

AN ABSTRACT OF THE THESIS OF

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Daniel D. Roby

To assess the impact of low-altitude jet overflights on parental care, we examined nest attendance, time-activity budgets, and provisioning rates of 21 Peregrine Falcon (*Falco peregrinus*) pairs breeding along the Tanana River, Alaska in 1995 and 1996. Several intrinsic and extrinsic factors influenced attributes of nesting behavior. Female nest attendance declined substantially with progression of the nesting cycle, while male attendance patterns were consistent throughout the nesting cycle. Further, although females typically performed most of the incubating, male attendance at the nest area varied considerably among breeding pairs. Both prey item delivery rates and estimated prey mass delivery rates increased with brood size. Prey item delivery rates per nestling, however, decreased with increasing brood size; yet estimated prey mass delivery rates per nestling did not vary with brood size. Peregrine Falcons apparently maintained constant provisioning rates per nestling as brood size increased by increasing average prey size.

We found evidence that nest attendance and time-activity budgets of Peregrine Falcons differed during periods of overflights compared with reference nests, but

differences depended on stage of the nesting cycle and gender. Males had lower nest ledge attendance during periods when overflights occurred than males from reference nests when data from the incubation and early nestling-rearing stages of the nesting cycle were combined. Females apparently compensated for lower male ledge attendance by attending the ledge more during overflown periods compared to females from reference nests, although this trend was not significant. During late nestling-rearing, however, females perched in the nest area less during periods when overflights occurred than females from reference nests. We did not see a relationship between nest attendance and the number of overflights, the cumulative number of exposures experienced by each nesting pair, or the average sound exposure level of overflights. Nor did we find evidence that nestling provisioning rates were affected by overflights. Low altitude jet overflights did not markedly affect nest attendance, time-activity budgets, or nestling provisioning rates of breeding Peregrine Falcons.

Parental Care of Peregrine Falcons in Interior Alaska and the
Effects of Low-Altitude Jet Overflights.

by

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Angela G. Palmer, Author

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CONTRIBUTION OF AUTHORS

Dr. Daniel D. Roby was involved with the design and editing of each manuscript. Dana L. Nordmeyer contributed to data collection for the study and was an integral part of the idea development leading to each manuscript.

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Prayer For The Great Family

Gratitude to Mother Earth, sailing through night and day--
and to her soil: rich, rare, and sweet
in our minds so be it.

Gratitude to Plants, the sun-facing light-changing leaf
and fine root-hairs; standing still through wind
and rain; their dance is in the flowing spiral grain
in our minds so be it.

Gratitude to Air, bearing the soaring Swift and the silent
Owl at dawn. Breath of our song
clear spirit breeze
in our minds so be it.

Gratitude to Wild Beings, our brothers and sisters, teaching
secrets, freedoms, and ways; who share with us their
milk; self-complete, brave, and aware
in our minds so be it.

Gratitude to Water: clouds, lakes, rivers, glaciers;
holding or releasing; streaming through all
our bodies salty seas
in our minds so be it.

Gratitude to the Sun: blinding pulsing light through
trunks of trees, through mists, warming caves where
bears and snakes sleep--he who wakes us--
in our minds so be it.

Gratitude to the Great Sky
who holds billions of stars--and goes yet beyond that--
beyond all powers, and thoughts
and yet is within us--
Grandfather Space.
The Mind is his Wife.

so be it.

after a Mohawk prayer

Gary Snyder

Parental Care of Peregrine Falcons in Interior Alaska and the Effects of Low-Altitude Jet Overflights

GENERAL INTRODUCTION

The United States Air Force (USAF) maintains low-altitude Military Training Routes (MTRs) and Military Operations Areas (MOAs) in areas of sparse human settlement in Interior Alaska. A proposal to expand the MOAs has been met with concern from residents and resource management agencies regarding the potential effects of low-altitude jet aircraft overflights on wildlife (Galdwin et al. 1987). As a result of these concerns, in combination with requirements of the National Environmental Policy Act (NEPA) (1969) and the Endangered Species Act (ESA) (1973), the USAF sponsored several research projects to document the effects of aircraft activity on wildlife populations. One taxon of concern was raptors (Falconiformes).

Raptors were of particular concern to wildlife management agencies for several reasons. First, as higher order consumers, they serve as indicators of ecosystem health and general environmental conditions (Newton 1979). Second, many raptor populations have experienced dramatic declines in the last 40 years, leaving some species (e.g., Peregrine Falcons (*Falco peregrinus*) and Bald Eagles (*Haliaeetus leucocephalus*)) threatened with extinction (Hickey 1969, Bird 1983). Finally, raptors are sensitive to human disturbance during nesting (Fyfe and Olendorf 1976, Steenhof and Kochert 1982, Steidl and Anthony 1995).

This thesis is part of a larger study on effects of jet overflights on behavior and reproductive success of Peregrine Falcons. Components of the larger study examine

immediate reactions and reproductive success of Peregrine Falcons exposed to low altitude jet overflights. In addition, the larger study seeks to validate a model designed to predict the potential effects of aircraft overflights and sonic booms on the reproduction of endangered raptorial birds (Bowles et al. 1990). The portion of the project described in this thesis, however, focuses on parental care behavior. While some responses by nesting raptors to aircraft overflights may be overt, such as attack or panic flights (Fyfe and Olendorf 1976, Ritchie 1987), other responses may be subtle and more difficult to detect (Platt 1975, Ellis et al. 1991). These subtle responses may result in changes in parental behavior and care of offspring that ultimately affect nesting success as much as immediate responses. Subtle responses to disturbances could lead to insidious impacts on nesting success, such as reallocation of time to nest attendance and various breeding activities, and declines in the rate at which parents provision their young. Few studies have examined these types of longer term responses by nesting raptors to potential disturbance (Awbrey and Bowles 1990).

Parent birds must adequately care for nidicolous young to ensure success of a breeding attempt. Parental care involves allocating time towards protecting the nest, brooding the eggs or young, and acquiring food for young, while at the same time meeting parental energy and nutrient requirements. In order to maximize fitness, parents must maintain themselves for future reproductive attempts. Adult birds must make decisions throughout the breeding season involving the trade-off between investment in their own survival and that of their young (Trivers 1972). Species with nidicolous young, like Peregrine Falcons, provide an opportunity to study how parents allocate time

among the competing functions of self maintenance, protection of progeny, and provisioning progeny with energy and other nutrients. One of the effects of disturbance is its potential effect on how a parent allocates its time and resources toward reproduction.

To understand the potential effects of overflights on nest attendance, time-activity budgets, and nestling provisioning rates, we must first understand the factors that influence these aspects of breeding behavior in the absence of overflights. In chapter 1, we assessed how Peregrine Falcons allocated their time during the breeding season to nest attendance and various categories of activity. In chapter 2, we examined how Peregrine Falcons provisioned their young and the factors that help explain variation in provisioning rates. Finally, in chapter 3, we investigated effects of low-altitude jet overflights on nest attendance, time-activity budgets, and nestling provisioning rates of Peregrine Falcons.

If nest attendance and behavior of adult Peregrine Falcons are influenced by low-altitude jet overflights, we would expect attendance and time-activity budgets of falcons to differ between periods immediately following overflights and periods when no overflights occur, and between nests that are exposed to overflights and those that are not. If overflights inhibit Peregrine Falcons from either 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, and lower at nests that were overflowed compared to nests that were not overflowed.

CHAPTER 1.
FACTORS INFLUENCING NEST ATTENDANCE AND TIME-ACTIVITY
BUDGETS OF PEREGRINE FALCONS IN INTERIOR ALASKA

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ABSTRACT

An essential prerequisite to examining the impacts of anthropogenic disturbance on nesting activities is the understanding of intrinsic and extrinsic factors that influence allocation of time to breeding behaviors. We examined factors influencing nest attendance and time-activity budgets of 21 Peregrine Falcon (*Falco peregrinus*) pairs breeding along the Tanana River, Alaska in 1995 and 1996. First, we found that for female peregrines activities with low energetic cost, like incubating and brooding, decreased dramatically as the nesting cycle progressed, while more energetically costly activities, like flying, increased during the nestling-rearing stage. Second, as is typical of most bird species with nidicolous young and biparental care, females attended the nest ledge and nest area more than males, and female attendance decreased with progression of the nesting cycle to levels similar to males. Third, nest area attendance followed a circadian rhythm, with attendance in the nest area lower during early morning, a prime hunting period, compared to late morning. Finally, while females typically performed most of the incubating, we found that male attendance at the nest area during incubation differed considerably among pairs.

INTRODUCTION

In nidicolous species, a parent's time is mainly partitioned 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). Attending adults defend young against predators and provide shelter from severe weather. The major cost to adults of nest attendance is lost foraging time, while the major cost to adults of foraging away from the nest area is the increased exposure of eggs and young to potential nest predation. The optimal allocation of time and energy to nest attendance versus foraging by a breeding pair influences overall reproductive success (King 1974, Nur 1987), a key component of fitness.

Allocation of time and energy to various activities is dependent on intrinsic and extrinsic factors. Intrinsic factors include age, hunting skills, and physiological condition of each member of a pair (Rijnsdorp 1981, Deerenberg et al. 1995, Marzluff et al. 1997). Extrinsic factors may include time of day, weather conditions, presence of potential nest predators, and human-related disturbance (Platt 1975, Ritchie 1987, Masman et al. 1988, Steidl and Anthony 1995). Different activities require different rates of energy expenditure (Gessaman 1987, Goldstein 1988), and disturbance to a breeding pair may lead to increased energetic 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 prior to examining the impacts 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. 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.

Raptors are of particular interest as subjects for investigations into the allocation of time and energy for reproduction. First, as higher order consumers raptors are useful bioindicators of ecosystem health (Newton 1979). Second, many raptor populations have experienced dramatic declines in the last 40 years, leaving some species (e.g., Peregrine Falcons and Bald Eagles (*Haliaeetus leucocephalus*)) threatened with extinction (Hickey 1969, Bird 1983). Third, raptors are characterized by distinctive reverse sexual size-dimorphism (Mueller and Meyer 1985) and are well-suited for investigation of gender differences in nesting behavior.

We posed several hypotheses regarding nest attendance and time-activity budgets in breeding Peregrine Falcons. First, due to 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. Second, the sexual size dimorphism in Peregrine Falcons (Mueller and Meyer 1985) may be associated with pronounced gender differences in nest attendance and time-activity budgets. Third, 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), and higher during more inclement weather when maintenance energy costs of young are higher (Buttemer et al. 1986). Finally, due to their high trophic level and complex

behavior, we predicted that individual pairs might differ in how the sexes allocated time to nest attendance and other reproductive tasks.

METHODS

We collected data in the field during the 1995 and 1996 breeding seasons from 13 May through 17 August, and from 13 May through 3 September, respectively. Two separate crews of two to four observers recorded data at Peregrine Falcon nest sites in each year of the study.

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). Locations along the river were identified by distance (km) from the river's source near Tok. In 1995, the study area extended from Tanacross (km 155) to Sawmill (km 305). We located 13 active Peregrine Falcon nests along this stretch of the river, and of these, 10 were accessible and afforded adequate visibility for observations. In 1996, we included an additional section of the river from Delta (km 379) to Salcha (km 443). We located a total of 19 active nests along the two sections of river. In 1996, we observed six nests that were observed in 1995 and six additional nests along the new section of river. Nests were situated on bluffs overlooking the river. We selected nests for observation based on

access to observation sites opposite nest cliffs and visibility of the nest ledge from observation sites.

We established observation sites across at least one channel of the river and 300-750 m from nests to permit observation of the behavior of breeding adults and nestlings. Observation distance depended on available observation sites and the sensitivity of individual falcons to observer presence. In an attempt to minimize the disturbance associated with the approach of observers, field crews approached observation sites indirectly and along a consistent path by foot or boat. In addition, we used tents as blinds at sites where adults were more sensitive to observer presence and to protect gear from inclement weather. As the breeding season progressed, water levels rose due to glacial runoff and submerged some observation sites. Observation distances increased to as much as 1500 m late in the 1995 season. River levels peaked at lower levels in 1996.

Nest Attendance and Time-activity Budgets

Observations were made with the aid of binoculars, 15-60 X spotting scopes, and 90 X Questar telescopes. During incubation, two observers operated video equipment and recorded data on nest attendance and time-activity budgets. In 1995, two observers recorded data during the nestling-rearing period, while in 1996 the number of observers was increased to three during nestling-rearing. There were four observers during the post-fledging stage of the nesting cycle when young were not restricted to the nest ledge.

We used the instantaneous scan method to sample activity (Altmann 1974, Tacha et al. 1985) at one-minute intervals for each parent. Scans contributed data to both nest attendance and time-activity budgets. For nest attendance, we distinguished between attendance at the nest ledge or scrape, attendance in the nest area (within 200 m of the nest ledge), and away from the nest area (greater 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 1.1. For analysis we lumped primary activities into 6 activity categories (Table 1.1). Incubation, brooding, and shading activities were combined because they all involve thermoregulation of eggs/young. Perching, feeding self, feeding young, flying, and unknown were the other activity categories used in analyses. We categorized birds as out of sight (OS1 or OS2--see Table 1.1) for no longer than 5 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 3 stages of the Peregrine Falcon nesting cycle: incubation, nestling-rearing, and post-fledging. The duration of other stages (courtship and pre-laying, laying, and hatching) is comparatively short, and sample sizes of observation blocks during these stages were correspondingly small. Of the 10 nests observed in 1995, we observed 5 during incubation, 9 during nestling-rearing, and 4 during post-fledging. One nest was observed during all three stages. In 1996, we sampled behavior during incubation, nestling-rearing, and post-fledging at 7 of 11 nests.

Table 1.1. Activity categories for time-activity budgets of Peregrine Falcons breeding along the Tanana River, Alaska.

Activity Categories ^a	Primary Activities
Incubating/ Brooding/ Shading	<u>incubating</u> : prone posture covering eggs <u>out of sight (OS1)</u> : on the nest ledge/scrape, but out of sight, e.g., in a cavity at the nest ledge <u>brooding</u> : covering nestlings, wing may be slightly off to the side <u>shading young</u> : shielding nestlings from direct sunlight
Perching	<u>perching</u> : standing on one or both feet <u>out of sight (OS2)</u> : 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	<u>feeding self</u> : consuming prey
Feeding Young	<u>feeding young</u> : feeding prey to nestlings or known to be feeding young but out of view, possibly in a cavity
Flying	All flight behaviors: <u>flapping</u> : active flight that involves wing flapping <u>soaring or gliding</u> : passive flight with little to no wing movement <u>stooping</u> : wings tucked, in downward pursuit of prey from altitude <u>diving</u> : Aggressive attack on prey or predator
Unknown	<u>location unknown</u> : assumed to be away from the nest site in flight foraging or perching

^a Other behaviors (lying: with sternum resting on the ground, walking, and running) occurred less than 1 % of time.

The other 4 nests were not sampled during each of the three stages because 2 nests failed following incubation and were replaced by 2 other nests.

For analysis, the nestling-rearing phase was further subdivided into three stages, early nestling-rearing (0-10 days post-hatch), mid nestling-rearing (11-24 days), and late nestling-rearing (25-42 days). Consequently, we conducted analyses on 5 stages of the nesting cycle: incubation; early, mid, and late nestling-rearing; and post-fledging. Stage of the nestling-rearing phase was determined by the estimated age of the oldest chick, based on measurements taken during banding visits to the nest in the mid nestling-rearing period.

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. During the early and late stages of the breeding season, lack of daylight precluded some observations in the first time-block. We sampled activity for a minimum of one hour within each time-block at each nest during each phase. In both years, however, observations were concentrated between 8:00 and 17:00 ADT.

For analysis purposes, we grouped one-minute scan samples by specific 4-hour time-blocks, 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 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 447 observation blocks over the two years. Observations of adults at the same nest, but in different years were considered independent.

Two video cameras equipped with 250 mm lenses and 2X extenders were employed to continuously record behaviors of adults at or near the nest scrape during observations. In 1995 we used Canon L2 Hi-8 mm and Sony CCD-FX430 8 mm video cameras, while in 1996 we used Canon L2 cameras exclusively. During incubation and nestling-rearing periods, one camera was focused on the nest ledge, while the other was focused on the attending adult. During the post-fledging period, we focused on visible fledglings or adults as their visibility allowed. Video tapes confirmed ledge attendance during periods when incubating or brooding adults were not directly visible to observers.

We measured weather parameters every hour from the observation site, including temperature ($^{\circ}\text{C}$), wind speed (km/h), and precipitation. Precipitation was assessed as none, low (drizzle or light rain), medium (steady rain), or high (down pour). Temperature and wind speed were averaged over each observation block, while for precipitation we used the highest level that occurred in each observation block.

Finally, we recorded the presence or absence of avian intruders (i.e., conspecifics, other raptors, and ravens) within 200 m of the nest ledge during each observation block, and scored whether intruders elicited flight responses from attending adults.

Sample Units and Statistical Analyses

To calculate ledge attendance by each member of the 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. As with ledge attendance, 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. Likewise, we used female plus male area attendance to estimate total area attendance by the pair. Similarly, 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 examined the significance of three weather variables (temperature, wind speed, and precipitation) on attendance using linear regression. For analysis of patterns in ledge attendance, we did not include data from the post-fledging stage of the nesting cycle because ledge attendance was rare. To investigate gender roles in nesting activities we examined the ratio of female attendance to total attendance for departures from 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 with stage 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 homogeneity to test for differences between sexes. All tests were conducted at the 0.05 α level. Means are reported as $\bar{x} \pm \text{SE}$.

