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Source: Journal of Raptor Research, 45(2) : 150-159

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-09-13.1

J. Raptor Res. 45(2):150–159

RECOVERY AND TRENDS OF PEREGRINE FALCONS BREEDING IN THE YUKON-TANANA UPLANDS, EAST-CENTRAL ALASKA, 1995–2003

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ABSTRACT.—We conducted intensive helicopter-supported surveys to assess the distribution, occupancy, and reproductive rate of Peregrine Falcons (*Falco peregrinus anatum*) in the Yukon-Tanana uplands of interior Alaska 1995–2003. We surveyed specific reaches of Birch Creek and the Goodpaster and Salcha rivers in this remote area to monitor this nesting species. Each year, we visited potential cliff-nesting areas and known nesting territories during early incubation (late May) to assess occupancy and nesting activities, and during the late-nestling period (mid-July) to count young, document nesting success, and measure reproductive rate. We identified 55 different nest cliffs occupied by Peregrine Falcons during at least one year of our survey. The number of occupied nesting territories detected each year increased from a low of 12 in 1995 to a high of 38 in 2002. Reproductive rate averaged 1.6 young/occupied territory and 2.4 young/successful territory for the nine-year period. The percentage of successful territories each year ranged from 42% to 81% (mean = 65%). Little is known about Peregrine Falcon numbers and distribution in the Yukon-Tanana uplands prior to the DDT-induced decline, but they are currently the most abundant cliff-nesting raptor in the region. Monitoring these remote areas may provide a valuable tool to alert us to population declines before they occur in larger drainages.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *Alaska*; *detectability*; *nesting*; *occupancy*; *population*; *reproductive rate.*

RECUPERACIÓN Y TENDENCIAS DE *FALCO PEREGRINUS ANATUM* ANIDANDO EN LAS TIERRAS ALTAS DE YUKÓN-TANANA, ESTE DE ALASKA CENTRAL, 1995–2003

RESUMEN.—Realizamos muestreos intensivos desde un helicóptero para evaluar la distribución, ocupación y tasa reproductiva del halcón *Falco peregrinus anatum* en las tierras altas de Yukon-Tanana en el interior de Alaska, entre 1995 y 2003. Muestreamos sectores específicos de aguas abiertas de Birch Creek y de los ríos Goodpaster y Salcha en esta área remota para monitorear halcones anidando. Cada año, visitamos áreas de acantilado potencialmente usadas para anidar y territorios de anidación conocidos de *F. p. anatum* al principio de la incubación (fines de mayo), para evaluar la ocupación y las actividades de anidación, y a finales del período de pichones (mediados de julio) para contar a los juveniles, documentar el éxito de anidación y medir la tasa reproductiva. Identificamos 55 nidos diferentes ocupados por *F. p. anatum* en los acantilados, durante al menos un año de nuestro muestreo. El número de territorios de anidación ocupados detectado cada año aumentó desde un mínimo de 12 en 1995 a un máximo de 38 en 2002. La tasa reproductiva promedió 1.6 juveniles/territorio ocupado y 2.4 juveniles/territorio exitoso para el período de nueve años. El porcentaje de parejas exitosas de cada año varió entre 42% y 81% (promedio = 65%). Se sabe poco sobre los números y la distribución de estos halcones en las tierras altas de Yukon-Tanana que existía antes de la disminución inducida por el DDT, pero *F. p. anatum* es actualmente el ave rapaz más abundante que anida en los acantilados de la región. El monitoreo de estas áreas remotas puede brindar una herramienta valiosa para alertarnos sobre disminuciones poblacionales antes de que éstas ocurran en cuencas mayores.

[Traducción del equipo editorial]

The great rivers of east-central Alaska, the Yukon, Tanana, and Porcupine rivers, have long histories of traditional use by the Peregrine Falcon subspecies *Falco peregrinus anatum* (e.g., Osgood and Bishop 1900, Williams 1925, Cade 1960, Cade et al. 1976, Haugh 1976). Peregrine Falcons have been studied along these rivers since the early 1970s, some time after the dramatic DDT-induced decline of these and other Peregrine Falcon subpopulations in North America (Cade et al. 1971, Kiff 1988). Much

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of our understanding of the status and eventual recovery of this species' population in Alaska is derived from data from these main rivers (e.g., Ambrose et al. 1988, Enderson et al. 1995).

