

Effects of jet aircraft overflights on parental care of peregrine falcons

Angela G. Palmer, Dana L. Nordmeyer, and Daniel D. Roby

Abstract Concerns voiced by resource managers caused us to examine the hypothesis that low-altitude jet aircraft overflights affect parental care by peregrine falcons. Specifically, we studied effects on nest attendance, time-activity budgets, and provisioning rates of peregrine falcons (*Falco peregrinus*) breeding along the Tanana River, Alaska in 1995, 1996, and 1997. We detected subtle effects of jet overflights on peregrine falcon parental behavior, but found no evidence that overall attendance patterns differed depending on exposure to overflights. Nest attendance and time-activity budgets of peregrine falcons during periods of overflights differed from those of peregrines at reference nests (nests rarely overflown). Differences depended on stage of the nesting cycle and gender. During the incubation and brooding stages of the nesting cycle, males attended the nest ledge less when overflights occurred than did males from reference nests. Females attended the nest ledge more during overflown periods compared to females from reference nests. Additionally, while females were still brooding nestlings, they were less likely to be absent from the nest area during periods when overflights occurred than females from reference nests. Although we found differences in nest attendance and time-activity budgets between overflown and reference nests, we did not observe differences between periods with overflights and periods without overflights at the same nests. Nor did we detect a relationship between nest attendance and the number of overflights occurring within a given time period, the cumulative number of above-threshold noise events at each nest, or the average sound-exposure level of overflights. Furthermore, we found no evidence that nestling provisioning rates were affected by overflights.

Key words Alaska, *Falco peregrinus*, low-altitude jet overflights, nest attendance, nestling provisioning rates, peregrine falcon, time-activity budgets

Disturbance to nesting birds may result in changes in parental behavior and care of progeny that ultimately affect nesting success. Few studies have examined subtle long-term behavioral responses of nesting raptors to potential overflight disturbance (Awbrey and Bowles 1990). Due to concerns expressed by resource managers, the United States Air Force funded a study on effects of jet overflights on behavior and reproduction of raptors (Palmer 1998, Nordmeyer 1999, Murphy et al.

2001). As a part of this study, we examined the effects of overflights on parental care by peregrine falcons in interior Alaska. Nordmeyer (1999) examined overflight parameters, the immediate reaction of nesting peregrine falcons to overflights, and the impact of overflights on nesting success. Here we measure effects of overflights on components of parental care including nest attendance (amount of time parents are near the nest), time-activity budgets (amount of time parents allocate to various

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activities), and nestling provisioning rates (the rate at which parents deliver food to young).

We examined the hypothesis that low-altitude jet aircraft overflights affect peregrine falcon parental care. If nest attendance and behavior of adult peregrines are influenced by low-altitude jet overflights, we would expect time-activity budgets of falcons to differ between periods immediately following overflights and periods when no overflights occur and between nests exposed to overflights and those that are not. Additionally, because the stage of the nesting cycle plays a prominent role in falcon breeding behavior, we would predict that behavioral responses to overflights would change as the nesting cycle progresses. Also, if overflights affect behavior, we would expect a higher frequency of overflights to lead to more pronounced changes in allocation of time to breeding activities. If overflights inhibit peregrine falcons from hunting or delivering prey to young, we would expect nestling provisioning rates to be lower during periods following overflights than during periods when no overflights occurred. Finally, we would expect a negative correlation between number of overflights and prey provisioning rates.

Study area

The Tanana River is a wide, braided, glacially fed river in interior Alaska. The valley floor was covered in boreal forest of predominantly white spruce (*Picea glauca*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*), with many boggy areas and small thaw lakes. Schist and granite cliffs, ranging in height up to several hundred meters, intermittently bounded the northern bank of the Tanana River. These south-facing slopes were warmer, sunnier, drier, and had a longer growing season than did low-lying areas and back-sides of cliffs (Wahrhaftig 1965). These slopes or

cliffs also were where peregrine falcons most frequently located their nests. Most occupied cliffs overlooked the river, and all were near lakes, ponds, marshes, or other expanses suitable for hunting. Population monitoring along the Tanana River has been documented since the 1950s (Cade 1960, White 1969, Ambrose et al. 1988, Bente and Wright 1995, Wright and Bente 1999). These surveys indicated a steady annual increase of occupancy and productivity of traditional nest sites (territories with a breeding pair; Steenhof 1987).

