In order to examine the potential impact of military jet overflights and other disturbances on productivity of peregrine falcons (*Falco peregrinus*), we observed behavioral reactions of peregrines to disturbances at nests along the Tanana River, Alaska during the 1995-1997 breeding seasons. Military jets conducted low-altitude flights over a sample of nests under observation in each year (experimental nests), while other nests were not intentionally overflown (reference nests). Other disturbances occurred at random. Animal noise monitors (ANMs), which collect and store data on noise disturbance levels, were deployed at each observed nest. A total of 878 above-threshold (≥ 85 dB) overflights were recorded by the ANMs during the course of the study. A total of 401 close (defined as ≤ 1000 m slant distance from the nest) overflights by subsonic F-16, F-15, A-10, Harrier, Jaguar, or Tornado jet aircraft were recorded during observations. Close overflights by military jets accounted for 63% of all observed potential disturbances at experimental nests; they accounted for 2.6% of all observed potential disturbances at reference nests. Other potential disturbances at reference nests included civilian fixed-wing aircraft (41%), boats (33%), avian predators (17%).
helicopters (5%), and mammalian predators (1%). Peregrine falcons responded differently to animate and inanimate sources of disturbance, and responded most intensely and most frequently to other raptors, particularly conspecifics. Flight reactions were common, but not in response to inanimate sources. Among inanimate potential disturbances, falcons responded most intensely to boats (6% of reactions involved flight), and least intensely to helicopters (3%) and fixed-wing aircraft (2%). Intensity of reactions to military jets was indistinguishable from that to either boats or other aircraft. Intense behavioral responses (including flight reactions) to military jet overflights were rarely observed in this study, even at slant distances <500 m, and no intense behavioral responses were observed at slant distances >550 m. Peregrine falcon productivity (number of fledglings produced per nesting attempt) in the study area was within the normal range for Interior Alaska and the Tanana River. Dose of jet aircraft disturbance was not correlated with productivity. Productivity was, however, negatively correlated with reactivity of both individual falcons and mated pairs. Those falcons that responded more intensely to overflights tended to have lower productivity. The sensitivity of breeding peregrine falcons to low-altitude jet overflights is a better indicator of subsequent productivity than actual dose of overflights. This is likely a reflection of lower parental quality/investment among breeding pairs with high reactivity (i.e., younger, less experienced parents are less likely to be productive).
Effects of Jet Aircraft Overflights and Other Potential Disturbances on Behavioral Responses and Productivity of Nesting Peregrine Falcons

by

Dana L. Nordmeyer

A THESIS submitted to Oregon State University in partial fulfillment of the requirements for the degree of Master of Science

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Dana L. Nordmeyer, Author
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CONTRIBUTION OF AUTHORS

Dr. Daniel Roby was involved in the design of the study and in the writing of each manuscript. Angela Palmer assisted in data collection for the study and was an integral part of the idea development leading to each manuscript.
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LIST OF ABBREVIATIONS

AFB--Air Force Base
AGL--Above Ground Level
ANM--Animal Noise Monitor
dB--Decibels
dBA--A-weighted Decibels
EIAP--Environmental Impact Assessment Process
EIS--Environmental Impact Statement
FAA--Federal Aviation Administration
FAC--Forward Air Controller
FIM--Flight Intention Movement
Lmax--Maximum Sound Pressure Level
MOA--Military Operations Area
MTR--Military Training Route
NEPA--National Environmental Policy Act
NSBIT--Noise and Sonic Boom Impact Technology Program
SEL--Sound Exposure Level
SELa--A-weighted Sound Exposure Level
USAF--United States Air Force
USFWS--United States Fish and Wildlife Service
To Dr. Homer Sharp
An excellent teacher, a wonderful person, and
one of the main inspirations behind my decision to pursue biology instead of chemistry

also

In memory of Beng Bong
A profound influence on my whole being

“Jedes Erlebnis, das Gott uns schenkt,
jeder Mensch, den er uns in Leben schickt,
ist die vollkommene Vorbereitung auf die Zukunft,
die allein er sehen kann.”
--Corrie ten Boom
CHAPTER 1: Introduction

As human populations increase and encroach on undeveloped lands, their impact on wildlife and wildlife habitat increases. These changes force resident wildlife to either move, adapt to the changing environment, or suffer lower survival and/or productivity. The world is becoming smaller, and as people have realized this, they have also begun to recognize the fragility of the world around them. This concern has led to an increasing number of studies on the effects of human disturbance on wildlife.

Humans can disturb wildlife in a number of ways. Webster defines “disturb” as “to interfere with” or “to destroy the tranquility or composure of.” Random House defines it as “to interrupt the quiet, rest, or peace of.” One obvious way that humans can “destroy the tranquility” or “interrupt the quiet” of wildlife is by making noise. Planes, trains, and automobiles; boats; construction activities; and military training exercises are just a few of the ways that humans create noise disturbance. Neil et al. (1975) defined human disturbance as any human activity that raises the physiological costs of survival and/or lowers the chances of successful reproduction. In order to determine that a noise event (or events) has caused a measurable disturbance, it must be shown to ultimately affect the survival or productivity of the subjects. This can be either a direct effect (e.g., burst ear drum) or an indirect effect (e.g., long-term changes in behavior; Janssen 1980).

One type of noise disturbance that has been the subject of public concern for several years is caused by low-altitude military jet overflights. Several studies have been
conducted, yet more information on potential impacts of low-altitude overflights is needed. The Environmental Impact Assessment Process (EIAP) was initiated in 1972 after the passage of the National Environmental Policy Act (NEPA). As part of this process, the United States Air Force (USAF) must document the effects of aircraft activity on animal populations and must prepare Environmental Impact Statements (EISs) for the U.S. Fish and Wildlife Service (USFWS), among other agencies, to review. The Noise and Sonic Boom Impact Technology Program (NSBIT) was formed by the USAF in response to this growing area of concern and specifically to study the potential effects of aircraft noise.

Aircraft noise is potentially disturbing to a variety of wildlife, including birds of prey (raptors), waterfowl, shorebirds, gamebirds, marine mammals, rodents, bats, and ungulates (Manci et al. 1988). Wildlife in general seem to be more sensitive to noise than are humans (Borg 1981). Avian species tend to be more affected by noise than mammals, while reproduction in wild animals seems to be more affected by noise disturbance than that of their domestic counterparts (Manci et al. 1988).

A high proportion of top trophic level consumers are classified as threatened or endangered because toxic substances bioaccumulate in apex predators. Raptors are threatened with extinction more than many other types of birds (Ehrlich et al. 1988), largely because of their high trophic level. Because of their threatened status, many apex predators, including raptors, may be especially sensitive to all types of human disturbance, including noise. Possible detrimental effects of noise disturbance on raptors can include: 1) abandonment of nest sites, 2) decreased hatchability of eggs, 3) damage to
eggs or nestlings from startle responses of the parents, 4) premature fledging, 5) physiological stress, and 6) behavioral changes (Fyfe and Olendorf 1976, Manci et al. 1988, Awbrey and Bowles 1990).

The USAF wants to expand its Military Operations Areas (MOAs) in Alaska, and the EIAP requires an assessment of the effects of aircraft activity on wildlife populations. Defensible model-based predictions of the potential effects of aircraft activity on reproductive success and population demography require empirical studies that quantify the relationship between levels of disturbance and negative effects on reproduction. In 1990, a provisional model was developed “to predict the potential effects of aircraft overflights and sonic booms on the reproduction of endangered raptorial birds” (Bowles et al. 1990). Because empirical studies on the effects of aircraft noise on raptors were inadequate to develop a reliable predictive model, a hypothetical model was created based on the worst-case scenario. This model is based on the assumption that aircraft disturbance affects the behavior of the breeding pair, which, at some threshold, adversely affects productivity.

Several relationships needed to be explored and quantified to validate the model developed by Awbrey and Bowles (1990). First, there was a lack of studies that have included low-altitude military operations and also specifically examined the correlations between disturbance variables (including precise sound-exposure data), raptor behavioral responses, and reproductive effects. Second, the relationship between disturbance and reproductive effects needed to be quantified directly, and it needed to be determined whether the magnitude of disturbance or raptor behavioral response to that disturbance is
the best predictor of effects. Lastly, the frequency and intensity of aircraft activity or noises that cause or are correlated with reproductive effects needed to be quantified, and the effects of other factors, such as phase of the nesting cycle, previous experience with aircraft, and sex needed to be identified. Effects of overflight variables, such as sound level, distance from the nest, and number of exposures, on reproductive success were unknown. These variables needed to be related to the probability of a response of a given type and intensity. A great diversity of responses to noise disturbance exists, ranging from minor behavioral reactions to drastic changes in behavior and habitat use (Manci et al. 1988). Because the behavioral response of raptors may influence reproductive success, the probability of an effect after any given response also needed to be determined.

Disturbance may not have a large, obvious effect on reproductive success in raptors (Hennessy 1978, Awbrey and Bowles 1990). Awbrey and Bowles (1990) hypothesized that an effect on the order of a 5-35% reduction in reproductive output may be detectable. Reoccupation of nest sites may be affected by disturbance, although this might not have a large effect on reproductive success because raptors often maintain several nesting sites in areas exposed to high levels of disturbance (Newman et al. 1977).