In contrast, less is known about Peregrine Falcons nesting in more remote areas of interior Alaska, where historical records are limited or where very low numbers were recorded after the population decline. For instance, the Yukon-Tanana uplands physiographic province (Wahrhaftig 1965), the mountainous region between the Yukon and Tanana rivers, includes numerous off-river (i.e., outside the floodplains) cliffs on many tributaries that appear suitable for nesting, but few records existed for this species in these areas. Some of these off-river areas had records of Peregrine Falcon nests before the pesticide-induced decline (e.g., Grinnell 1909, Osgood 1909, Blackwelder 1919, Williams 1925), but early survey coverage was not adequate to clearly establish rates of recovery or to know whether recent increases represent population recovery or range expansion. There is some evidence that numbers of the nesting populations decreased less along major rivers than they did along their smaller tributaries in Alaska (e.g., Cade and White 1976). During the early to late 1970s, when Peregrine Falcons declined in interior Alaska, numerous surveys reported only occasional nesting pairs with numerous, apparently suitable, cliff areas unoccupied in the Yukon-Tanana uplands (e.g., Cade 1976, White and Boyce 1978). By the 1990s, when the number of nesting Peregrine Falcons began to exceed what was once considered the historical level on the Yukon River (Ambrose et al. 1988), unpublished reports suggested increasing numbers in the Yukon-Tanana uplands as well.

In 1993, monitoring activities associated with proposed U.S. Air Force low-level jet-aircraft training exercises in Yukon Military Operation Areas (MOA) in interior Alaska provided an opportunity to acquire baseline data about nesting Peregrine Falcons in off-river locations. The objectives of our study included locating and monitoring off-river nests along specified drainage segments or reaches from 1995–2003. Here, we summarize information about these off-river areas and compare them with other regional subpopulations to better understand the Peregrine Falcon's current status in interior Alaska.

STUDY AREA

We conducted surveys for nesting Peregrine Falcons along portions of three tributaries of the Tanana (Salcha and Goodpaster rivers) and Yukon (Birch Creek) rivers in MOAs in east-central Alaska in 1995–2003 (Fig. 1). The three rivers are typical of watersheds within the Yukon-Tanana uplands (Wahrhaftig 1965), with pool and riffle structures generally confined to one channel within a narrow alluvium-floored valley. The relatively narrow valleys of these tributaries are mosaics of boreal forest and wetlands that are shaped by frequent wildfires and permafrost. Vegetation (Interior Highlands ecoregion) was characterized by open needle-leaf forests dominated by white (*Picea glauca*) and black (*P. mariana*) spruce mixed with hardwoods such as aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) (Gallant et al. 1995). Areas above tree line included dwarf scrub, alpine communities, and barren areas. Floodplain elevations ranged from approximately 200 m in lower Birch Creek to 640 m along the upper Salcha River and were typically surrounded by rounded, even-topped ridges and compact, rugged mountains (1200–1500 m elevation; Wahrhaftig 1965).

The cliff-nesting raptor and Common Raven (*Corvus corax*) community in the Yukon-Tanana uplands was more diverse than that along the Tanana and Yukon rivers. On those rivers, Common Ravens were the primary cliff nesters, along with Peregrine Falcons. In contrast, the higher-elevation cliffs along the three surveyed drainages in the Yukon-Tanana uplands were occupied by Gyrfalcons (*Falco rusticolus*), Golden Eagles (*Aquila chrysaetos*), and Common Ravens. Avian prey and their habitats were similar to those found along the Yukon River (Hunter et al. 1988), but waterbirds were less common upriver and away from the floodplains of the Yukon and Tanana rivers.

METHODS

Nesting Terminology. For this study, we defined terms as follows: (1) *nest*: structure made or the place used by birds for laying their eggs and raising their young, (2) *nest cliff*: a distinct cliff or bluff with at least one confirmed nesting attempt by Peregrine Falcons during the course of the study, (3) *off-river nest cliff*: a nest cliff located on tributaries in the uplands between the Tanana and Yukon rivers.

We further defined reproductive terms, based on Steenhof and Newton (2007) as follows: (1) *Nesting territory*: an area that contained, or historically contained, one or more nests within the home range of a single, territorial pair; (2) o*ccupied territory*: a nesting territory where a single or pair of adults that