We logit transformed ($\log(Y/(1-Y))$) non-normal data. When logit transformations were necessary for total nest 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 scrape, by twice the number of minutes per observation block for total ledge attendance. Similarly, we divided the number of minutes the female plus the number of minutes the male spent either at the nest ledge or in the nest area (within 200 m of the ledge or scrape), by twice the number of minutes per observation block to calculate total area attendance. 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 ($F_{3,337} = 244$, $P < 0.0001$; Fig. 1.1a). During incubation, total ledge attendance averaged 0.99 ± 0.004 among nests. During the early nestling-rearing stage, total ledge attendance was initially high but gradually decreased to chick age 10 days ($r^2 = 0.84$, $P = 0.0008$; Fig. 1.2). Most visits to the nest ledge during subsequent stages were limited to prey deliveries and feeding of young; thus ledge attendance was low following the early nestling-rearing stage (Fig. 1.1a). Similarly, area attendance declined with nesting stage, after controlling for nesting pair, but not as markedly ($F_{4,446} = 40$, $P < 0.0001$; Fig. 1.1b), 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 among nesting stages, after accounting for nesting pair ($F_{3,274} = 6.36$, $P = 0.004$; and $F_{4,402} = 11.33$, $P < 0.0001$, respectively; Fig. 1.3). The ratio of female ledge attendance to total ledge attendance was greater than 0.50 during incubation, early nestling-rearing, and mid nestling-rearing, but not different from 0.50 during late nestling-rearing (Fig. 1.3a). Unlike the ratio of female ledge attendance to total ledge attendance, which increased

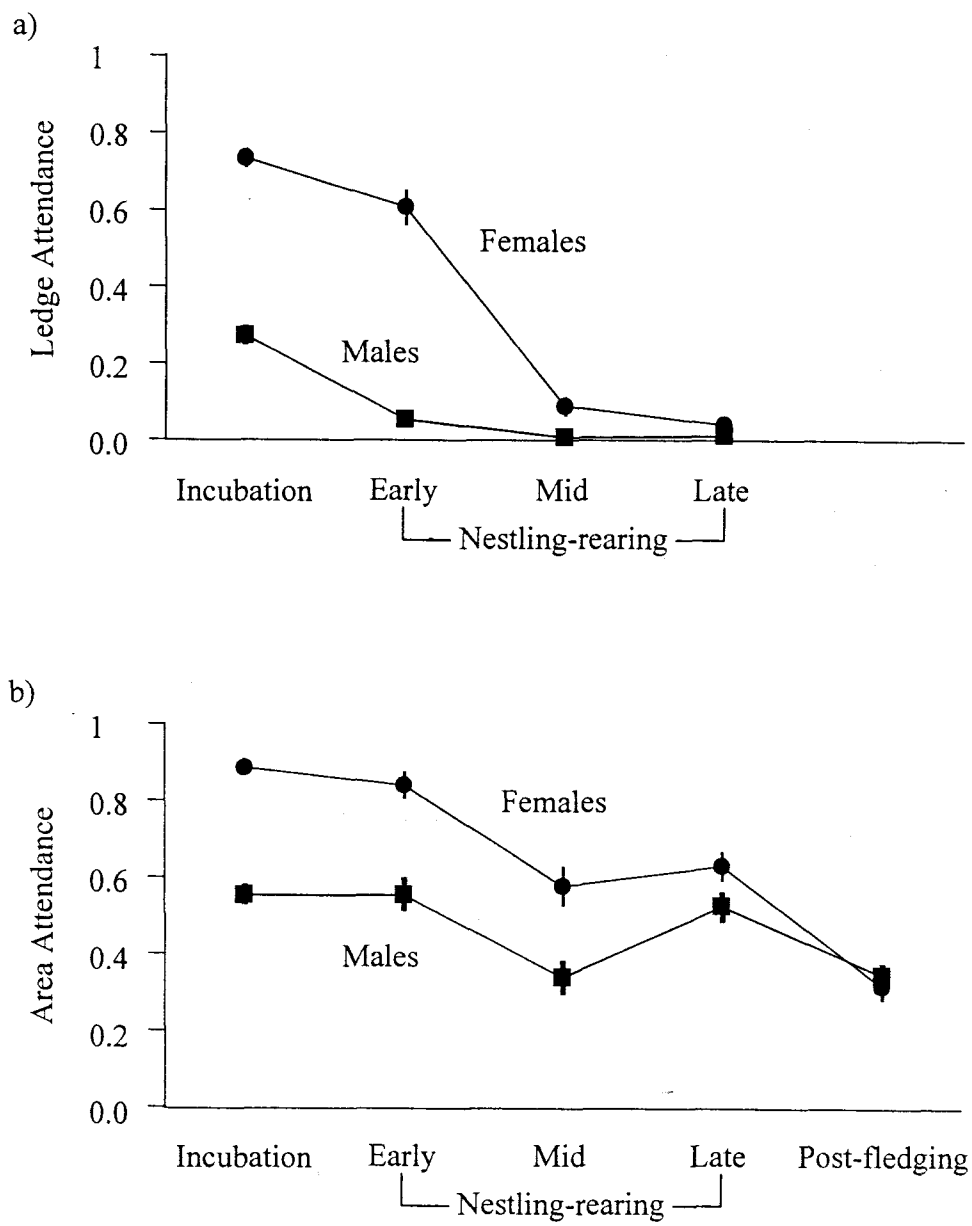


Figure 1.1. Nest attendance (\pm SE) as a function of stage of the nesting cycle by Peregrine Falcons breeding along the Tanana River, Alaska.

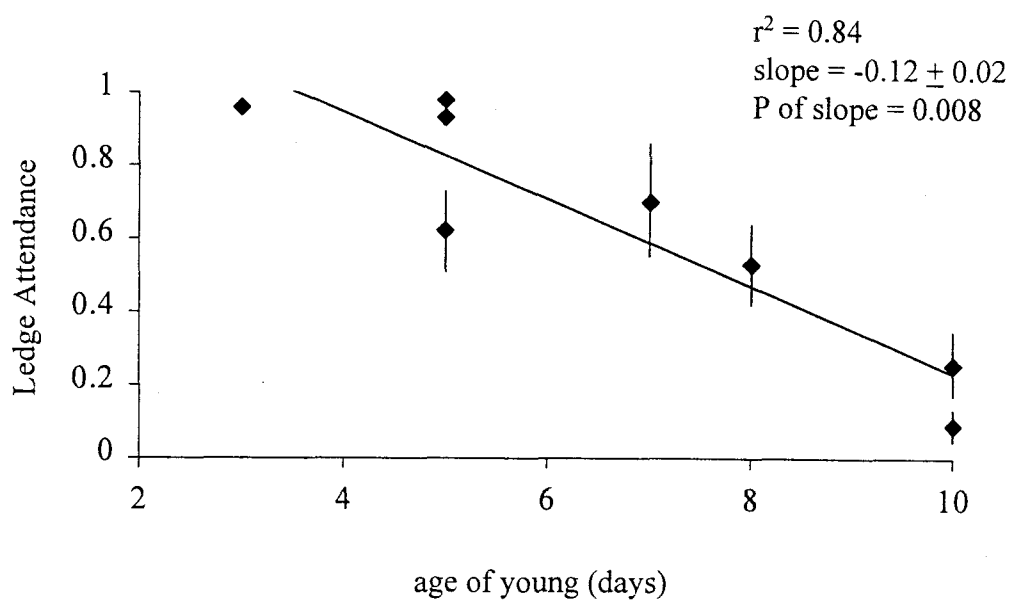


Figure 1.2. Total ledge attendance (\pm SE) per nest during early nestling-rearing in relation to chick age by Peregrine Falcons breeding along the Tanana River, Alaska.

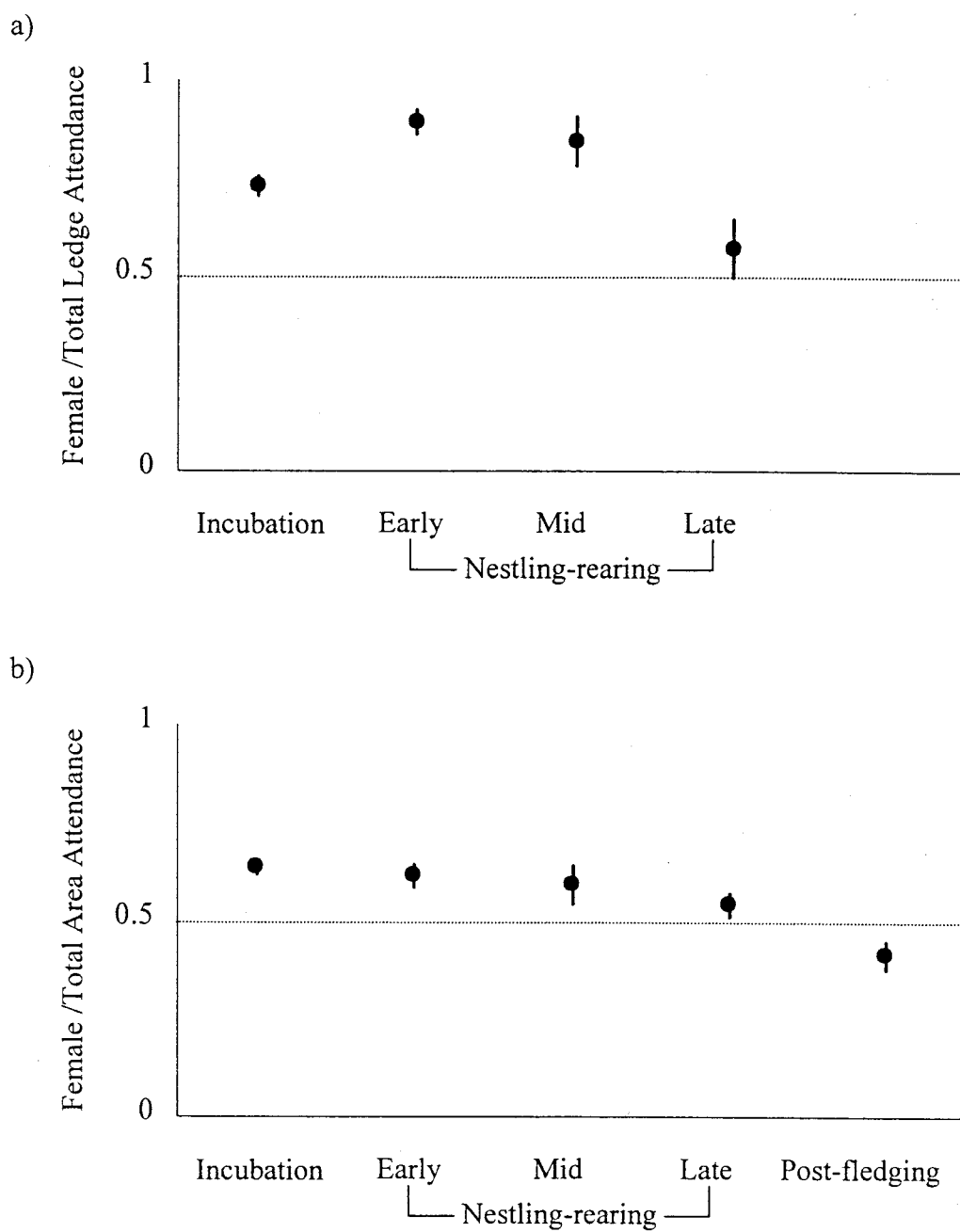


Figure 1.3. The ratio of female attendance to total attendance (\pm SE) as a function of nesting stage of Peregrine Falcons breeding along the Tanana River, Alaska.

from incubation to early nestling-rearing ($P < 0.05$) and then decreased in subsequent stages of the nesting cycle, 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. 1.3b). During post-fledging the ratio of female area attendance to total area attendance was actually less than 0.50 (95% confidence interval: 0.34 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 ($F_{5, 337} = 1.15$, $P = 0.33$); however, area attendance did differ among time-blocks ($F_{5, 446} = 2.32$, $P = 0.0428$). Specifically, area attendance was lower ($P < 0.05$) during time-block 1 (0:00 hrs to 04:00 hrs; $1.05 (\pm 0.11)$) than time-block 3 (08:00 hrs to 12:00 hrs; $1.20 (\pm 0.046)$).

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 was most obvious during incubation. During this stage, differences in area attendance among pairs were highly significant ($F_{13, 138} = 4.41$, $P < 0.0001$). When separated by sex, differences in area attendance among males were highly significant ($F_{13, 138} = 3.51$, $P = 0.0001$), yet differences among females were not ($F_{13, 138} = 1.01$, $P = 0.4455$; Fig. 1.4). During incubation, at least one member of each pair attended the nest ledge nearly all the time. Although average female ledge attendance during incubation varied considerably among individuals (0.51 ± 0.25 to 0.98 ± 0.03 ; Fig. 1.5), due to small sample sizes and high variability among observation blocks

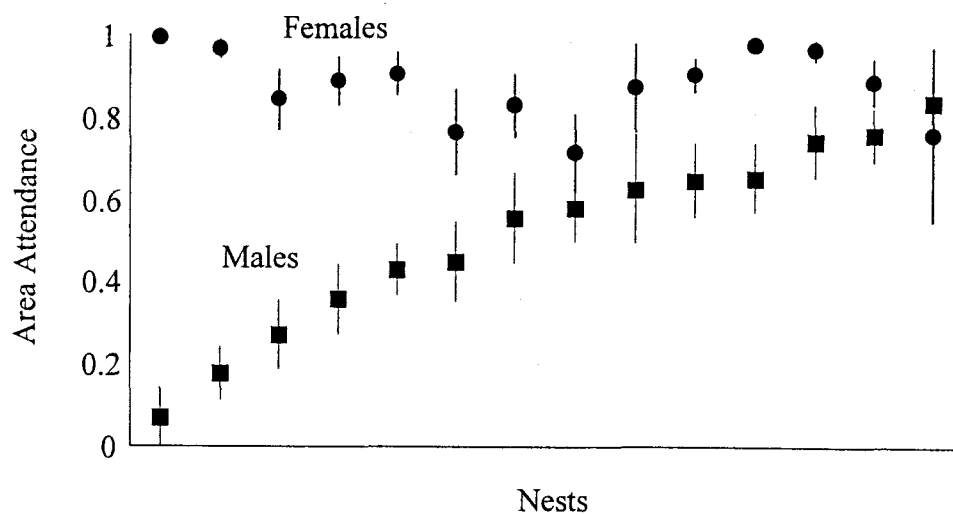


Figure 1.4. Differences in area attendance (\pm SE) during incubation among Peregrine Falcon pairs breeding along the Tanana River, Alaska, in ascending order of male area attendance.

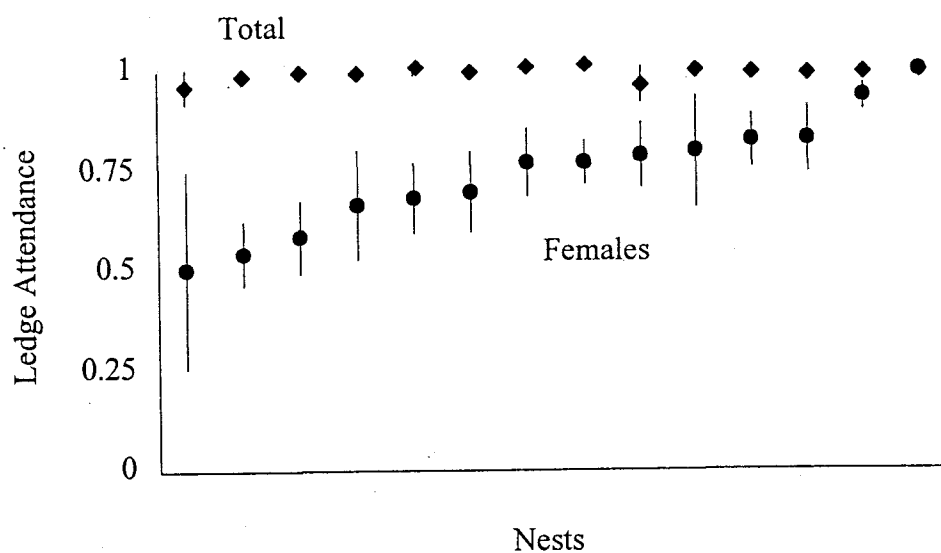


Figure 1.5. Differences in ledge attendance (\pm SE) during incubation among Peregrine Falcon pairs breeding along the Tanana River, Alaska, in ascending order of female ledge attendance.

for individual females, among-female differences in ledge attendance were not significant ($F_{13, 138} = 1.39$, $P = 0.1723$).

Gender differences in nest attendance were especially apparent when potential avian predators were present. Of the 42 intrusions by raptors observed within Peregrine Falcon territories during incubation, 36 occurred at just two nests. Intruders at these nests included other Peregrine Falcons, Common Ravens (*Corvus corax*), Bald Eagles, Golden Eagles (*Aquila chrysaetos*), and a Merlin (*Falco columbarius*). The two breeding pairs that experienced the majority of the intrusions reacted differently. Intruders elicited flight responses from both the female and male at nest 205 (10 and 8 times out of 21 intrusions, respectively), while at nest 221 the female rarely flew (twice in 15 intrusions) compared to the male's 9 flights out of 15 intrusions. During intrusions, these differences were reflected in ledge attendance (Fig. 1.6). Female ledge attendance during incubation differed between the two nests, depending on the presence of intruders ($P = 0.0014$, t-test for an interaction, $df = 1$). At nest 205, observation blocks with intruders had lower female ledge attendance than observation blocks without intruders ($P = 0.0027$, t-test, $df = 9$), while at nest 221 there was a trend for higher female ledge attendance when intruders were present compared to when they were absent.

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 activity categories

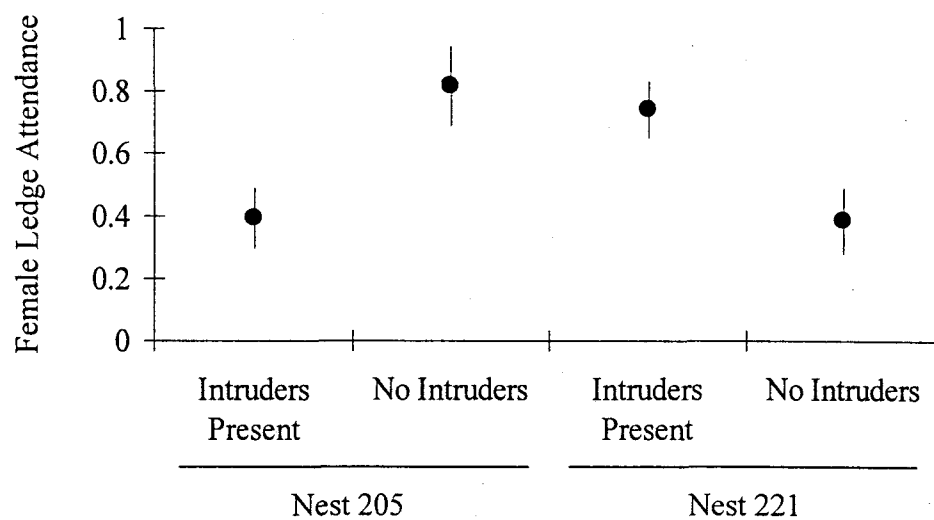


Figure 1.6. Female ledge attendance during incubation, when intruders were present and absent, at two Peregrine Falcon nests along the Tanana River, Alaska.

feeding self (both sexes) and flying (males only), after accounting for nesting pair (Tables 1.2., 1.3., and 1.4). Females spent over twice as much time incubating ($71.4 \pm 2.56\%$) as males ($26.4 \pm 2.51\%$; $P < 0.0001$, paired t-test). Females brooded young much more than males during early nestling-rearing (Fig. 1.7a), though levels of this activity were lower than during incubation for both sexes ($P < 0.05$ for both).

Perching time also differed among 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. 1.7b). Perching time in males was lower during incubation and post-fledging than during early and late nestling-rearing, while perching time during mid nestling-rearing was not significantly different from either group ($P < 0.05$). Comparing the incidence of perching between the sexes, females perched less than males during incubation and early nestling-rearing ($P = 0.012$ and $P = 0.00086$, respectively; paired signed rank tests), but more than males during mid nestling-rearing ($P = 0.029$; paired signed rank test; Fig. 1.7b). During late nestling-rearing and post-fledging, the incidence of perching did not differ between the sexes ($P = 0.067$ and $P = 0.38$, respectively; paired signed rank tests; Fig. 1.7b).

