Hills[c]	Askinuk Mountains[d,e]	Ingakslugwat Hills[e]	Ingakslugwat Hills[e]
Type	**Remains**	**Remains**	**Remains[f]**	**Remains**	**Remains**	**Pellets**
Nests	**1**	[g]	**8**	**15**	**16**	**16**
Species						
American Wigeon *Anas americana*					1	
Northern Pintail *Anas acuta*					1	
Green-winged Teal *Anas crecca*		1		1		
Surf Scoter *Melanitta perspicillata*	1					
Red-breasted Merganser *Mergus serrator*				1		
unidentified anatid	2	1		29	5	6
Spruce Grouse *Falcipennis canadensis*		1	3			
ptarmigan spp. *Lagopus* spp.	1	20	24	107	420	166
Gyrfalcon *Falco rusticolus*					4	
golden-plover sp. *Pluvialis,* sp.					1	7
Surfbird *Aphriza virgata*		1				
Western Sandpiper *Calidris mauri*				2		
Pectoral Sandpiper *Calidris melanotos*				1		
Dunlin *Calidris alpina*				1		
Wilson's Snipe *Gallinago delicata*				1		
Red-necked Phalarope *Phalaropus lobatus*				1		
unidentified shorebird				14		7
Sabine's Gull *Xema sabini*				2		
Mew Gull *Larus canus*				1		
Arctic Tern *Sterna paradisaea*				1		
Parasitic Jaeger *Stercorarius parasiticus*	1					
Long-tailed Jaeger *Stercorarius longicaudus*				1		
Unidentified larid				3		

Table 6. continued

	Anvik River[a]	Tuluksak River[b]	Kilbucks and Nulato Hills[c]	Askinuk Mountains[d,e]	Ingakslugwat Hills[e]	Ingakslugwat Hills[e]
Type	**Remains**	**Remains**	**Remains[f]**	**Remains**	**Remains**	**Pellets**
Nests	**1**	**[g]**	**8**	**15**	**16**	**16**
Species						
Belted Kingfisher *Megaceryle alcyon*		1				
Gray Jay *Perisoreus canadensis*	1					
Swainson's Thrush *Catharus ustulatus*	1					
American Robin *Turdus migratorius*	1	2				
Varied Thrush *Ixoreus naevius*	2					
Lapland Longspur *Calcarius lapponicus*						1
unidentified warbler					1	
Savannah Sparrow *Passerculus sandwichensis*				1		
Pine Grosbeak *Pinicola enucleator*	1					
unidentified redpoll *Acanthis,* sp.				1		
unidentified passerine				15	6	4
unidentified bird					1	20
unidentified mustelid					1	
Snowshoe Hare *Lepus americanus*			3			3
unidentified hare					1	
Arctic Ground Squirrel *Spermophilus parryii*	2	13	10			
Nelson's Collared Lemming *Dicrostonyx nelsoni*						1
Tundra Vole *Microtus oeconomus*						1
unidentified vole			2			
small mammal					2	17
unidentified mammal						1
Total individuals	13	40	42	183	444	234
Total species	$\geq$ 9	$\geq$ 7	$\geq$ 5	$\geq$ 14	$\geq$ 9	$\geq$ 7
% ptarmigan	8	50	57	58	95	71

[a] White and Boyce 1978 (Anvik River is east of the Andreafsky watershed).
[b] Petersen et al. 1991 (Tuluksak River is in the northern Kilbuck Mountains just north of our study area).
[c] Mindell 1983.
[d] White and Springer 1965.
[e] This study.
[f] May have included pellets as well.
[g] Number not specified in text.

Table 7. Mean number of observed occupied territories (± SD) of Rough-legged Hawks, Golden Eagles, Gyrfalcons, and Common Ravens in the Askinuk Mountains, Ingakslugwat Hills, and Kisaralik corridor, Yukon-Kuskokwim Delta, Alaska, 2000 to 2004.