In order to more accurately investigate the role of disturbance caused by low-altitude military jets, the effects of other disturbances must also be examined. This could include noises from civilian aircraft, helicopters, and boats, as well as the presence of humans and other potential nest predators. These potential sources of disturbance have been shown to induce behavioral changes in various avian species (White and Sherrod
The peregrine falcon (*Falco peregrinus*) is an excellent subject for studies of the effects of noise disturbance on raptors. First, peregrine falcons are protective of their nests and display obvious defensive behavior in response to disturbance. Secondly, peregrine falcons do not depend on cyclic prey, such as microtine rodents and snowshoe hares (*Lepus arcticus*), and are therefore not subject to the same population fluctuations that would confound studies of reproductive success and productivity of many other raptor species in Alaska. Thirdly, an extensive historical database has been collected on peregrine falcons nesting in Interior Alaska since the drastic decline of this species in the 1960s. Additionally, a relatively large population of peregrine falcons currently nests along the Tanana River in Interior Alaska, which offers accessibility for scientific studies and is located in an area where the USAF conducts training exercises. Finally, peregrine falcons are a species of concern and the subspecies that breeds in Interior Alaska (*F. p. anatum*) is listed as endangered under the Endangered Species Act (1973).

In 1994, the USAF began funding a study on the effects of jet aircraft overflights on the behavior and productivity of peregrine falcons (Ritchie et al. 1998). The study had two main components: an on-river (nests along the Tanana River) component to examine the effects of overflights on behavior and productivity, and an off-river (nests not on major drainages) component, which looked exclusively at productivity as a function of exposure to overflight noise. As part of this larger study, I specifically
investigated acute behavioral reactions to overflights and their potential effects on nesting success and productivity at nest sites along the Tanana River. A companion study investigated time-activity budgets, attendance, and prey provisioning rates to nestlings by adult peregrine falcons to evaluate hypotheses related to changes in parental care following exposure to low-altitude jet overflights.

In Chapter 2, I examine the behavioral responses of peregrine falcons to military jet aircraft overflights. Specifically, I evaluate what types of responses peregrine falcons exhibit in response to jets and the correlations among various types/intensities of response and characteristics of the overflights (e.g., type of aircraft, distance of overflight from the nest, and sound exposure level). In Chapter 3, I examine the relationship between behavioral responses and overall nesting success and productivity. I also address the hypothesis that raptor behavioral response to disturbance, rather than the magnitude of that disturbance, is the best predictor of effects. In Chapter 4, I investigate how nesting peregrine falcons react to naturally-occurring and anthropogenic sources of disturbance, and how these compare with responses to low-altitude jet overflights. I also test the hypothesis (Awbrey and Bowles 1990) that frequency of flight responses is an indicator of reduction in productivity of peregrine falcons.
CHAPTER 2

Behavioral Responses of Nesting Peregrine Falcons to Low-Altitude Jet Aircraft Overflights

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ABSTRACT

We examined the effects of low-altitude military jet overflights on the behavior of peregrine falcons (*Falco peregrinus anatum*) nesting along the Tanana River, Alaska during the 1995-1997 breeding seasons. Animal Noise Monitors (ANMs), which collect and store data on noise exposure level, were deployed at 11-12 active nest sites in each year. Six to nine of the study nests each year were located in Military Training Routes (MTRs) and were subject to low-altitude jet overflights (experimental nests). The other three to five study nests were reference nests located outside MTRs, where jet aircraft were subject to altitude restrictions. The ANMs recorded a total of 878 above-threshold noise events during the course of the study. A total of 401 close overflights (defined as ≤1000 m slant distance from a nest) by subsonic F-16, F-15, A-10, Harrier, Tornado, or Jaguar jet aircraft were recorded during observations over the course of the three breeding seasons. Observers recorded acute behavioral responses of peregrine falcons to jet overflights. The majority (78%) of all observed responses by peregrine falcons to close overflights were classified as minimal (either no apparent reaction or attentive to the overflight), while 17.5% of observed responses consisted of alert reactions. Intense reactions (flight intention movements, stand, or crouch/cower) accounted for 2% of all observed reactions to close overflights during the study. Males generally reacted more intensely to overflights than did females. Flight reactions to jet overflights were exhibited only by males and accounted for 5% of all male responses to close jet overflights. Of the overflight variables examined, maximum sound pressure level (Lmax), sound exposure level (SELa), and slant distance were the best predictors of falcon response to overflights and explained a significant amount of the
variation in both male and female response. Male reaction intensity was positively and significantly correlated with number of overflights in rapid succession, while this correlation was only marginally significant for females. Male reaction intensity varied significantly with phase of the nesting cycle, while the correlation was again only marginally significant for females. If acute, short-term behavioral responses are indicative of damage caused by potential disturbance, then the low level of overt behavioral responses observed in this study suggests a low sensitivity by nesting peregrine falcons to low-altitude jet aircraft overflights.

INTRODUCTION

The strong response of peregrine falcons (*Falco peregrinus*) to intruders near their nests is well-known (Monneret 1974, Olsen and Olsen 1980). They will attack humans, bears, mink, foxes, ravens, other peregrine falcons, eagles, and virtually any other potential predator of their eggs or nestlings. It follows that peregrine falcons may respond to inanimate intruders, such as aircraft, that may be perceived by adults as threatening to their young. In fact, peregrines have been known to attack both fixed-wing aircraft and helicopters that have made close approaches to active nests during nest surveys (White and Sherrod 1973, Cade and White 1976).

Noise disturbance of animals, particularly from jet aircraft, has been an issue of public concern for a number of years. A great diversity of responses to noise disturbance has been described, ranging from minor behavioral reactions to drastic changes in behavior and habitat use (Manci et al. 1988, Awbrey and Bowles 1990). Flushing as a
result of aircraft noise exposure has been documented in spotted owls (*Strix occidentalis*), red-tailed hawks (*Buteo jamaicensis*), bald eagles (*Haliaeetus leucocephalus*), and peregrine falcons, as well as other non-raptorial bird species (Andersen et al. 1989, Ellis 1991, Delaney et al. 1997, Grubb and Bowerman 1997, Stalmaster and Kaiser 1997). Bowles et al. (1990) postulated that an increase in flight responses induced by noise disturbance could lead to a decrease in productivity. Lower productivity could result from exposure of eggs or nestlings to stressful or lethal ambient conditions, increased predation risk, failure of the parents to care for eggs or nestlings properly, or some other unknown mechanism. Flight responses may also indicate enhanced stress levels or declining physiological condition in a breeding bird, assuming that deleterious effects of disturbance are indicated by changes in behavior (A.E. Bowles, pers. comm.).

The objective of this study was to evaluate the responses of nesting peregrine falcons to jet aircraft overflights, and then to determine which characteristics of overflights explain most of the variation in the magnitude and type of response observed. We wanted to quantify those disturbance factors (e.g., slant distance from the nest, noise level) that may best explain variation in falcon responses and assess the relative importance of other factors (e.g., sex, phase of the nesting cycle, previous experience with overflights, nest location) that may also influence response levels.

The overall hypothesis that we sought to test was that stronger stimuli associated with overflights elicit more intense behavioral reactions from breeding peregrine falcons. We hypothesized that a logistic relationship exists between intensity of disturbance, as estimated by altitude, distance, and sound exposure level (SEL), and intensity of response
(ranging from no visible reaction to evasive flight). We made several predictions about the characteristics of overflights that would elicit intense reactions from peregrine falcons.

First, we predicted that louder overflights would elicit more intense behavioral reactions from breeding peregrine falcons (Awbrey and Bowles 1990). The loudness of an overflight can be measured by the sound exposure level (SEL), or the total sound energy experienced over the duration of a noise event. Ward and Stehn (1989) found that noise level was a better predictor of behavioral responses to overflights in brant (Branta bernicla nigricans) than were visual cues. Brown (1990) found that responses by crested terns (Sterna bergii) depended on the noise level of simulated aircraft introduced to the colony.

Secondly, we predicted that closer jet overflights (as determined by slant distance from the nest) would elicit more intense reactions from peregrines. Olsen and Olsen (1980) observed that peregrine falcons defended their nests against humans more intensely at smaller approach distances. In spotted owls, unlike in brant, distance generally was a better predictor of response to helicopter overflights than was SEL (Delaney et al. 1997).

Based on observations by Monneret (1974), we predicted that males would respond more intensely than females during the incubation and early nestling-rearing phases. This is because females are responsible for the majority of incubation and brooding of young during these stages of the nesting cycle. Once the young are old enough for the female to leave the nest, the female begins to assume most of the nest
defense while the male is out hunting. We also predicted that males would be increasingly absent (away from the nest to hunt) once the female was able to take over the defense role (Monneret 1974). When both adults are present in late season, we predicted they would respond with equal intensity.

Finally, we predicted that peregrines that are rarely exposed to overflights would respond more intensely to the same overflight than would those in frequently overflown areas. In a Colorado study area with a long history of helicopter overflights, only 8% of red-tailed hawks flushed in response to helicopter overflights (Andersen et al. 1989). In an area where overflights were newly introduced, however, 53% of the hawks flushed. Similarly, we predicted that peregrines would respond with decreasing intensity as the number of consecutive days of overflights increased. By comparing reactions of peregrine falcons within and among areas with different exposures to overflights, we sought to account for potential effects of habituation.