Other activities that occurred infrequently either differed with nesting stage, 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 ($P < 0.05$ for both females and males, Fig. 1.7c). 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), $P = 0.0006$ (mid), and $P =$

Table 1.2. Means (\bar{x}) and standard errors (SE) of % time per observation block females spent engaged in each activity category for each stage of the nesting cycle among Peregrine Falcons nesting along the Tanana River, Alaska.

Activity	Incubation (n ^a = 139)		Nestling-rearing						Post-fledging (n = 109)	
	\bar{x}	SE	Early (n = 69)		Mid (n = 53)		Late (n = 77)		\bar{x}	SE
Incubating/Brooding	71.4	2.6	44.6	4.6	2.1	0.9	0.0	0.0	0.0	0.0
Perching	17.2	2.0	30.5	3.7	47.8	4.7	57.7	3.9	29.9	3.3
Feeding Self	0.48	0.13	0.24	0.08	0.15	0.06	0.38	0.21	0.80	0.28
Feeding Young			4.44	0.65	2.12	0.53	1.40	0.36	0.23	0.11
Flying	0.73	0.12	2.21	0.72	1.87	0.31	2.74	0.68	1.60	0.35

^a n = number of observation blocks per stage for all nests combined.

Table 1.3. Means (\bar{x}) and standard errors (SE) of % time per observation block males spent engaged in each activity category for each stage of the nesting cycle among Peregrine Falcons nesting along the Tanana River, Alaska.

Activity	Incubation (n ^a = 139)		Nestling-rearing						Post-fledging (n = 109)	
	\bar{x}	SE	Early (n = 69)		Mid (n = 53)		Late (n = 77)		\bar{x}	SE
Incubating/Brooding	26.3	2.5	0.70	0.40	0.0	0.0	0.0	0.0	0.0	0.0
Perching	27.1	2.5	48.4	4.2	30.5	4.0	48.3	3.9	33.2	2.9
Feeding Self	0.12	0.23	0.13	0.33	0.09	0.13	0.12	0.29	0.07	0.20
Feeding Young			0.39	0.95	0.08	0.12	0.11	0.21	0.0	0.0
Flying	1.57	0.22	2.73	0.59	1.78	0.50	0.64	3.00	3.09	0.41

^a n = number of observation blocks per stage for all nests combined.

Table 1.4. Significance of differences in proportion of time spent in activities (logit (proportion of time per observation block)) among stages of the nesting cycle, after accounting for nesting pair, for female and male Peregrine Falcons nesting along the Tanana River, Alaska, 1995-1996.

logit (Activity)	females			males		
	F (Stage)	df	P	F (Stage)	df	P
Incubate/Brood/Shade	72.91	2, 260	< 0.0001 ^a	62.09	1, 207	< 0.0001 ^b
Perch/out of sight	21.28	4, 446	< 0.0001 ^c	4.58	4, 446	0.0012 ^c
Feed Self	0.34	4, 446	0.8490 ^c	0.49	4, 446	0.7424 ^c
Feed Young	21.23	3, 307	< 0.0001 ^d	4.19	3, 307	0.0202 ^d
Fly	5.50	4, 446	0.0003 ^c	0.31	4, 446	0.2983 ^c

^a Females did not incubate, brood, or shade during late nestling-rearing or post-fledging, thus these stages were not included in the analysis.

^b Males did not incubate, brood, or shade after early nestling-rearing, thus the subsequent stages were not included in the analysis.

^c All stages were included in the analysis.

^d Analysis includes early, mid, and late nestling-rearing and post-fledging.

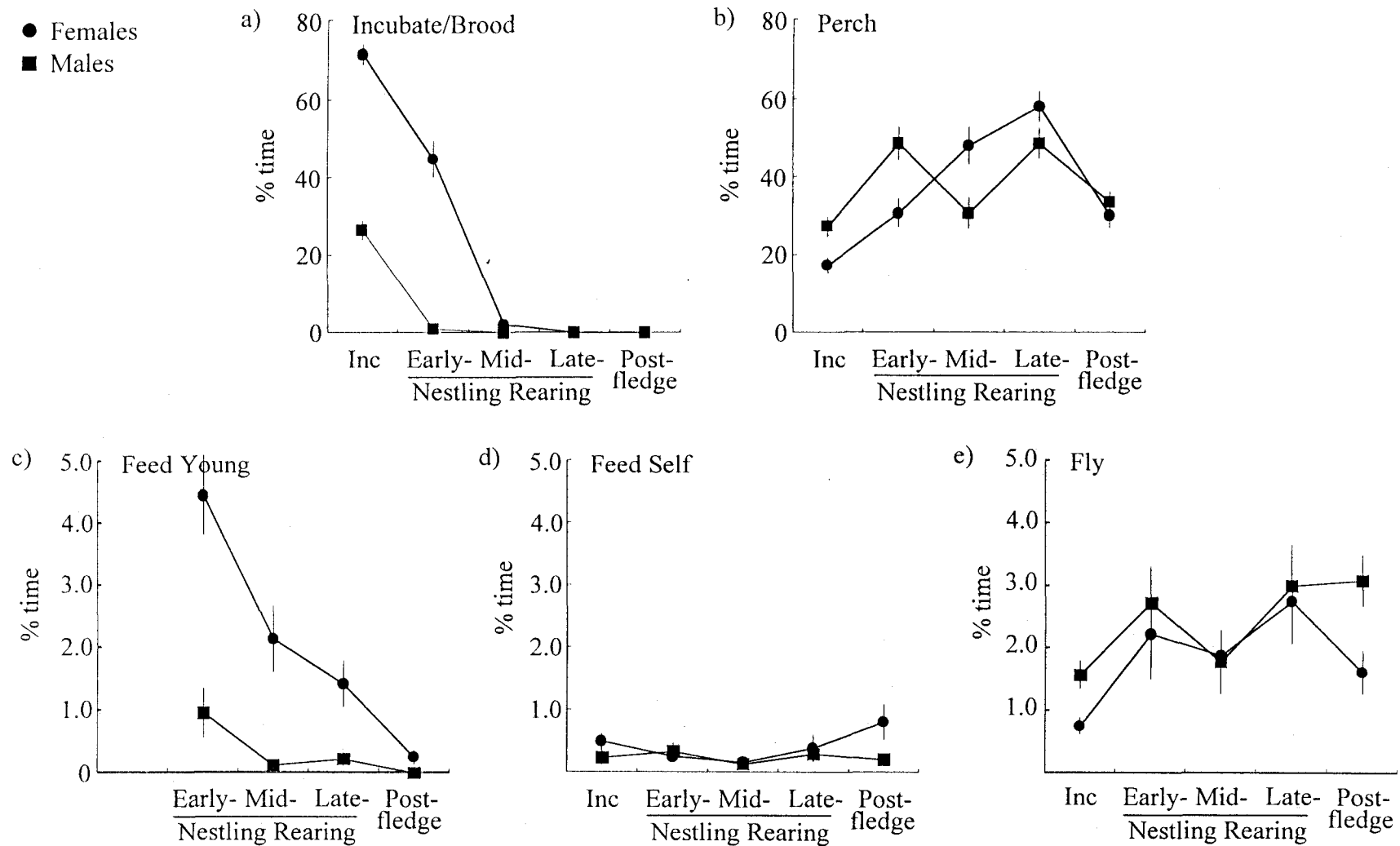


Figure 1.7. Time-activity budgets (\pm SE) in relation to stage of the nesting cycle for Peregrine Falcons breeding along the Tanana River, Alaska.

0.0215 (late); χ^2 tests for homogeneity). Females fed themselves in the nest area during more observation blocks (61 of 447) than males (38 of 447), a difference of 37% ($\chi^2 = 6.0$, $df = 1$, $P = 0.014$, test for independence between sex and activity; Fig. 1.7d). Finally, the proportion of time spent flying by females ($1.6 \pm 0.19\%$) and males ($2.4 \pm 0.20\%$) was low overall, and the incidence of flying was higher for females during mid and late nestling-rearing than during incubation and post-fledging ($P < 0.05$; Fig. 1.7e).

DISCUSSION

Stage of the nesting cycle was a prominent factor influencing nest attendance and time-activity budgets (Figs. 1.1, 1.2, and 1.7). Nest attendance and activities with low energetic cost, like incubating and brooding, decreased dramatically with stage of the nesting cycle (Figs. 1.1 and 1.7a), while perching and flying by females increased through the nestling-rearing stage (Figs. 1.7b and 1.7e). During the post-fledging stage, nest area attendance was lower than during other stages. Low attendance during post-fledging may have reflected avoidance by parents of begging young (Sherrod 1983). As young gained the coordination to feed themselves during nestling-rearing, the amount of time parents fed young decreased (Fig. 1.7c). These attendance and activity patterns are typical of other raptors (Collopy 1984, Collopy and Edwards 1989, Levenson 1981, Wakeley 1978)

Sexual differences in nest attendance are also typical of most bird species with nidicolous young and biparental care. Female Peregrine Falcons attended the nest ledge

and nest area more than males (Fig. 1.1), and their rate of attendance declined with progression of the nesting cycle down to levels similar to males (Fig. 1.3).

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 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 1995 and 1996 breeding seasons, the vast majority of observation blocks did not include extreme weather conditions. Indeed, average wind speed was below 7 mph for 90% of observation blocks, 80% of average temperatures were between 9^o C (48^o F) and 22.5^o C (72.5^o 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).

While female Peregrine Falcons typically perform most of the incubating (Cade 1960, Nelson 1970, this study), we found that some males guarded the nest area assiduously and some males participated nearly equally in incubation duties (Fig. 1.4). Differences among pairs in gender roles may be attributable to a variety of conditions, such as mate quality, territory quality, food availability, or the degree of sexual size dimorphism. One element that influences how a pair partitions attendance responsibilities may be related to the reactivity of the pair to intruders in the nest area. We found that two pairs of nesting falcons had different strategies for dealing with avian intruders; at one nest both members of the pair flew to intercept avian intruders, while at another the male responded to intruders more than the female. These strategies were reflected in differences in the way the two pairs partitioned ledge attendance responsibilities in the presence of avian intruders (Fig. 1.6).

In summary, we found that several intrinsic and extrinsic factors influenced nest attendance and time-activity budgets of nesting Peregrine Falcons. We observed prominent 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, sexual differences became negligible after the young fledged. Nest area attendance was lowest during early mornings, coinciding with periods when prey were most active. Some males vigilantly attended the nest area during incubation, while others did not. Gender roles in defending the nest from avian intruders were very different at the two

nests where most intrusions occurred. The level of variability in attendance patterns among pairs is an example of the complexity of behavioral systems at higher trophic levels. This complexity must be understood prior to testing for effects of human disturbance. Further investigations should document individual differences in reactivity to intruders on a broader scale, and assess the importance of other factors that may cause differences among breeding pairs in the division of labor between the sexes.

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CHAPTER 2.
FACTORS INFLUENCING NESTLING PROVISIONING RATES OF PEREGRINE
FALCONS IN INTERIOR ALASKA

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ABSTRACT

We examined factors influencing nestling provisioning rates among 19 Peregrine Falcon (*Falco peregrinus*) pairs breeding along the Tanana River, Alaska in 1995 and 1996. Perching birds (Passeriformes) composed the majority (51.9%) of prey items, while ducks and grebes composed the majority of the prey biomass (63.0%). Both prey item delivery rates and estimated prey mass delivery rates increased with brood size, after accounting for stage of the nesting cycle. Additionally, average prey size increased from broods of 1 to broods of 3, and we did not observe large prey items being delivered to broods of one. The length of time an adult was absent from the area of the nest prior to delivery of a prey item (foraging trip duration) was positively correlated with prey size, supporting the prediction of optimal foraging theory that prey size should increase as distance traveled to obtain prey increases. Finally, we found that while prey item delivery rates per nestling decreased with increasing brood size, estimated prey mass delivery rates per nestling did not vary with brood size. Peregrine Falcons apparently maintained per nestling provisioning rates as brood size increased by increasing average prey size.

INTRODUCTION

Parent birds must maintain adequate nestling provisioning rates to ensure growth and survival of nidicolous young. Because nestlings are especially vulnerable to predation, parents should attempt to provision nestlings with sufficient food to minimize the duration of the nestling period (Ricklefs 1984). Parents are limited in their ability to

adequately provide for nestlings by both environmental conditions and physiological constraints. Thus, parents must make decisions about the size and type of prey items to capture and deliver to nestlings in order to forage optimally for their brood (Pyke et al. 1977). Also, parents confront a trade-off between investing in present versus future reproduction (Trivers 1972). Investing too much in the present nesting attempt may decrease options for future reproduction. Maximizing lifetime production of fledglings should confer a selective advantage to parents (Krebs and Davies 1987). Deerenberg et al. (1995) supported the existence of a trade-off between present and future reproduction by showing that daily energy expenditure of breeding European Kestrels (*Falco tinnunculus*) increased with artificially enhanced brood size, and was negatively correlated with subsequent survival of parents. In addition, although parents raising larger broods contribute more offspring to the population, the fitness of each fledgling from large broods may be lower than the fitness of fledglings from smaller broods. Dijkstra et al. (1990) demonstrated that European Kestrel nestlings from enlarged broods had lower growth rates in comparison to those from either natural or reduced broods. Provisioning broods with less food per nestling presumably reduces both pre- and post-fledging survival and thus current reproductive success (Drent and Daan 1980).

Lack (1954) and Gibb (1955) proposed that parent birds work as hard as they can to feed young, and that chicks from larger than average broods are fed less than nestlings in average-sized broods. According to their hypotheses, provisioning rates per nestling should decline in a convex curve with increasing brood size. Royama (1966) argued that larger broods are fed less because they have less surface area per unit volume and greater

thermal inertia, and thus need less food to maintain homeothermy. Nur (1984) found that feeding frequency per nestling declined with a concave curve in studies on Blue Tits (*Parus caeruleus*), suggesting that nestlings from larger than average broods were fed less than nestlings in average-sized broods. A survey of the literature on nestling feeding frequencies indicated that concave declines in per nestling feeding frequencies with increasing brood size are the norm (Nur 1987).

Literature on feeding frequency has primarily focused on small passerines (e. g., Nur 1984), and these relationships are not well understood for raptors. As part of a larger study of factors influencing nesting behavior and reproductive success of Peregrine Falcons (*Falco peregrinus*), a cosmopolitan, high trophic level predator, we sought to test hypotheses about the relationships between prey item delivery rate, prey size, prey mass delivery rate, and brood size. First, if Peregrine Falcon pairs are flexible in how they meet nestling food requirements, we would expect to find differences among pairs in prey delivery rates and prey size in relation to brood size. We tested the hypothesis that prey provisioning rates (g/hr), which are a function of prey item delivery rates (items/hr) and prey size (g/item), increase with increasing brood size.

Second, Peregrine Falcons select a wide variety of predominantly avian prey species and sizes, and hunt over large local geographical areas (Enderson and Craig 1997, Ratcliffe 1993); thus they are good subjects to examine prey size-distance relationships in foraging. Optimal foraging theory predicts that prey size should increase as distance traveled to obtain prey increases (Pyke et al. 1977, Schoener 1979). For instance, Martindale (1983) found that foraging distance was positively correlated with prey size

among Gila Woodpeckers (*Melanerpes uropygialis*). Because it requires more time to commute to and from foraging areas further from the nest site, we assumed that the time an adult was away from the nest cliff prior to a prey delivery (foraging trip duration) was proportional to distance traveled. Thus, we predicted a positive correlation between foraging trip duration and size of prey item delivered.

Finally, raising larger broods can produce more fledglings, but can also be more energetically costly for parents (Deerenberg et al. 1995). We would expect parents to deliver more food to larger broods, but due to the energetic costs of provisioning, pairs with larger broods would not be expected to provide as much food per nestling as pairs with smaller broods. Alternatively, if parents fully compensate for each additional nestling in a brood, we would expect per nestling provisioning rates to be similar, regardless of brood size.

METHODS

Study Area

The study area included a 250 km stretch of the Tanana River between Tok and Fairbanks, Alaska (from 63° 8' N, 143° 36' W to 64° 18' N, 148° 45' W). Locations along the river were identified by distance (km) from the source. In 1995 the study area extended from Tanacross (km 155) to Sawmill (km 305). We located 13 active Peregrine Falcon nest sites along this stretch of the river. Of these, we selected 10 for observation.

In 1996, we included an additional section of the river from Delta (km 379) to Salcha (km 443). We located a total of 19 active nests along these two sections of river. In 1996, we observed 5 nests that were observed in 1995 and 4 additional nests from the new section of river. Nests are situated on bluffs overlooking the river. We selected nests for observation based on access to observation sites opposite cliffs and visibility of the nest ledge from the observation sites.

We collected field data during the breeding seasons from 13 May through 17 August 1995, and from 13 May through 3 September 1996. A crew of two to four observers recorded data at each Peregrine Falcon nest and two separate crews were in the field throughout the season.

We established observation sites across at least one channel of the river and 300-750 m from nests to permit observation of prey deliveries. Observation distance from nests depended on available observation sites and the sensitivity of individual falcons to observer presence. As the breeding season progressed, water levels rose due to glacial runoff and submerged some observation sites. Consequently, observation distances increased to as much as 1500 m from nests late in the 1995 season. River levels peaked at lower levels in 1996. We used tents to protect gear from inclement weather and as blinds at sites where adults were more sensitive to observer presence.

Provisioning Rates

We used binoculars, 15-60 X spotting scopes, and Questar telescopes to aide our observations. In 1995, two observers recorded data during the nestling-rearing period, and in 1996 the number of observers was increased to three. Four observers recorded nestling provisioning rates during the post-fledging stage of the nesting cycle, when fledglings could be widely scattered over the nest cliff.

We recorded the number of deliveries, the estimated size class of each item, and the type of prey delivered (identified to species whenever possible). As a measure of provisioning rates, we estimated the mass of those prey that were identified to species using the average body mass of that species in Dunning (1993). For prey that could be identified only to genus or family, we used the mean mass of all the species of that genus or family (Dunning 1993) that regularly occurred in the study area, except in the case of shorebirds, which span a wide range of masses. We classified shorebirds and prey items that could not be identified to species, genus, or family into the following size classes: small (9-50 g), medium (51-200 g), large (201+ g), or unknown, in order to assign them an estimated mass. For shorebirds and prey items that could be identified only to size-class, we used the median mass of all species of that size class known to regularly occur in the study area (30 g, 125 g, and 641 g for small, medium, and large items, respectively). Prey items that were of unknown size-class were categorized as medium-sized prey items. For analysis of prey item size in relation to brood size, we included only those prey items that could be identified at least down to the level of family and

classified them as small (9-50 grams), medium (51-200 g), or large (201+ g), based on the above method of mass assignments.