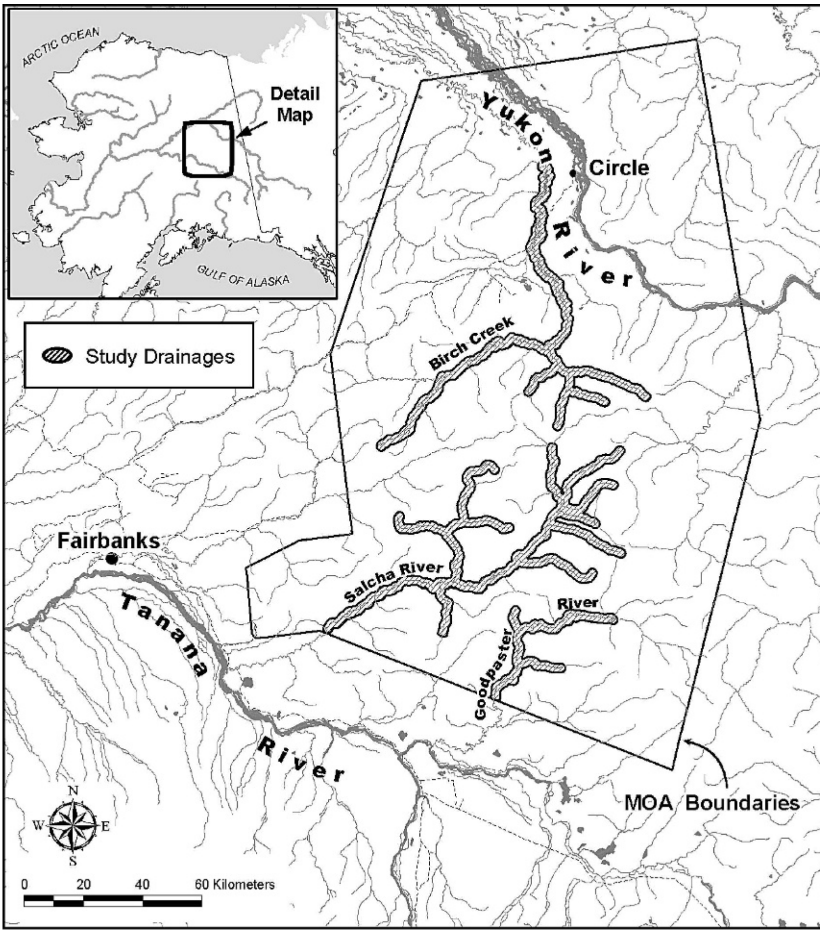

Figure 1. Yukon-Tanana uplands study area, east-central Alaska.

have defensive/territorial behaviors at a cliff, an incubating adult, eggs, or young were observed during surveys; (3) *successful territory* (or *successful pair*, in historical accounts): a nesting territory where at least one live nestling (regardless of age) was observed during the productivity survey; (4) *nesting success*: the proportion of occupied territories that raise at least one young (regardless of age) in a given season; and (5) *reproductive rate* (or *productivity*, in Steenhof and Newton 2007): the number of young (regardless of age) produced per occupied territory in a particular year.

Field Surveys. In 1994, we flew a preliminary aerial survey using a fixed-wing aircraft to identify suitable nesting cliffs and to determine the extent of river reaches to include in our multiyear study. Between 1995 and 2003 we used a Hughes 500D or Robinson R44 helicopter twice each breeding season to assess the occupancy of nesting territories, nesting success, and reproductive rate of Peregrine Falcons. Occupancy surveys occurred in the last week of May, after the majority of adults had initiated incubation (Cade 1960). Productivity surveys were flown in mid-July, when nestlings were generally large and conspicuous (>3 weeks old) but still confined to nests. Two observers seated on the same side of the aircraft participated in each survey. Survey efforts were comparable among all years.

Standard survey procedures included flying along the center of a drainage, then angling toward prospective and/or traditional nests when the aircraft was approximately 0.8–1.6 km from a cliff. A slow (30–60 km/hr) approach and pass were made along the cliff 25–50 m from potential nests. Multiple passes or hovering flights were made to inspect nests only when incubating adults were not detected. During occupancy surveys, the non-incubating adult often would fly as we approached, but incubating birds rarely left the nest. We followed a similar survey protocol during July to count young. All nesting cliffs and other cliffs within the study area were revisited, regardless of their status during the first survey, to maximize the detection of occupied territories that may have been missed during the occupancy survey.

For each survey, we recorded locations of raptor nests on USGS 1:63 360 maps and obtained coordinates of known and potential nests with an onboard Global Positioning System (GPS). Information on several cliff attributes were collected including elevation, cliff height, and aspect of slope. Measurements of some of these physical characteristics (e.g., cliff height) were estimates made from the aircraft and this lack of precision should be considered when comparing them to other studies where more precise measurements were made (e.g., Wightman and Fuller 2005).

Data Analysis. We estimated the detectability of occupied nest cliffs by comparing the numbers of nest cliffs characterized as occupied or unoccupied during the first and second visits. We classified each of 488 pairs of nest cliff visits into one of four possible nest status categories based on observations during the May and July surveys: (1) occupied-occupied; (2) occupied-unoccupied; (3) unoccupied-occupied; or (4) unoccupied-unoccupied. We then calculated the probability of a nest cliff being occupied in each category based on three parameters:

ψ = probability a nest cliff was occupied;
p = probability that an occupied territory was detected at a nest cliff on a given survey (given that it was present and not previously detected);
ε = probability that a nest cliff was occupied at the first visit and was unoccupied on the second visit (failed breeding).

