Factors Influencing Nest Attendance and Time-Activity Budgets of Peregrine Falcons in Interior Alaska

ANGELA G. PALMER,[1,2] DANA L. NORDMEYER[1,3] and DANIEL D. ROBY[1]

ABSTRACT. An essential prerequisite to examining the impacts of anthropogenic disturbance on avian nesting activities is understanding the intrinsic and extrinsic factors that influence the birds' allocation of time to breeding behaviors. We examined factors influencing nest attendance and time-activity budgets of peregrine falcons (*Falco peregrinus anatum*) breeding along the Tanana River in Alaska in 1995, 1996, and 1997. First, as is typical of most bird species with nidicolous young and biparental care, females attended the nest more than males and, as the nesting cycle progressed, female attendance decreased to levels similar to those of males. Second, nest area attendance followed a circadian rhythm; parents attended the nest area less during early morning and late evening, which are prime hunting periods, than during late morning. Finally, although females typically performed most of the incubating, the division of labor between males and females during incubation differed among pairs. Higher attendance in the nest area by females during incubation appeared to be associated with more young fledged among successful pairs.

Key words: peregrine falcon, *Falco peregrinus*, time-activity budgets, nesting success, nest attendance, Interior Alaska

RÉSUMÉ. Une condition indispensable pour examiner les retombées de la perturbation anthropique sur la nidification aviaire est la compréhension des facteurs intrinsèques comme extrinsèques qui influencent le temps consacré par l'oiseau à des comportements reproducteurs. On a étudié les facteurs qui ont influencé la présence au nid et les budgets temps-activités des faucons pèlerins (*Falco peregrinus anatum*) nichant le long de la rivière Tanana en Alaska en 1995, 1996 et 1997. Tout d'abord, comme on doit s'y attendre de la plupart des espèces aviaires dont les petits sont nidicoles et où les soins sont biparentaux, les femelles étaient présentes au nid plus que les mâles et, à mesure que le cycle de nidification avançait, la présence des femelles diminuait à des niveaux semblables à ceux de la présence des mâles. Deuxièmement, la présence aux environs du nid suivait un rythme circadien, les parents passant moins de temps près du nid au début de la matinée et en fin de soirée – temps forts de la chasse – qu'en fin de matinée. Enfin, même si en général les femelles se chargeaient en grande partie de la couvaison, la répartition du travail entre mâles et femelles durant l'incubation différait selon les paires. Durant l'incubation, la présence plus affirmée des femelles dans la zone du nid semblait être associée à un nombre supérieur de petits qui prenaient leur envol chez les paires qui avaient réussi à se reproduire.

Mots clés: faucon pèlerin, *Falco peregrinus,* budgets temps-activités, succès reproducteur, présence au nid, intérieur de l'Alaska

Traduit pour la revue *Arctic* par Nésida Loyer.

INTRODUCTION

In nidicolous bird species, parents divide their time mainly between attending the nest site and foraging for food away from the nest area. Most behaviors performed in the nest area, such as incubating and brooding, are associated with relatively low metabolic costs or low activity levels (Goldstein, 1988). Adults attending the nest also defend young against predators and provide shelter from severe weather. Thus the major cost to adults of nest attendance is lost foraging time, whereas the major cost of foraging away from the nest area is increased exposure of eggs and young to potential nest predation. The relative allocation of parents' time and energy to nest attendance versus foraging influences overall reproductive success (King, 1974; Nur, 1987), a key component of reproductive fitness.

Allocation of time and energy to various activities depends on both intrinsic and extrinsic factors. Intrinsic factors include age, hunting skills, and physiological condition of both members of a breeding pair (Rijnsdorp et al., 1981; Deerenberg et al., 1995; Marzluff et al., 1997). Extrinsic factors may include time of day, weather conditions, presence of potential nest predators, prey abundance, quality of territory, and human-related disturbance (Platt, 1975; Ritchie, 1987; Masman et al., 1988; Steidl, 1995). Different activities require different rates of energy expenditure (Gessaman, 1987; Goldstein, 1988), and disturbance to a breeding pair may lead to increased energy

demands, reduced hunting efficiency, or suboptimal allocation of time to nest attendance and foraging. It is essential to understand the underlying intrinsic and extrinsic factors that influence the time-activity budgets of nesting birds before examining the effects of potential disturbance factors on breeding behavior.

As part of a larger study of the effects of disturbance on reproduction and nesting behavior in peregrine falcons, we examined factors influencing nest attendance and time-activity budgets of breeding adults in Interior Alaska. Historical research on peregrine falcons in Alaska has focused on reproductive parameters and population status (Cade, 1960; White, 1969; Ambrose et al., 1988; Wright and Bente, 1999). Additionally, Ritchie (1987) investigated peregrine behavior on the Sagavanirktok River, Alaska, in response to disturbances; however, sample sizes were small. In this study we had a larger sample size. We investigated differences in parental attendance at the nest as a function of nesting stage, gender, time of day, weather, and nesting pair. In addition, we studied variation in time-activity budgets associated with nesting stage and gender.

We posed several hypotheses regarding nest attendance and time-activity budgets in breeding peregrine falcons. First, because of changing requirements for parental care by eggs and chicks as they develop, we expected shifts in parental attendance and time-activity budgets over the course of the breeding cycle, and between genders. Second, parental nest attendance should exhibit circadian patterns and be influenced by abiotic factors, such as weather. We expected attendance to be lower towards dawn and dusk, prime hunting times when the avian prey of peregrines are more active (Armstrong, 1954). Furthermore, we expected higher attendance during more inclement weather, when maintenance energy costs of young are higher (Buttemer et al., 1986), prey are less active, and energetic costs of hunting are likely higher. Finally, we predicted that individual pairs might differ in how the sexes allocated time to nest attendance and other reproductive tasks. Differences among pairs in nest attendance and time-activity budgets may be related to reproductive parameters like the number of young fledged per nesting attempt.

METHODS

Study Area

The study area encompassed a 250 km stretch of the Tanana River between Tok and Fairbanks (from 63°8′ N, 143°36′ W to 64°18′ N, 148°45′ W). In 1995, the study area extended from Tanacross to Sawmill, or approximately 110 km. Thirteen active peregrine falcon nest sites were found along this stretch of the river. Of these, we selected 10 for observation. In 1996 and 1997, we included an additional 65 km section of the river from Delta to Salcha.