	Rough-legged Hawk	Golden Eagle	Gyrfalcon	Common Raven
Askinuks[a]	16.8 (± 13.05)	2.3 (± 0.50)	8.8 (± 0.96)	9.8 (± 1.89)
Ingakslugwat Hills	8.6 (± 4.10)	3.8 (± 0.84)	9.6 (± 1.14)	3.4 (± 2.30)
Kisaralik corridor	2.0 (± 1.41)	15.4 (± 4.34)	5.4 (± 2.07)	0.6 (± 0.55)

[a] Askinuks not censused in 2002.

Table 8. Mean densities of occupied territories (per 1000 km^2) of Rough-legged Hawks, Golden Eagles, Gyrfalcons, and Common Ravens in the Askinuk Mountains, Ingakslugwat Hills, and Kisaralik corridor, Yukon-Kuskokwim Delta, Alaska, 2000 to 2004 (see Table 9 for SD of annual estimates).

	Rough-legged Hawk	Golden Eagle	Gyrfalcon	Common Raven
Askinuks[a]	40.5	4.4	21.1	23.6
Ingakslugwat Hills	12.2	5.4	13.6	4.8
Kisaralik corridor	5.9	45.4	15.9	1.8
Mean	19.51	18.39	16.88	10.04
SD	18.41	23.42	3.87	11.80

[a] Askinuks not censused in 2002.

Table 9. Standard deviations of annual density estimates of occupied territories (per 1000 km^2) of Rough-legged Hawks, Golden Eagles, Gyrfalcons, and Common Ravens in the Askinuk Mountains, Ingakslugwat Hills, and Kisaralik corridor, Yukon-Kuskokwim Delta, Alaska, 2000 to 2004.

	Rough-legged Hawk	Golden Eagle	Gyrfalcon	Common Raven
Askinuks[a]	31.52	0.92	2.31	4.57
Ingakslugwat Hills	5.80	1.18	1.61	3.26
Kisaralik corridor	4.17	12.79	6.12	1.62
Mean	13.83	4.96	3.35	3.15

[a] Askinuks not censused in 2002.

the predominance of taiga in this watershed just east of the Delta (White and Boyce 1978), quite different from the tundra-dominated landscape of the upper Andreafsky watershed 40 km to the west. Finally, we have also found the remains of Black-legged Kittiwakes (*Rissa tridactyla*) and common murres (*Urea aalgae*) around an eyrie on the west coast of Nunivak Island.

Co-occurring Cliff-nesting Species.–Rough-legged Hawks, Golden Eagles, and Common Ravens occur in all four of our study areas, and Gyrfalcons use the nests of all three species in each of those areas. The relative abundance of the species varies tremendously among the three primary study areas (Table 7). Rough-legged Hawks are, on average, the most abundant breeding raptor in the Askinuks, while Golden Eagles predominate along the Kisaralik River. Such differences are also conspicuous when the mean numbers of occupied territories are converted to densities (Table 8). The highest mean densities of Rough-legged Hawks, Golden Eagles, and Common Ravens are 6.9, 10.3, and 13.1 times higher than in the study areas with the lowest mean densities of these three species. Gyrfalcons, however, stand out as occurring at relatively comparable density in all three study areas, with the highest density in the Askinuk Mountains being only 55% higher than in the Ingakslugwat Hills with the lowest density. Not only did Gyrfalcons exhibit the least spatial variation in density, they also showed the least variation among years of the three true raptors (Table 9).

With the exception of TLB's work in the Ingakslugwat Hills (e.g., Booms et al. 2008b), most of our work consisted of 1–2 days of aerial censusing in spring and summer. In effect, our observations were simply "snapshots" of Gyrfalcon occurrence in our study areas. As a result, beyond documenting that Gyrfalcons regularly use the nests of all three species, we have few observations of direct interactions between Gyrfalcons and the other cliff-nesting species. We did observe three cases, however, in which sites initially occupied by Gyrfalcons were occupied by other species later in the same season. On 10 May 2001, a pair of Gyrfalcons was seen near a nest with a single Gyrfalcon egg on the inside rim of one of the major cones in the Ingakslugwat Hills. Minutes later, we observed a dark morph Rough-legged Hawk at a small spatter cone 1.3 km away. When we returned to the study area on 12 May, a light morph Rough-legged Hawk was alarm-calling and courtship flying directly above the Gyrfalcon nest. A falcon was seen briefly over the crater, but not subsequently. The hawk flew east and returned 10 minutes later with a dark morph hawk; the latter bird flew directly to the Gyrfalcon nest site and landed, at which time we saw that the Gyrfalcon egg was gone. When we checked the lower spatter cone later that day, we found a Gyrfalcon pair at that site.