The probability (Pr) of the four different nest status categories (11, 10, 01, and 00; where 1 indicates that an occupied territory was detected and 0 indicates that an occupied territory was not detected) was estimated using the formulas:

$$\Pr(11) = \psi p(1-\varepsilon)$$

$$\Pr(10) = \psi\, p\, \varepsilon$$

$$\Pr(01) = \psi(1-p)(1-\varepsilon)p$$

$$\Pr(00) = (1-\psi) + \psi(1-p)\varepsilon + \psi(1-\varepsilon)(1-p)^2$$

We assumed that the probability of detecting an occupied territory for the first time in a year is equal during the first and second surveys and that the probability of detecting an occupied territory (i.e., still-occupied nest cliff) on the second survey was 100%. We also assumed that the probability of detecting an occupied territory was equal at all nest cliffs (i.e., there was no heterogeneity among nest cliffs). If a significant degree of heterogeneity among nest cliffs existed, the true detectability of occupied territories may be lower or higher than our estimates but we had insufficient data available to test that assumption.

We used the likelihood function for a multinomial distribution and the number of nest cliffs within each category to derive the log likelihood function. We then optimized the log-likelihood using the optim function in the statistical software package R (R Development Core Team 2009).

Linear regression was used to identify temporal trends in nearest neighbor distance, numbers of pairs, nesting success, and reproductive rate (mean number of young/occupied territory). Analysis of covariance (ANCOVA) was used to compare annual trends between Yukon and Tanana drainages and to determine whether occupancy and reproductive rate (weighted by nest) in the two areas differed significantly. We accepted a significance level (α) of 0.05 in all statistical comparisons. Statistical analyses were conducted with SPSS software (SPSS 2002, ver. 11.5). Prior to analyses, percentages of successful nests were arcsine-transformed (Zar 1999). Cliff aspect was summarized following procedures for circular statistics with the program Oriana (Kovach 2003).

We included summaries of estimated cliff height, elevation, cliff aspect, and horizontal distance from nearest neighbor. We selected these characteristics because they provided insights into the regional nesting environment and have not been published for other studies of Peregrine Falcons in Alaska.

RESULTS

Cliff and Nest Attributes. We identified 55 different cliffs occupied by nesting Peregrine Falcons during at least one year of our surveys 1995–2003. Cliff faces on which nests were located ranged from approximately 15 to 250 m in height (mean = 66.4 m, median = 50 m). Over half (60%) were ≤50 m in height. Nest cliffs generally fit into one of three

Table 1. Occupancy, nesting success, and reproductive rate of Peregrine Falcons along the Birch, Salcha, and Goodpaster drainages, Yukon Tanana uplands, Alaska (1995–2003).

Year	Single Adults	Occupied Territories No.	Occupied Territories (%)[1]	Successful Territories No.	Successful Territories (%)	No. Young	Young/ Occupied Territory	Young/ Successful Territory
1995	5	12	25	8	67	23	1.92	2.88
1996	4	20	42	12	60	34	1.70	2.83
1997	4	21	44	17	81	39	1.86	2.29
1998	2	25	52	17	68	42	1.68	2.47
1999	3	29	60	18	62	46	1.59	2.56
2000	1	33	69	15	45	31	0.94	2.07
2001	3	35	73	23	66	48	1.37	2.09
2002	2	38	79	30	79	74	1.95	2.47
2003	2	36	75	25	69	60	1.67	2.40
Mean	2.9 ± 0.4	27.7 ± 2.9	57.6 ± 6.1	18.3 ± 2.2	66.4 ± 3.5	44.1 ± 5.2	1.63 ± 0.10	2.45 ± 0.095

[1] Percent of the total available territories (n = 48) in the study area that were occupied in one year.

categories: (1) large (>100 m high) riparian cliffs; (2) isolated granite tors (<25 m high) and limestone outcrops (>50 m high) outside the main floodplains; and (3) extensive dirt bluffs and crumbling schist cliffs (often <20 m high) within the floodplains. The average aspect of the main nesting cliff face was southern (179 ± 60.3 degrees; mean ±SD, n = 55). Over 75% of all cliffs used by nesting Peregrine Falcons were within a range of southwest to southeastern aspects.

Mean nest elevation was 512 m (calculated using the highest known nest on each cliff; median = 488 m, range 229–1067 m) and 84% of nests were between 300 and 700 m elevation. Only 11% of nests were at elevations >700 m, with two nests >800 m in height. The highest nest was located on an alpine cliff in the upper Salcha River drainage at 1067 m.