We found a total of 19 active nests in 1996 and 21 in 1997, along both stretches of river. In both 1996 and 1997, we observed six nests in the upper stretch and five nests in the lower stretch. Nests were situated on bluffs overlooking the river. Our selection of nests for observation was based on access to observation sites opposite cliffs and visibility of the nest ledge from the observation sites. Observations were initiated each year in mid-May, as soon as it was safe to travel on the river after ice breakup, and continued until late August or early September, when the young had fledged and left the nest area. A crew of two to four observers recorded data at each peregrine falcon nest, and two separate crews were in the field throughout each season. We observed the behavior of adults and nestlings at a distance of 300 m from the nests and across at least one channel of river.

Nest Attendance and Time-Activity Budgets

We made observations with the aid of binoculars, 15–60× spotting scopes, and 90× Questar® telescopes. During incubation, two observers recorded data on nest attendance and time-activity budgets. In 1995, two observers recorded data during the nestling-rearing period. In 1996 and 1997, the number of observers was increased to three during nestling-rearing. In all years, there were four observers during the post-fledging stage of the nesting cycle when young were not restricted to the nest ledge. The number of chicks fledged per nesting attempt was recorded at each nest site.

We used the instantaneous scan method (Altmann, 1974; Tacha et al., 1985) to sample activity for each parent at one-minute intervals. Scans contributed data to both nest attendance and time-activity budgets. For nest attendance, we distinguished between attendance at the nest ledge or scrape, in the nest area (within 200 m of the nest ledge), and away from the nest area (more than 200 m from the nest ledge or scrape, or not observed within the nest area). For time-activity budgets, we recorded adult activity as one of the 16 mutually exclusive primary activities listed in Table 1. For analysis, we lumped primary activities into six categories (Table 1). Incubation, brooding, and shading activities were combined because they all involve thermoregulation of eggs or young. The other activity categories used in analyses were perching, feeding self, feeding young, flying, and unknown. We categorized birds as out of sight (OS1 or OS2, see Table 1) for no longer than five minutes after they were last seen. Adults were classified as "unknown," or away from the nest area if they were not seen again within 5 minutes.

We collected observations during three phases of the peregrine falcon nesting cycle: incubation, nestling-rearing, and post-fledging. The duration of other phases (courtship and pre-laying, laying, and hatching) is comparatively short, and sample sizes during these stages were correspondingly small. Of the 10 nests selected in 1995, we observed 5 during incubation, 9 during nestling-rearing,

TABLE 1. Activity categories for time-activity budgets of peregrine falcons breeding along the Tanana River, Alaska.

Activity Categories[1]	Primary Activities
Incubating/Brooding/Shading	*incubating*: prone posture covering eggs *out of sight (OS1)*: on the nest ledge/scrape, but out of sight, e.g., in a cavity at the nest ledge *brooding*: covering nestlings, wing may be slightly off to the side *shading young*: shielding nestlings from direct sunlight
Perching	*perching*: standing on one or both feet within 200 m of nest sight *out of sight (OS2)*: known to be on nest cliff, but out of sight, e.g, obscured by vegetation or rock outcrop; adults were classified as unknown if their location was not verified after five minutes.
Feeding Self	*feeding self*: consuming prey
Feeding Young	*feeding young*: feeding prey to nestlings or known to be feeding young but out of view, possibly in a cavity
Flying	All flight behaviors: *flapping*: active flight that involves wing flapping *soaring or gliding*: passive flight with little to no wing movement *stooping*: wings tucked, in downward pursuit of prey from altitude *diving*: Aggressive attack on prey or predator
Unknown	*location unknown*: assumed to be away from the nest site in flight, foraging, or perching

[1] Other behaviors—*lying* (with sternum resting on the ground), *walking*, and *running*—occurred less than 1% of the time.

and 4 during post-fledging. Only one nest was observed during all three phases. In 1996, we sampled behavior during incubation, nestling-rearing, and post-fledging at 7 of 11 nests. The other four nests were not sampled during each of the three phases because two nests failed following incubation and were replaced by two other nests initiated by different pairs. In 1997, we sampled behavior during all three phases at 9 of 11 nests; of the remaining nests, one failed after incubation and was replaced by another pair's nest during nestling-rearing.

For analysis, the nestling-rearing phase was further subdivided into three stages: early (0–10 days), mid (11–24 days), and late (25–42 days) after hatching. Consequently, we conducted analyses on five stages of the nesting cycle: incubation; early, mid, and late nestling-rearing; and post-fledging. Stage of the nestling-rearing phase was determined by estimating the age of the oldest chick. Estimates were made during banding visits to the nest in mid nestling-rearing period and were based on feather development and comparisons to Nelson's (1970) drawings of chicks.

We divided the day into six 4-hour time-blocks covering the 24-hour period. The first 4-hour time-block began at midnight Alaska Daylight Time (ADT), two hours before solar midnight in Interior Alaska. Lack of daylight precluded some observations during the first time-block. Where possible, we sampled activity for a minimum of one hour within each time-block at each nest during each phase. In all years, however, observations were concentrated between 8:00 and 17:00 ADT. We sampled behavior during 37, 65, 183, 175, 141, and 59 observation blocks from time-blocks 1 through 6, respectively.

For analyses, we grouped one-minute scan samples within specific 4-hour time-blocks. These groupings were referred to as "observation blocks." We grouped scans to avoid autocorrelation in the data from one-minute scans.

Scans were eliminated from the total number in an observation block if visibility was poor or if gender of the parent falcons was indistinguishable. Observation blocks were discarded if the total number of scans within a given observation block was less than 60, if visibility was poor, or if the sexes remained indistinguishable throughout the observation block. Thus, the data used in analyses were collected during a total of 660 observation blocks over the three years. Observations of adults at the same nest, but in different years, were considered independent.

Two video cameras equipped with 250 mm lenses and 2× extenders were employed to record behaviors of adults continuously at or near the nest scrape during observations. During incubation and nestling-rearing phases, one camera was focused on the nest ledge, while the other was focused on the attending adult. During the post-fledging phase, we focused on fledglings or adults as their visibility allowed. Videotapes confirmed ledge attendance during periods when incubating or brooding adults were not directly visible to observers.