In the Askinuk Mountains, an adult Gyrfalcon was observed in incubation posture on a cliff-side stick nest on 13 May 2003, but on 17 July there were four large (but still partially downy) Rough-legged Hawk nestlings in that nest. In the same study area on the same dates, a pair of Gyrfalcons flushed from a cliff with a two-egg clutch in May, but the cliff was occupied by an adult and a sub-adult Golden Eagle in July. In none of these cases do we know if the Gyrfalcons abandoned the site independently, or if interactions with the other species led to the Gyrfalcons' departure.

Competition for food and/or nest sites with Golden Eagles may be a regular feature of Gyrfalcon ecology on the Delta. In the Ingakslugwat Hills, breeding Gyrfalcons consistently outnumber Golden Eagles (Tables 7, 8). At this site, where squirrels are absent and hares are rare, Gyrfalcons overwhelmingly exploit ptarmigan for food (Table 6), and more than half of Golden Eagle prey items in our sample of remains and pellets were of ptarmigan as well. This is consistent with our anecdotal observations in that study area in other years, in which ptarmigan were the most frequently detected prey items seen in eagle nests (BJM and TLB, unpublished). Thus, it seems that dietary overlap between the two species is unusually high in this region; depending on the magnitude and extremes of fluctuations in the ptarmigan population, competition between the two raptor species may occur. In the Kilbuck Mountains, however, dietary overlap between the two species may be less. Along the Tuluksak River, which flows through the Kilbuck Mountains north of our study area, half of Gyrfalcon prey remains were ptarmigan (Table 6), but ptarmigan made up only 6% of the diet of Golden Eagles, while squirrels and hares made up 86% of the eagle diet (Mindell 1983, Petersen et al. 1991).

Despite the apparent reduction of dietary overlap between the two species in the Kilbucks relative to the Ingakslugwat Hills, the ecology of these two species may be linked in other ways. Between 1991 and 2004, the number of laying pairs of the two species in the Kisaralik corridor were significantly correlated (adjusted r^2=0.23, P=0.047). Between 1999 and 2004, when we determined the number of occupied territories for both species, the relationship was even stronger (adjusted r^2=0.39, P=0.049). Occupancy and productivity metrics for the two species were most similar in the worst years. Between 1991 and 2004 in the Kisaralik corridor, we detected the fewest occupied Gyrfalcon territories and laying pairs in 2002, and found no fledged young that year. For Golden Eagles in the Kisaralik corridor in 2002, we also detected the fewest occupied territories, laying pairs, successful pairs, and fledged young of the entire 14-year study. The year 2003 was nearly as bad. Although seven Gyrfalcon territories were occupied, and six pairs produced eggs in 2003, no young fledged in the Kisaralik corridor. Similarly, for Golden Eagles, 2003 matched 2002 for the fewest young produced overall (only 3 fledged in each of those years from 9 and 17 occupied territories, respectively); it was the lowest year for young fledged per occupied territory, laying pair, and successful pair.

Not only were there positive correlations between annual reproductive success in the two species, but there was also circumstantial evidence suggesting that they may compete for nesting areas. A consideration of the four long-term Gyrfalcon territories in the Kisaralik corridor revealed that the reduced frequency of occupancy by Gyrfalcons was paralleled by an increased frequency of occupancy by Golden Eagles. From 1977 to 1982, Gyrfalcons were present at nesting cliffs in those territories in 14 of 16 site-years (11 laying pairs, 3 lone birds), and Golden Eagles were never observed. In contrast, between 1999 and 2004, Gyrfalcons nested much less frequently. Five of the six nesting records for Gyrfalcon during that 6-year interval occurred on just one of the four territories. On the other three territories, there was only a single Gyrfalcon observation (a laying pair) among 18 site-years. Over the same period, however, Golden Eagles were present on those three territories during 16 of 18 site-years (including 10 nests, 4 pairs, and 2 lone birds), and fresh greenery had been added to one of the nest sites in another year, also most likely by a Golden Eagle. Given that there is no evidence for an overall change in the breeding population size of either species in the Kisaralik corridor area over the study period, Gyrfalcons are still present in comparable numbers but are apparently choosing not to nest in those territories any longer. Although we suspect that those decisions are a result of interactions with, and displacement by, Golden Eagles, we cannot rule out the possibility that eagles are simply taking advantage of Gyrfalcons vacating those territories for other reasons.