Occupancy. Although we recorded 55 distinct cliffs that were occupied by nesting Peregrine Falcons during at least one year between 1995–2003, the annual history of use during our study suggests that some nesting territories contained one or more alternate nest cliffs. Therefore, we used 48 nesting territories as the estimate of maximum territories in the study area during our studies. Occupancy of these territories ranged from 25% in 1995 to 79% in 2002, and the number of single adults ranged from 5 in 1995 to 1 in 2000. Average occupancy in the last three years of surveys was 76% for these 48 territories (Table 1).

We used 488 pairs of nest cliff visits to estimate detectability including 168 nest cliffs that were occupied during both surveys, 19 that were first recorded occupied on the second survey (i.e., missed on the May survey), 61 that were occupied on the first survey but not on the second survey, and 240 that were not occupied during either survey. The probability of detecting an occupied nest given that a nest cliff was occupied (p) was 0.887 (SE = 0.0274), the probability that a given nest cliff was occupied during at least one survey (ψ) was 0.529 (SE = 0.0246), and the probability that a nest cliff that was occupied during the first survey would fail before the second survey (ε) was 0.266 (SE = 0.0292). Therefore, we estimate that a total of eight (MLE = 7.77) occupied nests were missed on the first survey and failed prior to the second survey and two (MLE = 2.42) occupied nests were not detected during either survey even though they were occupied. The total number of occupied nests for all years was estimated to be 258 and 10 were not detected during either survey. This resulted in an overall detectability rate of 96.1%. We felt this was sufficient to assume 100% detectability in subsequent analyses.

Nearest Neighbor Distances. The mean nearest neighbor distance between Peregrine Falcon nests in occupied territories in the Yukon-Tanana uplands study area decreased by 0.437 km/yr during 1995–2003 ($y = -0.437\times + 10.865$; $R^2 = 0.875$, $P < 0.001$; Fig. 2). Mean nearest neighbor distances ranged from a maximum of 10.1 km (±2.7 km) in 1997 to a minimum of 6.7 km (±1.0 km) in 2001. The shortest distances between occupied nests was 1.3 km in 2001 (both nests were successful), and another pair of nests both occupied in 2001 and 2002 were only 1.3 km apart. Mean nearest neigh-

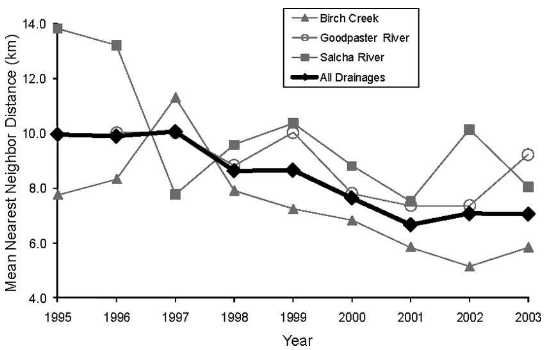

Figure 2. Mean nearest neighbor distances for nesting Peregrine Falcon pairs along the Birch, Goodpaster and Salcha drainages, Yukon-Tanana uplands study area, Alaska (1995–2003).

bor distances equaled 5.8 km, 8.0 km, and 9.2 km in the last year of the study, for Birch Creek and the Salcha and Goodpaster rivers, respectively (Fig. 2).

Population Trend. The number of occupied territories of Peregrine Falcons in the study area increased from 12 in 1995 to 38 in 2002 (Fig. 3, 4). The mean annual rate of increase of the number of occupied territories in the study area was 16% for nine years of surveys and ranged from 5% to 67%, with most of the increase occurring in the first six years of the study. The trend slowed to 3%/yr after 2000; fewer occupied territories (36) were recorded during the last survey in 2003.

The number of Peregrine Falcon occupied territories substantially increased from 1995–2003 (R^2 = 0.936, $P < 0.001$; Fig. 4). The rate of increase did not differ between the Yukon drainage versus the Tanana drainages ($F = 0.19$, df = 1, $P = 0.67$).

Nesting Success and Reproductive Rate. Data on nesting success and reproductive rate were collected for 249 Peregrine Falcon nesting attempts (i.e., 12–38 occupied territories per year from 1995–2003). Nesting success varied annually and ranged from 45% to 81% (Table 1). Mean nesting success was 66.4% ± 3.5 (SE) for the entire nine-year study period.

Nesting success showed no trend over the study period ($R^2 = 0.0152$, $P = 0.70$). Nesting success also did not differ between the Yukon and Tanana drainages ($F = 2.47$, df = 1, $P = 0.14$). Annual mean reproductive rates ranged from 0.9–2.0 young/occupied territory and 2.1–2.9 young/successful territory (Table 1). Mean reproductive rates for all years combined equaled 1.6 ± 0.1 young/occupied territory and 2.5 ± 0.01 young/successful territory. Similar to nesting success, there was no linear trend in young/occupied territory over the study period (R^2 = 0.0368, $P = 0.89$). There were no detectable differences in mean annual reproductive rate between Yukon and Tanana drainages ($F = 0.41$, df = 1, P = 0.54).