STUDY AREA

We conducted field observations at peregrine falcon nest sites along the Tanana River, Alaska, during the summers of 1995, 1996, and 1997. Observations were initiated each year as soon as it was safe to travel on the river after ice break-up in mid-May, and continued until young had fledged and left the area of the nest (late August/early September). The Tanana River between Tok and Salcha (from 63°8'N, 143°36'W to 64°18'N, 148°45'W) supports over 30 active peregrine falcon nests and is crossed by three Military Training Routes (MTRs; Fig. 2.1). These MTRs are air corridors between Air
Force bases and Military Operations Areas (MOAs). Low-altitude training flights can be conducted in these areas without special clearance from the Federal Aviation Administration (FAA) and, as Eielson Air Force Base is nearby, many training missions could be modified to fly over particular nests in the MTRs. Nests within MTRs were considered “experimental nests,” while those outside of MTRs, where jets were subject to altitude restrictions, served as “reference nests.” Baseline observations were recorded at experimental nests on days when no overflights were observed. Nests were identified by river km, with the source at river km 0.

During the 1995 field season, we recorded observations at five experimental nests within MTRs 940 and 926 and six reference nests (Fig. 2.1). All of these nests were located along an approximately 110-km stretch of the Tanana River between Tok and Sawmill Landing (hereafter the “upper stretch”). In 1996 and 1997, the study area was expanded to include another 100-km stretch of the Tanana River between Delta Junction and Salcha (hereafter the “lower stretch”). The lower stretch is crossed by MTR 1928 (Fig. 2.1), located closer to Eielson AFB, and potentially subject to a higher volume of military aircraft traffic. Because we were working with the USAF on a non-interference basis (flights could not be scheduled over nests solely for the purposes of this study, but overflights could be included as part of existing training missions), it was important that field crews put themselves in the path of as many missions as possible. In 1996 and 1997, nine experimental nests and three reference nests were observed. Six of these nests were located in the upper stretch of the study area, and six were in the lower stretch.
Fig. 2.1. The study area along a 300-km stretch of the Tanana River between Tok and Salcha, Interior Alaska.
The Tanana River is a braided, glacially-fed river in Interior Alaska. The valley floor is covered in boreal forest of predominately white spruce (*Picea glauca*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*), with many boggy areas and small thaw lakes. The northern bank of the Tanana River is intermittently bounded by schist and granite cliffs ranging in height up to several hundred meters. These south-facing slopes are warmer, sunnier, drier, have a longer growing season, and support a different assortment of plants than do low-lying areas and the backsides of cliffs (Wahrhaftig 1965). These slopes/cliffs are also where peregrine falcons most frequently locate their nests. Some occupied cliffs overlook wide, braided areas of the river, while others are located near lakes, ponds, marshes, or other expanses suitable for hunting.

METHODS

Field crews conducted behavioral observations of breeding peregrines and their young and collected data on overflight characteristics during the 1995, 1996, and 1997 nesting seasons. Two field crews were present in the field in all years, although the number of observers per field crew doubled after the first year. This increase in numbers of individuals per crew from two to four allowed us to increase the number of hours of observation at each nest, while also providing better coverage during each observation session. Field crews traveled to the various nests using river boats (21-foot or 24-foot Alwelds with 150-hp jet outboards). We made observations from across at least one channel of the river, between 300 and 750 m from each nest. Observation sites were
generally located on sandbar islands, and due to late-season flooding each year, observations were sometimes made at greater distances by the end of the season. Observation distance also depended on the sensitivities of each pair of peregrines to observer presence. Crews camped out of view (but within 5 km) of each observation site, but generally left equipment in a tent-blind at each site. Approximately an hour before each session, we either walked or boated to the observation site.

The nesting cycle was divided into four phases: 1) pre-incubation (including arrival, courtship, and egg-laying), 2) incubation, 3) nestling-rearing (including hatching), and 4) fledging (from the first observed flight by a nestling until all fledglings had left the nest area). In addition, we treated failed nests as a separate phase of the nesting cycle for purposes of data analysis. Most data were collected during the incubation, nestling-rearing, and fledging phases due to the inaccessibility of nests prior to ice break-up on the Tanana River, which occurs around the peak of laying.

We recorded the behavioral responses of adult peregrine falcons to disturbances on data sheets. These observations were made with the aid of 10x binoculars, 15-45x spotting scopes, and Questar telescopes. We also recorded responses to overflights using two Canon L2 Hi-8 mm video cameras. These cameras continuously recorded behavioral data during observation periods in order to have a video record of responses to overflights and other disturbances. Each camera was mounted on a tripod and equipped with a 250 mm telephoto lens, 2x teleconverter, a DC-S10 12V adapter, and a 12V deep-cycle battery. The cameras used Hi-8 mm video tapes, which record for up to 2 hours. One camera was focused on the nest ledge at all times. During the incubation and nestling-
rearing periods, we focused the second camera on which ever adult was not at the nest ledge. If both adults were in sight, but away from the nest ledge, we focused the second camera on the female. Late in the fledging period, when the nest ledge was rarely occupied, cameras were focused on the two birds (or groups of birds) that were most easily viewed.

We recorded responses to disturbance as one of the following categories: unknown reaction, no reaction, attentive, alert/alarmed, flight intention movement, stand up, crouch/cower, unknown flying, defensive flying, or evasive flying. Definitions of response categories were as follows, in order of increasing intensity:

**Unknown reaction**: the individual was not in view of the observers during the potential disturbance

**No reaction (Response category 0)**: continued previous activities, including perching, dozing, preening, feeding, or soaring

**Attentive (1)**: aware of stimulus; looked up briefly and watched stimulus source; sometimes looked about with intermittent head movements

**Alert/alarmed (2)**: looked about in search of stimulus with quick head jerks in rapid succession; sometimes followed by an intense stare; tucked leg might drop to perch

**Flight Intention Movement (3)**: showed intention to fly but did not fly; became alert and then exhibited head-bobbing, leaned forward, defecated, and/or raised wings

**Stand up (3)**: stood up, particularly from an incubating or brooding posture for adults

**Crouch/cower (4)**: adult lowered profile while perching, incubating, or brooding
**Unknown flying (5):** flight appeared to be neither defensive or evasive; conversely, the bird left its perch but its flight was not observed

**Defensive Flying (6):** flew in a defensive manner; could include vocalization, diving, or attacking source of disturbance

**Evasive flying (7):** flew in an evasive manner; could include avoidance escape, low profile/low altitude flight, or rapid disappearance from view

Response categories 0 and 1 were classified as “minimal.” Response categories 3 and 4 were classified as “intense” whereas response categories 5, 6, and 7 were classified as “flight.” Behavioral responses to potential disturbances were classified in the same way, regardless of the type of potentially-disturbing stimulus.

Overflights of nests in the MTRs by subsonic A-10, F-15, and F-16 military jets were coordinated with existing missions of the 11th Air Force from Eielson and Elmendorf Air Force Bases. Several British jets (Harriers, Tornados, or Jaguars) involved in joint training exercises were also engaged in overflights. Prior to the beginning of each field season, a preliminary schedule was prepared of days when we could expect overflights at each nest (training missions, weather, and real-life military situations permitting). Overflights could not be scheduled during Cope Thunder exercises (joint training exercises occurring each summer in Interior Alaska), although we did receive incidental, unscheduled overflights while Cope Thunder exercises were being conducted. During Cope Thunder periods (two weeks at a time, 3-4 times per breeding season), we concentrated on baseline observations at overflown nests, as well as observations at reference nests. Each week during potential overflight periods, we used
cell phones to call the Eielson AFB scheduling office (cell coverage permitting) to receive a schedule of half-hour time blocks when we could expect overflights.

Type III Standard and Compact Animal Noise Monitors (ANMs; Hill 1995, Kugler 1996) were deployed near the nests for the duration of the breeding season and were used for monitoring noise levels during overflights. In addition, a portable Larson Sound Monitor 870 or an ANM was deployed near the observers in 1995. These extra monitors served as a backup during behavioral observations and also provided some index for checking the accuracy of cliff-deployed ANMs. Two ANMs were deployed at each experimental nest as a backup in case of ANM failure, while only one was deployed at each reference nest. The ANMs were set to record any sound event that exceeded a threshold of 85 dBA (A-weighted decibels) and lasted more than two seconds, but less than two minutes. These criteria were chosen in order to record noise events that were likely to be jet aircraft, while screening out noise events that were unlikely to be jet aircraft (Kugler 1996). ANMs measured the intensity of noise events and provided back-up information on number, timing, and frequency of these events. The ANMs recorded the following noise dose variables:

- A- and C-weighted sound exposure level (SELa and SELc)
- duration of above-threshold sound levels
- maximum sound pressure level ($L_{\text{max}}$)

ABR, Inc. provided technical assistance for deploying and retrieving data from ANMs. Krisand Consulting and Research (KCR) screened the ANM data. All noise events recorded on the weekend (when military jet overflights only rarely occurred) and all noise
events that could not be interpreted as military jet overflights were removed from the database by KCR.

Air Force personnel (Forward Air Controllers, or FACs) were present in the field during much of the 1996 and 1997 field seasons. The FACs directed scheduled flights over nests, called in extra aircraft that happened to be in the area, and helped with data collection (particularly for overflight variables such as distance, altitude, and airspeed). The FACs communicated with pilots and were often able to obtain altitude and airspeed readouts from the cockpit. They also were able to direct pilots for multiple passes at varying altitudes and angles of approach in relation to an active nest. Each pass by an aircraft or group of aircraft was treated as a separate overflight.

Scheduled jets were requested to fly directly over nests at altitudes between 170 m (500 ft., which was the lower limit in the MTR) and 330 m (1000 ft.) AGL (above ground level) and at power settings of 90% full power. If possible, scheduled jets were asked to fly over nests from multiple directions, several passes in succession.