Discussion

On the Yukon-Kuskokwim Delta, we found Gyrfalcons breeding wherever suitable cliff habitat occurred within a landscape dominated by open tundra and associated shrublands. The only major expanse of potential nesting habitat on the Delta not known to support breeding Gyrfalcons is the extensive series of cliffs and bluffs along the north bank of the Yukon River from the inland border of the Delta downstream as far as Mountain Village (Mindell 1983, Payer and Ritchie 2001). Peregrine Falcons (*F. peregrinus*), however, nest commonly along this stretch of the lower Yukon (Payer and Ritchie 2001). The absence of Gyrfalcons from this area is likely due to the presence of extensive boreal forest, rather than tundra, along most of this portion of the Yukon River.

The concentration of Gyrfalcons in the Andreafsky Wilderness, particularly along the upper East Fork of the Andreafsky River, is noteworthy. According to the Alaska Gyrfalcon distribution model (Booms et al. 2010a), the Andreafsky region was in the lowest category of predicted Gyrfalcon occurrence (< 20%), and within the range of predicted occurrence (0 to 40%) that was assumed to support no breeding Gyrfalcons. Breeding Gyrfalcons have also been found in seven of 16 watersheds draining the Nulato Hills to the north and east of the Andreafsky Wilderness (White and Boyce 1978, Mindell 1983). Those drainages were also included in the lowest category of predicted occurrence by Booms et al. (2010a), even though one of those rivers (the Ungalik) was thought to support densities of Gyrfalcons (and Golden Eagles) comparable to high density areas elsewhere in Alaska (White and Boyce 1978). These data, as well as ours, suggest that the Alaska nest distribution model can be improved; as noted by Booms et al. (2010a), the model is just a first step in our efforts to understand Gyrfalcon breeding habitat and predict their distribution.

The local densities of Gyrfalcons on the Delta are among the highest reported in the published literature, whether considering territories per km^2 or nearest neighbor distances (Swem et al. 1994, Booms et al. 2008a). Again, the East Fork of the Andreafsky is noteworthy because our density estimate there is for an area that has been only partially searched to date; a comprehensive census would almost certainly result in a higher density.

At our three primary study sites, true densities may also be higher than we report because our territory occupancy estimates are minimum values (except in 2002 in the Ingakslugwat Hills, when all known territories were confirmed as occupied). Territories where we only detected lone birds were not recorded as occupied, although at least some of those "single" birds were almost certainly paired. In addition, our annual occupancy estimates were usually derived from single-day censuses in the early spring. Territorial pairs and even incubating females can be missed during one-time searches if the pairs are away from the cliff (Mossop and Hayes 1994), flush from the cliff prior to detection, or remain motionless and cryptic, particularly if nesting in novel microhabitats (TLB and BJM, unpubl. obs.). Indeed, Booms et al. (2010b) estimated the detection probability from aircraft for Gyrfalcons in the Kilbucks and Ingakslugwat Hills to be 0.79. If we correct our occupancy estimates by dividing by the empirically-derived detection probability estimate, the adjusted mean occupancy rate estimates actually exceed 100% in both the Askinuks and the Ingakslugwat hills, and climb from 53% to 67% in the Kilbucks. Applying the detection probability to all years individually suggests that true occupancy exceeded 90% in all years from 2000 to 2004 in both the Askinuks and the Ingakslugwat Hills, and may have exceeded 75% in half of the years between 1991 and 2004 along the Kisaralik corridor.