DISCUSSION

Attributes of Cliffs and Nests. The majority of nesting cliffs found in the Yukon-Tanana uplands were generally similar to cliffs used by Peregrine Falcons along major rivers in interior Alaska (e.g., Yukon, Tanana; Cade 1960, Ritchie 1976). One notable difference was that many of the nesting territories used in the upper reaches of the Yukon-Tanana uplands were at higher elevations and more remote from the main floodplains than typically was associated in the boreal region of Alaska. Cade (1960) suggested that limiting factors (i.e., prey availability) prevented them from nesting at elevations greater than 610 m (2000 ft) in Alaska. Interestingly, this is the same distinct upper limit for most breeding Peregrine Falcons in Britain, where conditions ''can be truly arctic at nesting'' (Ratcliffe 1993:174). Cade (1960:162) also noted that ''occasional pairs probably also nest on cliffs away from the immediate vicinity of water … but there is no known instance of such a nesting in Alaska.'' He also stated ''when more ornithological work has been done in the mountains of Alaska, some Peregrine Falcons may be found [at higher elevations]'' (Cade 1960:161). Our observations and other recent observations (e.g., Nation and Kandik rivers; C. McIntyre pers. comm.) suggest that nesting at higher elevations occurs more frequently than in historical reports. Further, we expect that more cliffs in alpine areas and areas removed from the main floodplains of rivers will be identified as used by Peregrine Falcons as raptor surveys expand in those areas.

Occupancy. Occupancy rates in the study ranged from 25% in 1995 to 79% in 2002 and averaged 76% in the last three years of surveys. In stable populations, especially prior to the pesticide-induced decline pre-1970, Peregrine Falcons may have occupied 80–90% of all nesting territories in any year (Ratcliffe 1993, Enderson et al. 1995). During the pesticide-induced decline, occupancy rates in interior Alaska probably dropped to approximately 17%, increasing to 30–40% during early stages of recovery on the Yukon River (late 1970s to 1985;

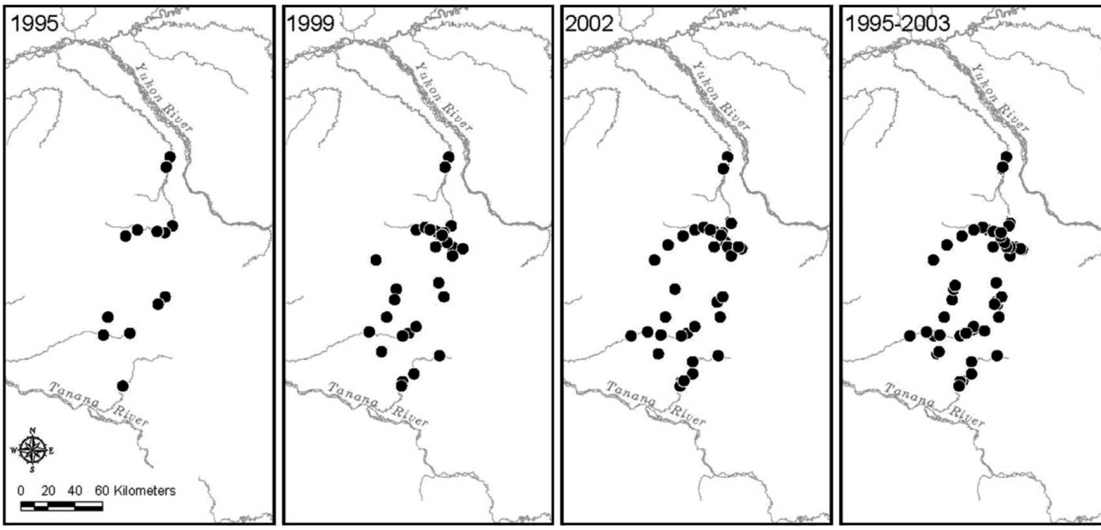

Figure 3. Number and distribution of nesting cliffs occupied by territorial pairs of Peregrine Falcons in the Yukon-Tanana uplands study area, Alaska (represented by three years [1995, 1999, 2002] and pooled for all years).

Ambrose et al. 1988). Currently the number of occupied territories along the Yukon River exceeds the number reported in historical information (R. Ambrose pers. comm.). Occupancy during the recovery period of the Peregrine Falcon has exceeded historical levels in other populations as well (Ratcliffe 1988, 1993, Murphy 1990, Enderson et al. 1995).