We measured provisioning rates during the nestling-rearing and post-fledging phases of the Peregrine Falcon nesting cycle. Of the 10 Peregrine Falcon nests that were observed in 1995, we observed all 10 during nestling-rearing, and 4 during post-fledging. In 1996, we sampled nestling provisioning rates at 8 of 9 nests during nestling-rearing. One nest failed prior to fledging; we observed the 7 remaining nests plus a replacement nest during the post-fledging stage. For analysis, the nestling-rearing stage was further subdivided into: early nestling-rearing (0-10 days post-hatch), mid nestling-rearing (11-24 days), and late nestling-rearing (25 days to fledging). Stage was determined by the estimated age of the oldest chick based on visits to the nest to band young.

We sampled provisioning rates during most of the daylight period at each nest observed during nestling-rearing and again at each nest observed during post-fledging, with the exception of one nest during nestling-rearing that was observed during only one 4-hour period. In both years, however, observations were concentrated from 8:00 to 17:00 Alaska Daylight Time (ADT).

Two video cameras equipped with 250 mm lenses and 2X extenders were employed to record prey deliveries continuously during observation sessions. In 1995, we used Canon L2 Hi-8 mm and Sony CCD-FX430 8 mm video cameras, and in 1996 we used Canon L2 cameras exclusively. During the nestling-rearing stage, one camera was focused on the nest ledge, while the other was focused on the attending adult. During the post-fledging stage, we focused on fledglings or adults as their visibility allowed.

We estimated prey mass delivery rates during each stage of the nesting cycle (early, mid, and late nestling-rearing, and post-fledging) for each nest by averaging total prey mass delivered during 4-hour observation sessions. Similarly, we calculated prey item delivery rates during each stage for each nest by averaging total number of prey items delivered during 4-hour observation sessions. Finally, to estimate average prey mass per nest per stage, we first divided the total estimated mass of prey delivered by the total number of items delivered per 4-hour observation session, and then calculated the mean for the total number of observation sessions. During a given stage of the nesting cycle we conducted an average of 5 ($SD = 2.6$) 4-hour observation sessions at a given nest, for a total of 182 observation sessions. Observation sessions were excluded from analyses if poor visibility persisted throughout the session. Nests were treated independently between years.

In addition, we examined the relationship between the length of time an adult was absent from the area of the nest prior to a delivery (foraging trip duration), and the estimated mass of the prey item delivered. For this analysis we excluded the first item of every observation session and included only prey items identified to species, genus, or family.

Average brood size among successful study nests during the study period was 2.71 ($SD = 0.96$, range = 1 - 4 nestlings), similar to average brood size throughout Interior Alaska (Cade 1960, Ambrose et al. 1988, Bente 1995). Our average included two nests that experienced reductions in brood size: one from 3 to 1 chick and the second from 4 to 3 chicks.

Statistical Analyses

We used linear regression to assess the relationships of estimated prey mass delivery rate, prey item delivery rate, and average estimated prey mass as a function of brood size, and of estimated prey mass as a function of foraging trip duration. Additionally, we used a χ^2 test to examine the relationship between prey size and brood size. Analyses were conducted at the 0.05 α level. Means are reported as $\bar{x} \pm \text{SE}$. We weighted means based on the sample size of 4-hour observation blocks per stage. Although we log transformed prey mass delivery rates to meet the assumptions of the statistical test, we report data on the non-transformed scale.

RESULTS

Taxonomic Composition of Prey

Of the 215 prey items observed being delivered to nestlings, 133 could be identified to some taxonomic group. Most of these prey (51.9%) were perching birds (Passeriformes), with shorebirds (24.1%), ducks and grebes (14.3%), and gulls and terns (9.0%) comprising most of the remainder (Fig. 2.1, Table 2.1). Ducks and grebes were the most important prey category on a biomass basis, comprising nearly two-thirds (63.0%) of total estimated prey biomass. Shorebirds followed at 13.0%, gulls and terns were 11.2%, and perching birds were only 11.1% of total prey biomass.

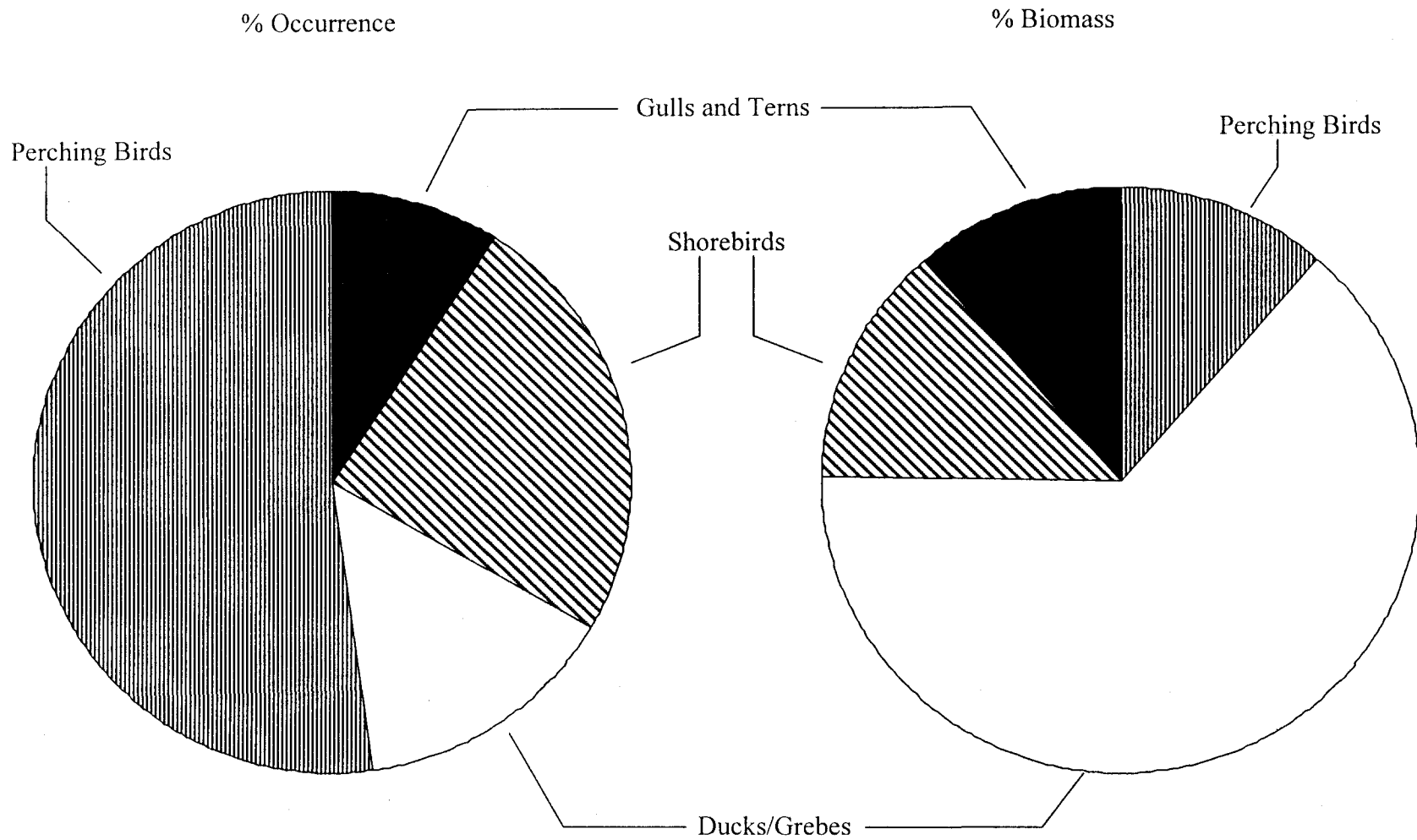


Fig. 2.1 Taxonomic composition of prey delivered to Peregrine Falcon nestlings along the Tanana River, Alaska

Table 2.1. Frequencies of prey items observed and identified upon delivery to Peregrine Falcon nestlings at nests along the Tanana River, Alaska in 1995 and 1996.

Common Name (<i>Scientific Name</i>)	Age/Sex	Frequency	% Occurrence	Body Mass g ^a	% Total Prey Mass
Grebe spp. (Red-necked, or Horned) (<i>Podiceps</i> spp.)	-	3	2.3	738	10.9
Mallard (<i>Anas platyrhynchos</i>)	female	2	1.5	1082	10.7
American Wigeon (<i>Anas americana</i>)	female	1	0.8	719	3.5
American Wigeon (<i>Anas americana</i>)	male	2	1.5	792	7.8
American Green-winged Teal (<i>Anas crecca</i>)	male	1	0.8	364	1.8
American Green-winged Teal (<i>Anas crecca</i>)	-	1	0.8	340	1.7
Scaup spp. (Greater or Lesser) (<i>Aythya</i> spp.)	male	1	0.8	891	4.4
Duck spp. (Anatinae spp.)	female	1	0.8	722	3.6
Duck spp. (Anatinae spp.)	-	3	2.3	746	11.0
Duckling (Anatinae spp.)	Juvenal	2	1.5	30	0.3
Duck/Grebe spp. (Anatinae spp. or <i>Podiceps</i> spp.)	-	2	1.5	745	7.3
Total Ducks and Grebes (Anatinae and Podicipedidae)		19	14.6		63.0
Red-necked Phalarope (<i>Phalaropus lobatus</i>)	-	1	0.8	34	0.2

Table 2.1. Continued

Common Name (<i>Scientific Name</i>)	Age/Sex	Frequency	% Occurrence	Body Mass g ^a	% Total Prey Mass
Least Sandpiper (<i>Calidris minutilla</i>)	-	2	1.5	23	0.2
Lesser Yellowlegs (<i>Tringa flavipes</i>)	-	2	1.5	81	0.8
Yellowlegs spp. (Greater or Lesser) (<i>T. flavipes</i> or <i>T. melanoleuca</i>)	-	5	3.8	126	3.1
Solitary Sandpiper (<i>Tringa solitaria</i>)	Juvenal	1	0.8	48	0.2
Upland Sandpiper (<i>Bartramia longicauda</i>)	-	1	0.8	150	0.7
Spotted Sandpiper (<i>Actitis macularia</i>)	-	5	3.8	32	0.8
Spotted Sandpiper (<i>Actitis macularia</i>)	Juvenal	2	1.5	32	0.3
Shorebird spp. (Scolopacidae spp.) small	-	3	2.3	30	0.4
Shorebird spp. (Scolopacidae spp.) medium	-	10	7.5	125	6.2
Total Shorebirds (Scolopacidae)		32	24.3		12.9
Mew Gull (<i>Larus canus</i>)	-	1	0.8	404	2.0
Bonaparte's Gull (<i>Larus philadelphia</i>)	-	1	0.8	212	1.0
Gull spp. (Mew or Bonaparte's) (<i>Larus</i> spp.)	-	2	1.5	308	3.0
Gull nestling (<i>Larus</i> spp.)	-	2	1.5	125	1.2

Table 2.1. Continued

Common Name (<i>Scientific Name</i>)	Age/Sex	Frequency	% Occurrence	Body Mass g ^a	% Total Prey Mass
Arctic Tern (<i>Sterna paradisaea</i>)	-	5	3.8	110	2.7
Gull/Tern spp. (<i>Larus</i> spp or <i>Sterna</i> spp.)	-	1	0.8	242	1.2
Total Gulls and Terns (<i>Laridae</i> or <i>Sternidae</i>)		12	9.2		11.1
Rock Dove (<i>Columba livia</i>)	-	1	0.8	355	1.7
Northern Flicker (<i>Colaptes auratus</i>)	-	1	0.8	142	0.7
Bohemian Waxwing (<i>Bombycilla garrulus</i>)	-	1	0.8	56	0.3
Black-billed Magpie (<i>Pica pica</i>)	-	2	1.5	178	1.8
Gray Jay (<i>Perisoreus canadensis</i>)	-	3	2.3	73	1.1
Gray Jay (<i>Perisoreus canadensis</i>)	Juvenal	1	0.8	73	0.4
Dark-eyed Junco (<i>Junco hyemalis</i>)	-	2	1.5	20	0.2
Cliff Swallow (<i>Hirundo pyrrhonota</i>)	-	1	0.8	22	0.1
Violet-green Swallow (<i>Tachycineta thalassina</i>)	-	2	1.5	14	0.1
Violet-green Swallow (<i>Tachycineta thalassina</i>)	Juvenal	1	0.8	14	0.1

Table 2.1. Continued

Common Name*(<i>Scientific Name</i>)	Age/Sex	Frequency	% Occurrence	Body Mass g ^a	% Total Prey Mass
Bank Swallow (<i>Riparia riparia</i>)	-	1	0.8	15	0.1
Tree Swallow/Violet-green Swallow (<i>Tachycineta bicolor</i> or <i>T. thalassina</i>)	-	2	1.5	17	0.2
Swallow spp. (Cliff, Tree, Violet-green, or Bank) (Hirundinidae spp.)	-	25	18.8	18	2.2
Swallow spp. (Hirundinidae spp.)	Juvenal	6	4.5	18	0.5
Yellow Warbler (<i>Dendroica petechia</i>)	-	1	0.8	10	0.1
Black-capped Chickadee (<i>Parus atricapillus</i>)	-	1	0.8	11	0.1
Swainson's Thrush (<i>Catharus ustulatus</i>)	-	1	0.8	31	0.2
Varied Thrush (<i>Ixoreus naevius</i>)	-	1	0.8	77	0.4
American Robin (<i>Turdus migratorius</i>)	-	1	0.8	77	0.4
Thrush spp. (Gray-checked, Swainson's, or Hermit) (<i>Catharus</i> spp.)	-	1	0.8	32	0.2
small Passerine spp. (Passeriformes spp.)	-	15	11.3	30	2.2
Total Perching Birds (Passeriformes)		68	51.3		10.6
Unknown Avian spp.	-	82	-	-	-
Total	-	(215)	133=100%	20,294 g=100%	

Table 2.1. Continued

^a In the case of prey items identified to species, we estimated prey mass using the average body mass of that species directly from the literature (Dunning 1993). For prey that could be identified only to genus or family, we used the mean mass of all the species of that genus or family (Dunning 1993) that regularly occur in the study area, except in the case of shorebirds which span a wide range of masses. We classified shorebirds into small (9-50 g) or medium (51-200 g) size classes based on estimated size in the field and assigned them the median mass of all species of that size class known to regularly occur in the study area (30 g and 125 g, respectively).

Prey Size

Of the 215 prey items that we observed being delivered to young, 133 items (61.9%) were identified to prey size category (Table 2.1). Overall, more small items (76 or 57.1%) were delivered than either medium (36 or 27.1%) or large (21 or 15.8%) items (χ^2 goodness of fit test = 34.89, $df = 2$, $P < 0.0001$). When all prey items were combined, there was a trend towards lack of independence between brood size and size of prey item (χ^2 contingency test = 10.98, $df = 6$, $P = 0.0890$).

The average mass of individual prey items increased from broods of 1 to broods of 3, but decreased between broods of 3 to 4 (Fig. 2.2). This convex relationship was evident from the negative coefficient of the quadratic term, $\text{brood size}^2 = -45.2 (\pm 22.1)$, after accounting for stage of the nesting cycle ($r^2 = 18.8$). Despite the large standard error and the low coefficient of variation, the coefficient of $(\text{brood size})^2$ was significant ($P = 0.0493$; Fig. 2.2).

We did not observe parents of 1-chick broods delivering large items, and analysis of standardized residuals indicated a trend towards fewer medium-sized items brought to broods of 2 ($P = 0.1556$), and more medium-sized items brought to broods of 4 ($P = 0.0614$). Although this analysis does not account for differences in the number of 4-hour observation sessions among brood sizes, together with data on average prey mass it suggests that Peregrine Falcons provisioning brood sizes of 2 and 3 delivered larger items to their young than those with broods of 1. Broods of 4 maintained higher provisioning rates by increasing both prey item delivery rates and average prey mass.

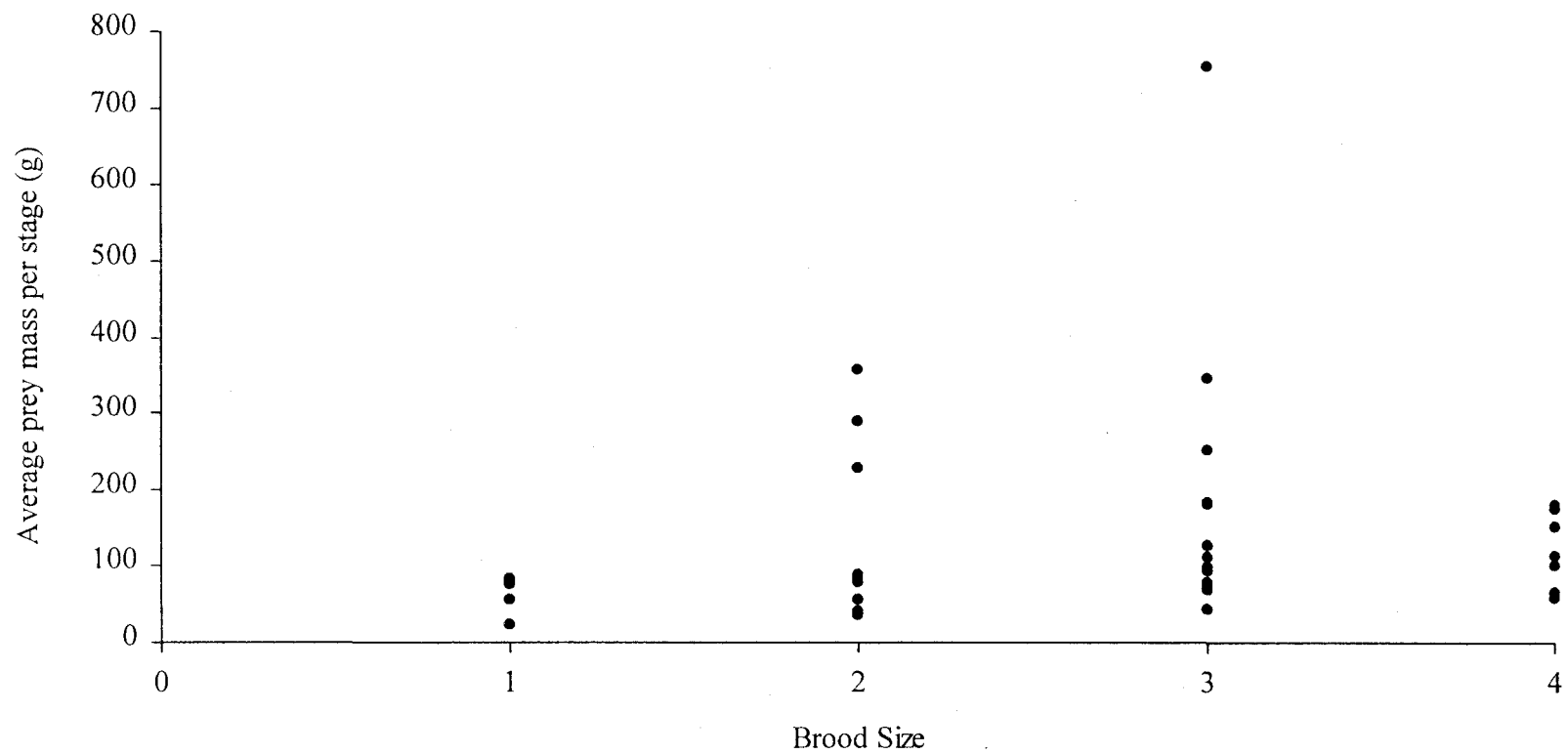


Figure 2.2. Average estimated mass of prey items delivered per stage of the nesting cycle to Peregrine Falcon broods of various sizes along the Tanana River, Alaska.