We recorded the type of aircraft, altitude, estimated minimum lateral distance from nest, and weather conditions (percent cloud cover, wind speed and direction, precipitation, and temperature) for each overflight. Slant distances were calculated for each overflight by combining the minimum altitude of an overflight above a nest with the minimum lateral distance of an overflight from the nest. Close overflights, defined as \( \leq 1000 \) m slant distance from a nest, were used to examine the effects of jet overflight parameters on behavior of peregrine falcons. We chose this slant distance as the criterion for a close overflight because all but one of the observed jet overflights that exceeded the
thresholds of the ANMs were within 1000 m slant distance of the nest. All but one above-threshold A-10 overflight was within 500 m slant distance; F-series and British jets were louder and were picked up by the ANMs at greater distances. Additionally, only minimal responses (no reaction or attentive reaction) by peregrine falcons were observed for overflights beyond 1000 m slant distance.

STATISTICAL ANALYSIS

Graphical displays were used for preliminary examination of the data. We used the NCSS97 statistical package (Hintze 1997) to perform statistical analyses, including descriptives for means, standard deviations, and ranges; regression analyses; two sample t-tests; Mantel-Haenszel tests; one-way ANOVAs; and Duncan’s multiple comparison tests. We explored the relationship between overflight parameters (aircraft type, altitude, lateral distance, slant distance, SELa, duration of sound, maximum sound pressure level) and peregrine falcon response with multiple linear regression, while controlling for number of jets, consecutive days of above-threshold noise events, number of overflights in rapid succession (i.e., multiple passes by one aircraft or group of aircraft), sex, phase of the nesting cycle, nest-year, inclusion in an MTR, stretch of the river, and time of day.

We reported P-values for all statistical tests. If \( P \leq 0.05 \), we considered the test significant. We chose to consider tests with \( 0.05 < P \leq 0.10 \) as marginally significant, in order to avoid type II errors. If a difference existed, we wanted to avoid the possibility of incorrectly overlooking that difference.
We chose a-weighted sound exposure level (SELa) over SELc as the primary noise dose variable. SELa is often used in studies of noise effects on wildlife, and is therefore convenient for comparing results among studies (Black et al. 1984, Johnson 1988, Ward and Stehn 1989). Also, this is the weighting commonly used to measure aircraft noise levels and is an appropriate variable to use when making management recommendations (Brown 1990, Hill 1995), as SELa emphasizes those frequencies to which humans are most sensitive. Birds and humans are generally sensitive to similar sound frequencies, so a-weighting would be more appropriate than would c-weighting (Schwartzkopff 1973).

Altitude and lateral distance were examined separately in regressions, and also in combination (slant distance). This was done in order to account for possible “sound shadow effects” (Ward and Stehn 1989). Although counter-intuitive, overflights at greater slant distances can be louder than low-altitude overflights at smaller slant distances due to shadow zones caused by wind. Sound from low-altitude overflights can also be more attenuated by topography (“barrier effect”; Trimper et al. 1998).

RESULTS

Jet Overflight Disturbance

A total of 1414 jet noise events, defined as any jet sound audible to the observers, was recorded by field crews at active nest sites during the course of the study. Of these jet noise events, 214 (15%) were barely audible (<15 dB) and the source was out of sight. Another 470 (33%) were observed to be military jets, but noise levels were low (<40 dB)
and the source too distant (>2 km) for the type of jet to be determined. The remaining 730 overflights (51%) were from identified military jets, including F-15's or F-16's (305 overflights); A-10's (322 overflights); and British Harriers, Tornados, or Jaguars (103 overflights). Many of these identified overflights were greater than 1000 m slant distance from the nest, and most were below the 85 dB threshold for recording by the ANMs.

A total of 401 of the identified jet overflights (55%) were defined as close, or within 1000 m slant distance of a nest (Fig. 2.2). Of these close overflights, 132 (33%) exceeded the 85 dB threshold and were recorded by the ANMs. A-10's greater than 500 m slant distance accounted for 55 (20.4%) of the close overflights that were not recorded by the ANMs, and British aircraft accounted for 18 (6.7%) of these overflights. Multiple overflights in rapid succession by the same jet formations sometimes triggered only one, longer-duration ANM record. These accounted for 33 (12.3%) of the close overflights that were not recorded by the ANMs. The remaining close overflights that were not recorded by ANMs comprised 40% of the total and consisted of F-series (F-15 and F-16) jets. The noise from these louder jets was apparently attenuated by sound shadow or sound barrier effects before reaching the ANMs.

A total of 878 above-threshold noise events were recorded by ANMs during the study (Fig. 2.3). Military jet formations generally flew over several nests while they were in the area and although ANMs were set up at each nest, observers were present at only one nest at a time. Of the 257 ANM-recorded noise events that occurred when observers were present, 91% (235 noise events) agreed with observed jet overflights. These 235 noise events consisted of 132 sets of rapid-succession overflights by several
Fig. 2.2. Number of close (≤ 1000 m slant distance from a nest) military jet overflight events (n=401) recorded by field crews at each peregrine falcon nest in each year of the 3-year study.
Fig. 2.3. Number of jet overflight events $\geq 85$ dB noise level ($n=878$) recorded by Animal Noise Monitors (ANMs) at each peregrine falcon nest in each year of the 3-year study.
planes in a group, many of which were recorded by the ANMs as separate events. Four of these observations (1.5% of total) were not Air Force jets, but instead were boats, helicopters, or small fixed-wing aircraft. An additional 4% (10 events) were possible matches (less than 5 minutes time difference between observer log and ANM record). Only 12 of the ANM-recorded noise events (4% of those that occurred when field crews were present) could not be matched with an event recorded by field crews. Although some discrepancies were inexplicable (i.e., the 12 instances when observers were present at the nest site but did not observe a noise event) and some of the ANMs experienced technical difficulties, these discrepancies accounted for a small percentage of ANM records. The ANM records generally provided an accurate measure of the level of noise exposure that peregrine falcons on the Tanana River experienced as a result of jet aircraft overflights (Kugler 1996).

As a whole, nests were exposed to more above-threshold overflights in 1997 than in previous years (Fig. 2.3). The nests on the lower stretch of the river and the nests farthest downstream in the upper stretch (nests 280, 281, and 288) received the bulk of the close overflights in 1996 and 1997 (Figs. 2.2 and 2.3). Two of the upper-stretch nests within MTRs (nests 205 and 221.5; Fig. 2.3) experienced low numbers of above-threshold overflights in 1996 and 1997, similar to nests outside of MTRs.

**Peregrine Falcon Reactions to Jet Overflights**

Adult peregrine falcons were not always in view when jets flew over active nests. Of the 1414 jet noise events recorded by field crews, we were able to observe responses
for both the male and female parent in 508 of the events (36%). Reactions were observed for only one of the two parents in 354 cases (25%), while reactions were observed for neither parent during 552 events (39%). Of the 401 close overflights (≤1000 m slant distance from the nest) by military jets, we were able to record responses for both parents during 98 (24%) of the overflights. Only the female was visible during 93 (23%) close overflights, and neither parent was in view during 210 (52%) of the close jet overflights.

A total of 35% of all known responses by parents to close military jet overflights were listed as “no reaction.” An additional 43% were categorized as attentive (a minimal response demonstrating that the birds were aware of the jet overflights, but also suggesting that they were not threatened or disturbed). Alert reactions accounted for 17.5% of all known responses to close jet overflights, while only 2% of all reactions were classified as intense (stand, crouch/cower, flight intention movement). Flight reactions accounted for 2.5% of the total reactions by adult peregrine falcons to close overflights. No flight reactions by adult female peregrine falcons in response to jet overflights were observed, while 8 responses by males to close overflights (5%) were flight reactions (Fig. 2.4).

Reaction Intensity and Overflight Characteristics

In order to test our original hypotheses, we compared reaction intensity with slant distance, SELa, and type of jet aircraft, while controlling for sex, nesting phase, and nest. We also examined the proportion of intense or flight responses by males and females as a function of slant distance, SELa, and aircraft type. We had 83 complete records of
Fig. 2.4. Proportion of several behavioral reaction types observed in response to jet aircraft overflights (slant distance ≤ 1000 m) by female (n=191) and male (n=98) peregrine falcons during the 1995-1997 breeding seasons.
overflights, i.e., records of overflights where noise level was above-threshold and where the reaction of at least one adult falcon was visible. These data were used to investigate the relative role of SELa for explaining variation in behavioral reactions of peregrine falcons to overflights. We had 508 records for audible jet overflight events when the reactions of both adult peregrines were visible; 98 of these records were for close overflights. This larger data set was useful for examining the role of other overflight parameters (i.e., slant distance, jet type) in relation to falcon reaction.

**Altitude**

A trend of decreasing reaction intensity with increasing altitude was evident in graphical displays of altitude versus reaction intensity, regardless of sex. A regression of reaction intensity on altitude (controlling for nesting phase and nest) was significant for both females ($F_{1,638} = 55.11, P < 0.001$) and males ($F_{1,535} = 54.53, P < 0.001$).

No intense reactions were observed at overflight altitudes greater than 300 m AGL. No flight reactions were observed at overflight altitudes greater than 240 m AGL.

**Lateral distance**

A trend of decreasing reaction intensity with increasing lateral distance was evident in graphical displays of lateral distance versus reaction intensity ($n=862$), regardless of sex. A regression of reaction intensity on lateral distance (controlling for nesting phase and nest) was significant for both females ($F_{1,638} = 71.20, P < 0.001$) and males ($F_{1,535} = 64.15, P < 0.001$).
No intense reactions or flight reactions were observed in response to overflights at lateral distances greater than 400 m.