We measured weather parameters, including temperature (°C), wind speed (km/h), and precipitation, every hour from the observation site. Precipitation was assessed as none, low (drizzle or light rain), medium (steady rain), or high (downpour). For temperature and wind speed, we averaged measurements over each observation block. For precipitation, we used the highest level that occurred in each observation block.

Sample Units and Statistical Analyses

To calculate ledge attendance by each member of a pair, we divided the number of minutes the female or male spent at the nest ledge or scrape by the number of minutes in the observation block. We used female plus male ledge attendance as a measure of total ledge attendance by a pair.
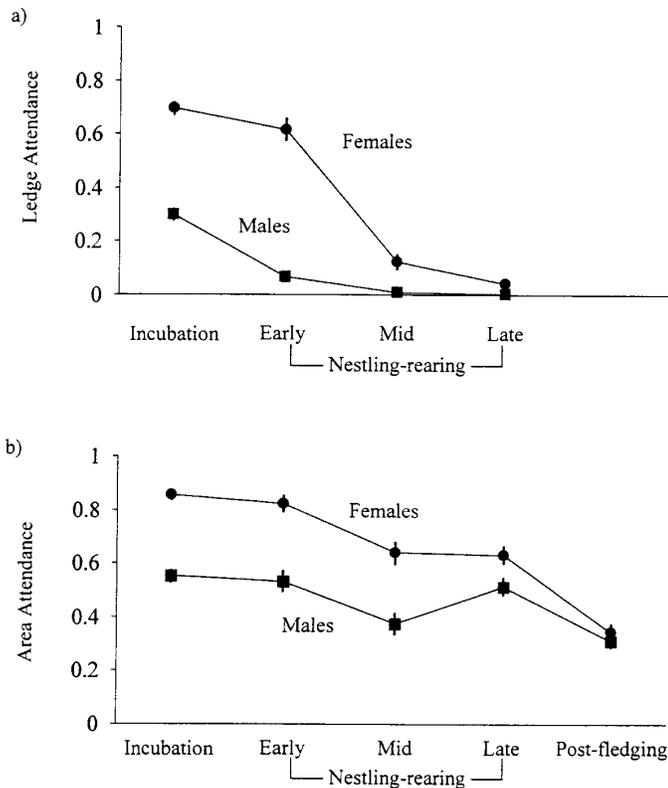
a)

b)

FIG. 1. Nest attendance (± SE) as a function of stage of the nesting cycle for peregrine falcons breeding along the Tanana River, Alaska.

Similarly, we measured area attendance of each parent by dividing the number of minutes each parent spent at the nest ledge or in the nest area (within 200 m of the ledge or scrape) by the number of minutes in the observation block and used female plus male area attendance to estimate total area attendance by the pair. The sample unit for time-activity budgets was the number of minutes the parent spent performing a particular activity divided by the total number of minutes per observation block.

We used analysis of variance (ANOVA) and Bonferroni's multiple comparison procedure to detect differences in attendance patterns among stages of the nesting cycle, time-blocks, and nesting pairs. We also used linear regression to examine the significance of three weather variables (temperature, wind speed, and precipitation) for attendance. For analysis of patterns in ledge attendance, we did not include data from the post-fledging stage of the nesting cycle, when ledge attendance was rare. To investigate gender roles in nesting activities, we examined the ratio of female attendance to total attendance for departures from 0.50, which would indicate unequal attendance by the two sexes. We also assessed changes in the ratio across stages.

We used ANOVAs and Bonferroni's multiple comparison procedure to assess differences in time-activity budgets between stages of the nesting cycle and paired t-tests (or paired signed rank tests for non-normal data) to compare time-activity budgets between the sexes. For activities that were performed infrequently, we used χ^2 tests for
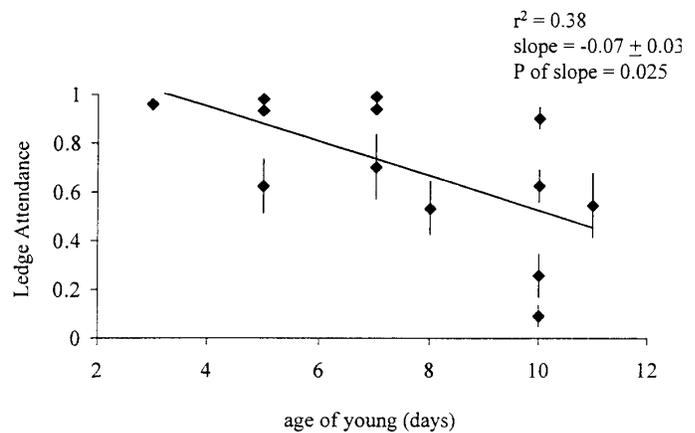

FIG. 2. Total ledge attendance (± SE) per nest during early nestling-rearing in relation to chick age for peregrine falcons breeding along the Tanana River, Alaska.

homogeneity to test for differences between sexes. All tests were conducted at the 0.05 α level. Means are reported as x (± SE).

We used logit transformations $(\log(Y/(1-Y)))$ to normalize data where necessary. When logit transformations were necessary for total nest attendance, we converted total attendance to a true ratio for both ledge attendance and area attendance. In the case of total ledge attendance, we divided the number of minutes the female spent at the nest ledge or scrape, plus the number of minutes the male spent at the nest ledge or scrape, by twice the number of minutes per observation block. Similarly, to calculate total area attendance, we divided the number of minutes the female spent either at the nest ledge or in the nest area (within 200 m of the ledge or scrape), plus the number of minutes the male spent either at the nest ledge or in the 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, we report arithmetic means and standard errors calculated from untransformed data.