The study area encompassed a 250-km stretch of the Tanana River between Tok and Fairbanks (Figure 1). In 1995 the study area extended from Tanacross to Sawmill, an approximately 110-km stretch of river, and included two Military Training Routes (MTRs) that crossed the river. In 1996 and 1997, we included an additional 65-km section of the river from near Delta Junction to the Salcha River, which included an additional MTR. Nest sites were located along these stretches of the river. In 1995 we selected 9 nests for observations, 4 of them located in MTRs and subjected to low-altitude overflights. In both 1996 and 1997, we observed 6 nests in the upper stretch and 4 nests in the lower stretch. Five and 7 of these 10 observed nests were exposed to overflights and within MTRs in 1996 and 1997, respectively. Two nests (nests 205 and 221), located within an MTR and overflowed in 1995 and 1997, were not overflowed in 1996.

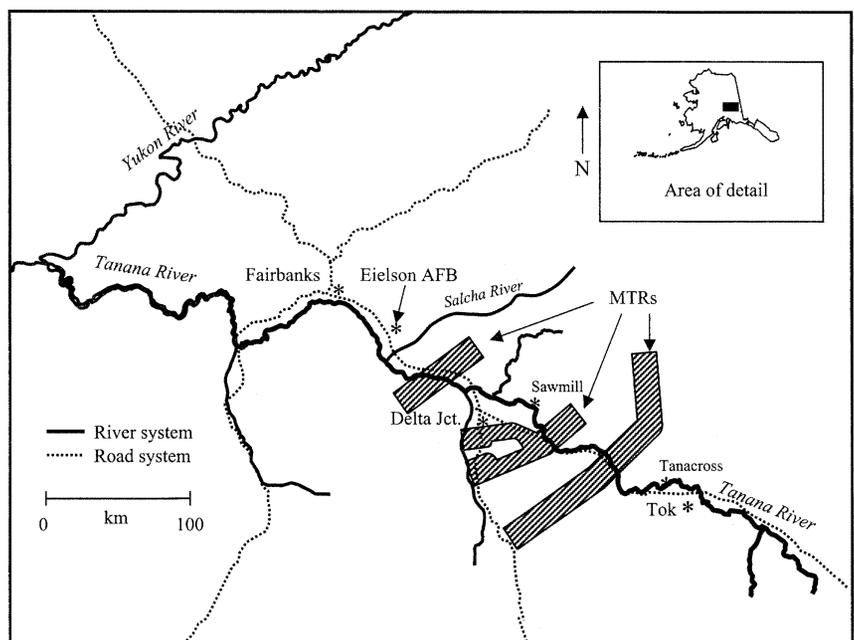


Figure 1. Study area for peregrine falcons nesting along a 250-km stretch of the Tanana River between Tok and Fairbanks, Alaska, 1995, 1996, and 1997.

Methods

Overflights

The eleventh United States Air Force (USAF) provided jet aircraft overflights directed at peregrine falcon nests located in the MTRs. We provided the USAF with the latitude and longitude of nests and marked their locations on photographs and United States Geological Survey topographic maps. We coordinated with the USAF to schedule overflights during periods when field crews were present. The USAF was able to provide the majority of overflights to nests during three 2.5-week periods each year. The first overflight period in each year coincided with incubation, the second with mid to late nestling rearing, and the third with post-fledging. In 1996 and 1997, forward air controllers from Ft. Wainwright joined field crews on the ground to enhance the proximity of overflights to observed nests.

The military uses the MTRs as corridors to travel to and from Military Operation Areas (MOAs). The Federal Aviation Administration permits low-altitude jet overflights in MTRs without special clearance. During this study we requested pilots to fly at or below 150 m directly at specific nest cliffs within the MTRs. Because the MTRs in this study have been in place since 1994 (ENSR Consulting and Engineering 1992), it was impossible to know previous exposure of nesting peregrines in the study area to overflights, though some exposure was likely; however, exposure to directed overflights probably was relatively low.

We deployed Animal Noise Monitors (ANMs; Wildlife Computers, Redmond, Wash.), which measure several noise-dose variables including sound-exposure level (SEL), on the cliffs near each active nest ledge to measure noise dose (two ANMs were deployed at each nest within MTRs and one at each nest outside MTRs). The ANMs had the capacity to store 2,000 sound profiles of noise events that occurred over a minimum dB level. We set this threshold level at 85 dB for all ANMs. ANMs recorded noise events if they were >2 sec and <2 min duration. We chose these criteria in order to record noise events likely to be jet aircraft while screening out events unlikely to be jet aircraft.