_Slant distance_

Slant distance of an overflight is a combination of altitude above a nest and lateral distance from the nest. A trend of decreasing reaction intensity with increasing slant distance was evident in graphical displays of slant distance versus reaction \((n=862)\), regardless of sex (Fig. 2.5). A regression of reaction intensity on slant distance (controlling for nesting phase and nest) was significant for both females \((F_{1,638}=93.74, P<0.001)\) and males \((F_{1,535}=84.64, P<0.001)\). Slant distance explained more of the variation in falcon response intensity than did either altitude or lateral distance alone. Slant distance alone explained 14% of the variation in male reaction intensity to jet overflights and 13% of the variation in female reaction intensity when all audible overflights were included.

No alert/alarmed reactions were observed in response to overflights at slant distances greater than 700 m, and no intense reactions were observed in response to overflights at slant distances greater than 550 m. No flight reactions were observed in response to overflights at slant distances greater than 400 m.
Fig. 2.5. Mean female (n=731) and male (n=636) peregrine falcon behavioral reactions to jet aircraft overflights as a function of slant distance. Reactions, in order from 0-7, include: no reaction, attentive, alert/alarmed, stand/flight intention movement, crouch/cower, unknown flying, defensive flying, and evasive flying.
Sound exposure level (SELa)

A trend of increasing reaction intensity with increasing a-weighted SEL (SELa) was visible in graphical displays of SELa versus reaction intensity for both males and females (Fig. 2.6). A regression of reaction intensity on SELa also indicated that reaction intensity was positively and significantly related to SELa for females ($F_{1,37}=10.10$, $P=0.0024$), but the regression was only marginally significant for males ($F_{1,42}=4.05$, $P=0.0506$), largely because of a few outliers (Fig. 2.6). It is likely that with a larger sample size the regression for males would be significant. SELa explained 15% of the variation in female response to above-threshold jet overflights and 10% of the variation in male response. When we only used those data where both the male and the female were present for the same overflight, SELa was still significant for females ($F_{1,23}=9.63$, $P=0.0047$), but not for males ($F_{1,23}=1.22$, $P=0.2806$). Inclusion of SELa in a multiple regression model with slant distance resulted in SELa explaining a significant proportion of the residual variation in reaction intensity for females ($F_{2,26}=4.96$, $P=0.0103$), but not for males ($F_{2,21}=2.16$, $P=0.1280$).

One intense reaction by a male occurred in response to an overflight that was not recorded by the ANMs, and so was probably under 85 dB. An additional five overflights that induced intense responses occurred after ANMs had been retrieved (failed nests) or when they were no longer functioning (one nest). Of the remaining nine overflights that elicited intense responses, the average SELa was 99.7 dB (range = 89.0-110.3 dB, $n=9$). No flight reactions were observed at SELa’s less than 89.0 dB (mean = 100.5 dB, range = 89.0-110.3 dB, $n=5$).
Fig. 2.6. Female ($n=63$) and male ($n=47$) peregrine falcon behavioral reactions to jet aircraft overflights as a function of a-weighted sound exposure level (SELa). Reactions, in order from 0-7, include: no reaction, attentive, alert/alarmed, stand/flight intention movement, crouch/cower, unknown flying, defensive flying, and evasive flying.
Duration of sound and maximum sound pressure level

Duration of sound did not explain a significant proportion of the variation in reaction intensity of males or females (females, $F_{1,57} = 0.0093$, $P = 0.9236$; males, $F_{1,42} = 0.3386$, $P = 0.5638$). A-weighted maximum sound pressure level, however, did explain a significant proportion of the variation in reaction intensity of females, and a marginally significant proportion in males (females, $F_{1,57} = 11.29$, $P = 0.0014$, $R^2 = 0.1653$; males, $F_{1,42} = 3.32$, $P = 0.0756$, $R^2 = 0.0733$).

Type of jet aircraft

F-series and British jets produced higher SELa’s on average than did A-10s, even after controlling for slant distance ($F_{1,130} = 9.03$, $P = 0.0032$), and airspeeds were greater as well. After controlling for effects of SELa, however, type of jet did not explain a significant proportion of the variation in peregrine falcon response intensity. Type of jet was also not a significant factor after controlling for effects of either slant distance or a combination of altitude and lateral distance.

Amounts of jet aircraft disturbance

The total number of aircraft in an overflight formation (i.e., 1-ship, 2-ship, 4-ship, 8-ship) did not explain a significant proportion of the variation in peregrine falcon response to overflights. The number of overflights in rapid succession (number of passes), however, explained a significant proportion of the variation for males
There was a positive correlation between number of overflights in rapid succession and reaction intensity of male peregrine falcons. The regression was only marginally significant for females ($F_{1,253}=3.68$, $P=0.0561$, $R^2=0.0143$; Fig. 2.7).

**Reaction Intensity and Peregrine Falcon Characteristics**

**Sex**

Males exhibited a higher proportion of intense responses to jet overflights than did females (Fig. 2.8). When both males and females were present during an overflight, the reaction intensity of males was significantly higher than for females (1-tailed paired t-test, $P=0.0002$, $df=1014$). Males also exhibited significantly more flight reactions than did females (1-tailed paired t-test, $P=0.0041$, $df=1012$, Fig. 2.8). In fact, females were not observed exhibiting any flight responses as a result of jet overflights during the course of the three-year study. Gender differences in reaction intensity were evident in graphical displays of reaction intensity on altitude, lateral distance, slant distance, SELa, total number of overflights in rapid succession, and phase of the nesting cycle (Figs. 2.5-2.8).

Breeding males were more likely to be absent from the area of their nest when jet overflights occurred than were females (Mantel-Haenszel test, $P<0.001$). In fact, males spent less time attending the nest than females up until the fledging phase (Palmer et al., unpubl. ms.). During incubation and nestling-rearing, males, when present, responded more intensely than did females (1-tailed paired t-test, $P=0.0029$, $df=152$ and $P=0.0071$, $df=348$, respectively). Females and males did not, however, respond differently during
Fig. 2.7. Behavioral reactions by female and male peregrine falcons in relation to number of jet aircraft overflights in rapid succession.
Fig. 2.8. Proportion of known intense (stand, flight intention movement, or crouch/cower) or flight reactions by female and male peregrine falcons to all audible jet aircraft overflights as a function of phase of the nesting cycle.
fledging (1-tailed paired $t$-test, $P=0.4840, \, df=120$). When both males and females were present at failed nests, they also did not respond differently to jet overflights (2-tailed paired $t$-test, $P=0.5669, \, df=160$).

Phase of the nesting cycle

Differences in reaction intensity of females to audible overflights as a function of phase of the nesting cycle were marginally significant (1-way ANOVA, $F_{3,727}=2.28, \, P=0.0783$). Reaction intensity of males differed among phases of the nesting cycle (1-way ANOVA, $F_{3,629}=5.28, \, P=0.0013$). Males exhibited significantly higher reaction intensities during the incubation and nestling-rearing phases than they did during fledging (Duncan’s Multiple Comparison Test, $P<0.05$). But the reaction intensity of males at failed nests was not different from males during the fledging phase, nor was there a difference in male reaction intensity between incubation and nestling-rearing (Duncan’s Multiple Comparison Test, all audible overflights included in analyses, $P>0.05$). Results were similar when we examined only reactions to close overflights; females did not exhibit a difference in reaction intensity across phases of the nesting cycle ($F_{3,188}=1.82, \, P=0.1452$), whereas males did ($F_{3,189}=3.01, \, P=0.0322$). No intense or flight reactions were observed in response to overflights during fledging, regardless of sex (Fig. 2.8).

In order to better examine gender differences in reaction intensity during each phase of the nesting cycle, we calculated a derived variable from the difference in the male’s reaction and the female’s reaction for each overflight where both parents were visible. When only close overflights were analyzed, no differences were detected across
the phases of the nesting cycle (1-way ANOVA, \( P=0.5964 \)). When all audible jet overflights (where both parents were present) were included in the analysis, incubation was significantly different from the other two phases (1-way ANOVA, \( P<0.0001 \), Duncan’s Multiple Comparison Test, \( P<0.05 \)). This means that gender differences in reaction intensity were greatest during incubation.

**Time of day or year**

Neither time of day nor year explained a significant proportion of variation in reaction intensity for males (1-way ANOVA, \( P=0.5444 \) for close overflights) or females (1-way ANOVA, \( P=0.1194 \) for close overflights).

**Previous exposure to overflights**

There was not a large enough sample of banded adult peregrines among the study nests to test for significant effects of individual exposure history on intensity of response to overflights. In order to assess the role of habituation as a factor influencing reaction intensity, we instead examined reaction intensity as a function of consecutive days of above-threshold noise events and consecutive days of close jet overflights. These two independent variables were identical. The number of consecutive days of close, above-threshold overflights did not explain a significant proportion of the variation in reaction intensity (females: \( F_{1,190}=0.418, P=0.8382 \); males: \( F_{1,152}=0.4337, P=0.5112 \)).
Location of nests

Reaction intensity to similar overflights did not differ between experimental and reference nests (2-tailed, 2-sample t-test, females, \(df=190, P=0.5422\); males, \(df=152, P=0.8591\)). Reaction intensity also did not differ between nests located on the upper stretch of the Tanana River study area compared with those located on the lower stretch (2-tailed, 2-sample t-test, females, \(df=190, P=0.6598\); males, \(df=152, P=0.3954\)).