These estimates of occupancy suggest not only that Gyrfalcon densities and occupancy rates are high on the Delta; they are also relatively stable in space and time. The difference in density among study areas was lower among Gyrfalcons than either Rough-legged Hawks or Golden Eagles, and annual variation in territory occupancy was lower in Gyrfalcons than in either of the other two cliff-nesting raptors. These patterns are consistent with Nielsen's (1999) conclusion that raptors that respond to cyclic mammals (e.g., microtine rodents and hares for Rough-legged Hawks and Golden

Eagles, respectively; McIntyre and Adams 1999, Bechard and Swem 2002, Kochert et al. 2002) should fluctuate more dramatically than Gyrfalcons because the magnitude of fluctuations in the falcons' preferred prey (i.e., ptarmigan) is generally much less than among populations of cyclic mammals (Krebs et al. 1992, Nielsen 1999; but see McIntyre and Adams 1999 for fluctuations of comparable magnitude in sympatric hare and ptarmigan populations). Variation in annual Gyrfalcon territory occupancy on the Delta at the regional level is even less than at the scale of individual study areas, because occupancy rates did not vary synchronously among study areas.

Comparing Gyrfalcon population stability among different studies can be problematic. Studies that conduct searches during the nestling phase can underestimate territory occupancy and laying frequency, because such efforts miss non-breeding and failed pairs (e.g., Swem et al. 1994). Studies vary in their use of terminology, duration of study, and numbers of nests sampled (e.g., Tømmeraas 1993, Mossop and Hayes 1994, Nielsen 1999), all of which obscure comparison. Nevertheless, overall occupancy rates among 35 Gyrfalcon territories on the Delta exceeded 70% in each of the four common study years, and occupancy probably exceeded 90% in most years and study areas, suggesting that the Delta's Gyrfalcon population is indeed relatively stable for a high-latitude raptor.

A number of factors may contribute to such stability on the Delta. First, our main study areas occur from lat 60°13'N to lat 61°50'N; this range is near the southern limit of breeding Gyrfalcons (Booms et al. 2008a). One consequence of this southern distribution is that, even in midwinter, days are relatively long. On the winter solstice at our latitude, there are 5.5 h between sunrise and sunset, and 7.5 h between the onset of civil twilight at dawn and the end of civil twilight at dusk. As a result, up until the vernal equinox, Gyrfalcons at this latitude have more (and in mid-winter, considerably more) opportunities for diurnal foraging than those that winter farther north. This may result in greater territory fidelity and/or territory occupancy, reduced winter dispersal, improved body condition as the birds approach the onset of breeding in late winter, and perhaps even higher survival. The combination of latitude and proximity to the Bering Sea also produces milder winter temperatures than those in more Arctic or continental areas; this, too, may improve the condition of wintering Gyrfalcons prior to the onset of breeding, which may have effects on breeding territory occupancy and breeding success (Nielsen 2004, Selås and Kålås 2007). A third factor that may contribute to relatively stable density and occupancy rates among Delta Gyrfalcons is the abundance and diversity of prey in this subarctic region. In addition to multiple species of ptarmigan, squirrels, rabbits, and voles, the Delta supports very large and diverse populations of waterbirds. Along with asynchrony in the population peaks of cycling mammal species (BJM, unpublished), the abundance and diversity of alternate prey may buffer Gyrfalcons from the consequences of population declines in favored prey items, particularly ptarmigan.

Unfortunately, we do not have quantitative regional or local estimates of ptarmigan abundance from which to infer patterns of temporal change in ptarmigan population size. Anecdotal observations over the last several decades provide no evidence of cyclic population change in ptarmigan, but depending on the magnitude of annual variation, such changes could escape detection by casual observers. The annual subsistence harvest of ptarmigan on the Delta between 1988 and 2008 varied by a factor of nearly seven, but in most years, the harvest levels differed little from the long-term mean (Naves 2010). The annual harvest exceeded one standard deviation from the mean in only 6 of 21 years, and in half of the years, the harvest was within 0.5 standard deviation of the mean. In addition, the timing of high and low harvest years did not exhibit a cyclic pattern. Ultimately, however, even these data cannot provide strong inferences about the population patterns of the ptarmigan because harvest levels can be determined as much by the need and storage capacity of the subsistence hunters as by the availability of their prey. Thus, we simply do not know whether or not ptarmigan populations on the Delta are cyclic, or over what range of population sizes they fluctuate.