We categorized each nest each year as either overflown or reference. Overflown nests were those located within MTRs and exposed to a minimum of 7 overflights per season that exceeded the 85-dB threshold. We classified as an overflight any

military jet or helicopter that was ≤ 300 m above a nest and ≤ 400 m laterally from a nest during our observations. This was equivalent to a 500-m slant distance, where slant distance was the shortest distance from aircraft to nest. Eighty-five percent of noise events detected by ANMs when observers were present had slant distances of ≤ 500 m. Overflown nests received up to 28 observed overflights spread throughout a single breeding season (Table 1). In 1995 a maximum of 6 additional noise events per nest were recorded by ANMs when observers were not present (Table 1). In 1996 and 1997, an average of 17 additional noise events were recorded by ANMs when observers were not present (Table 1), mostly due to the proximity of the new MTR to Eielson Air Force Base. These numbers likely were accurate for jet overflights but underestimated the number of helicopter overflights. Due to their sound profiles, helicopter noise events were undetected in some instances. Only 3% of the 252 observed overflights were attributable to helicopters.

Reference nests were those that received a maximum of 5 above-threshold noise events, either in the presence or absence of observers (Table 1). All but 3 nest sites met this criterion. One nest in 1996 (nest 379) and 2 nests in 1997 (nests 181.7 and 379) received >5 noise events detected by ANMs and were thus excluded from the analyses.

Behavioral observations

Nests were situated on bluffs overlooking the river. We selected study nests based on access to observation sites on gravel bars opposite cliffs and across at least 1 channel of the river. We located observation sites about 300 m from nests to permit viewing of the nest ledge without disturbing the breeding pair. We initiated observations each year after ice break-up in mid-May and continued until the young had fledged and left the nest area (late August–early September). A crew of 2 to 4 observers recorded data at each peregrine falcon nest, and 2 separate crews were in the field throughout each season. We discarded observations if visibility was poor or if the sex of adults could not be determined.

We used binoculars, 15–60X spotting scopes, and 90X Questar® telescopes (Questar Corporation, New Hope, Pa.) to aid our observations during 3 phases of the peregrine falcon nesting cycle: incubation, nestling rearing (0–42 days post-hatch), and post-fledging (42+ days post-hatch). We used

Table 1. The number of overflights to which overflow and reference peregrine falcon nests were exposed along the Tanana River, Alaska, in 1995, 1996, and 1997.

Year	Nest type Nest number	Number of overflights per nesting cycle phase			Total
		Incubation	Nestling rearing	Post-fledging	
1995	Overflow nests				
	205 ^a	11 (2) ^b	8 (0)	no obs.	19 (2)
	221 ^a	8 (2)	12 (0)	5 (0)	25 (2)
	281 ^a	no obs.	10 (6)	3 (no ANM)	13 (6)
	288 ^a	2 (2)	3 (0)	no obs.	5 (2)
	Reference nests				
	243	0 (1)	0 (1)	0 (no ANM)	0 (2)
	247	0 (0)	0 (1)	no obs.(no ANM)	0 (1)
	258	no obs. (0)	0 (1)	no obs.(no ANM)	0 (1)
	269	no obs. (0)	0 (1)	0 (no ANM)	0 (1)
299	no obs. (4)	0 (1)	no obs. (no ANM)	0 (5)	
1996	Overflow nests				
	280.5 ^a	18 (9)	4 (7)	0 (0)	22 (16)
	288.5 ^a	1 (4)	23 (11)	4 (1)	28 (16)
	427 ^a	9 (12)	4 (20)	15 (2)	28 (34)
	431 ^a	2 (14)	nest failure		
	438.6 ^a	1 (12)	15 (14)	4 (0)	20 (26)
	Reference nests				
	205 ^a	0 (0)	nest failure		0 (0)
	221 ^a	0 (1)	0 (1)	0 (0)	(2)
	258	no obs. (no ANM)	no obs. (no ANM)	0	0
269.5	0 (0)	0 (0)	0 (0)	0 (0)	
379 ^c	0 (5)	0 (7)	2 (13)	2 (27)	
1997	Overflow nests				
	205 ^a	1 (0)	1 (4)	0 (1)	2 (7)
	221 ^a	3 (2)	2 (8)	0 (2)	5 (17)
	280.5 ^a	24 (2)	0 (0)	2 (4)	26 (32)
	288.5 ^a	7 (9)	2 (32)	0 (4)	9 (54)
	427 ^a	0 (21)	0 (34)	12 (15)	12 (70)
	431 ^a	0 (15)	6 (47)	17 (12)	23 (74)
	436 ^a	10 (23)	nest failure	nest failure	10 (23)
	Reference nests				
	181.7 ^c	1 (2)	0 (6)	0 (2)	1 (10)
269.5	0 (4)	0 (0)	0 (1)	0 (5)	
379 ^c	0 (11)	0 (1)	0 (0)	0 (12)	

^a These nests fell within Military Training Routes.