Complete Model

The factors that were significant (or at least approached significance) in explaining variation in reaction intensity of adult peregrine falcons to jet overflights were sex, slant distance, a-weighted sound exposure level (SELa), a-weighted maximum sound pressure level (Lmax), number of overflights in rapid succession, and phase of the nesting cycle. When we ran a stepwise regression on these five factors for the overflights with complete records (i.e., included noise level measurements), the complete model for females included only Lmax \((R^2=0.1735, F_{1,56}=11.76, P=0.0011\)). Nothing was significant for males. When we ran a stepwise regression on slant distance, number of overflights in rapid succession, and phase of the nesting cycle for all close overflights (in order to increase sample size), the complete model included slant distance for both females and males (female: \(R^2=0.0559, F_{1,190}=11.25, P=0.0009\); male: \(n=154\), partial \(R^2=0.0613\)). In addition, the complete model for all close overflights included number of overflights in rapid succession for males (\(n=154\), partial \(R^2=0.0482\); complete model \(R^2=0.0936, F_{2,151}=7.80, P=0.0005\)).
DISCUSSION

The overall hypothesis that we sought to test was that stronger stimuli associated with jet overflights elicit more intense behavioral reactions from breeding peregrine falcons. This hypothesis was supported by the results. Both males and females showed similar trends of increasing reaction intensity with decreasing altitude, lateral distance, and slant distance. Additionally, both SELa (a-weighted sound exposure level) and Lmax (a-weighted maximum sound pressure level) were significantly and positively correlated with reaction intensity in females and marginally so for males.

The highly significant negative correlation between peregrine falcon reaction intensity and slant distance indicates that closer overflights elicit more intense reactions, in agreement with other studies (Olsen and Olsen 1980, Johnson 1988, Ward and Stehn 1989, Yalden and Yalden 1989, Grubb and Bowerman 1997). Slant distance, however, only explained about 6% of the variation in reaction intensity to close (< 1000 m slant distance) overflights for either sex, when other variables were taken into consideration.

A-weighted SEL was a significant source of variation in female peregrine falcon response to overflights, and marginally significant for males. Males responded intensely to overflights at all measurable SELa levels (>85 dB). This supports the hypothesis that the greater average reaction intensity of males is related to their greater role in nest defense throughout most of the breeding season. Male reaction intensity may be more closely related to visual cues than to auditory ones, as they are normally perched near the nest where vantage is good. Females, on the other hand, are more frequently at the nest ledge, where the view of the surroundings can be quite restricted. The sample of
overflights with SELa measurements is a small sample of very close and very loud overflights. This helps explain why female reaction intensity varied with noise level, while male reaction intensity did not.

Duration of sound did not significantly affect intensity of peregrine falcon reactions to overflights. This result likely reflects a greater sensitivity to the maximum noise level experienced, rather than the duration of sound.

We predicted that males would respond to overflights more intensely than females during incubation and nestling-rearing because males are usually responsible for nest defense and females normally sit tight while brooding eggs or nestlings (Monneret 1974). Clear differences were detected in the reactions of the two sexes to jet overflights. These differences are probably related to the pronounced sexual dimorphism in peregrine falcons and differences in the roles of the two sexes during reproduction (Monneret 1974). Males displayed higher frequencies of both intense and flight reactions than did females in each year of the study. The mean intensity of male reactions was also higher than that of females. Cade and White (1976) found that incubating peregrine falcons responded less to disturbance than did non-incubating peregrines, and that it was difficult to get incubating peregrine falcons to move off the nest scrape.

During the fledging phase, neither sex responded as intensely to overflights, and there was no gender difference in reaction intensity. This could be a result either of habituation by males to overflights or a decrease in protectiveness of the nest and young once the young have fledged.
Interestingly, males responded to jet overflights with the same intensity whether their nest had failed or their young had fledged. This intensity of response was significantly less than when males were caring for eggs or nestlings. This supports Olsen and Olsen’s (1980) finding that defensive behaviors were greatest when a pair had eggs or nestlings. They also found that while non-breeding pairs sometimes defended their territory, they usually did not.

Males tended to react more than females, regardless of location of the nest, time of day, or noise level of the overflight. Besides slant distance, the one factor that explained a significant proportion of variation in male reaction intensity was the number of aircraft overflights in rapid succession (number of passes). The number of passes was positively correlated with intensity of male reaction. Perhaps repeated passes increased the stress level of males or sensitized them to additional passes, at least in the short-term.

Females did not react as strongly or as often as males. Slant distance was the only variable that explained a significant proportion of the variation in female reaction intensity. There was more variation among individual females in reaction intensity compared to males. Perhaps females reacted most when their mate needed assistance (or when the male was not present) because the cost of flight reactions may be high in terms of exposing eggs or young. The cost of flight reactions by males is comparatively low and so they may react more intensely to a wider range of jet overflight intensities. In order to examine this possibility, we ran an ANOVA on reactions of females to close jet overflights when males were present versus when they were absent. The mean reaction
intensity of females was significantly greater when their mates were out of sight of the observers ($F_{1,85}$=8.08, $P=0.0050$).

The lack of a difference in reaction intensity between peregrines whose nests were within MTRs and those whose nests were not is partly because location of a nest within an MTR did not guarantee that it would be exposed to many overflights. Three nests within MTRs were exposed to less than 10 above-threshold overflights in a given season, while five nests within MTRs were exposed to less than 15 audible overflights during observation periods in a given season. Conversely, nests outside MTRs were sometimes exposed to significant numbers of overflights. Three nests outside of MTRs were exposed to more than 10 overflights that exceeded the 85 dB threshold of the ANMs in a single season.

The lack of a difference in reaction intensity between experimental and control nests suggests that peregrine falcons are experiencing neither habituation nor sensitization at this level of exposure to jet overflights. If peregrine falcons tended to habituate to jet overflights, one would expect a lower average reaction intensity from those peregrines nesting in flight corridors (i.e., MTRs) than from those nesting in areas where jets are subject to altitude restrictions. If peregrines were, on the other hand, sensitizing to jet overflights, one would expect a higher average reaction intensity from those peregrines nesting in flight corridors.

Of all the overflight parameters, noise parameters such as $L_{max}$ and $SEL_{A}$ were the best predictors of reaction intensity of nesting peregrine falcons to jet aircraft overflights. $L_{max}$ was a better predictor of reaction intensity than was $SEL_{A}$, but $L_{max}$ still only
explained 7% and 17% of the variation in male and female reaction intensities, respectively. In the absence of quantified noise data, slant distance of the aircraft from the nest was the best predictor. Even with the numbers of loud, close overflights observed in this study, however, intense reactions by peregrine falcons to military jet overflights were rarely observed. If acute, short-term behavioral responses are indicative of damage caused by disturbance, then the observed low level of overt behavioral reactions to jet aircraft overflights by nesting peregrine falcons suggests a low overall sensitivity to this potential source of disturbance. Despite the significant contribution of slant distance, noise exposure, sex, and phase of the nesting cycle in explaining variation in reaction intensity to jet overflights, most of the variation remained unexplained and was presumably related to individual differences in sensitivity to overflights.

CONCLUSIONS

1. Intense behavioral responses (including flight responses) were rarely observed in this study, even at slant distances <500 m, and no intense behavioral responses were observed at slant distances >550 m.

2. No flight responses were observed in female peregrine falcons in response to jet overflights, and females responded with a lower mean reaction intensity than did males.

3. Lmax was a better predictor of reaction intensity than slant distance, for those overflights where both measurements were available. When no noise
measurements were available, slant distance was clearly the next best predictor of reaction intensity to overflights.

4. Reactions to jet overflights may be less overt for females brooding eggs or young because of their dominant role in protecting offspring at the nest ledge, whereas males generally assume more the role of attacking intruders within the nest area.

5. Most of the variation in reaction intensity of nesting peregrine falcons to jet aircraft overflights remained unexplained.

LITERATURE CITED


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CHAPTER 3

Relationship of Peregrine Falcon Responses to Jet Aircraft Overflights and Nesting Success

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ABSTRACT

Behavioral responses of nesting raptors to potential disturbances have been used as indicators of the impact of disturbance on nesting success. The purpose of this study was to determine if the intensity of acute behavioral reactions by breeding peregrine falcons (Falco peregrinus) to jet aircraft overflights is associated with lower productivity. We observed behavioral reactions of peregrines to overflights at 12 nests along the Tanana River, Alaska during each of the 1995-1997 breeding seasons. Military jet aircraft conducted low-altitude flights over a sample of active nest sites under observation in each year (experimental nests), while other nests were not intentionally overflown (reference nests).

Productivity did not differ between experimental and reference nests (1.96 fledglings and 1.92 fledglings per nesting attempt, respectively) and was within the normal range for peregrine falcons in Interior Alaska. Productivity also did not differ between nests exposed to >20 close overflights per season compared with those exposed to <20 close overflights per season, nor between nests with an average daily sound exposure level (SELa) of >90 dB compared with those with average daily SELa of <90 dB. Productivity did differ, however, between nests located along the upper stretch vs. the lower stretch of the study area. Adult peregrine falcons exhibited little or no overt behavioral reaction to the majority (78%) of close military jet overflights (≤1000 m slant distance from the nest). Only 5.5% of reactions were classified as intense (stand, crouch/cower, flight intention movement) or flight. There were significant differences
among individual nesting peregrines in the intensity of reaction to close overflights, after controlling for gender and slant distance. The average reactivity of both individual peregrine falcons and mated pairs to close jet overflights was negatively correlated with productivity and explained a significant proportion of the variation in productivity among nests. These results suggest that the sensitivity of breeding peregrine falcons to low-altitude jet overflights is a better indicator of subsequent productivity than actual dose of overflights. Such a relationship might result from lower productivity among pairs not habituated to overflights (i.e., higher intensity reactions interfere with parental duties) because of scant previous exposure to overflights. The available evidence, however, supports the hypothesis that higher reactivity is associated with lower parental investment, presumably in younger, less experienced parents, and these parents are also less likely to be productive.