As a result, we can only speculate about some of the ecological relationships of the Gyrfalcons on the Delta. For example, in the Ingakslugwat Hills, the coexistence of a dense and productive Gyrfalcon population with Golden Eagles seems paradoxical given the relatively low diversity of potential ptarmigan and mammalian prey. In most other areas where Golden Eagles have been studied, population density and breeding success of that species are usually tied to the abundance of medium-sized mammals such as hares and squirrels (Watson 2010), taxa which are rare and absent, respectively, from the Ingakslugwat Hills. Our estimate of Willow Ptarmigan density in the Ingakslugwat Hills (16.1 birds per km^2) is intermediate between the densities recorded in the tundra and shrub communities in the Askinuk Mountains, and also intermediate between the high and low densities reported elsewhere (Hannon et al. 1998). Because we do not know where the ptarmigan density we measured in a single year falls relative to the mean or range of annual densities in the Ingakslugwat Hills, we cannot draw inferences about the mechanism by which Gyrfalcons and eagles manage to co-exist in that area; instead, we can only hypothesize. For example, if Willow Ptarmigan, the primary prey for both species of raptors in the Ingakslugwat Hills, usually vary only over a range of relatively high densities, ptarmigan may rarely become a limiting resource for nesting raptors at this site, thus reducing foraging competition between the falcons and eagles.

Another apparent paradox concerns the status of Gyrfalcons in the Kilbuck Mountains relative to those in the Askinuks and Ingakslugwat Hills. Compared to Gyrfalcons in those two study areas, falcons in the Kilbucks have the lowest average occupancy rate and the lowest maximum occupancy rate whether we consider the entire Kilbuck time series (1991 to 2004) or the study period common to all three study areas (2000 to 2004). Kilbuck Gyrfalcons also have the lowest laying frequency, estimate of clutch size, nest success (per territorial pair and laying pair), and number of young fledged. Such consistently low reproductive metrics are surprising given the diversity and apparent abundance of both ptarmigan and potential mammalian prey in the Kilbucks, which exceeds the diversity in our other two study areas.

Through their effects on the Golden Eagle population, however, the diversity and abundance of prey in the Kilbucks may actually solve the paradox. The rich prey base and the abundance of suitable nesting habitat in the Kilbucks support an extremely high density of Golden Eagles, particularly in the Kisaralik corridor (mean annual density of 45 pairs per 1000 km^2). These densities increase the probability of interactions between eagles and falcons, and we suspect that such interactions may account for the relatively low occupancy and success of breeding Gyrfalcons in the Kilbucks. In fact, during the three years when we searched all18 Gyrfalcon territories in the expanded Kilbuck study area, the occupancy rate in the eight territories outside the Kisaralik corridor was virtually identical to the average rates in our other two study areas, but it was 25% higher than in the 10 territories within the adjacent Kisaralik corridor. This difference suggests that the factor(s) contributing to reduced occupancy and productivity in the Kisaralik corridor (e.g., interactions with Golden Eagles) may be a very local effect not exhibited elsewhere in the Kilbucks (where Golden Eagle density is lower; BJM unpublished data).

Golden Eagles could negatively affect Gyrfalcons in several ways, including appropriating nest sites, stealing prey, directly killing Gyrfalcons (adults, nestlings, or recently fledged young), and depressing local prey abundance. Unfortunately, we lack such observations, as well as data on prey abundance and seasonal availability. As a result, the dynamics and significance of falcon-eagle interactions in the Kilbucks remain hypothetical.