RESULTS

Nest Attendance

Ledge attendance differed among stages of the nesting cycle. Through the course of the nesting cycle, ledge attendance declined, after controlling for nesting pair $(F_{3,504} = 774, p < 0.0001$; Fig. 1a). During incubation, total ledge attendance averaged 0.99 (± 0.018) among 24 nests. During the early nestling-rearing stage, total ledge attendance was initially high but gradually decreased to chick age 11 days ($r^2 = 0.38, p = 0.025$; Fig. 2). Most visits to the nest ledge during subsequent stages were limited to prey
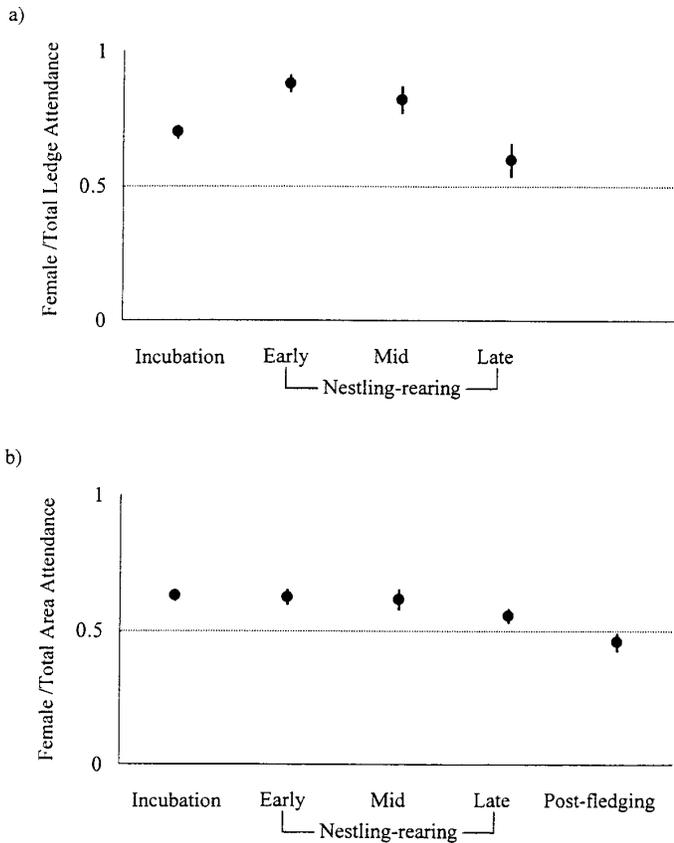
a)

b)

FIG. 3. The ratio of female attendance to total attendance (± SE) as a function of nesting stage of peregrine falcons breeding along the Tanana River, Alaska.

deliveries and feeding of young; thus ledge attendance was low following the early nestling-rearing stage (Fig. 1a). Similarly, area attendance declined with nesting stage, after controlling for nesting pair, but not as markedly ($F_{4, 661} = 63$, $p < 0.0001$; Fig. 1b), with lowest levels during post-fledging ($p < 0.05$).

The ratio of female attendance to total attendance is an indication of the division of labor within a pair. Both the ratio of female ledge attendance to total ledge attendance and the ratio of female area attendance to total area attendance differed from 0.50 (t-stat = 11.9, $p < 0.0001$, n = 660 and t-stat = 9.3, $p < 0.0001$, n = 660, respectively). Furthermore, these ratios for both ledge and area attendance differed among nesting stages, after accounting for nesting pair ($F_{3, 411} = 6.18$, $p = 0.0004$; and $F_{4, 632} = 11.22$, $p < 0.0001$, respectively; Fig. 3). The ratio of female ledge attendance to total ledge attendance was greater than 0.50 during all stages of the nesting cycle (Fig. 3a). The ratio increased from incubation to early nestling-rearing ($p < 0.05$) and then decreased in subsequent stages of the nesting cycle (Fig. 3). Unlike the ratio of female ledge attendance to total ledge attendance, the ratio of female area attendance to total area attendance decreased with each consecutive stage of the nesting cycle, after accounting for nesting pair (Fig. 3b). During post-fledging, the ratio of female area attendance to total area attendance was actually less than 0.50 (95% confidence interval: 0.38 to 0.49).

There was no difference in total ledge attendance among different time-blocks, after accounting for stage of the nesting cycle and nesting pair ($p > 0.05$ for family-wise comparisons); however, area attendance did differ among time-blocks ($F_{5, 659} = 4.81$, $p = 0.0003$). Specifically, area attendance was lower ($p < 0.05$) during time-block 1 (0:00 hrs to 04:00 hrs; 0.87 (± 0.11)) and time-block 6 (20:00 hrs to 24:00 hrs; 1.01 (± 0.4)) than during time-block 3 (08:00 hrs to 12:00 hrs; 1.26 (± 0.06)). Although both sexes exhibited this attendance pattern in the nest area, it was significant only among males. Males had higher attendance during time-block 3 than during other time-blocks ($F_{5, 659} = 5.02$, $p = 0.0002$).

None of the three weather variables (temperature, wind speed, or precipitation) explained a significant proportion of the variation in attendance while controlling for nesting stage and nesting pair.

Differences in nest attendance among pairs were most obvious during incubation. During this stage, differences in area attendance among pairs were highly significant ($F_{23, 209} = 4.45$, $p < 0.0001$). Differences in area attendance were highly significant among both males ($F_{23, 209} = 2.48$, $p = 0.0004$) and females ($F_{23, 209} = 2.36$, $p = 0.0009$) when separated by sex (Fig. 4). However, there was no correlation between a female's area attendance and that of her mate (two-sided t-test for a test that the slope is zero = -0.53, $p = 0.60$). Among successful pairs, females that attended the nest area more during incubation raised more young, but this trend only approached significance (two-sided t-test for a test that the slope is zero = 2.0, $p = 0.061$; Fig. 5). Male area attendance was negatively correlated with female ledge attendance (two-sided t-test for a test that the slope is zero = -4.61, $p = 0.0001$). Finally, while total ledge attendance did not differ among pairs (Kruskal-Wallis test statistic = 29.09, $p = 0.18$), the division of labor between the sexes did vary among pairs: for differences among females, $F_{23, 209} = 1.83$, $p = 0.0155$; among males, $F_{23, 209} = 1.77$, $p = 0.0208$ (Fig. 6).

Time-activity Budgets

For both females and males, mean proportion of time spent in each activity per observation block changed significantly with nesting stage, except for the activity category "females feeding self," after accounting for nesting pair (Tables 2 and 3). On average, females spent over twice as much time incubating (68.4 ± 2.2%) as males did (29.0 ± 2.1%; $p < 0.0001$, paired t-test). Females brooded young much more than did males during early nestling-rearing ($p < 0.0001$, paired t-test; Fig. 7a), though levels of this activity were lower than during incubation for both sexes ($p < 0.05$ for both).