INTRODUCTION

Human disturbance of wildlife can be defined as any human activity that raises the physiological costs of survival or lowers the chances of successful reproduction (Neil et al. 1975). One potential link between a disturbance and its effect on productivity of wildlife is its immediate effect on behavior. Flemming et al. (1988) found that disturbance-induced behavioral changes in piping plover chicks led to increased chick mortality. Hamm (1967) attributed aircraft noise-induced reductions in egg production of domestic fowl to changes in behavior, not stress-related physiological changes. Similarly,
Stadelman (1958) found that an isolated low-altitude flyover triggered a violent behavioral response in poultry, which resulted in chick loss.

It has been well-documented that low-altitude aircraft overflights affect the normal behavior of wildlife and elicit a variety of behavioral responses (Manci et al. 1988, Andersen et al. 1989, Ward et al. 1989, Ellis 1991, Maier et al. 1998). A provisional model for effects of jet aircraft overflights on nesting success of raptors proposed by Awbrey and Bowles (1990) was based on the assumption that the acute behavioral responses to aircraft noise can cause lower productivity in raptors. Does the magnitude of behavioral response to overflights have measurable effects on nesting success of raptors? In other words, can we use the reactions of raptors to jet aircraft overflights to assess the magnitude of disturbance and the corresponding deleterious effects on survival and reproduction?

In this study we sought to determine if the observed behavioral reactions of nesting peregrine falcons to low-altitude jet aircraft overflights were correlated with subsequent nesting success. We attempted to test the hypothesis that the behavioral reactions of nesting peregrine falcons to jet aircraft overflights represent a measurable cost for the current reproductive attempt. This hypothesis predicts that the frequency and intensity of behavioral reactions to disturbance are negatively correlated with nesting success and productivity of breeding peregrine falcons. In this case, the sensitivity of parent peregrine falcons may be a better predictor of the magnitude of disturbance than the actual dose of potential disturbance. An alternative hypothesis is that peregrine falcons that are highly responsive to jet aircraft overflights have a high motivation to
defend young, which is indicative of a high level of parental investment in the current reproductive attempt. This hypothesis predicts that the frequency and intensity of behavioral reactions to disturbance are positively correlated with nesting success and productivity.

STUDY AREA

We conducted field observations at peregrine falcon nests along the Tanana River, Alaska, during the breeding seasons of 1995-1997. Observations were initiated as soon as safely possible after ice break-up on the river (early May) and continued until the young had fledged and left the nest area (late August/early September). The Tanana River between Tok and Salcha (from 63° 8'N, 143°36'W to 64°18'N, 148°45'W) supports a high density of active peregrine falcon nests and is crossed by three Military Training Routes (MTRs). These MTRs are air corridors between Air Force bases and Military Operations Areas (MOAs), where jet aircraft training exercises occur. Low-altitude training flights can be conducted in MTRs, and many training missions from Eielson AFB could be modified to fly over particular nests in the MTRs (see Chapt. 2).

Nests within MTRs were referred to as “experimental,” while nests outside MTRs were considered “reference” nests. Baseline observations were collected at experimental nests during days without overflights. During the 1995 field season, five nests within MTRs 940 and 926 and six reference nests were observed. All of these nests were located along an approximately 110-km stretch of the Tanana River between Tok and
Sawmill Landing (hereafter the “upper stretch”). In 1996 and 1997, the study area was expanded to include another 100-km stretch of the Tanana River between Delta Junction and Salcha (hereafter the “lower stretch”). The lower stretch is crossed by MTR 1928, located closer to Eielson AFB, and potentially subject to a higher volume of military aircraft traffic. In 1996 and 1997, nine experimental nests and three reference nests were observed. Six nests were observed in both the upper and lower stretches of the river. Nests were identified by river km, with the source being km 0.

The Tanana River is a braided, glacially-fed river in Interior Alaska. A more detailed description of the study area and the nesting habitat of peregrine falcons along the river is presented in Chapter 2.

METHODS

Field crews conducted occupancy checks, collected data on nesting success and productivity, and recorded data on jet aircraft overflights and the reactions of peregrine falcons to those potential disturbances. Two field crews were present in the field in all three years of the study. Field crews traveled to the various nests using river boats (21-foot or 24-foot Alwelds with 150-hp jet outboards). Observations were made from across at least one channel of the river, between 300 and 750 m from each nest. Observation sites were generally located on sandbar islands, and due to late-season flooding each year, observations were sometimes made at greater distances by the end of the season. Observation distance also depended on the sensitivities of each pair of peregrines to observer presence.
The nesting cycle was divided into four phases: 1) pre-incubation (including arrival, courtship, and egg-laying), 2) incubation, 3) nestling-rearing (including hatching), and 4) fledging (from the first observed flight by a nestling until all fledglings had left the nest area). In addition, we treated failed nests as a separate phase of the nesting cycle for purposes of data analysis. Most data were collected during the incubation, nestling-rearing, and fledging phases due to the inaccessibility of nests during ice break-up on the Tanana River.

Observations of behavioral responses of peregrine falcons to disturbances were made with the aid of 10x binoculars, 15-45x spotting scopes, and Questar telescopes. Responses to overflights were also recorded on tape using two Canon L2 Hi-8 mm video cameras (see Chapt. 2).

Behavioral responses to overflights were recorded as one of the following categories: unknown reaction, no reaction, attentive, alert/alarmed, flight intention movement, stand up, crouch/cower, unknown flying, defensive flying, or evasive flying. Definitions of response categories were as follows, in order of increasing intensity:

**Unknown reaction**: the individual was not in view of the observers during the potential disturbance

**No reaction (Response category 0)**: continued previous activities, including perching, dozing, preening, feeding, or soaring

**Attentive (1)**: aware of stimulus; looked up briefly and watched stimulus source; sometimes looked about with intermittent head movements

**Alert/alarmed (2)**: looked about in search of stimulus with quick head jerks in rapid succession; sometimes followed by an intense stare; tucked leg might drop to perch
**Flight Intention Movement (3):** showed intention to fly but did not fly; became alert and then exhibited head-bobbing, leaned forward, defecated, and/or raised wings

**Stand up (3):** stood up, particularly from an incubating or brooding posture for adults

**Crouch/cower (4):** adult lowered profile while perching, incubating, or brooding

**Unknown flying (5):** flight appeared to be neither defensive or evasive; conversely, the bird left its perch but its flight was not observed.

**Defensive Flying (6):** flew in a defensive manner; could include vocalization, diving, or attacking source of disturbances

**Evasive flying (7):** flew in an evasive manner; could include avoidance escape, low profile/low altitude flight, or rapid disappearance from view

Response categories 0 and 1 were classified as “minimal.” Response categories 3 and 4 were classified as “intense” whereas response categories 5, 6, and 7 were classified as “flight”.

Overflights of nests in the MTRs were coordinated with existing missions of the 11th Air Force from Eielson and Elmendorf Air Force Bases. Air Force personnel (Forward Air Controllers, or FACs) provided support in the field during much of the 1996 and 1997 field seasons. The FACs directed overflights and helped with data collection (see Chapt. 2 for more detail on flight scheduling, FAC responsibilities, and overflight data).

Type III Standard and Compact Animal Noise Monitors (ANMs) were deployed near the nests for the duration of the breeding season and were used for monitoring noise
levels during overflights (see Ch. 2). The ANMs were set to record any sound event that exceeded a threshold of 85 dBA (A-weighted decibels) and lasted more than two seconds, but less than two minutes. These criteria were chosen in order to record noise events that were likely to be jet aircraft, while screening out other types of noise events. The ANMs recorded several noise dose variables, including a-weighted sound exposure level (SELa).

Productivity data were collected during observations of nests and during two nest visits to each active nest in each breeding season. The first nest visit took place in early to mid-May (depending on timing of river break-up and ice conditions) in order to perform an occupancy check, install ANMs, and determine clutch size (if possible without causing excessive disturbance to the breeding pair). The second nest visit took place in mid- to late July to check productivity, band young, and collect prey remains. These productivity checks coincided with the mid nestling-rearing phase, when the young are least vulnerable to disturbance as they are capable of thermoregulation but still sedentary.

The following nesting success/productivity variables were measured for each nest under observation:

1) **hatch date**: median date on which eggs hatched. This date was used to estimate laying date by back-dating. Hatch date was estimated by back-dating from estimated age of nestlings at banding, if hatch date was unknown.

2) **nestling survival**: proportion of hatchlings that survived to 25 days post-hatch.

3) **nesting success**: whether a breeding pair successfully fledged at least 1 young.

4) **productivity**: number of young fledged per nesting attempt.
STATISTICAL ANALYSIS

Graphical displays were used for preliminary examination of the data. We used the NCSS97 statistical package to perform statistical analyses, including descriptives for means, standard deviations, and ranges; frequency tables; regression analyses; correlation analyses; t-tests; one-way ANOVAs; and Duncan's multiple-comparison tests (Hintze 1997).