Similarly, the paucity of information on prey abundance precludes definitive conclusions about the reproductive failures in the Kilbuck Mountains for both species in 2002, an atypically wet period on the Delta. April and May snowfall totals in Bethel, 85 km from our Kilbuck study area, were 1.8 and 4.5 times the long-term (1923 to 2007) averages, respectively. Overall precipitation totals for April and May were 2.2 and 3.8 times the long-term average, respectively; the May total of 92 mm was the wettest May on record. RAWS (remote automated weather station) data from a site at the south end of our Kilbuck study area also revealed that late April and early May, when Gyrfalcon females are producing clutches, was wetter in 2002 than any other year of our study (Western Regional Climate Center 2011). Such wet conditions in April and May could reduce reproductive success via several mechanisms during the period from follicle development and clutch production through late incubation and the early nestling phase. For example, in Canada, the survival of Snowshoe Hares in late winter and early spring is negatively correlated with the number of days with snowfall (Meslow and Keith 1971), and in the Peregrine Falcon, certain types of hunting are less successful during inclement weather (White et al. 2002). In a spring with high snowfall and poor weather, the effects of reduced prey abundance and/or reduced hunting success early in the breeding season could reduce a male Gyrfalcon's effectiveness at provisioning his mate, thereby negatively impacting her ability to produce a clutch of eggs and/or maintain incubation constancy. Not surprisingly, egg and chick survival in the Peregrine Falcon decline during late, cold, and wet springs (White et al. 2002); the same may hold true for its larger congener. Despite the logic of this weather hypothesis, however, we cannot confidently attribute the 2002 reproductive failures in Gyrfalcons and Golden Eagles to the unusual spring weather because we have neither documented direct effects of the weather nor ruled out other competing or complementary hypotheses.

The need for both extensive and intensive quantitative data on diet and prey abundance is essential for developing a better understanding of the ecology of Gyrfalcons on the Yukon-Kuskokwim Delta. Even in lieu of such data, however, we can make an important generalization about Gyrfalcons in this region. The concentrations of breeding Gyrfalcons on the Delta exhibit an impressive range of ecologies. At the landscape level, local concentrations exploit oases of cliff-nesting habitat (e.g., the Askinuk Mountains and Ingakslugwat Hills, the sea cliffs of Nunivak and Nelson islands) as well as larger blocks of extensive mountainous terrain (e.g., the Kilbuck Mountains and southern Nulato Hills). Prey communities vary dramatically among areas, from the seabird colonies on the Bering Sea coast to the inland mountains supporting diverse populations of ptarmigan, squirrels, and hares, and from the species-rich coastal wetlands and waters surrounding the Askinuks to the far less diverse volcanic uplands of the Ingakslugwat Hills. Although the suite of co-occurring, cliff-nesting species is shared across the Delta, the relative abundance of those species varies dramatically among sites. Whereas Rough-legged Hawks, Golden Eagles, and Common Ravens all provide potential nest sites for Gyrfalcons, they can also compete with Gyrfalcons for those nest sites, and potentially for food as well. Because of the spatial variation in abundance of those species, the opportunities and challenges for Gyrfalcons co-existing with them must also vary among sites. The propensity for, and success of, tree-nesting among Gyrfalcons in the Ingakslugwat Hills is a good example. Finally, we have identified apparent differences among the regions in reproductive metrics that may be related to biotic and/or abiotic factors.

Such ecological diversity across a relatively small geographic region has two important implications. First, because of the locally high densities of, and proximity among, Gyrfalcon concentrations on the Delta, this region is a natural laboratory for testing hypotheses about the factors that regulate Gyrfalcon populations in the subarctic. In effect, the diverse ecological settings can serve as natural "treatments" for teasing out the importance of different elements of the Gyrfalcon's biology. This might be particularly important if we seek to both measure and predict the effects of climate change on Gyrfalcon population trajectories. The potential effects of climate change will vary along several gradients—from the Bering Sea coast to the inland boreal forest, from sea level to mountains, from wet tundra and meadow communities to xeric sites, from species-rich to species-poor communities, and from areas underlain by permafrost to those where permafrost is absent. Our current study areas span those gradients and provide an excellent opportunity for initiating more quantitative, hypothesis-driven investigations of Gyrfalcon ecology and population dynamics.