Perching time at the nest area also differed among nesting stages and between sexes. Mean proportion of time spent perching by females during incubation, early nestling-rearing, and post-fledging was lower than during mid and late nestling-rearing ($p < 0.05$; Fig. 7b). Perching time
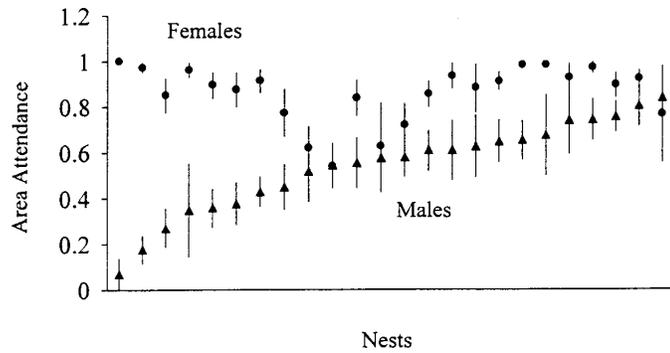
FIG. 4. Differences in area attendance (± SE) during incubation among peregrine falcon pairs breeding along the Tanana River, Alaska, in ascending order of male area attendance.
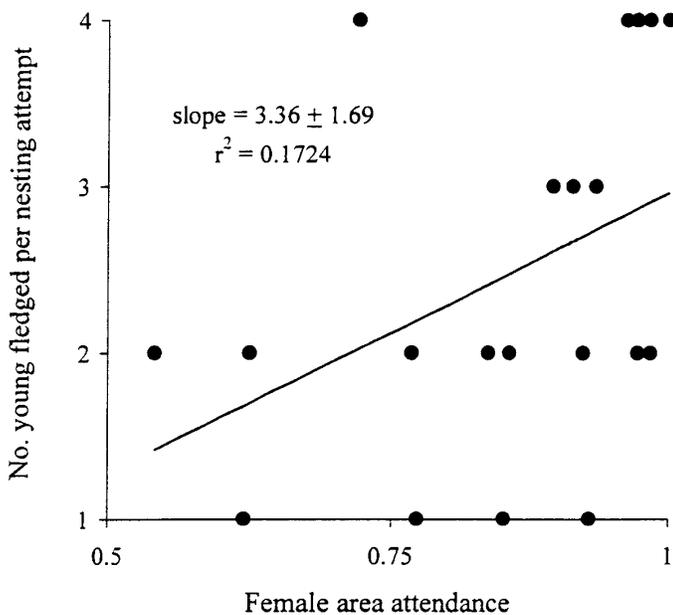

FIG. 5. Number of young fledged per nesting attempt among successful nests in relation to female area attendance during incubation in peregrine falcons breeding along the Tanana River, Alaska.

in males was lower during incubation and post-fledging than during early and late nestling-rearing, whereas perching time during mid nestling-rearing was not significantly different from perching time during early and late nestling-rearing ($p < 0.05$). Comparing the incidence of perching between the sexes, females perched less than males during incubation and early nestling-rearing ($p = 0.022$ and $p = 0.0078$, respectively; paired signed rank tests), but more than males during mid and late nestling-rearing ($p = 0.029$ and $p = 0.0006$, respectively; paired signed rank tests; Fig. 7b). During post-fledging, the incidence of perching did not differ between the sexes ($p = 0.78$; paired signed rank tests; Fig. 7b).

Other activities that occurred infrequently differed either with nesting stage, or gender, or both. Mean proportion of time spent feeding young gradually decreased with stage of the nesting cycle for both females and males, most dramatically between early and mid nestling-rearing for

females ($p < 0.05$, Fig. 7c). Comparing sexes, females fed young during a greater proportion of observation blocks than males in each stage of the nestling-rearing period ($p < 0.0001$ (early), $p < 0.0001$ (mid), and $p = 0.0088$ (late); χ^2 tests for homogeneity). Males fed themselves in the nest area more during nestling-rearing than during both incubation and post-fledging. Females fed themselves in the nest area during more observation blocks (79 of 660) than males (51 of 660), a difference of 35.4% ($\chi^2 = 6.2$, df = 1, $p = 0.013$, test for independence between sex and activity with Yates' correction; Fig. 7d). Finally, the proportion of time spent flying by females ($1.6 \pm 0.19\%$) and males ($2.4 \pm 0.20\%$) was low overall. The incidence of flying was higher for females during nestling-rearing than during incubation ($p < 0.05$; Fig. 7e) and higher for males during late nestling-rearing and post-fledging than during incubation ($p < 0.05$; Fig. 7e).

DISCUSSION

Stage of the nesting cycle and gender were prominent factors influencing nest attendance and time-activity budgets (Figs. 1–3 and 7). Nest attendance and activities associated with low energetic cost dominated early stages of the nesting cycle (Figs. 1a and 7a). This implies that nesting success during incubation and chick brooding could be disproportionately affected by factors like disturbance, because disturbance may shift activities away from thermoregulation of eggs and young chicks and towards territorial defense. Indeed, peregrine chicks are sensitive to extreme temperatures during breeding (Palmer, 1988). Following chick brooding, perching by females and flying by both sexes increased through the nestling-rearing stage (Figs. 7b and 7e). For females, this likely allowed for increased hunting (both perch-hunting and flight-hunting) when chicks were larger and had higher physiological demands. Similarly, males spent more time flying, an activity linked to hunting (Ratcliffe, 1993), perhaps to provision older chicks.

The increasing energetic requirements of large chicks, combined with the declining physiological state of parents, may dictate gender roles as well (Court et al., 1990). The increased proportion of female ledge attendance to total ledge attendance from incubation to early nestling-rearing may reflect the new pressure on males to provide for both young chicks and females, while the chicks still require brooding, performed primarily by the female. General accounts of peregrine breeding behavior indicate that females assume the majority of incubating and brood rearing, and males conduct most of the hunting (Palmer, 1988; Ratcliffe, 1993). Our results on nest attendance and time-activity budgets concur with these results. However, our results also show a steady decline in the ratio of female area attendance to total area attendance with the progression of the nesting cycle, which may indicate that larger chicks compel females to hunt for larger or more prey.

TABLE 2. Time-activity budgets in relation to stage of the nesting cycle for female peregrine falcons breeding along the Tanana River, Alaska. Significant differences are reported.