Foraging Trip Duration

There was a positive correlation between foraging trip duration (minutes) and estimated mass of the delivered prey item (slope = 0.197 min/g, 95% confidence interval: 0.05 to 4.2, $P = 0.0001$, $r^2 = 0.22$, $df = 61$; Fig. 2.3). This is driven by the inverse relationship between prey item delivery rate and average prey mass (slope = -3.04, 95% confidence interval: -2.2 to -3.4, $P < 0.0001$, $r^2 = 65.5$, $df = 34$) measured per stage per nest.

Stage of the Nesting Cycle and Prey Provisioning Rates

Prey item delivery rates did not differ among stages of the nesting cycle ($P > 0.10$, P -value for family-wise multiple comparisons). Average prey size also did not differ among stages ($F_{3,35} = 1.36$, $P = 0.2726$). Prey mass delivery rates were not significantly different among stages ($F_{3,35} = 1.41$, $P = 0.2575$), although there was a trend toward lower prey mass delivery rates during post-fledging (Fig. 2.4).

Brood Size and Prey Provisioning Rates

There was a positive correlation between brood size and both prey item delivery rate ($r^2 = 0.51$, $P = 0.0055$, Fig. 2.5a) and prey mass delivery rate ($r^2 = 0.25$, $P = 0.0225$, Fig. 2.6a), after accounting for stage of the nesting cycle in both analyses. Lack of Fit F-tests were not significant for either prey item delivery rate ($P = 0.41$) or prey mass

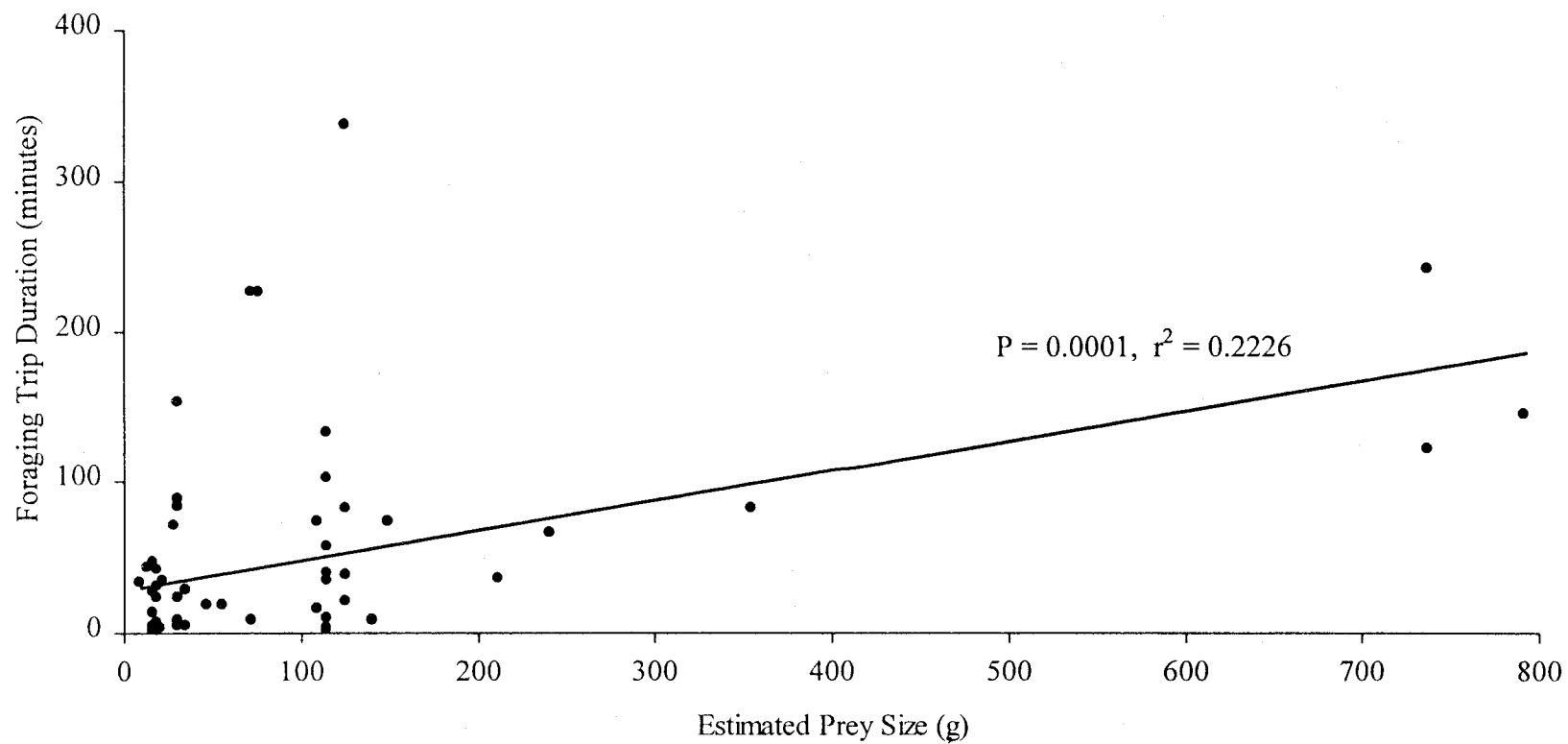


Figure 2.3. Foraging trip duration (minutes away from nest cliff prior to prey item delivery) as a function of estimated prey size for Peregrine Falcons nesting along the Tanana River, Alaska.

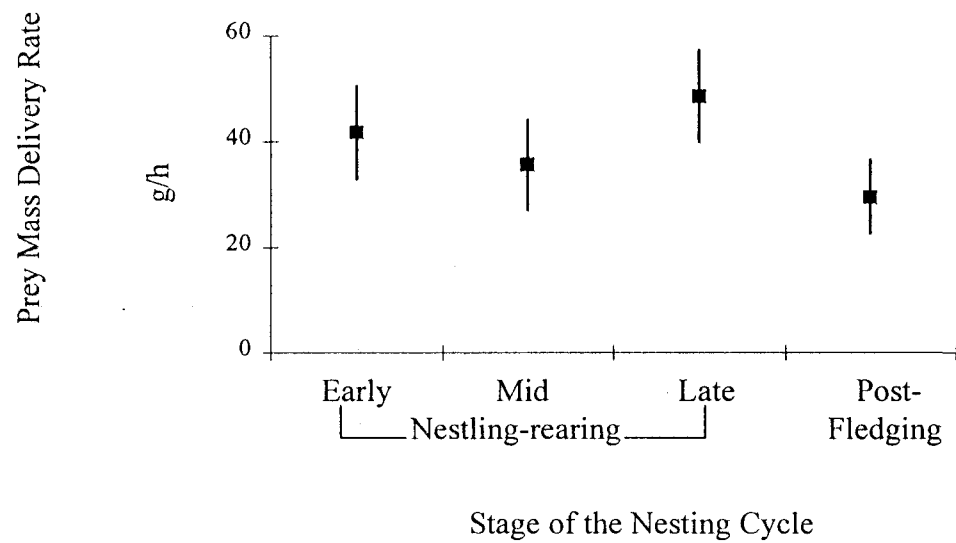


Figure 2.4. Estimated prey mass delivery rate versus stage of the nesting cycle in Peregrine Falcons nesting along the Tanana River, Alaska.

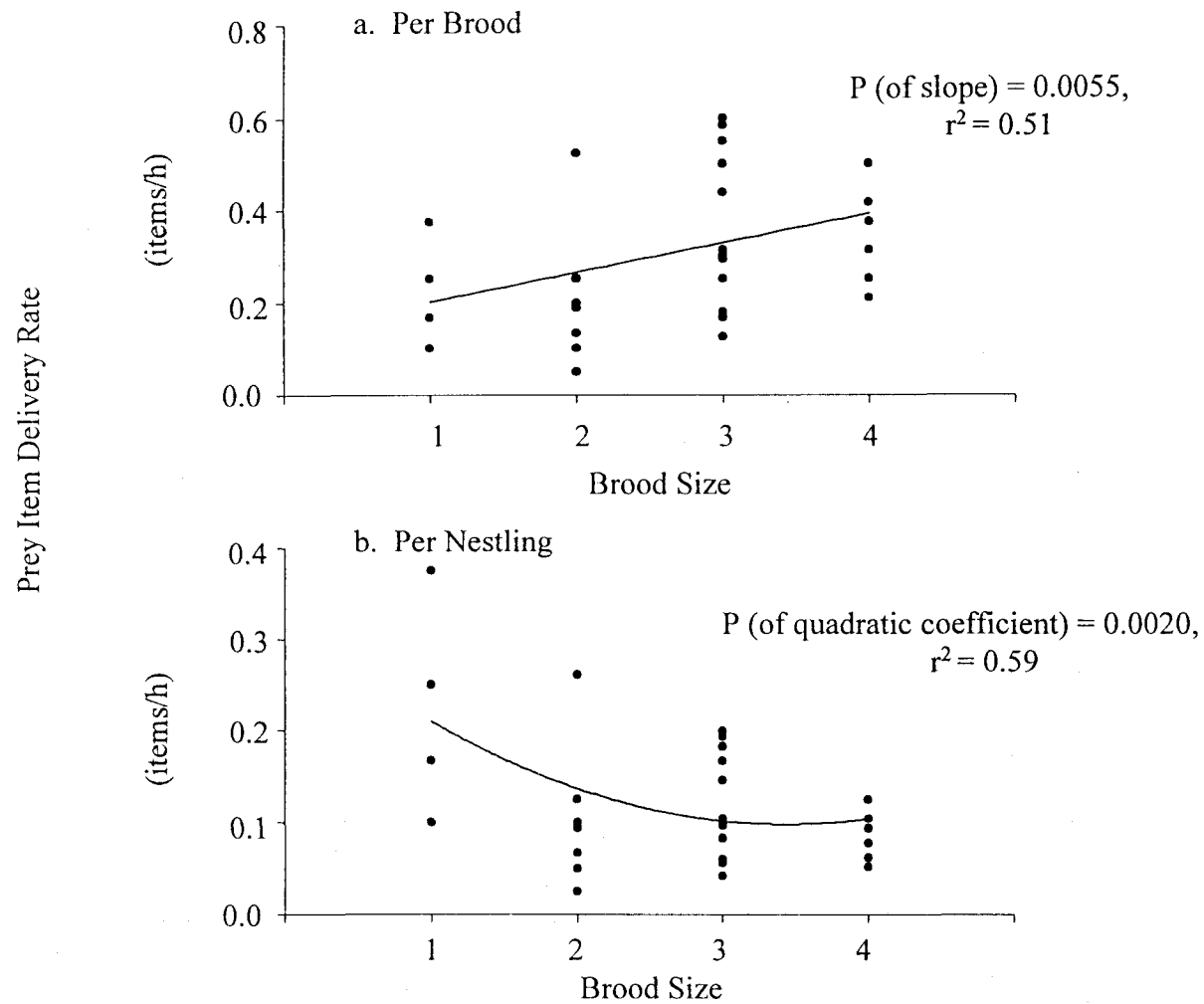


Figure 2.5. Prey item delivery rate per brood (a) and per nestling (b) as a function of brood size in Peregrine Falcons nesting along the Tanana River, Alaska.

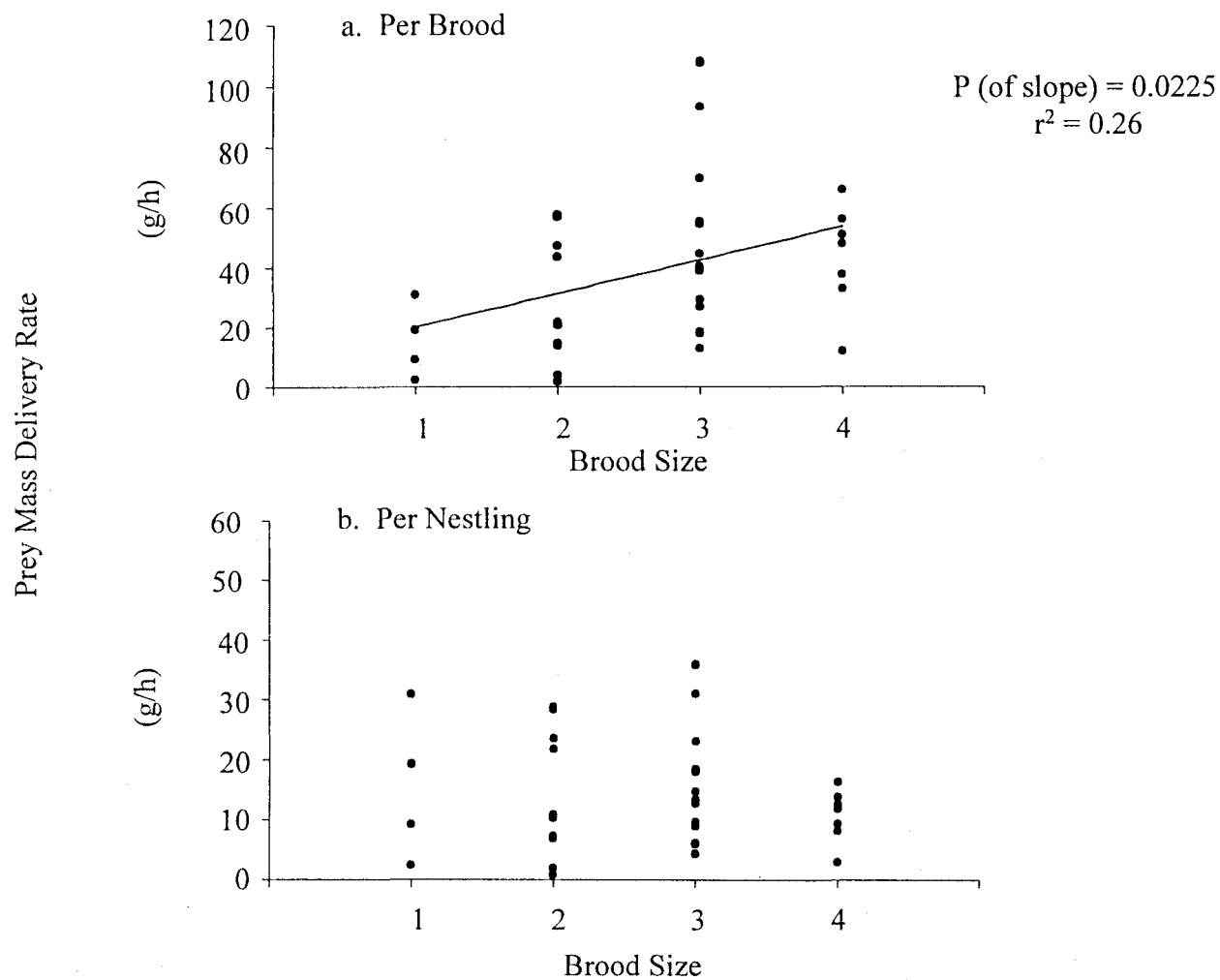


Figure 2.6. Estimated prey mass delivery rate per brood (a) and per nestling (b) as a function of brood size in Peregrine Falcons nesting along the Tanana River, Alaska. P-value and r^2 in (a) based on model using log transformed data.

delivery rate ($P = 0.77$), suggesting a linear relationship between provisioning rates and brood size.

Prey Provisioning Per Nestling

Prey item delivery rates per nestling declined with increasing brood size, after accounting for stage of the nesting cycle (Fig. 2.5b). In contrast, prey mass delivery rates per nestling appeared to remain constant with increasing brood size (Fig. 2.6b). As brood size increased from 1 to 3 chicks, prey item delivery rate per nestling decreased, but no such decrease was apparent from brood size 3 to 4 (Fig. 2.5b). The relationship between prey item delivery rate per nestling and brood size after accounting for stage of the nesting cycle was concave, as indicated by including a quadratic term (brood size)² in the model ($P = 0.0011$ for the positive coefficient of (brood size)²; Fig. 2.5b). In contrast, the slope of the regression of prey mass delivery rate per nestling on brood size did not differ from zero, after accounting for nesting stage (2-sided test, $P = 0.3897$ for the coefficient of brood size on prey mass delivery rate per nestling; Fig. 2.6b). Consequently, breeding pairs did not fully compensate for larger broods by proportionately increasing the rate of prey item delivery, but instead increased the size of prey delivered.

DISCUSSION

Our results are consistent with the hypothesis that parents must work harder to provide for larger broods. Pairs with larger broods not only had higher prey item delivery

rates (Fig. 2.5a), but also had higher prey mass delivery rates, after accounting for stage of the nesting cycle (Fig. 2.6a). Per nestling prey item delivery rates declined, however, with increasing brood size, indicating that parents did not fully compensate for larger broods by capturing more prey (Fig. 2.5b). The lack of a correlation between per nestling prey mass delivery rates and brood size (Fig. 2.6b) suggests that parents of larger broods compensated for lower per nestling prey item delivery rates by delivering larger prey items on average. In support of this interpretation, average prey mass increased between broods of 1 to 3 (Fig. 2.2), parents of small broods did not deliver any large items, and there was a trend toward parents of broods of 4 delivering more medium-sized items than those of broods of 1 to 3. Consequently, different brood sizes were associated with different parental foraging strategies.

We found evidence for a positive relationship between foraging trip duration and size of prey delivered (Fig. 2.3). If foraging trip duration is proportional to distance traveled from the nest, then this prediction of optimal foraging theory was supported. In other words, Peregrine Falcons delivered larger prey items when foraging at greater distances from the nest. Parent falcons routinely took swallows (*Tachycineta* spp. or *Hirundo* spp.; Table 2.1) that were breeding on the nest cliffs, while ducks and grebes were delivered infrequently and were never observed being captured within view of the nest. Nevertheless, ducks and grebes comprised the majority of prey mass delivered to nestlings, at least in brood sizes greater than one.

While foraging trip duration and prey size were significantly correlated, much of the variability in foraging trip duration was not explained. This is likely because many

other variables, such as hunger level of brood (Tinbergen and Drent 1980), prey availability (Hunter et al. 1988, Meese and Fuller 1989, Rosenfield et al. 1995), prey handling time (Beissinger 1983), foraging efficiency (Winkler and Allen 1995), and weather conditions (Steidl and Anthony 1995) affected foraging trip duration or prey size. In general, with constant prey mass delivery rates the relationship between prey item delivery rate and average prey size is inverse, i.e., the time required to retrieve a given mass of prey in many smaller prey items captured right at the nest may be more than the time required to retrieve the equivalent mass of prey in a single large item (Fig. 2.3). Large prey may only be caught at some distance from the nest, or it may require a longer time to kill and pluck large prey.