Second, the ecological diversity of settings in which Gyrfalcons occur on the Delta suggests that they may have more flexibility for responding to the stressors of climate change than some other northern vertebrates. This potential for local flexibility is reflected at the global level as well. For example, although most Gyrfalcon populations apparently exhibit some level of dependence upon ptarmigan, the mechanism of that dependence varies geographically. In some areas, there is no apparent relationship between breeding Gyrfalcons and ptarmigan population changes; in others, Gyrfalcon numbers track ptarmigan numbers directly; and in still other areas, Gyrfalcons show a delayed density-dependent numerical response to changing ptarmigan numbers (Nielsen 1999, Selås and Kålås 2007). Such variation is paralleled by other aspects of Gyrfalcon biology, including their broadly holarctic distribution, the geographical diversity of preferred habitats, and regional variation in nesting sites. Considered together, this ecological diversity suggests that, at least at the metapopulation level, Gyrfalcons might find ways to persist over a fairly broad range of climate-induced changes.

Ultimately, however, the fate of most Gyrfalcon populations may still hinge on their relationship with ptarmigan when male falcons are provisioning females during the critical prebreeding window in the late winter and early spring. Gyrfalcons are often characterized as having population dynamics linked to the cycles of, or at least to the dramatic fluctuations in the size of, ptarmigan populations (Nielsen 1999, Booms et al. 2008a, Mossop 2011). Reductions in the amplitude, and even the virtual disappearance, of population cycles have been reported among other first-order consumers in the arctic, with markedly negative effects on the predator populations that depend on them (e.g., Ims and Fuglei 2005, Gilg et al. 2009). Recent work suggests that the amplitude of ptarmigan population peaks may be declining similarly, perhaps as a result of climate change, and perhaps with a similarly negative effect on Gyrfalcon populations (e.g., Mossop 2011).

A reduction in the amplitude of prey cycles by itself, however, does not necessarily result in a negative effect on their predators. The specific effect of a dampened prey cycle on a predator population will depend upon several factors, including the relative contribution of predator reproduction in peak prey years to mean lifetime reproduction, the mean annual level of preferred prey abundance relative to the threshold required for initiating and/or maintaining a successful breeding effort, changes in the phenology of alternate prey, and the effects of reducing or eliminating very poor years for predator survival and/or reproduction (if prey populations no longer decline to extremely low levels). Regarding the latter factor, life stage simulation analysis suggests that, depending upon the range over which the variance of predator vital rates might decline, reduced variance in prey population numbers could increase the population growth rate for the predator (see Wisdom et al. 2000). The various ways in which changing prey population dynamics might impact predators will vary among species and, geographically, within species as well.

In the case of Gyrfalcons, it is not difficult to envision a scenario in which gradually dampening ptarmigan cycles simply lead to less interannual variability in Gyrfalcon reproductive success, with no net impact on annual mean productivity or lifetime reproductive success. Because ptarmigan numbers often have no impact on the mean brood size of Gyrfalcons (Nielsen 1999), the crucial factor may be whether or not there is a change in the frequency of years in which sufficient numbers of ptarmigan are available to trigger the initiation of Gyrfalcon breeding in late winter and early spring. If most of the historical late-winter and early-spring fluctuations in ptarmigan numbers in a particular region occurred at or above that threshold level, dampened oscillations should not negatively affect long-term Gyrfalcon population dynamics. If, however, reduced amplitude of peaks is coupled with a reduction in the annual mean population levels of ptarmigan, Gyrfalcons could be negatively impacted. Quantitatively estimating the threshold densities of ptarmigan needed for Gyrfalcons to initiate successful breeding on the Delta will require a creative mix of laboratory, field, and modeling efforts.

As stated previously, we do not know if ptarmigan populations actually cycle on the Delta. If our anecdotal observations (i.e., no obvious cycling) actually represent biological reality, it could be because cycles never occurred in this subarctic environment or because climate change at this latitude has already resulted in the elimination of conspicuous cycles. In either case, the Delta presently supports high local densities of breeding Gyrfalcons, and the relative stability of occupancy rates suggests that Gyrfalcons on the Delta may not be as sensitive to fluctuations in the abundance of ptarmigan as falcon populations elsewhere. At the same time, however, the Delta's location near the southern limit of the species' breeding range suggests that Gyrfalcons in this region may be among the first to experience new challenges as potential competitors and disease vectors extend northward. Thus, it remains to be seen if the behavioral and ecological plasticity of the Delta's Gyrfalcons is sufficient to keep up with the rate at which their environment will be changing in the coming decades.

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