^b Noise events recorded on Animal Noise Monitors (ANMs) when observers were not present are in parentheses.

^c These reference nests were excluded from analyses due to the number of above threshold noise events recorded by ANMs when observers were absent.

Canon L2 Hi-8 mm (Canon, Inc., Tokyo, Japan) and Sony CCD-FX430 8 mm (Sony Corporation, Tokyo, Japan) video cameras equipped with 250-mm lenses and 2X extenders to record behaviors. During incubation and nestling-rearing periods, we focused 1 camera on the nest ledge and the other on the attending adult. During the post-fledging period, we focused on visible fledglings or adults. We recorded nest attendance and time-activity budgets during incubation and nestling rearing and recorded prey provisioning rates during nestling rearing

and post-fledging. Of 9 nests observed in 1995, we observed 4 during incubation, 8 during nestling rearing, and 4 during post-fledging. We conducted observations during incubation, nestling rearing, and post-fledging at 7 of 10 nests in 1996 and 8 of 10 nests in 1997. In 1996 the 3 other nests were not sampled during all 3 phases of the nesting cycle because 2 nests failed following incubation and we replaced them with a nest initiated by another pair. Similarly in 1997, of the remaining 2 nests, 1 failed after incubation and we replaced it with another nest initiated by a different pair. Failures occurred during incubation, and the rate of failure was not outside the normal rate for the Tanana River or interior Alaska (Nordmeyer 1999, Wright and Bente 1999). For analysis, the nestling-rearing phase was further subdivided into 3 stages, early- (0-10 days post-hatch), mid (11-24 days), and late nestling rearing (25-42 days). We determined stages of the nestling-rearing phase during banding

visits by estimating age of the oldest chick based on feather development (Nelson 1970).

Nest attendance and time-activity budgets

We used the instantaneous scan method to sample activity at 1-min intervals for each adult (Altmann 1974, Tacha et al. 1985). For nest attendance we distinguished between nest ledge (the ledge or scrape where eggs or chicks are located), ledge attendance (an adult attending the ledge),

nest area (<200 m of the nest), area attendance (an adult attending the nest area), and away from the nest area (>200 m from the nest, or not observed within the nest area). For time-activity budgets we recorded adult activity as 1 of 6 categories (incubating or brooding or shading, perching, feeding self, feeding young, flying, unknown; Palmer et al. 2001). An observation block refers to a group of 1-min scan samples that fell within a 1- to 4-hr time period. We grouped scans in this way to avoid autocorrelation in the data from 1-min scans.

We compared nest attendance and time-activity budgets between overflown blocks (when overflights occurred) and 2 controls: 1) baseline blocks from overflown nests when overflights did not occur, and 2) reference blocks from reference nests. These 2 types of controls helped to distinguish between 2 different types of variability in nesting behavior. Comparisons of behavior between exposed and unexposed nests controlled for bias from previous exposure to overflights (Gravetter and Wallnau 1988, Trimper et al. 1998). In contrast, within-nest comparisons (baseline vs. overflown) compensated directly for behavioral differences among pairs but may have been biased due to previous exposure to overflights (Gravetter and Wallnau 1988, Trimper et al. 1998).

We collected behavioral data during 405 observation blocks during incubation and nestling rearing. We restricted analyses, however, to 73 overflight blocks, 73 baseline blocks, and 78 reference blocks. We selected baseline and reference blocks to correspond with the same stage of the nesting cycle and time of day as overflight blocks as much as possible; however, observation blocks during mid-nestling rearing were underrepresented at reference nests. Additionally, within the 1- to 4-hr range in observation blocks, we truncated the length of baseline and reference blocks so as to match the length of overflown blocks from the same stage of the nesting cycle and time of day. Most overflights occurred between 0800 and 1700 hr Alaska Daylight Time; thus, we also restricted inclusion of data to observation blocks that overlapped this 9-hr period.

We set the beginning of observation blocks by the timing of the day's first overflight or to coincide with 3 times of day (0800 hrs, 1200 hrs, or 1600 hrs). The first overflight to occur after the first 4-hr overflown block marked the start of the next 4-hr overflown block. We matched baseline observation blocks to overflown blocks by selecting observa-

tions during the 4 hours preceding an overflight or from days without overflights that corresponded to the nesting stage and time of day when overflights occurred. Fourteen of the 73 baseline blocks occurred on days following overflights rather than before.