Lower rates of occupancy between off-river nesting territories and those on the Yukon and Tanana rivers may reflect a number of factors, including differences in habitat and carrying capacity, and

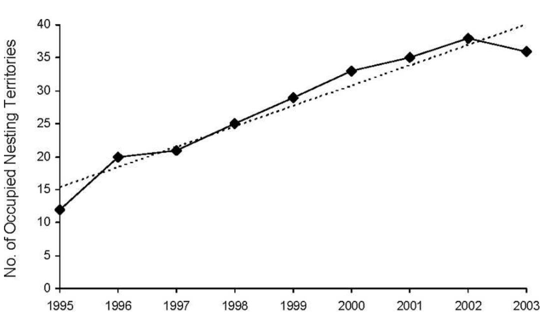

Figure 4. Population growth (number of occupied nesting territories) of Peregrine Falcons in the Yukon-Tanana uplands study area, Alaska (1995–2003; trendline indicated by dashed line: y = 3.10× − 6169.23; $R^2 = 0.936$, $P < 0.001$).

the current status of recovery in each region. For instance, as noted above, Peregrine Falcons used alpine cliffs for nesting in the study area. Use of alpine areas might be more limited than lower-altitude areas due to factors such as harsher environmental conditions and/or increasing competition with other raptors that are not regular occupants along the main rivers. Higher-elevation nest cliffs may be less attractive as nests due to delayed snow melt and lower diversity and abundance of avian prey (e.g., Rahbek 1995). In regard to prey availability, alpine cliffs in the study area were adjacent to prime riverine habitats of prey species, well within the hunting range of alpine-nesting Peregrine Falcons (Enderson and Craig 1997, White et al. 2002), so we would not expect large differences in prey availability. We also expect that ameliorating influences of climate change (e.g., earlier snow melt and warming temperatures) might mitigate some of the differences in environmental conditions between areas at lower and higher elevations.

Competition for nest cliffs or territorial antagonism with other species also may affect the occupancy of nest cliffs for Peregrine Falcons, particularly at higher elevations where Golden Eagles and Gyrfalcons are more abundant. Peregrine Falcons tend to avoid Golden Eagles as close neighbors (Poole and Bromley 1988, Ratcliffe 1993, White et al. 2002). Gyrfalcons, resident in the study area's uplands, nest earlier and are not dislodged easily by Peregrine Falcons (Cade 1960). Isolated alpine cliffs, such as those in the upper reaches of study area streams, might not afford enough space for both species (Burnham and Mattox 1984). On three occasions in our study area, when Gyrfalcons were recorded occupying nest cliffs regularly used by Peregrine Falcons, only one species ever occupied the cliff during any single breeding season, suggesting competitive exclusion. Further, some ''first class'' cliffs (Hickey 1942) in alpine areas had no historical record of occupancy by Peregrine Falcons and no recorded occupancy when we completed our surveys in 2003. These large, high-elevation cliffs did, however, often have nesting Gyrfalcons, Gyrfalcon perches, and unoccupied Golden Eagle nests.

Finally, differences in occupancy of Peregrine Falcon nest cliffs between the Yukon-Tanana uplands and the Yukon and Tanana rivers also may be due to the status of the peregrines' recovery in both areas. Although they occupied more nesting cliffs than indicated in historical records on the Yukon River, recovery may still be occurring in more remote areas including our study area, as suitable unoccupied cliffs are still present (see below).

Population Trend. The substantial population growth we witnessed in the study area (16%/yr), with higher rates in the first half of the period compared to the second half, was similar to or greater than rates of increase recorded during the expansion or recovery stages in some other Peregrine Falcon studies. In southwestern Scotland, a fairly discrete nesting population showed a mean increase of ~12% per year from 1974–82 (Newton and Mearns 1988). Annual growth rate was 16% for a population augmented by captive releases in New York and New England (Corser et al. 1999), with growth rates slowing after releases were stopped. Slower rates of growth were recorded during the Peregrine Falcon recovery in England: 3.8% (1971–81) and 5.3% (1981–91) per year (Ratcliffe 1993). On the upper Yukon River, Alaska, the mean annual increase in the number of occupied territories was 11% per year during the first years of recovery (1975–84; Ambrose et al. 1988), slowed to 6% from 1985–94 and to 2% from 1995–2003 as the population may have started to stabilize when nesting locations became limited (R. Ambrose pers. comm.). Similarly, by the start of our surveys in 1995, population growth on the Tanana and Porcupine rivers in east-central Alaska had slowed after substantial growth in the previous two decades (D. Payer pers. comm., R. Ritchie unpubl. data).