Theory suggests that raising the maximum possible number of young causes reductions in parental survival, and thus natural brood sizes are lower than maximum in order to optimize future survival and thus maximize lifetime reproductive output (Dijkstra 1990). Deerenberg et al. (1995) demonstrated a direct relationship between increased individual work rate in parents with enlarged broods and local survival rate. They proposed that an optimal work rate may be a proximate control mechanism for brood size, because high work rates may entail physiological weakening, leading to lower survival rates. Nur (1984, 1987) demonstrated that per nestling provisioning rates in blue tits decrease with increasing brood size, producing a concave curve. The decline in per nestling provisioning rates is predicted because it does not maximize fitness to provide each nestling in large broods proportionally, given the energetic costs of increased provisioning rates.

A major difference between these studies and the present study is that this study did not manipulate brood size. Nevertheless, the results from this study were similar; per nestling prey delivery rates as a function of brood size decreased in a concave curve (Fig. 2.6b). Per nestling prey mass delivery rates, unlike per nestling prey item delivery rates, were constant across the range of natural brood sizes seen in this study.

One possible explanation for constant per nestling prey mass delivery rates, regardless of brood size, is that parents of smaller broods were working far below maximum sustained working capacity (Dijkstra 1990, and see Stearns 1992 for a review). This, in turn, could be because prey were readily available and easy to acquire. An alternative explanation is that pairs with larger broods were better providers and able to regularly kill larger prey and transport it to the nest.

To raise large broods, parents must not only be efficient enough hunters to capture and deliver prey at adequate provisioning rates, but they also need to maintain a work rate that does not excessively impinge on future survival and thus reduce lifetime reproductive output (Deerenberg 1995). If natural brood size is an indication of optimal work load per pair then brood size may reflect parental foraging efficiency. In general, we observed more prey items and larger prey items delivered to larger broods. Larger prey required longer foraging trips due either to distance traveled to capture larger prey or to increased handling time for larger prey. Thus, in natural broods, we found parents had equal provisioning rates per nestling regardless of brood size, presumably maximizing both their present and future reproductive output. Distinguishing between parental hunting

efficiency and prey availability as they influence prey provisioning rates will be essential to test foraging theory as it relates to Peregrine Falcons feeding young.

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CHAPTER 3.
EFFECTS OF JET AIRCRAFT OVERFLIGHTS ON NEST ATTENDANCE, TIME-
ACTIVITY BUDGETS, AND NESTLING PROVISIONING RATES OF PEREGRINE
FALCONS

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ABSTRACT

Few studies have examined the effects of disturbances on nest attendance, time-activity budgets, and nestling provisioning rates by breeding raptors. Subtle changes in these parameters could potentially lead to insidious impacts on nesting success. In this study we examined the effects of low-altitude jet aircraft overflights on nest attendance, time-activity budgets, and provisioning rates of 19 Peregrine Falcon (*Falco peregrinus*) pairs breeding along the Tanana River, Alaska in 1995 and 1996. Nest attendance and time-activity budgets of Peregrine Falcons during periods of overflights differed from those of peregrines at reference nests, but differences depended on stage of the nesting cycle and gender. During the incubation/nestling-brooding stage of the nesting cycle, males attended the nest ledge less when overflights occurred than did males from reference nests. Females apparently compensated for low male ledge attendance by attending the ledge more during overflown periods compared to females from reference nests, although this trend was not significant. 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. During late nestling-rearing, however, females perched in the nest area less 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 to occur within a given time period, the cumulative number of above threshold noise events experienced by each nesting pair, or the average sound exposure level of overflights. Furthermore, we found no evidence that nestling provisioning rates were affected by overflights.

INTRODUCTION

Human disturbance of wildlife is an increasing concern as human activities expand into wilderness areas. The United States Air Force (USAF) maintains low-altitude Military Training Routes (MTRs) and Military Operations Areas (MOAs) in areas of sparse human settlement in Interior Alaska. Residents and resource management agencies have voiced concern regarding the potential effects of low-altitude jet aircraft overflights on wildlife (Galdwin et al. 1987). As a result of these concerns, in combination with requirements of the National Environmental Policy Act (NEPA) (1969) and the Endangered Species Act (ESA) (1973), the USAF sponsored several research projects to document the effects of aircraft activity on wildlife populations. One taxonomic group of concern was raptors (Falconiformes).

Raptors were of particular concern to wildlife management agencies for several reasons. First, as higher order consumers, they serve as indicators of ecosystem health and general environmental conditions (Newton 1979). Second, many raptor populations have experienced dramatic declines in the last 40 years, leaving some species (e.g., Peregrine Falcons (*Falco peregrinus*) and Bald Eagles (*Haliaeetus leucocephalus*))

threatened with extinction (Hickey 1969, Bird 1983). Finally, raptors are sensitive to human disturbance during nesting (Fyfe and Olendorf 1976, Steenhof and Kochert 1982, Steidl and Anthony 1995). Steidl and Anthony (1995) found that prey consumption rates by Bald Eagle nestlings decreased with proximity of human recreational activities. It is widely accepted that birds are sensitive to disturbance during particular periods of the nesting cycle. In raptors these periods include early incubation, early nestling-rearing, and early fledging (Fyfe and Olendorf 1976); yet few studies have examined the effects of overflights at these times (Awbrey and Bowles 1990).

Some responses by nesting raptors to aircraft overflights are overt, such as attack or panic flights (Fyfe and Olendorf 1976, Ritchie 1987), while other responses may be subtle and more difficult to detect. Disturbance may result in changes in parental behavior and care of progeny that ultimately affect nesting success as much or more than immediate responses. Subtle, longer term responses to disturbances could lead to insidious impacts on nesting success, such as reallocation of time to nest attendance and various breeding activities, and declines in the rate at which parents provision their young. Few studies have examined these types of responses by nesting raptors to potential disturbance.

As part of a larger study on the effects of jet overflights on the behavior and reproduction of raptors, we studied Peregrine Falcons to investigate effects of overflights on several components of parental care, including nest attendance, time-activity budgets, and nestling provisioning rates. If nest attendance and behavior of adult Peregrine Falcons are influenced by low-altitude jet overflights, we would expect the time-activity

budgets of falcons to differ between periods immediately following overflights and periods when no overflights occur, and between nests that are exposed to overflights and those that are not. Additionally, because stage of the nesting cycle plays a prominent role in falcon breeding behavior (see Chapter 1), we would predict that behavioral responses to overflights would change as the nesting cycle progresses. Finally, if overflights affect behavior, we would expect a higher frequency and/or intensity of overflights to lead to more pronounced changes in allocation of time to various activities by breeding Peregrine Falcons.

In addition to nest attendance and time-activity budgets, another important aspect of parental care is nestling provisioning rates. If overflights inhibit Peregrine Falcons from either hunting or delivering prey to young, then we would expect nestling provisioning rates to be lower during periods following overflights than during periods when no overflights occurred, and lower at nests that were exposed to overflights compared to nests that were not. Acquiring larger prey items requires longer hunting forays further from nest sites (Schoener 1979, Chapter 2); thus, if overflights cause falcons to remain closer to their nests, their ability to provide larger prey items may be reduced. Finally, we would expect a negative correlation between number of overflights and prey provisioning rates.

METHODS

Study Area

The study area included 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 (Fig. 3.1). Locations along the river were identified by distance (km) from the source. In 1995, the study area extended from Tanacross (km 155) to Sawmill (km 305), and included two Military Training Routes (MTRs) that crossed the river; low-altitude military jet overflights were permitted without Federal Aviation Administration clearance in the MTRs. We identified 13 active Peregrine Falcon nest sites along this stretch of the river. Of these, 9 afforded adequate visibility for observations and 4 of these were located in MTRs and subjected to low-altitude overflights. In 1996, we included an additional section of the Tanana River from Delta (km 379) to Salcha (km 443), which included an additional MTR. We located a total of 19 active nests in 1996 and collected observations at 6 nests from the 1995 study area plus 4 nests in the new section of river. Five of these 10 observed nests were in MTRs and exposed to overflights. Two nests that were located within an MTR and were overflown in 1995 were not overflown in 1996.

Two crews of 2 to 4 observers recorded data at each Peregrine Falcon nest during two breeding seasons from 13 May through 17 August 1995, and from 13 May through 3 September 1996.

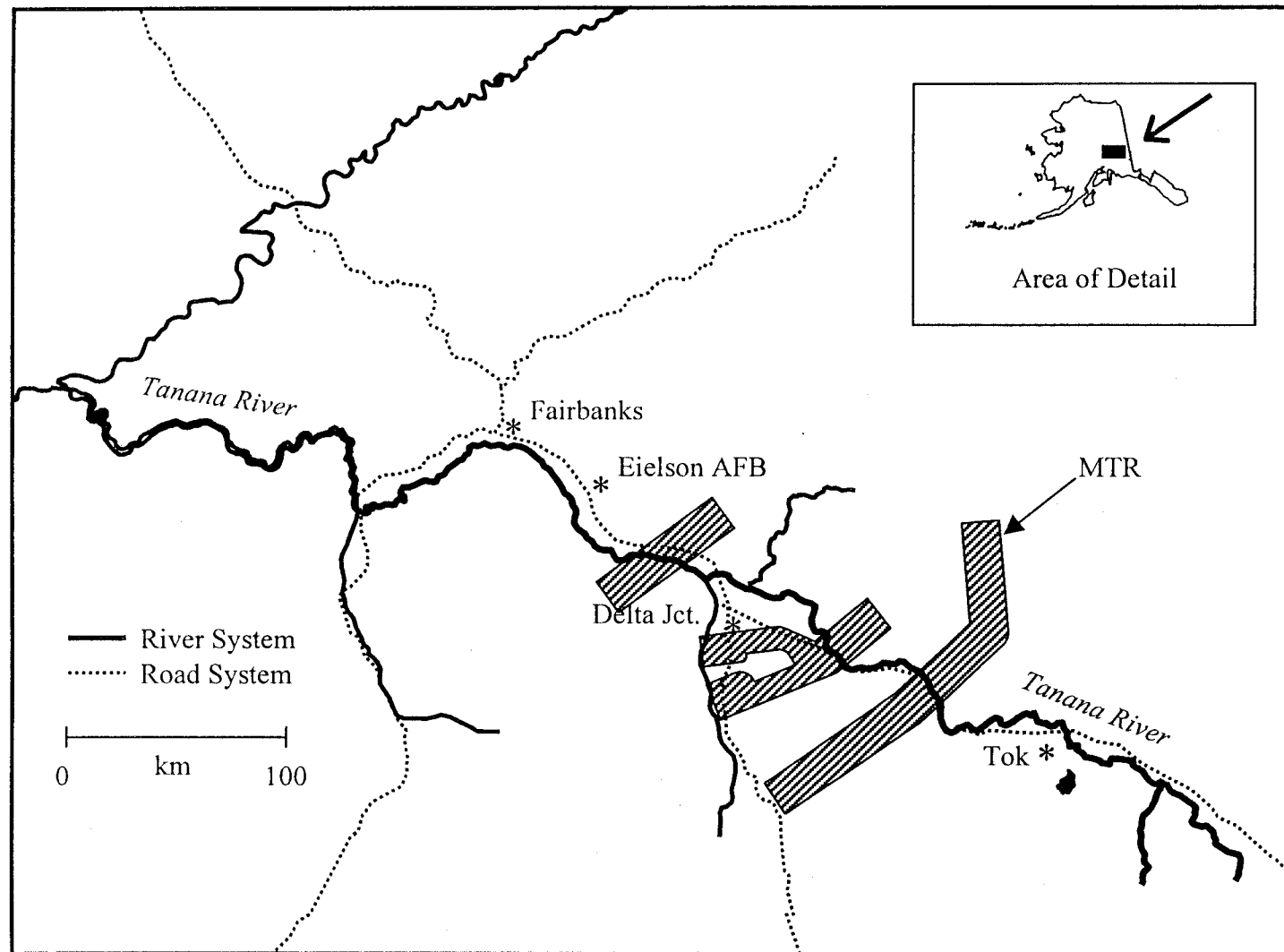


Figure 3.1. Study area along a 250-km stretch of the Tanana River between Tok and Fairbanks, Alaska.

Overflights

The 11th Air Force provided jet aircraft overflights directed at Peregrine Falcon nests that were located in the MTRs. We provided the Air Force with the latitude and longitude of nests, and marked their locations on USGS topographic maps and photographs. We coordinated with the Air Force to schedule overflights during periods when field crews were present and recording observations. The Air Force was able to provide the majority of overflights to nests during three 2.5-week periods each year (5 - 16 June, 5 - 21 July, and 7 - 17 August in 1995; 24 May - 5 June, 24 June - 10 July, and 29 July - 23 August in 1996). Overflights were less likely to occur during the interim periods because of major training exercises known as Cope Thunder. 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, the proximity of overflights to active nests was enhanced by Forward Air Controllers (FAC's) from the 3rd ASOS at Ft. Wainwright, who joined field crews on the ground.

Animal Noise Monitors (ANMs), which measure several noise dose variables, including sound exposure level (SEL), were deployed on the cliffs near each active nest ledge or scrape 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 2000 sound profiles of noise events that occurred over a minimum dB level. This threshold level was set at 85 dB for all ANMs. Noise events were only recorded if they exceeded 2 seconds and were less than 2 minutes duration.

We categorized each nest each year as either overflown or reference. Overflown nests were those located within MTRs and exposed to a minimum of 5 overflights that exceeded the 85 dB threshold. In addition, we classified as an overflight any military jet or helicopter that was ≤ 300 m (1000 ft) in altitude above an nest and ≤ 400 m (1300 ft) lateral distance from an nest during our observations. This is equivalent to a 500 m slant distance, where slant distance is the closest distance from aircraft to nest. Ninety-five percent of observed overflights within this slant distance were detected by ANMs in 1995 (Nordmeyer et al. unpubl. ms.). In 1996, it is likely that a similar percentage of overflights within 500 m slant distance were above the 85 dB threshold, though the exact percentage is unclear due to malfunction of some ANMs. Overflown nests received up to 28 observed overflights spread throughout a single breeding season (Table 3.1). In 1995, a maximum of 6 additional noise events per nest were recorded by ANMs when observers were not present (Table 3.1). In 1996, 14 to 36 above-threshold noise events occurred at nests when observers were not present (Table 3.1), due mostly to the proximity of the new MTR to Eielson Air Force Base. These numbers are likely accurate for jet overflights, but underestimate the number of helicopter overflights. Due to their sound profiles, helicopter noise events were undetected in some instances.

Reference nests were those that received a maximum of 2 above-threshold noise events, either in the presence or absence of observers (Table 3.1). Four nests in 1995 and 4 nests in 1996 met these criteria, while 2 nests outside of MTRs, one each from 1995 and 1996, were excluded from the analyses due to exposure to at least 5 noise events

Table 3.1. The number of overflights^a that overflown^b and reference^c nests were exposed to in 1995 and 1996. Noise events recorded on Animal Noise Monitors (ANMs) when observers were not present are in parentheses.

1995	Stage of the Nesting Cycle			Total	Grand
	Incubation	Nestling-rearing	Post-fledging	Observed	Total
Overflown Nests					
205	11 (2)	8 (0)	no obs.	19	21
221	8 (2)	12 (0)	5 (0)	25	27
281	no obs.	10 (6)	3 (no ANM)	13	19
288	2 (2)	3 (0)	no obs.	5	7
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

Table 3.1 (Continued).

1996	Stage of the Nesting Cycle			Total	Grand
	Incubation	Nestling-rearing	Post-fledging	Observed	Total
Overflowed Nests					
280.5	18 (9)	4 (7)	0 (0)	22	38
288.5	1 (4)	23 (11)	4 (1)	28	44
427	9 (12)	4 (20)	15 (2)	28	62
431	2 (14)	nest failure	-	-	16
438.6	1 (12)	15 (14)	4 (0)	20	46
Reference Nests					
205	0 (0)	nest failure	-	0	0
221	0 (1)	0 (1)	0 (0)	2	2
258	no obs. (no ANM)	no obs. (no ANM)	0	0	0
269.5	0 (0)	0 (0)	0 (0)	0	0
379	0 (5)	0 (7)	2 (13)	2	2

Table 3.1 (Continued).

^a Overflights were classified as any military jet or helicopter that came within a 500 m slant distance of the nest, where slant distance is the closest distance from the aircraft to the nest.

^b Overflown nests are those that were exposed to a minimum of 5 overflights above the 85 dB threshold during a given breeding season.

^c Reference nests are those that were exposed to no more than 2 noise events above the 85 dB threshold during a given breeding season.

* This reference nest was excluded from analyses due to the number of above threshold noise events recorded by ANMs when observers were absent.

when observers were not present. One of the reference nests in 1996 did not have an ANM deployed nearby, but was likely not exposed to above-threshold noise events (1) because the location of the nest was remote with respect to MTRs, and (2) the exposure of the closest reference nest (10 km down-river) to above-threshold noise events was nil.

Behavioral Observations

We established observation sites across at least one channel of the river and 300-750 m from nests to permit observation of nest attendance, time-activity budgets, and prey deliveries without disturbing the breeding pair. Observation distance from nests depended on available observation sites and the sensitivity of individual falcons to human presence. As the breeding season progressed, water levels rose dramatically due to glacial runoff and submerged some observation sites. Due to high water levels, observation distances increased to as much as 1500 m for two nests late in the 1995 season. River levels peaked at lower levels in 1996.

We used binoculars, 15-60 X spotting scopes, and Questar telescopes to aide our observations during 3 stages of the Peregrine Falcon nesting cycle: incubation, nestling-rearing, and post-fledging. We recorded nest attendance and time-activity budgets during incubation and nestling-rearing, and measured prey provisioning rates during nestling-rearing and post-fledging. Of the 11 nests observed in 1995, we observed 5 during incubation, 9 during nestling-rearing, and 4 during post-fledging. In 1996, we conducted observations during incubation, nestling-rearing, and post-fledging at 7 of 11 nests. The

other 4 nests were not sampled during all three phases of the nesting cycle because 2 nests failed around hatching and were replaced by 2 other nests after hatching. For analysis, the nestling-rearing phase was further subdivided into three stages, early nestling-rearing (0-10 days post-hatch), mid nestling-rearing (11-24 days), and late nestling-rearing (25-42 days). Stage was determined by the estimated age of the oldest chick based on banding visits to the nest during mid nestling-rearing.

We used Canon L2 Hi-8 mm and Sony CCD-FX430 8 mm video cameras equipped with 250 mm lenses and 2X extenders to record nest attendance, adult behaviors, and prey deliveries during observations. During incubation and nestling-rearing periods, one camera was focused on the nest ledge, while the other was focused on the attending adult. During the post-fledging period, we focused on visible fledglings or adults. Video tapes provided additional data on behavior during times when instantaneous scans were insufficient to describe events. We used tents to protect gear from inclement weather and as blinds at sites where adults were more sensitive to human presence.