To calculate ledge attendance and area attendance, we divided number of minutes each adult spent at the nest ledge or nest area, respectively, by number of minutes in the observation block. We defined total ledge attendance as female plus male ledge attendance and, similarly, total area attendance as female plus male area attendance, as in Palmer et al. (2001). Because the male and female were rarely at the nest ledge together (<0.1% of time), total ledge attendance measures the time the nest ledge was attended by an adult. The sample unit for time-activity budgets was number of minutes the parent spent performing a particular activity divided by total number of minutes per observation block.

Nestling provisioning rates

We recorded number of deliveries, estimated size class of each item, and type of prey delivered (identified to species whenever possible) to each nest. A delivery was defined as any prey item brought to the nest area by a parent and delivered to young. We estimated prey mass using the average body mass reported in Dunning (1993) and by methods described by Palmer (1998). We based size classes on relative size of prey to the size of adult.

We estimated prey mass delivery rates as total prey mass delivered during 2-hr observation blocks. Similarly, we calculated prey item delivery rates as total number of prey items delivered during 2-hr observation blocks, and we calculated average estimated prey size as total prey mass delivered divided by number of prey items delivered. We used 2-hr blocks in order to standardize the amount of time used to calculate provisioning rates because peregrine falcons have relatively low delivery rates (about once every 2 hrs; Cade 1960) and to maximize number of available overflown blocks to include in analyses.

We compared nestling provisioning rates between overflown blocks and 2 controls: 1) baseline blocks, and 2) reference blocks, as for nest-attendance comparisons. We collected data during 284 blocks during the nestling-rearing and post-fledging phases but restricted analyses to 37 overflown blocks, 37 baseline blocks, and 38 reference

blocks in order to make comparisons among a similar number of overflown and control blocks. We selected and matched overflown and baseline blocks in the same manner as for nest-attendance comparisons, using 2 hr as the block length. We selected reference blocks from similar stages and times of day as overflown blocks.

Statistical analyses

We logit transformed $[\log\{Y/(1-Y)\}]$ non-normal proportion data and used log transformations on rates to meet the assumptions of statistical tests. When logit transformations were necessary for total ledge attendance (or total area attendance), we converted total attendance to a true ratio by dividing the number of minutes the female plus the number of minutes the male spent at the nest ledge (or nest area), by twice the number of minutes per observation block. Because response variables included many values equal to 0 or 1, we added 0.5 times the minimum value of the response variable to Y for each proportion to avoid zero in the denominator or numerator of the logit-transformed term. Although some analyses were performed with transformed data and accounted for variables such as stage of the nesting cycle, brood size, and among-pair differences, we report arithmetic means and standard errors calculated from raw data.

We tested for differences in nest attendance, time-activity budgets, and nestling provisioning rates between overflown and baseline blocks using analysis of variance (ANOVA) and between overflown and reference blocks using nested ANOVAs. For the latter, nesting pairs were nested within treatment. For nest attendance and frequently performed activities (females incubating, males and females perching, and males unknown), we accounted for among-pair variability and stage of the nesting cycle. We restricted ledge-attendance analyses to incubation and early nestling rearing, when eggs and chicks are most dependent on parents for thermoregulation (Cade 1960). For activities that occurred infrequently (i.e., <25% of the time on average), we used Mantel-Haenszel odds ratio tests with continuity correction for small sample sizes and stratified by stage of the nesting cycle (Ramsey and Schafer 2002). We were unable to account for among-pair variability for tests on infrequently performed behaviors due to small sample sizes. When tests were significant, we used Fisher's Exact tests to determine differences among stages

(Ramsey and Schafer 2002). Infrequent activities included females away from nest area, males incubating or brooding, males or females feeding, males or females feeding young, and males or females flying. For nestling provisioning rates, we controlled for effects of brood size and stage of the nesting cycle by including them in the model. We treated nest sites independently among years. We reported all statistical differences with a $P \leq 0.10$ to minimize Type II error.

We used linear regression to assess the effects of overflights on nest attendance and nestling provisioning rates of 1) the number of observed overflights during a given observation block, 2) the cumulative number of overflights (both observed events and above-threshold events recorded by ANMs) that particular nests had been exposed to up to and including that observation block, and 3) the average SEL of detected overflights to occur within each observation block. We also used linear regression to assess the effects of the cumulative number of overflights on nest attendance and nestling provisioning rates. We accounted for stage of the nesting cycle and among-pair variability.