A reduced rate of growth in the latter half of our survey period also may reflect the attainment of a population at carrying capacity, although there are suitable unoccupied cliffs in the area. Numerous (>20) dirt and shale bluffs in lower elevations of the study area were still unoccupied when we completed our surveys. It seems likely that at least some of these cliffs may be occupied if the number of nesting pairs of Peregrine Falcons continues to increase. Similar observations were reported along the Tanana River, where quarry cliffs and road cuts along the Alaska Highway have recently been occupied after the natural cliffs in the floodplain were occupied (Ritchie et al. 1998; H. Timm pers. comm.). Finally, with the recent discovery of nesting Peregrine Falcons using an old Bald Eagle nest in a tree in interior Alaska (Whitman and Caikoski 2008), these additional substrates suggest the potential for further, albeit more limited, increases in nesting territories.

Nesting Success and Reproductive Rate. Nesting success and reproductive rate varied considerably among years but fell within the range of other *F. p. anatum* populations in the boreal forest region of North America. In particular, mean brood size in the study area (2.4 young/successful territory) was similar to that in a number of drainages in northern Canada between 1975 and 1990 (Rowell et al. 2003), a period when Peregrine Falcons were recovering or expanding their range: 1.7–2.8 young/successful pair on the Porcupine River, 2.0–2.6 young/successful pair on the Yukon River, Canada, and 2.2–2.8 young/successful pair on the Mackenzie River. These values also are similar to historical records for brood size prior to the pesticide decline (2.5 young/successful pair [Great Britain: Ratcliffe 1993], 2.6 young/successful pair [southern Canada; Hickey 1942]), and 2.5 young/successful pair [arctic Alaska; Cade 1960]).

Nesting success in the study area fell within the range of other populations of Peregrine Falcons and was relatively high (>60%) in all but one of our study years (40%, 2000) with no trend over the nine-year period. In other areas, nesting success has varied: 60–88%, Rankin Inlet, Keewatin District, NWT (1981–85; Court et al. 1988); 40–66%, England (1980–91; Ratcliffe 1993), 40–100%, Washington coast (Wilson et al. 2000); and 38–94%, upper Yukon River, Alaska (R. Ambrose pers. comm.).

Recovery or Expansion? Peregrine Falcon populations have been increasing and/or recovering in North America for at least the last 30 years (Enderson et al. 1995, White et al. 2002, Rowell et al. 2003). In numerous closely monitored nesting populations, the number of occupied territories now exceeds the numbers of historical territories recorded prior to the decline (Ratcliffe 1993, Enderson et al. 1995). Populations along the Yukon River in Alaska and Canada are no exception, with more than twice the number of occupied territories today than were known in the 1960s and 1970s (Murphy 1990; R. Ambrose pers. comm.).

Although historical data are inadequate to evaluate population levels before the pesticide-induced decline, some evidence suggests that Peregrine Falcons were greatly reduced or possibly even extinguished in the study area during this era. For example, they were not reported during surveys in the late 1970s on the lower Salcha River and Birch Creek and Goodpaster River (White and Boyce 1978). Surveys on Birch Creek and its upper tributaries in late 1980s and early 1990s reported only a few nesting there (P. Kuropat pers. comm., C. McIntyre pers. comm.).

It is impossible to document whether Peregrine Falcons in the Yukon-Tanana uplands have exceeded historical numbers prior to the pesticide-induced decline. As they adjust to new opportunities and challenges, such as those associated with global climate change, it may become even more difficult to distinguish between a recovery to historical levels or an expansion in the Yukon-Tanana uplands. However, regularly assessing the numbers of nesting Peregrine Falcons in these off-river areas may be a valuable tool for documenting the status of their populations over the larger boreal forest region. If nesting territories last occupied are the first to be abandoned (Lohmus 2001) or recovery is slower in areas of lower density (Ratcliffe 1993), monitoring to detect changes in numbers at off-river territories might alert us to another decline before such changes are witnessed along larger rivers.

ACKNOWLEDGMENTS

This project was funded by the U.S. Air Force, 11th Air Force, Elmendorf Air Force Base, AK, through the National Park Service, Fort Collins, CO. Skip Ambrose of the National Park Service, Fort Collins, CO, was helpful throughout the project. Jonathan Laravee, Chris Soloy, and Richard Kimball of Prism Helicopters and Rick Swisher of Quicksilver Air provided expert flying for the helicopter surveys. At ABR, Alex Prichard performed statistical analyses, Betty Anderson and Robert Day edited drafts of this manuscript; Allison Zusi-Cobb and Will Lentz assisted with map and GIS database preparation. Clay White, Robert Day, and Robert Burgess reviewed and offered improvements to earlier drafts of this paper. Our efforts were coordinated with existing monitoring programs conducted on the Yukon River and some of its tributaries by the U.S. Fish and Wildlife Service and the U.S. National Park Service. Carol McIntyre, Tom Cade, Robert Steidl, and an anonymous reviewer read an earlier draft of this paper, greatly improving the final product.

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Received 7 March 2009; accepted 17 January 2011
Associate Editor: Carol L. McIntyre