Stage of the nesting cycle	n[1]	Activity category				
		Incubate/brood	Perch	Feed self	Feed young	Fly
Incubation	210	68.4 (2.2)[2]	18.4 (1.7)	0.33 (0.08)	–	0.7 (0.1)
Early Nestling-rearing	91	42.9 (4.1)	35.6 (3.5)	0.07 (0.07)	3.7 (0.5)	2.0 (0.6)
Mid Nestling-rearing	80	4.8 (1.9)	53.6 (4.0)	0.01 (0.06)	1.9 (0.4)	2.1 (0.4)
Late Nestling-rearing	122	–	59.6 (3.1)	0.33 (0.01)	1.0 (0.2)	2.7 (0.5)
Post-fledging	157	–	34.7 (2.9)	0.55 (0.02)	0.2 (0.8)	2.4 (0.7)
F[3]	–	86.1	28.2	0.42	25.0	7.9
dfn, dfd[4]	–	2, 349	4, 659	4, 659	3, 449	4, 659
p	–	< 0.0001	< 0.0001	0.80	< 0.0001	< 0.0001

[1] n = number of observation blocks per stage for all nests combined.

[2] mean percent time (SE).

[3] F-tests took into account differences among pairs.

[4] dfn = degrees of freedom numerator, dfd = degrees of freedom denominator.

- = not applicable.

TABLE 3. Time-activity budgets in relation to stage of the nesting cycle for male peregrine falcons breeding along the Tanana River, Alaska. Significant differences are reported.

Stage of the nesting cycle	n[1]	Activity category				
		Incubate/brood	Perch	Feed self	Feed young	Fly
Incubation	210	29.0 (2.1)[2]	25.8 (1.2)	0.16 (0.08)	–	1.4 (0.2)
Early Nestling-rearing	91	2.4 (0.9)	47.8 (3.7)	0.35 (0.14)	0.74 (0.30)	2.4 (0.5)
Mid Nestling-rearing	80	–	36.6 (3.7)	0.28 (0.11)	0.13 (0.07)	2.0 (0.4)
Late Nestling-rearing	122	–	49.3 (3.0)	0.25 (0.10)	0.14 (0.07)	2.9 (0.5)
Post-fledging	157	–	31.9 (2.4)	0.15 (0.05)	0.01 (0.01)	2.7 (0.3)
F[3]	–	40.9	10.76	2.32	3.05	3.08
dfn, dfd[4]	–	1, 300	4, 659	4, 659	3, 449	4, 659
p	–	< 0.0001	< 0.0001	0.056	0.029	0.016

[1] n = number of observation blocks per stage for all nests combined.

[2] mean percent time (SE).

[3] F-tests took into account differences among pairs.

[4] dfn = degrees of freedom numerator, dfd = degrees of freedom denominator.

- = not applicable.

Because they are larger than males, female raptors can deliver larger prey (Mearns, 1983; Palmer, 1988), and larger prey are sometimes associated with longer periods away from the nest area (Palmer, 1999). Alternatively, females may spend less time guarding the nest area as the nesting cycle progresses because the young are more independent and require less thermoregulation by parents.

During the post-fledging stage, parental area attendance was lower than during other stages. Low attendance during post-fledging may have reflected parents' avoidance of their begging young (Sherrod, 1983). As young gained the coordination to feed themselves during nestling-rearing, the amount of time parents spent feeding young decreased (Fig. 7c). Also, post-fledging brings on a stage when chicks are less attached to the nest area, and thus free to hunt and eat away from the nest area with parents (Sherrod, 1983), as they prepare for migration. These attendance and activity patterns are typical of other raptors (Wakeley, 1978; Levenson, 1981; Collopy, 1984; Collopy and Edwards, 1989)

Another factor that may influence peregrine falcon nest attendance is the daily rhythm of activity in their prey. Peregrines feed primarily on other birds (Ratcliffe, 1993), and passerines, shorebirds, and waterfowl display circadian rhythms of activity, even in the Arctic summer (Armstrong, 1954). Therefore, we expected falcons to trade off high levels of nest attendance for hunting opportunities early and late in the day (Pyke et al., 1977). The data supported this hypothesis; area attendance during early morning and late evening was lower than during late morning. The data were also in agreement with Bird and Aubry (1982), who reported more hunting attempts and more prey captured by peregrine falcons during the first hours of daylight.

Weather was not a significant factor influencing nest attendance, after accounting for stage of the nesting cycle and nesting pair. Although we observed parent peregrine falcons during inclement weather in the three breeding seasons, the vast majority of observation blocks did not include extreme weather conditions. Indeed, average wind
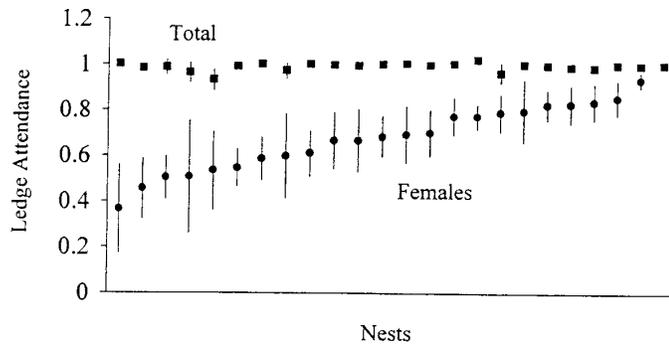
FIG. 6. Differences in ledge attendance (± SE) during incubation among peregrine falcon pairs breeding along the Tanana River, Alaska, in ascending order of female ledge attendance.

speed was below 7 mph for 90% of observation blocks, 80% of average temperatures were between 9°C (48°F) and 22.5°C (72.5°F), and 83% of observation blocks included no rainfall. In the absence of more observation blocks with adverse weather, it may be difficult to detect a significant correlation between weather conditions and behavior. However, weather can influence peregrine falcon breeding success and behavior. For example, periodic yet rare severe weather over the course of 13 years influenced chick survival of peregrine falcons in the Northwest Territories (Bradley et al., 1997).