Results

Nest attendance and time-activity budgets

We detected some differences in nest attendance by parent peregrine falcons between overflown and reference blocks but not between overflown and baseline blocks. Male ledge attendance was lower during overflown blocks than reference blocks ($F_{1,101} = 8.87, P = 0.008$; Figure 2). Total ledge attendance, however, did not differ between overflown and reference blocks ($F_{1,101} = 0.32, P = 0.58$). Females apparently compensated for lower male ledge attendance by attending the nest ledge more during overflown compared to reference blocks ($F_{1,101} = 6.32, P = 0.022$; Figure 2). Similarly, area attendance was lower for males during overflown blocks than reference blocks ($F_{1,150} = 3.15, P = 0.089$), and this difference was most obvious during incubation ($F_{1,72} = 6.03, P = 0.026$; Figure 3). These differences in male area attendance were small, and although female area attendance did not differ between overflown and reference blocks ($F_{1,150} = 0.27, P = 0.61$), total area attendance also did not differ between overflown and reference blocks ($F_{1,150} = 0.74, P = 0.40$). No differences between overflown and baseline blocks were observed

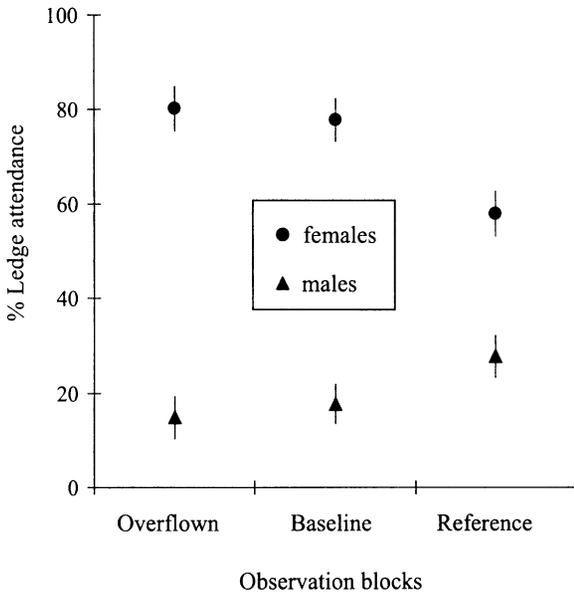


Figure 2. Average ledge attendance (\pm SE) during incubation and early nestling rearing for overflow, baseline, and reference observation blocks among peregrine falcons nesting along the Tanana River, Alaska, 1995, 1996, and 1997.

among any measure of nest attendance ($P > 0.5$ for all). Neither total ledge attendance nor total area attendance differed among years ($P > 0.5$ for both). Furthermore, neither was correlated with either the number of overflights per block, the average sound-exposure level (SEL) from overflights during

blocks, or the cumulative number of overflights to which a pair had been exposed ($P > 0.15$ for all).

We found little evidence that the incidence of frequently performed activities was influenced by overflights; differences corresponded with nest-attendance activities. Males spent more time away from the nest area during overflow blocks than reference blocks ($P = 0.066$). This was particularly evident during incubation ($P = 0.014$) and reflected male area attendance. There was no difference in the amount of time females spent incubating or males spent perching ($P > 0.25$ for all ANOVA tests).

Similarly, we found some evidence that infrequently performed activities differed between overflow and reference blocks but not between overflow and baseline blocks. Females were less likely to be away from the nest area during overflow than reference blocks ($\chi^2_1 = 4.55$, $P = 0.033$, Mantel-Haenszel test). This effect was most obvious during incubation and early nestling rearing ($P = 0.031$ and $P = 0.042$, respectively, Fisher's Exact Test; Figure 4), but by late nestling rearing there was no difference in the incidence of female "unknown" activities between overflow and reference blocks ($P = 0.63$, Fisher's Exact Test). Similar to attendance results, males were less likely to incubate during overflow than reference blocks ($\chi^2_1 = 2.77$, $P = 0.096$, Mantel-Haenszel test), and the trend was most obvious