Nest Attendance and Time-Activity Budgets

We used the instantaneous scan method to sample activity (Altmann 1974, Tacha et al. 1985) at one-minute intervals for each adult. Scans contributed data to both nest attendance and time-activity budgets. For nest attendance, we distinguished between attendance at the nest ledge or scrape, attendance in the nest area (within 200 m of the

nest ledge), and away from the nest area (greater 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 6 categories (See Chapter 1, Table 1.1). We categorized birds as “out of sight” for no longer than 5 minutes without confirmation of their location. Adult activity was classified as “unknown”, or away from the nest area, if they were not detected within 5 minutes.

We compared attendance and time-activity budgets between observation blocks when overflights occurred (overflowed blocks) and two types of control observation blocks: 1) from overflowed nests when overflights did not occur (baseline blocks) and 2) from reference nests (reference blocks) (Fig. 3.2). These two types of controls helped to distinguish between two different types of variability in nesting behavior. Comparisons of behavior between exposed and unexposed nests control for bias from previous exposure to overflights. In contrast, within-nest comparisons (internal controls) compensate directly for behavioral differences among pairs, but may be biased due to previous exposure to overflights.

An observation block refers to the group of one-minute scan samples that fell within a 1- to 4-hour time period. We grouped scans in this way to avoid autocorrelation in the data from one-minute scans. We collected behavioral data during 238 observation blocks during incubation and nestling-rearing. Analyses, however, were restricted to the 53 blocks when overflights occurred, 53 baseline blocks, and 58 reference blocks. Baseline and reference blocks were selected to correspond with the same stage of the nesting cycle and time of day as overflight blocks as much as possible; however,

Treatment

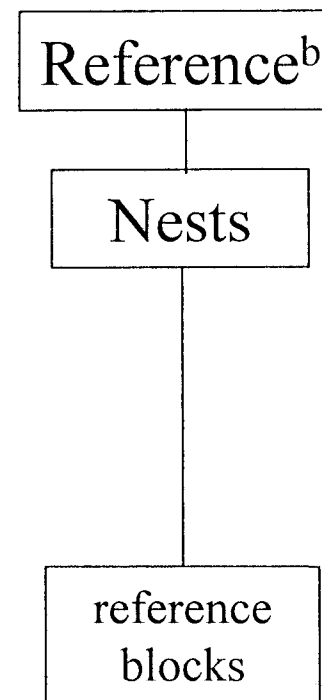
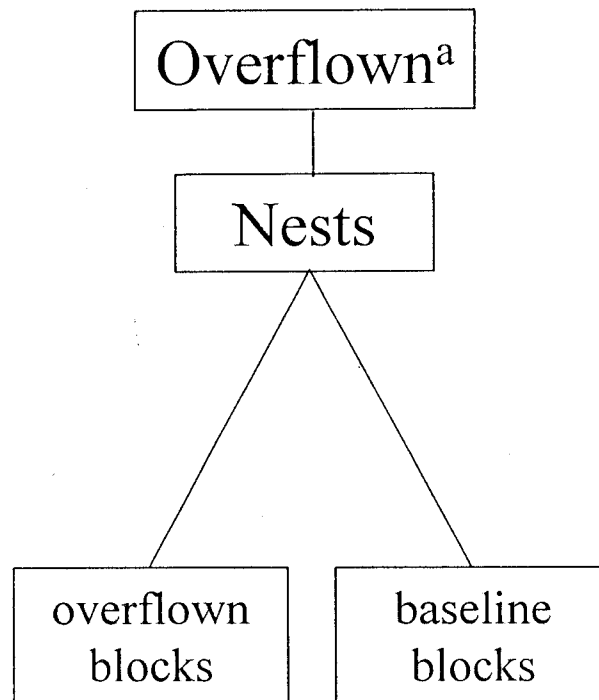


Figure 3.2. Study design for detecting effects of jet aircraft overflights on nest attendance, time-activity budgets, and nestling provisioning rates of Peregrine Falcons nesting along the Tanana River, Alaska.

^a Overflown nests were those that were exposed to at least 5 noise events that exceeded 85 dB per season.

^b Reference nests were those that were exposed to less than 2 noise events that exceeded 85 dB per season.

observation blocks during mid nestling-rearing were under-represented at reference nests. Additionally, within the 1- to 4-hour 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 hrs and 1700 hrs ADT; thus, we also restricted inclusion of data to observation blocks that overlapped this 9-hour period. Observation blocks were discarded if visibility was poor, or if the sex of adults was indeterminant throughout the block.

The beginning of observation blocks was set either by the timing of the day's first overflight or to coincide with three times of day (0800 hrs, 1200 hrs, or 1600 hrs), and were continued for up to four hours. The first overflight to occur after the first 4-hour overflown block marked the start of the next 4-hour overflown block. Baseline observation blocks were matched to overflown blocks either by selecting observations during the four hours preceding an overflight, or from days without overflights that corresponded to the nesting stage and time of day when overflights occurred. In the latter case, blocks began at 0800 hrs, 1200 hrs, or 1600 hrs. Reference blocks also began at 0800 hrs, 1200 hrs, or 1600 hrs.

To calculate ledge attendance by each member of the 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. As with ledge attendance, 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. Likewise, we 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.

Nestling Provisioning Rates

We recorded the number of prey deliveries, the estimated size class of each prey item, and the type of prey delivered (identified to species whenever possible). As a measure of provisioning rates, we estimated the mass of prey identified to species using the average body mass of that species in Dunning (1993). For prey that could be identified only to genus, family, size class, or unknown, we estimated prey mass based on methods discussed in Chapter 2.

We estimated prey mass delivery rates as the total prey mass delivered during 2-hour observation sessions. Similarly, we calculated prey item delivery rates as the total number of prey items delivered during 2-hour observation sessions, and we calculated average estimated prey size as total prey mass delivered divided by number of prey items delivered. A delivery was defined as any prey item brought to the nest ledge (or directly to post-fledging young) by a parent. Observation sessions were excluded from analyses if poor visibility persisted throughout the session. Nests were treated independently between years.

We compared nestling provisioning rates between 2-hour observation blocks when overflights occurred (overflown blocks) and two types of control 2-hour observation blocks: 1) from overflown nests when overflights did not occur (baseline blocks) and 2) from reference nests (reference blocks) (Fig. 3.2). We used 2-hour 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 hours; Cade 1960), and to maximize the number of available overflown blocks to include in analyses. We collected data during 159 blocks during the nestling-rearing and post-fledging phases, but restricted analyses to 31 overflown blocks, 31 baseline blocks, and 31 reference blocks.

Due to the timing of overflights, we restricted analyses to observations from 0700 hrs to 2000 hrs ADT. Overflown blocks began with the first overflight of the day. Baseline blocks were matched with overflown blocks either by selecting the observations 2-hours preceding an overflight, or from days without overflights that corresponded to the nesting stage and time of day when overflights occurred. 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 nest 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 scrape, by twice the number of minutes per observation block. Similarly, for total area attendance we divided the number of minutes the female plus the number of minutes the male spent either at the nest ledge or in the nest area (within 200 m of the ledge or scrape), 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 like 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 overflowed and baseline blocks using analysis of variance (ANOVA) and between overflowed 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 examined all data combined and separately by 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 (less than 25% of the time on average), we used Fisher's Exact tests and Mantel-Haenszel odds ratio tests with continuity correction for small sample sizes and stratified by stage of the nesting cycle. These tests determine if

the odds of an activity occurring during overflown blocks versus either baseline or reference blocks was the result of random chance or, alternatively, was more or less likely to occur. We were unable to account for between-pair variability with these tests due to small sample sizes. Infrequent activities included females unknown (away from nest area), males incubating or brooding, males or females feeding self, males or females feeding young, or males or females flying. For nestling provisioning rates, we controlled for effects of brood size by including brood size in the model as a continuous variable. We assumed independence between years in observations from the same nest site. All statistical differences with a P-value of 0.10 are reported in the results to minimize Type II error, but the p-values are reported for all tests.

We used linear regression to assess the effects 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 (cumulative number of overflights), 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.

RESULTS

Nest Attendance

We detected some differences in nest attendance by parent Peregrine Falcons between overflown and reference observation blocks, but not between overflown and baseline observation blocks. Male ledge attendance was lower during overflown blocks than reference blocks, after accounting for among pair variability and stage of the nesting cycle ($F_{1,59} = 3.78$, $P = 0.080$; Fig. 3.3). Total ledge attendance, however, did not differ between overflown and reference blocks ($F_{1,59} = 0.14$, $P = 0.71$), after accounting for among pair variability and stage of the nesting cycle. Females apparently compensated for lower male ledge attendance by attending the ledge more during overflown compared to reference blocks; however, this trend was not significant ($F_{1,59} = 1.82$, $P = 0.21$) after accounting for among pair variability and stage of the nesting cycle. When data were separated by stage, there was no difference in male ledge attendance between overflown and reference blocks during either incubation ($F_{1,43} = 1.34$, $P = 0.27$) or early nestling-rearing ($F_{1,27} = 2.18$, $P = 0.21$), likely due to smaller sample sizes.

The other measure of nest attendance, area attendance, did not differ between overflown and reference observation blocks ($F_{1,110} = 0.17$, $P = 0.69$) or between overflown and baseline observation blocks ($F_{1,105} = 1.62$, $P = 0.21$), after accounting for stage of the nesting cycle and among pair variability. We detected one difference in female area attendance, however, when data were separated by stage of the nesting cycle. Similar to

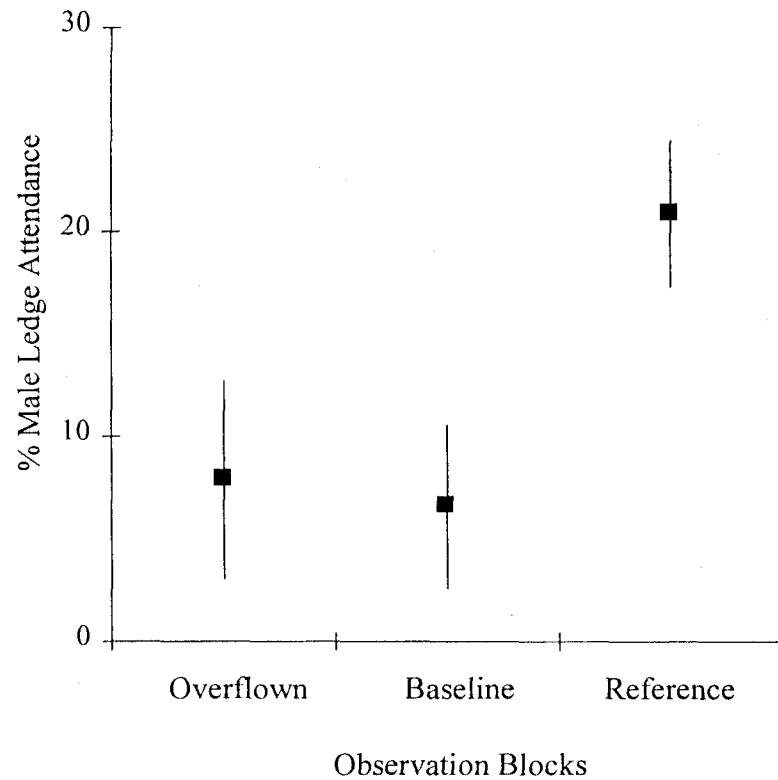


Figure 3.3. Average male ledge attendance (\pm SE) during incubation and early nestling-rearing for overflown, baseline, and reference observation blocks among Peregrine Falcons nesting along the Tanana River, Alaska.

male ledge attendance, which was lower for overflown blocks than for reference blocks during incubation and early nestling-rearing, female area attendance during late nestling-rearing was lower during overflown blocks than reference blocks ($F_{1,23} = 6.15$, $P = 0.056$). But, female area attendance was not significantly different between overflown blocks and baseline blocks during late nestling-rearing ($F_{1,29} = 0.25$, $P = 0.62$). We found no differences in area attendance between overflown blocks and the two types of control blocks during other stages of the nesting cycle for either sex.

While some differences in nest attendance between overflown observation blocks and reference blocks were found, total ledge attendance during either the first half of the nesting cycle (incubation and early nestling-rearing) or the second half of the nesting cycle (mid and late nestling-rearing) was not correlated with the number of overflights that occurred during each overflown block ($P = 0.357$, $df = 27$ and $P = 0.842$, $df = 26$, respectively). Additionally, total ledge attendance during either the first or second half of the nesting cycle was not correlated with average sound exposure level (SEL) from overflights during overflown blocks ($P = 0.159$, $df = 27$, and $P = 0.646$, $df = 26$, respectively). Likewise, total area attendance during the first or second halves of the nesting cycle was not correlated with the number of overflights to occur within observation blocks ($P = 0.719$, $df = 27$, and $P = 0.883$, $df = 26$, respectively). Also, total area attendance during the first or second half of the nesting cycle was not correlated with average SEL from overflights during overflown blocks ($P = 0.758$, $df = 27$, and $P = 0.631$, $df = 26$, respectively). Finally, neither total ledge nor total area attendance was correlated with the cumulative number of overflights that a pair had been exposed to,

after accounting for stage of the nesting cycle ($P = 0.534$, $df = 27$, and $P = 0.962$, $df = 52$, respectively).

Time-activity Budgets

We found little evidence that the incidence of frequently performed activities was influenced by overflights. There was no difference in the amount of time females spent incubating, males or females spent perching, or males spent performing “unknown” behaviors away from the nest area, after accounting for variability among pairs and stage of the nesting cycle ($P > 0.21$ for all ANOVA tests). When data were analyzed separately by stage, however, females perched less during overflown blocks than reference blocks during late nestling-rearing, after accounting for among pair variability ($P = 0.056$; Fig. 3.4a). This was associated with the lower area attendance by females during overflown blocks in late nestling-rearing (see above).

We found some evidence that infrequently-performed activities differed between overflown blocks and the two types of control blocks (Tables 3.2 and 3.3). Females were less likely to perform “unknown” activities (away from the nest area) during overflown observation blocks than reference observation blocks, after accounting for stage of the nesting cycle ($P = 0.09$, Mantel-Haenszel Test). This effect was most obvious during early nestling-rearing, when female activity was only 0.12 times as likely to be classified as “unknown” during overflown blocks compared with reference blocks (0.0048 to 0.83, 90% confidence interval, $P = 0.038$, Fisher’s Exact Test; Fig. 3.5a). Yet by late

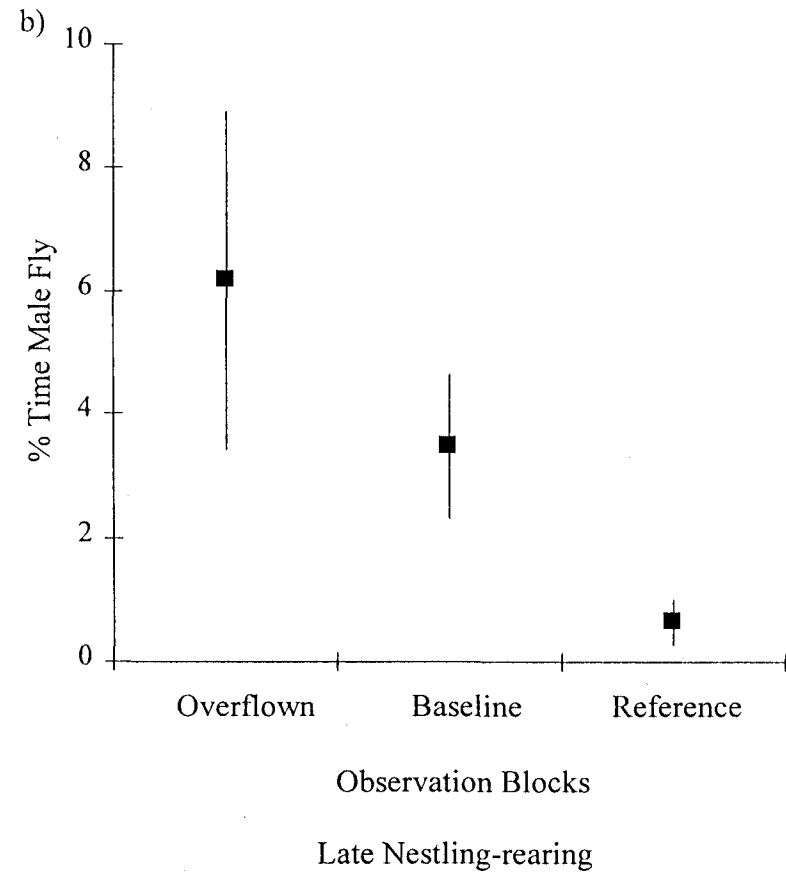
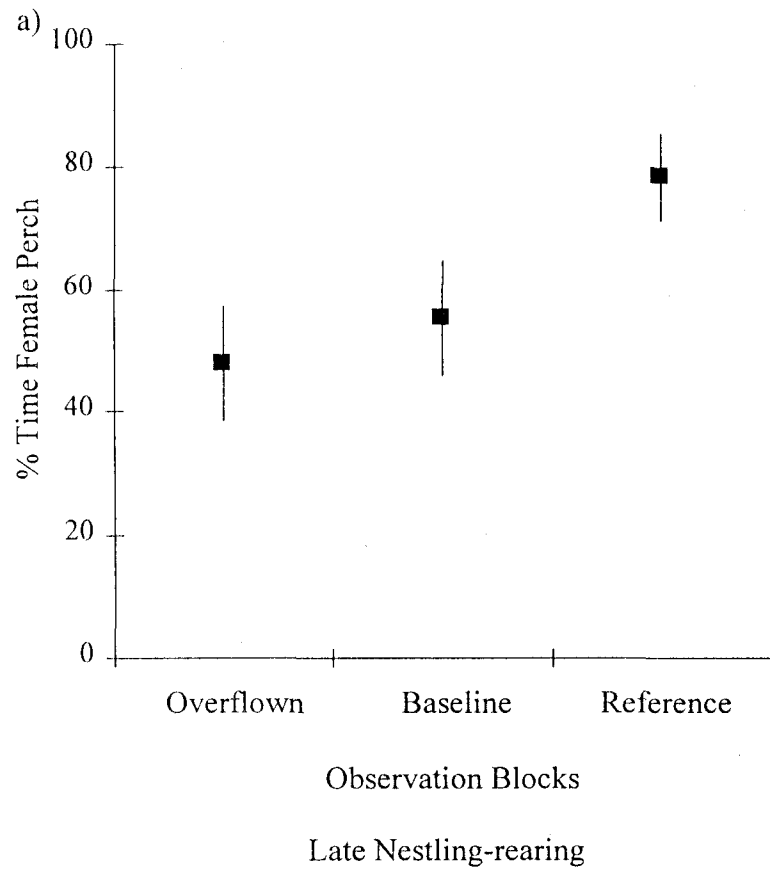


Figure 3.4. Average percent time a) females perched (\pm SE) and b) males flew (\pm SE) during overflown, baseline, and reference observation blocks during late nestling-rearing among Peregrine Falcons nesting along the Tanana River, Alaska.