Although female peregrine falcons typically perform most of the incubating (Cade, 1960; Nelson, 1970; Palmer,

1988; Ratcliffe, 1993; this study), we found gender roles were not consistent among pairs. Some females allocated nearly all of their time to incubation, while other pairs divided the role of incubation more evenly between the sexes (Fig. 6). Cade (1960) found similar variability in incubation sharing between the sexes among peregrines bred in captivity. Differences among pairs in gender roles may be attributable to a variety of conditions, such as mate quality, territory quality, food availability, or mate age. Males that allocate more time to hunting may enable females to focus on consistent nest guarding. We found that male area attendance was negatively correlated with female ledge attendance. "Quality" females that sat tight evidently had mates that hunted for them. In turn, this cooperation may have led to production of more young, as seen in the apparent relationship between higher female area attendance and more chicks fledged (Fig. 5).

Others report congruent findings for other raptors. Ward and Kennedy (1996) attributed higher nestling survival among supplementally fed northern goshawk (*Accipiter gentilis*) chicks to higher female nest attendance, which presumably deterred predators. Similarly, Newton (1986) remarked that high female nest attendance among sparrowhawks (*Accipiter nisus*) was associated with better chick growth and survival.

In summary, we found that several intrinsic and extrinsic factors influenced nest attendance and time-activity budgets of nesting peregrine falcons. We observed prominent
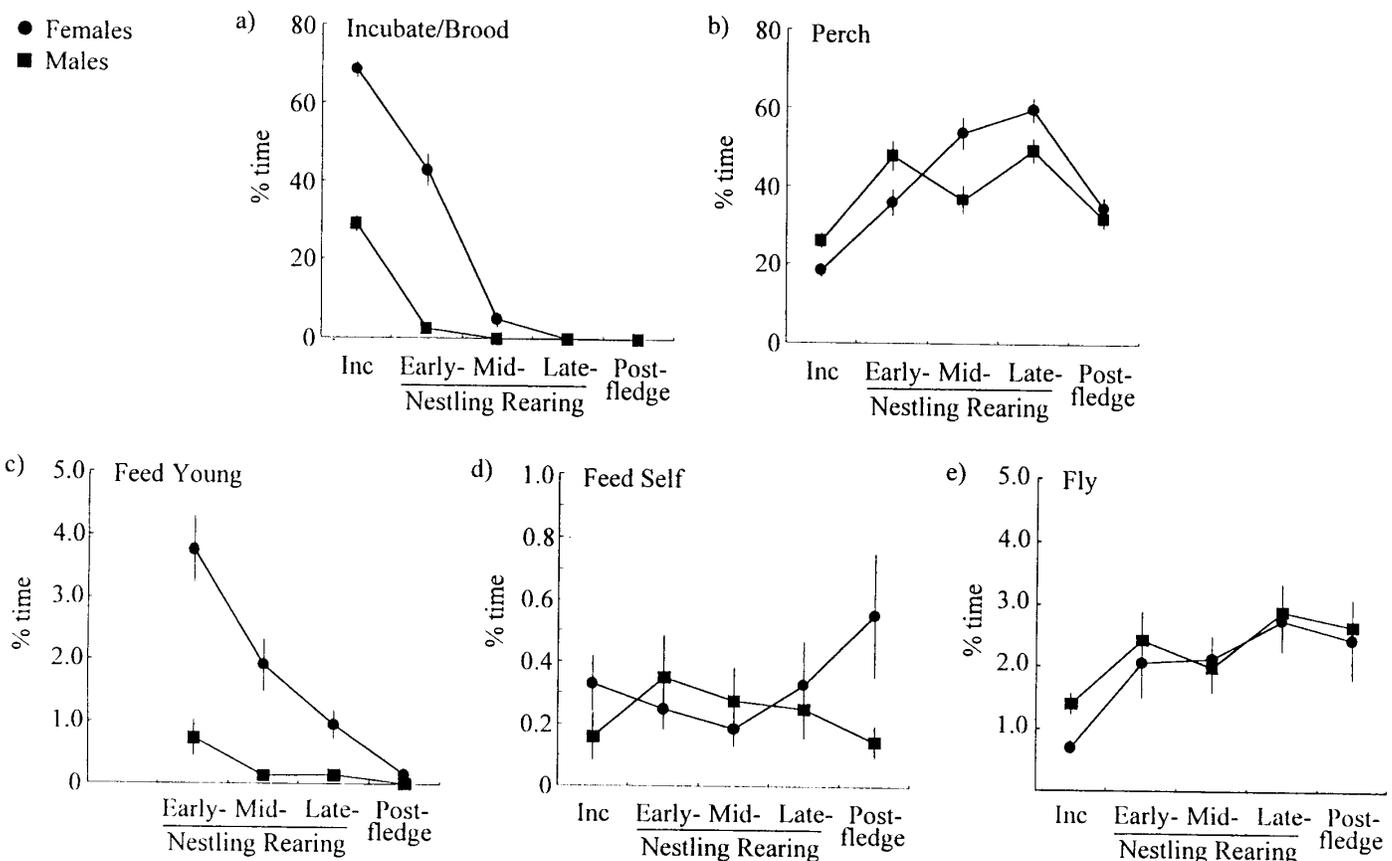

FIG. 7. Time-activity budgets (± SE) in relation to stage of the nesting cycle for peregrine falcons breeding along the Tanana River, Alaska.

differences among stages of the nesting cycle and between the sexes. While sexual differences in area attendance were pronounced during early stages of the nesting cycle, they became negligible after the young fledged. Nest area attendance was lowest during early mornings and late evenings, coinciding with periods when prey were most active. Finally, we found that gender roles varied among pairs. Among successful pairs, females with higher attendance in the nest area during incubation appeared more likely to fledge more young. Eggs appeared to require strict ledge attendance, yet variation in area attendance may also be linked to reproductive parameters like the number of chicks fledged. Further investigations should examine the influence of mate quality and territory quality on the division of labor in relation to reproductive success.

ACKNOWLEDGEMENTS

REFERENCES

ALTMANN, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49:227–267.

AMBROSE, R.E., RITCHIE, R.J., WHITE, C.M., SCHEMPF, P.F., SWEM, T., and DETTRICK, R. 1988. Changes in the status of peregrine falcon populations in Alaska. In: Cade, T.J., Enderson, J.H., Thelander, C.G., and White, C.M., eds. Peregrine falcon populations: Their management and recovery. Boise, Idaho: The Peregrine Fund, Inc. 73–82.

ARMSTRONG, E.A. 1954. The behavior of birds in continuous daylight. Ibis 96:1–30.

BIRD, D.M. 1983. Biology and management of bald eagles and ospreys. Ste. Anne de Bellevue, Quebec: Harpell Press.