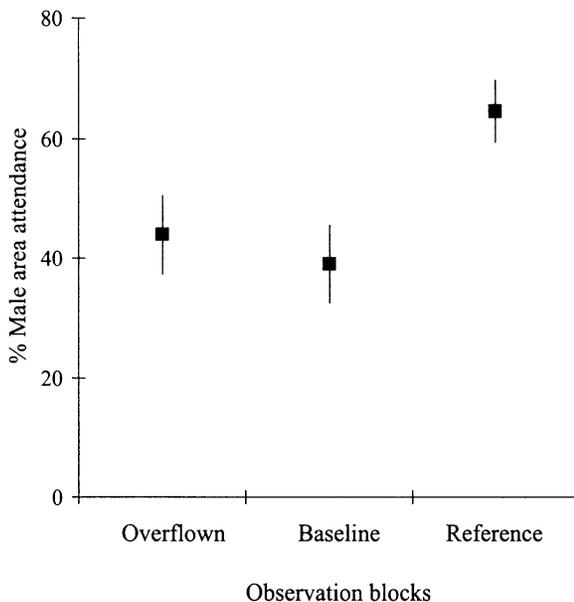


Figure 3. Average male area attendance (\pm SE) during incubation for overflow, baseline, and reference observation blocks among peregrine falcons nesting along the Tanana River, Alaska, 1995, 1996, and 1997.

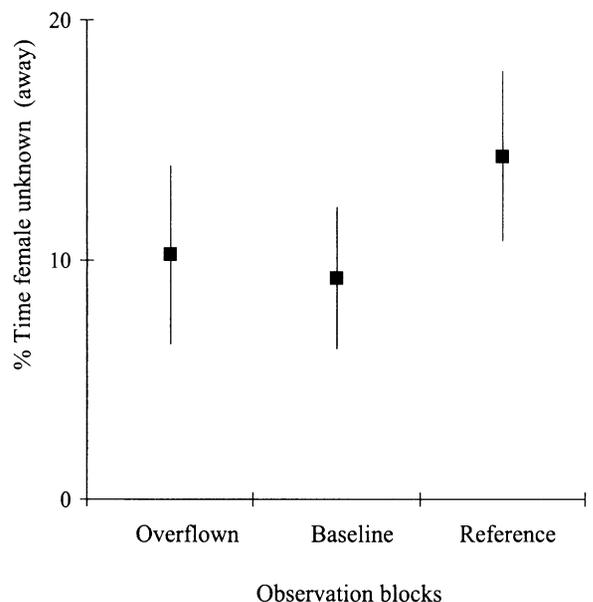


Figure 4. Average percent time females were "unknown" (away from nest area; \pm SE) during overflow, baseline, and reference observation blocks during incubation among peregrine falcons nesting along the Tanana River, Alaska, 1995, 1996, and 1997.

during incubation ($P=0.027$, Fisher's Exact Test). All other comparisons of infrequently performed activities among block types were not significant ($P>0.10$, for all Mantel-Haenszel tests).

Nestling provisioning rates

We found no evidence that overflights affected nestling provisioning rates. Neither prey-item delivery rates nor prey-mass delivery rates differed between overflown and baseline blocks or between overflown and reference blocks ($P>0.4$ for all ANOVA tests). Furthermore, we did not find a relationship between nestling provisioning rates and either the number of overflights per block or the average SEL from overflights during overflown blocks ($P>0.15$ for all tests).

Discussion

Our results provide very little support for the hypothesis that low-altitude jet aircraft overflights affect parental behavior of peregrine falcons. Our results suggest that peregrines exposed to low-altitude jet overflights may have adjusted their attendance patterns compared to reference nests. Males attended the nest ledge less during overflown than reference blocks, while total ledge attendance did not differ between overflown and reference blocks when all data were combined from incubation and early nestling rearing (Figure 2). In contrast, females attended more during overflown blocks than reference blocks (Figure 2) and were less likely to be away from the nest area during overflown blocks compared with reference blocks during incubation and early nestling rearing (Figure 4). Thus, peregrine falcon nest attendance and time-activity budgets differed during periods of overflights compared with reference nests, but differences depended on stage of the nesting cycle and gender and were not detected in comparisons between overflown and baseline blocks.

Among birds with bi-parental care, males generally allocate time and energy toward nest activities at a more constant rate through the course of the nesting cycle than females, whose time and energy allocated toward attending eggs and young during incubation and early nestling-rearing stages generally far exceed that of males. Females then shift to equal or lower attendance and provisioning rates compared with males following mid-nestling rearing (Trivers 1972, Collopy 1984). Decreased ledge attendance during overflown blocks as compared

to reference blocks early in the nesting cycle suggested that males were less likely to brood eggs or chicks during times of overflight disturbance, apparently requiring females to spend more time on these activities. Alternatively, females may have spent more time incubating or brooding during overflight disturbance. This was consistent with results from Nordmeyer (1999), who found that the incidence of flight reactions in response to overflights was higher in males than females and was related to stage of the nesting cycle. Females at overflown nests sat tighter on eggs and young and remained closer to the nest than those at reference nests. Other studies found early nestling rearing to be a stage when raptors generally are more sensitive to disturbance due to the high dependence of young on parents for defense and thermoregulation (Fyfe and Olendorff 1976).