Table 3.2. P-values of Fisher's Exact Tests that the difference in odds of females performing a particular activity during overflown vs. non-overflown blocks was not the result of random chance, and Mantel-Haenszel Tests with continuity correction for each activity stratified by stage of the nesting cycle.

Females		Activity Category							
		Feed Self		Feed Young		Fly		Unknown	
		O vs B ^a	O vs R ^b	O vs B ^a	O vs R ^b	O vs B ^a	O vs R ^b	O vs B ^a	O vs R ^b
Stage	Test								
Incubation	Exact	1.000	0.258	n.a. ^c	n.a. ^c	1.000	0.547	0.086*	0.208
Early Nestling-rearing	Exact	1.000	0.123	1.000	0.372	1.000	0.606	1.000	0.038*
Mid Nestling-rearing	Exact	1.000	0.565	0.400	1.000	0.414	0.517	0.590	1.000
Late Nestling-rearing	Exact	1.000	1.000	0.651	1.000	1.000	1.000	1.000	0.635
Mantel-Haenszel Test	(χ^2_1)	0.09	0.12	0.62	0.15	0.16	0.78	0.47	2.79
	P	0.77	0.72	0.43	0.70	0.69	0.38	0.49	0.095*

^a O vs B = Overflight block vs Baseline block

^b O vs R = Overflight block vs Reference block

^c n.a. = not applicable

* significant differences $\alpha \leq 0.10$

Table 3.3. P-values of Fisher's Exact Tests that the difference in odds of males performing a particular activity during overflown vs. non-overflown blocks was not the result of random chance, and Mantel-Haenszel Tests for each activity stratified by stage of the nesting cycle.

Males	Stage	Test	Activity Category							
			Feed Self		Feed Young		Fly		Incubate/Brood	
			O vs B ^a	O vs R ^b	O vs B ^a	O vs R ^b	O vs B ^a	O vs R ^b	O vs B ^a	O vs R ^b
	Incubation	Exact	1.000	0.409	n.a.	n.a.	1.000	0.761	all zeros	0.3613
	Early Nestling-rearing	Exact	0.200	0.409	1.000	all zeros	0.608	1.000	-	0.6508
	Mid Nestling-rearing	Exact	1.000	1.000	1.000	-	1.000	0.517	-	n.a.
	Late Nestling-rearing	Exact	1.000	1.000	0.598	-	1.000	0.092*	-	n.a.
	Mantel-Haenszel Test	(χ^2_1)	0.11	0.17	0.18	-	0.04	0.56	-	0.05
		P	0.74	0.68	0.67	-	0.84	0.34	-	0.83

^a O vs B = Overflight block vs Baseline block

^b O vs R = Overflight block vs Reference block

^c n.a. = not applicable

* significant differences $\alpha \leq 0.10$

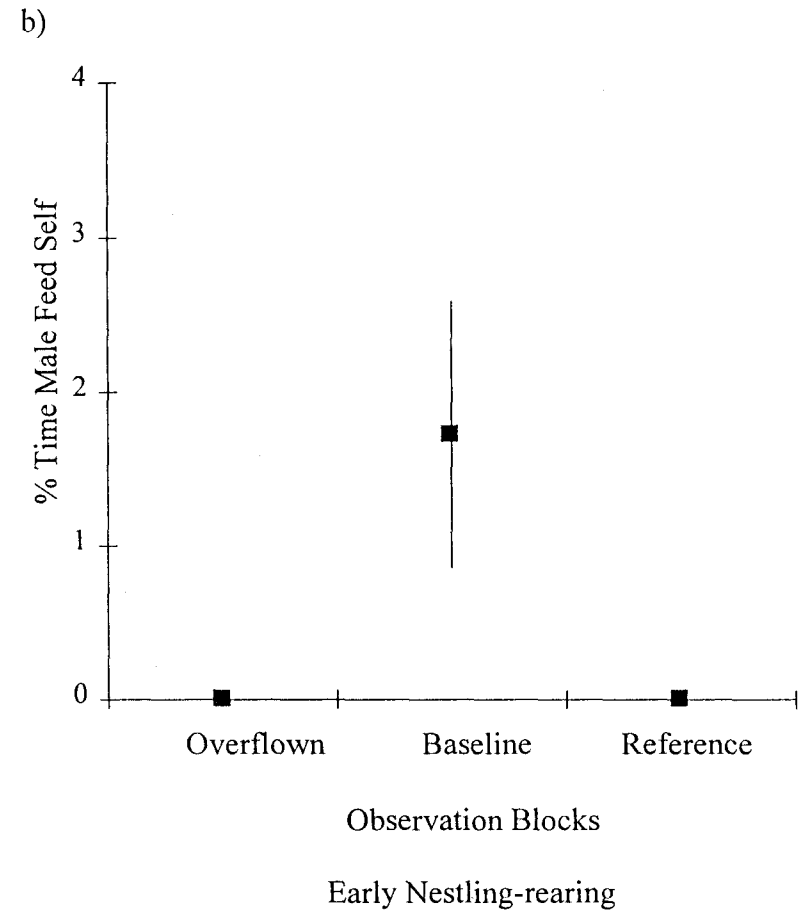
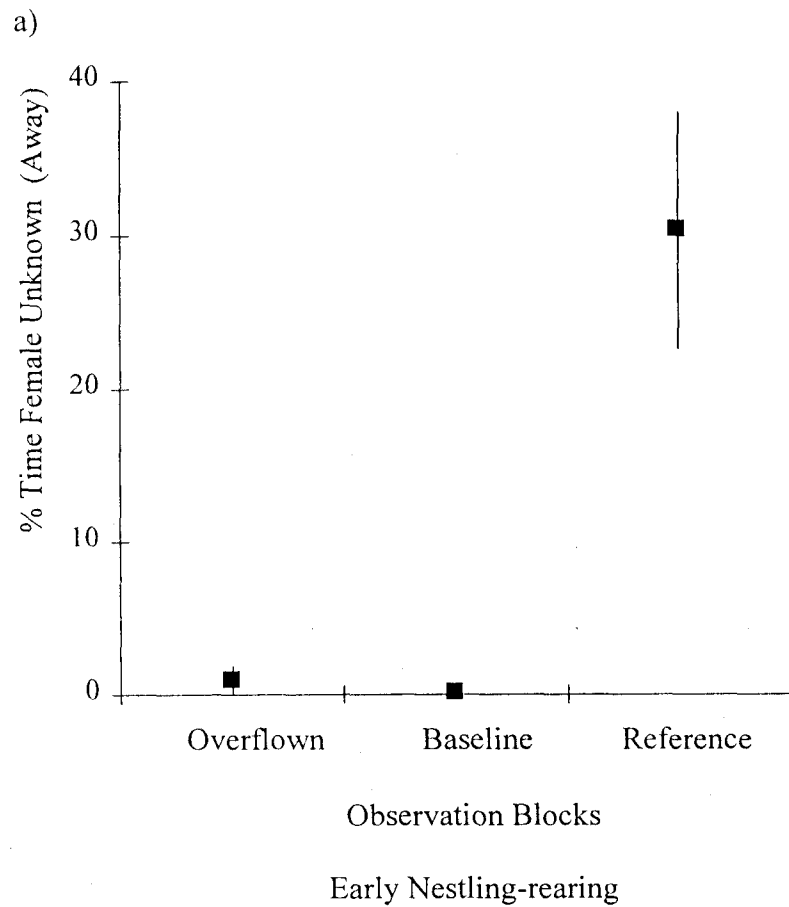


Figure 3.5. Average percent time a) females were “unknown” (away from nest area; \pm SE) and b) males fed themselves (\pm SE) during overflow, baseline, and reference observation blocks during early nestling-rearing among Peregrine Falcons nesting along the Tanana River, Alaska.

nestling-rearing there was no difference in the incidence of female “unknown” activities between overflown and reference blocks ($P = 0.63$, Fisher’s Exact Test). Also during incubation only, females were 0.24 times as likely to perform “unknown” activities (away from the nest area) during overflown blocks compared with baseline blocks (0.051 to 0.96, 90% confidence interval, $P = 0.086$, Fisher’s Exact Test), but the difference was not significant for the entire nesting cycle ($P = 0.36$, Mantel-Haenszel Test). In addition, during late nestling-rearing the incidence of flight among males was greater during overflown blocks than reference blocks ($P = 0.092$, Fisher’s Exact Test; Fig. 3.4b); however, the 90% confidence interval did not indicate odds different from 1 (0.88 to 39.7). Additionally, this pattern was not apparent throughout the nesting cycle ($P = 0.45$, Mantel-Haenszel Test, Table 3.3). Finally, during early nestling-rearing, males fed themselves at the nest site only during baseline observation blocks, not during either overflown or reference observation blocks, but this trend was not significant ($P = 0.20$, Fisher’s Exact Test; Fig. 3.5b). The incidence of other infrequent activities (males incubating or brooding, males or females feeding self, males or females feeding young, or females flying) during overflown blocks was not different than during either baseline or reference blocks, after accounting for stage of the nesting cycle (Mantel-Haenszel Tests, Tables 3.2 and 3.3).

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 observation blocks ($F_{1,72} = 0.07$, $P = 0.79$, and $F_{1,72} = 0.01$, $P = 0.91$, respectively), or between overflown and reference observation blocks ($F_{1,73} = 0.01$, $P = 0.93$, and $F_{1,73} = 0.11$, $P = 0.75$, respectively), after accounting for effects of brood size. Additionally, average estimated prey size did not differ between overflown and either baseline ($F_{1,72} = 0.56$, $P = 0.46$) or reference ($F_{1,73} = 0.11$, $P = 0.75$) observation blocks. Furthermore, we did not find a relationship between nestling provisioning rates and either the number of overflights or the average SEL from overflights to occur during overflown blocks. The number of overflights per block (among overflown blocks only) was not significantly correlated with either prey item delivery rate ($P = 0.200$, $df = 36$) or the log of prey mass delivery rate ($P = 0.228$, $df = 36$), after accounting for brood size and stage of the nesting cycle. Moreover, the average SEL of overflights per observation block was not significantly correlated with either prey item delivery rate ($P = 0.759$, $df = 33$) or the log of prey mass delivery rate ($P = 0.558$, $df = 33$), after accounting for effects of brood size and stage of the nesting cycle. Finally, the cumulative number of overflights to which nests were exposed was also not correlated with either prey item delivery rate ($P = 0.383$, $df = 36$) or prey mass delivery rate ($P = 0.494$, $df = 36$), after accounting for brood size and stage of the nesting cycle.

DISCUSSION

Our results provide some support for the hypothesis that low-altitude jet aircraft overflights affect the parental behavior of Peregrine Falcons. Several lines of evidence suggest that Peregrine Falcons exposed to low-altitude jet overflights adjusted their attendance patterns and time-activity budgets compared to reference nests. Males attended the nest ledge significantly less during overflown observation blocks than reference observation blocks when all data were combined from incubation and early nestling-rearing (Fig. 3.3). In contrast to males that attended less during overflown blocks, females during early nestling-rearing were less likely to be away from the nest area during overflown blocks compared with reference blocks (Fig. 3.5). The opposite effect was observed during late nestling-rearing, when females attended the nest area less and perched less during overflown blocks compared to reference blocks (Fig. 3.4a). Similarly, males during late nestling-rearing were more likely to fly during overflown blocks than reference blocks (Fig. 3.4b). 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 and then

shift to equal or lower attendance and provisioning rates compared with males following mid nestling-rearing (Trivers 1972, Collopy 1984, see Chapter 1). Decreased ledge attendance during overflown blocks compared with reference blocks early in the nesting cycle suggests that males were less likely to brood eggs or chicks during times of overflight disturbance, apparently forcing females to spend more time on these activities. Alternatively, females may have been less inclined to allow males to relieve them of incubation or brooding duties during overflight disturbance. This is consistent with results from Nordmeyer et al. (unpubl. ms.), who found that the incidence of flight reactions in response to overflights was much 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, apparently in response to greater perceived threat. Other studies found early nestling-rearing to be a stage when raptors are generally 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 perching and attending the nest area, and males were more likely to fly during periods with overflights (Fig 3.5). This suggests 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 towards potential predators (Nordmeyer et al. unpubl. ms.); thus, it is unlikely that Peregrine Falcons were perceiving 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, as many studies suggest nest defense towards potential predators increases late in the nesting cycle (Trivers 1972, Dawkins and Carlisle 1976, Knight and Temple 1986).

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-hour observation blocks. Alternatively, because baseline blocks are not independent from overflown blocks, differences between these types of blocks may be more difficult to detect. Additionally, we did not see a relationship between nest attendance and the number of overflights that occurred in the block, the cumulative number of exposures experienced by each nesting pair, or the average SEL of overflights. Nor did we find evidence that nestling provisioning rates were influenced by low-altitude jet overflights.

Effects of human disturbance on raptor breeding behavior are equivocal. For instance, Platt (1975) subjected gyrfalcons to close approaches by helicopters early in the nesting season and found that none of the 10 nest sites were reoccupied the subsequent year, while prior reoccupancy rates had been around 38%. Andersen et al. (1986) found

that an adult male Red-tailed Hawk (*Buteo jamaicensis*) apparently avoided parts of its home range due to ground-based military activities. In contrast, Holthuijzen et al. (1990) found incubation times in Prairie Falcons (*Falco mexicanus*) did not differ between pairs exposed to experimental dynamite blasts and controls, and that nest success and reoccupancy rates did not differ between experimental and control nests. Additionally, 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. Other studies have found minimal changes to time-activity budgets of birds exposed to aircraft or vehicular disturbance (Trimper et al. 1998, Conomy et al. 1998a, Plumpton and Lutz 1993). 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 overflowed blocks and the two 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 males and females partitioned attendance responsibilities differently in relation to exposure to overflights. It is likely, however, that two 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.

Although our data provided some support for the hypothesis that low-altitude jet overflights impact patterns of parental behavior at the observed intensity of overflights,

other studies have shown relationships between human disturbance and raptor reproductive success. Carpenter (1993) found that reproductive performance of American Kestrels (*Falco sparverius*) was significantly negatively affected by frequent human disturbances during a year with low prey availability. Additionally, Bednarz (1984) found that breeding Prairie Falcons (*Falco mexicanus*) were absent from an area with heavy mining and blasting activity, yet present in low impact areas, essentially free of mining. Low-altitude jet overflights are a type of potential disturbance that differs from direct human disturbance, and the Peregrine Falcons in the present study likely perceived overflights as a minimal threat to their progeny. Due to their short duration and dissimilarity with natural nest predators, it may take more consecutive overflights to elicit a detectable response (Nordmeyer et al. unpubl. ms.), compared with human disturbance at the nest site.

In this study, we detected subtle effects of jet overflights on Peregrine Falcon parental behavior, but there was no evidence that the magnitude of these effects was sufficient to result in reduced productivity of nesting pairs. Although the intensity and frequency of overflights experienced by some overflown nests in the present study was higher than raptor nests would normally be exposed to in MOAs, the results of this study cannot be extrapolated to nests exposed to higher overflight levels. In addition, 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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SYNOPSIS AND CONCLUSIONS

Low-altitude jet overflights did not markedly affect nest attendance, time-activity budgets, and nestling provisioning rates of breeding Peregrine Falcons in this study.

Several other intrinsic and extrinsic factors did, however, influence these attributes of nesting behavior. Nest attendance and time-activity budgets changed dramatically as a function of stage of the nesting cycle. As would be expected among monogamous birds with biparental care, both nest ledge and nest area attendance declined substantially as the breeding season progressed. In most breeding pairs, females attended the nest ledge substantially more than males. Male attendance in the nest area did not change significantly, while female area attendance declined substantially as the breeding season progressed. The decline in female area attendance was associated with decreasing incidence of incubating and brooding activities, which were mostly performed by females. During incubation, male nest attendance at the nest area varied considerably among breeding pairs. Differences among pairs in gender roles may be attributable to a variety of factors, such as age, mate quality, territory quality, food availability, or the degree of sexual size dimorphism.

Provisioning rates of food to broods were influenced by brood size. Prey item delivery rates and estimated prey mass delivery rates both increased with increasing brood size. There was a negative correlation, however, between brood size and prey item delivery rates per nestling. There was no significant correlation between brood size and

estimated prey mass delivery rates per nestling ($\text{g of food} \cdot \text{hr}^{-1} \cdot \text{nestling}^{-1}$), indicating that smaller broods received smaller prey items on average.

We detected few effects of overflights on nest attendance and time-activity budgets. Males attended the nest ledge significantly less during overflown observation blocks than reference observation blocks when all data were combined from incubation and early nestling-rearing. Contrastingly, females during early nestling-rearing were less likely to be away from the nest area at overflown nests compared to reference nests. The opposite effect was observed during late nestling-rearing, when females perched less and attended the nest area less at overflown nests compared to reference nests. Similarly, males during late nestling-rearing were more likely to fly at overflown nests during periods of overflights than at reference nests. We found no difference, however, between overflown nests and reference nests in either prey item or prey mass delivery rates, after accounting for differences in brood size. Thus, the differences in nest attendance and time-activity budgets between overflown nests and reference nests were not reflected in differences in provisioning rates to nestlings.

Although we found some differences in attendance and time-activity budgets between overflown and reference nests, we found no differences in nest attendance or provisioning rates in relation to either the number of overflights per observation block, the cumulative number of overflights experienced by a given pair to that point, nor the average sound exposure level of overflights during overflown blocks. At the frequency and intensity of jet aircraft overflights described in this study, we were unable to detect an

appreciable affect on general reproductive behavior of Peregrine Falcons, as represented by nest attendance, time-activity budgets, and nestling provisioning rates.

We should consider two possible reasons for small or undetectable effects of overflights on parental care. First, noise and visual stimuli associated with jet aircraft overflights are of short duration, and the limited number and intensity of overflights that occurred during this study may not have been sufficient to elicit notable changes in behavior. Second, Peregrine Falcons in this study may have habituated to overflights during exposures in previous years; however, the same may not be true of naive pairs. Thus, extrapolation of conclusions to situations beyond the scope of this study should be made with caution.

Despite these limitations, the repeated exposure of Peregrine Falcons in this study to jet overflights resulted in little or no detectable effects on the major parameters of parental care that are strongly associated with productivity. We found that Peregrine Falcons, like other raptors (Holthuijzen 1990, Plumpton and Lutz 1993), appear to be adaptable to potential disturbance such as overflights. Given that we observed some response in parental care to overflights, it will be essential in the future to determine possible thresholds at which changes in parental care induced by low-altitude overflights would impact reproductive success. Peregrine Falcons exhibited flexibility among pairs in nest area attendance males. This flexibility may contribute to their ability to adjust to potential disturbances, such as overflights.

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