BIRD, D.M., and AUBRY, Y. 1982. Reproductive and hunting behavior in peregrine falcons, *Falco peregrinus*, in southern Quebec. Canadian Field-Naturalist 96:167–171.

BRADLEY, M., JOHNSTONE, R., COURT, G., and DUNCAN, T. 1997. Influence of weather on breeding success of peregrine falcons in the Arctic. Auk 114:786–791.

BUTTEMER, W.A., HAYWORTH, A.M., WEATHERS, W.W., and NAGY, K.A. 1986. Time-budget estimates of avian energy expenditure: Physiological and meteorological considerations. Physiological Zoology 59:131–149.

CADE, T.J. 1960. Ecology of the peregrine and gyrfalcon populations in Alaska. University of California Publications in Zoology 63:151–290.

COLLOPY, M.W. 1984. Parental care and feeding ecology of golden eagle nestlings. Auk 101:753–760.

COLLOPY, M.W., and EDWARDS, T.C., Jr. 1989. Territory size, activity budget, and role of undulating flight in nesting golden eagles. Journal of Field Ornithology 60:43–51.

COURT, G.S., GATES, C.C., BOAG, D.A., MacNEIL, J.D., BRADLEY, D.M., FESSER, A.C., PATTERSON, J.R., STENHOUSE, G.B., and OLIPHANT, L.W. 1990. A toxicological assessment of peregrine falcons, *Falco peregrinus tundrius*, breeding in the Keewatin District of the Northwest Territories, Canada. The Canadian Field-Naturalist 104:255–272.

DEERENBERG, C., PEN, I., DIJKSTRA, C., ARKIES, B., VISSER, F.H., and DAAN, S. 1995. Parental energy expenditure in relation to manipulated brood size in the European kestrel *Falco tinnunculus*. Zoology 99:39–48.

GESSAMAN, J.A. 1987. Energetics. In: Giron Pendleton, B.A., Millsap, B.A., Cline, K.W., and Bird, D.M., eds. Raptor management techniques manual. Washington, D.C.: National Wildlife Federation. 289–320.

GOLDSTEIN, D.L. 1988. Estimates of daily energy expenditure in birds: The time-energy budget as an integrator of laboratory and field studies. American Zoologist 28:829–844.

KING, J. 1974. Seasonal allocation of time and energy resources in birds. In: Paynter, R.A., ed. Avian energetics. Cambridge, Massachusetts: Nuttall Ornithology Club. 4–85.

LEVENSON, H. 1981. Time and activity budget of ospreys nesting in northern California. Condor 81:364–369.

MARZLUFF, J.M., KIMSEY, B.A., SCHUECK, L.S., McFADZEN, M.E., VEKASY, M.S., and BEDNARZ, J.C. 1997. The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of prairie falcons. Condor 99:567–584.

MASMAN, D., DANN, S., and DIJKSTRA, C. 1988. Time allocation in the kestrel (*Falco tinnunculus*), and the principle of energy minimization. Journal of Animal Ecology 57:411–432.

MEARNS, 1983. The diet of the peregrine falcon *Falco peregrinus* in south Scotland during the breeding season. Bird Study 30:81–90.

NELSON, R.W. 1970. Some aspects of the breeding behavior of peregrine falcons on Langara Island, B.C. Unpubl. M.S. thesis, University of Calgary, Calgary, Alberta. 306 p.

NUR, N. 1987. Parents, nestlings and feeding frequency: A model of optimal parental investment and implications for avian reproductive strategies. In: Kamil, A.C., Krebs, J.R., and Pulliam, H.R., eds. Foraging behavior. New York: Plenum Press. 457–476.

PALMER, A.G. 1999. Parental care of peregrine falcons in interior Alaska and the effects of low-altitude jet overflights. Unpubl. master's thesis, Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon. 155 p.

PALMER, R.S. 1988. Peregrine. Handbook of North American birds, Vol. 5. New Haven, Connecticut: Yale University Press. 324–380.

PLATT, J.B. 1975. A study of diurnal raptors that nest on the Yukon North Slope with special emphasis on the behavior of gyrfalcons during experimental overflights by aircraft. Arctic Gas Biological Report Series 30:1–40.

PYKE, G.H., PULLIAM, H.R., and CHARNOV, E.L. 1977. Optimal foraging: A selective review of theory and tests. Quarterly Review of Biology 52:137–154.

RATCLIFFE, D. 1993. The peregrine falcon. London: T. & A.D. Poyser.

RIJNSDORP, A., DAAN, S., and DIJKSTRA, C. 1981. Hunting in the kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. Oecologia 50:391–406.

RITCHIE, R.J. 1987. Response of adult peregrine falcons to experimental and other disturbances along the Trans-Alaska pipeline system, Sagavanirktok River, Alaska, 1985, 1986. Unpubl. report for Alyeska Pipeline Service Company. Available at ABR, Inc., P.O. Box 90410, Fairbanks, Alaska 99708, U.S.A. 91 p.

SHERROD, S.K. 1983. Behavior of fledgling peregrines. Ithaca, New York: The Peregrine Fund Inc. 202 p.

STEIDL, R.J. 1995. Recreation and bald eagle ecology on the Gulkana National Wild River, Alaska. Unpubl. Ph.D. dissertation, Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, Oregon. 155 p.

TACHA, T.C., VOHS, P.A., and IVERSON, G.C. 1985. A comparison of interval and continuous sampling methods for behavioral observations. Journal of Field Ornithology 56:258–264.

WAKELEY, J.S. 1978. Activity budgets, energy expenditures, and energy intakes of nesting ferruginous hawks. Auk 95:667–676.

WARD, J.M., and KENNEDY, P.L. 1996. Effects of supplemental food on size and survival of juvenile northern goshawks. Auk 113:200–208.

WHITE, C.M. 1969. Breeding Alaskan and Arctic migrant populations of the peregrine. In: Hickey, J.J., ed. Peregrine falcon populations: Their biology and decline. Madison, Wisconsin: The University of Wisconsin Press. 45–51.

WRIGHT, J.W., and BENTE, P.J. 1999. Documentation of active peregrine falcon nest sites. Project SE-2-9, 10, and 11. Juneau: Alaska Department of Fish and Game, Division of Wildlife Conservation. 15 p.