Later in the season, differences in responses between males and females were less obvious and differed from effects observed early in the season. During late nestling rearing, females spent less time attending the nest area. This suggested avoidance of the nest area during periods of overflights late in the season, compared with reference nests. During late nestling rearing, when chicks can thermoregulate on their own, parents may have been inclined to avoid the nest area during periods of overflights, while not sensing a threat to their offspring from overflights. Immediate behavioral reactions by peregrine falcons to jet overflights rarely mimicked behavior typical of nest defense involving potential predators (Nordmeyer 1999); thus, it was unlikely that peregrine falcons perceived overflights as a threat to their offspring. This might explain why we observed avoidance responses to overflights rather than increased attendance for defensive purposes with progression of the nesting cycle, despite the fact that many studies suggest nest defense toward potential predators increases late in the nesting cycle (Trivers 1972, Dawkins and Carlisle 1976, Knight and Temple 1986).

Some reference nests were exposed to low numbers of noise events, yet they provided the best available nests for comparisons. Because military jet traffic was common in interior Alaska, it was unclear whether any nesting pair along the Tanana River contained truly naïve birds, even among nests outside of MTRs. The option of making comparisons with another major drainage like the lower Yukon River, which does not include military airspace, would introduce other uncontrolled variables like

prey availability, nest-site selection, and variable weather conditions. Overflown nests received more overflights than reference nests, and we made comparisons between overflown blocks at overflown nests and blocks from reference nests without overflights. In this study, reference nests provided the best controls in existence.

Although we found differences in nest attendance and time-activity budgets between overflown and reference nests, we did not detect differences between overflown and baseline blocks within the same nests. This may be due to a residual effect of overflights on nest attendance and time-activity budgets. Perhaps exposure to overflights caused pairs to alter their activity patterns beyond the length of 4-hr observation blocks. Alternatively, because baseline blocks were not independent from overflown blocks, differences between these types of blocks may have been more difficult to detect. Additionally, we did not observe a relationship among nest attendance and number of overflights that occurred in the block, cumulative number of exposures experienced by each nesting pair, or average SEL of overflights. Nor did we find evidence that nestling provisioning rates were influenced by low-altitude jet overflights. However, our results are interesting because effects occurred during incubation and nestling rearing and were more pronounced during these stages when direct human disturbance can be more detrimental to raptors (Fyfe and Olendorff 1976).

The literature indicates minimal effects of overflights on wildlife. Ellis et al. (1991) reported that peregrine falcons subjected to low-altitude jet aircraft overflights rarely exhibited direct responses to overflights, usually had minimal responses, and responses were never associated with reproductive failure. They did not examine nest attendance, time-activity budgets, or provisioning rates of peregrine falcons. Other studies have found minimal changes to time-activity budgets of birds exposed to aircraft or vehicular disturbance (Plumpton and Lutz 1993, Conomy et al. 1998a, Trimper et al. 1998). In particular, Trimper et al. (1998) reported no difference in osprey (*Pandion haliaetus*) nest attendance between pre- and post-jet overflight periods and control periods of observation. Similar to Trimper et al. (1998), we also did not observe differences between overflown blocks and the 2 types of control blocks in total ledge attendance or total area attendance. But our results differed from Trimper et al. (1998) in that we found that males and

females partitioned attendance responsibilities differently in relation to exposure to overflights. It was likely, however, that 2 different raptor species would have different responses to overflights; Conomy et al. (1998b), for instance, found that American black ducks (*Anas rubripes*) habituated to aircraft disturbance with time, while wood ducks (*Aix sponsa*) did not.

We detected subtle effects of jet overflights on peregrine falcon parental behavior, but there was no evidence that overall attendance patterns differed depending on exposure to overflights. Thus, the magnitude of these effects was insufficient to result in reduced productivity of nesting pairs (Nordmeyer 1999). The peregrine falcons in our study likely perceived overflights as a minimal threat to their progeny. Due to the short duration of overflights and their dissimilarity to natural nest predators, it may take more consecutive overflights to elicit a detectable response (Nordmeyer 1999). Given the number of overflights experienced by nesting peregrine falcon pairs in this study, measured effects appeared minor and depended on gender and stage of the nesting cycle. In the future, more efforts are needed to assess the roles of habituation and sensitization in the effects of jet aircraft overflights on raptor nesting behavior.

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