In addition to separating study nests into either experimental or reference treatments based on their location either within or outside the MTRs, we separated all study nests into either “many overflights” or “few overflights” treatments. Some nests within an MTR were exposed to fewer overflights than some nests outside an MTR. Nests in the “many overflights” treatment were those exposed to at least 20 close (<1000 m slant distance from the nest) overflights (median=27 overflights, n=12 nest years) during a breeding season, whereas nests in the “few overflights” treatment experienced <20 close overflights (median=2 overflights, n=13 nest years). In addition, we categorized study nests in either the “high noise” or “low noise” treatment. Nests in the “high noise” treatment were those that had an average daily SELa of at least 90 dB during the breeding season (median=98.9 dB, n=21 nest years), while those in the “low noise” treatment had an average daily SELa of less than 90 dB (median=78 dB, n=14 nest years). The “high noise” treatment also included nests that experienced at least 10 above-threshold noise events (>85 dB) during a breeding season. In order to check the validity of combining data from nests in the two parts of the study area (upper and lower stretch),
we compared the success and productivity of nests from these two areas. We also
compared productivity among years in order to test for longitudinal differences.

We developed an index of reactivity in order to examine variation among nests in
sensitivity of breeding adult peregrine falcons to overflights (reaction intensity after
controlling for slant distance and gender). First, we plotted reaction intensity vs. slant
distance for the population (separately by sex) and then used the average residual of
reaction intensity for each individual falcon as an index to that individual’s reactivity to
overflights. We then used one-way ANOVA to test for differences in average reactivity
among individuals. Next we ran Duncan’s multiple-comparison tests to determine which
individuals were different. We compared the average residuals of individual peregrines
in experimental vs. reference treatments, “many overflights” vs. “few overflights”
treatments, and “high noise” vs. “low noise” treatments.

Then we performed correlation analysis on the index of reactivity vs. several
variables related to productivity (hatch date, nestling survival, nesting success, and
productivity) to determine if reactivity and productivity were correlated. We also
performed correlation analysis on the index of reactivity for each female and its mate in
order to test for associations between the members of a breeding pair.

We reported $P$-values for all statistical tests. If $P \leq 0.05$, we considered the test
significant. We chose to consider tests with $0.05 < P \leq 0.10$ as marginally significant, in
order to avoid type II errors (i.e., we sought to reduce the possibility of incorrectly
overlooking a real difference).
RESULTS

_Peregrine Falcon Productivity_

Average productivity (number of young fledged per nesting attempt) for nests included in the study over the three years was 1.94 fledglings ($sd=1.28$, range=0-4, $n=35$ nest years). This was within the normal range for interior Alaska and the Tanana River (Ritchie et al. 1998). Average productivity of experimental nests (1.96 fledglings, $sd=1.40$, range=0-4, $n=23$ nest years) was not different from that of reference nests (1.92 fledglings, $sd=1.08$, range=0-4, $n=12$ nest years; 2-tailed, 2-sample $t$-test, $P=0.9264$, $df=28$). There were also no differences in productivity among years ($F_{2,28}=1.32$, $P=0.2817$), between nests in the “many overflights” (>20 overflights per year that were ≤1000m slant distance) and “few overflights” treatments (2-tailed, 2-sample $t$-test, $P=0.9342$, $df=21$), nor between the “high noise” (average daily SELa ≥90 dB) and “low noise” treatments (2-tailed, 2-sample $t$-test, $P=0.8383$, $df=26$). Additionally, no significant treatment effects were found for nestling survival, nesting success, or hatch date (Table 3.1). Nestling survival and nesting success were, however, significantly higher in the upper stretch of the study area than in the lower stretch (Table 3.1, Fig. 3.1). When data from all three years were combined, study nests in the upper stretch also had higher mean productivity (2.35 fledglings, $sd=1.07$, $n=23$, range=0-4) than those in the lower stretch (1.17 fledglings, $sd=1.34$, $n=12$, range=0-4; 1-tailed, 2-sample $t$-test, $P=0.0079$, $df=19$; Table 3.1, Fig. 3.1).
Table 3.1. Peregrine falcon nesting success and productivity along the Tanana River between Tok and Salcha, Alaska during the 1995-1997 breeding seasons in relation to treatment group.

<table>
<thead>
<tr>
<th>Nest Treatment</th>
<th>Median Hatch Date</th>
<th>Avg. Nestling Survival</th>
<th>Avg. Nesting Success</th>
<th>Avg. Productivity</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experimental*</td>
<td>6/20 P=0.1610</td>
<td>0.75 P=0.1991</td>
<td>0.74 P=0.3800</td>
<td>1.96 P=0.9264</td>
<td>23</td>
</tr>
<tr>
<td>Reference</td>
<td>6/17</td>
<td>0.91</td>
<td>0.92 (Fisher’s)</td>
<td>1.92 P=0.9264</td>
<td>12</td>
</tr>
<tr>
<td>Upper stretch†</td>
<td>6/20 P=0.3232</td>
<td>0.95 * P=0.0389</td>
<td>0.91 * P=0.0331</td>
<td>2.35 * P=0.0158</td>
<td>23</td>
</tr>
<tr>
<td>Lower stretch</td>
<td>6/17</td>
<td>0.61</td>
<td></td>
<td>1.17</td>
<td>12</td>
</tr>
<tr>
<td>Many overflights§</td>
<td>6/21 P=0.2251</td>
<td>0.78 P=0.7171</td>
<td>0.75 P=0.6697</td>
<td>1.92 P=0.9342</td>
<td>12</td>
</tr>
<tr>
<td>Few overflights</td>
<td>6/19</td>
<td>0.83</td>
<td>0.83 (Fisher’s)</td>
<td>1.96</td>
<td>23</td>
</tr>
<tr>
<td>High noise‡</td>
<td>6/20 P=0.3764</td>
<td>0.74 P=0.1453</td>
<td>0.76 P=0.6818</td>
<td>1.90 P=0.8383</td>
<td>21</td>
</tr>
<tr>
<td>Low noise</td>
<td>6/18</td>
<td>0.92</td>
<td>0.85</td>
<td>2.00</td>
<td>13</td>
</tr>
<tr>
<td>1995</td>
<td>6/19 X²=0.0862</td>
<td>0.92</td>
<td></td>
<td>2.40</td>
<td>11</td>
</tr>
<tr>
<td>1996</td>
<td>6/19 F²=0.40</td>
<td>0.77 F=0.6727</td>
<td>0.62</td>
<td>1.54 P=0.2817</td>
<td>12</td>
</tr>
<tr>
<td>1997</td>
<td>6/20</td>
<td>0.78</td>
<td>0.83</td>
<td>2.00</td>
<td>12</td>
</tr>
<tr>
<td>Total</td>
<td>6/20</td>
<td>0.81</td>
<td>0.80</td>
<td>1.94</td>
<td>35</td>
</tr>
</tbody>
</table>

* denotes significance. P-values obtained from 2-tailed, 2-sample t-tests (Wilcoxon signed-rank test in the case of hatch date) unless otherwise noted.

- a hatch date estimated in some cases by back-dating from estimated age of young at banding
- b located within an MTR
- c proportion of hatchlings that survived to 25 days post-hatch
- d number of young fledged per nesting attempt
- e located in the upstream stretch of the Tanana River, between Tok and Sawmill Landing
- f received ≥ 20 close overflights by military jets during a breeding season
- g experienced daily average sound exposure level ≥ 90 dB during a breeding season
Fig. 3.1. Mean nestling survival, nesting success, and productivity of peregrine falcon nests in the lower stretch compared with nests in the upper stretch of the study area along the Tanana River, Alaska during 1995-1997.
Peregrine Falcon Reactions to Overflights

A total of 401 military jet overflights by F-15, F-16, A-10, or British fighter jets within 1000 m slant distance of a nest were recorded by field observers during the course of the study (see Chapt. 2). Peregrine falcons were not always in view when jet aircraft overflights occurred. Of the 401 close overflights, reactions were not observed for either adult during 210 overflights (52% of total). A total of 35% of all known responses to close overflights were listed as "no reaction." An additional 43% were categorized as attentive, meaning that the adult noticed the overflight, but did not react strongly. Alert reactions accounted for 17.5% of all known responses to close overflights, while only 2% of all reactions were classified as stand, crouch/cower, or flight intention movement. No flight reactions by adult female peregrines were observed in response to jet aircraft overflights, while 8 responses by males (5%) were flight reactions (see Chapt. 2).

Peregrine Falcon Productivity in Relation to Behavioral Reactions

There was no correlation between the number of observed flight reactions to military jet overflights and productivity ($F_{8,25}=0.96, P=0.4889$). Females were not observed to fly in response to military jet overflights, so the results of this analysis hold for both individual males and for mated pairs.

We calculated an index of reactivity (average residual for each individual from the regression of reaction intensity versus slant distance) for males and females separately (Fig. 3.2). There were significant differences among females in the index of reactivity (1-way ANOVA, $P=0.0030$). Of the 22 nest-years, 13 had negative average residuals and
Fig. 3.2. Index of reactivity (average residual of behavioral reaction intensity for each individual from the regression of reaction intensity on slant distance) to close jet overflights at each nest by female and male peregrine falcons.
9 had positive average residuals (mean=-0.0037, n=189, range= -1.25 to 1.31). The index of reactivity did not differ among individual males (1-way ANOVA, \( P=0.4061 \)).

Positive indices of reactivity indicate a greater-than-average intensity of reaction to overflights after controlling for slant distance and gender, while negative indices indicate a lower-than-average reaction intensity. For either males or females, there was no significant difference in the average index of reactivity for adults from the upper stretch compared with adults from the lower stretch of the study area (Mantel-Haenszel; females, \( P=0.6919 \); males, \( P=0.8755 \), for those within an MTR compared with those outside MTRs (females, \( P=0.7364 \); could not run analysis on males), for those in the “many overflights” treatment compared with those in the “few overflights” treatment (females, \( P=0.7278 \), males, \( P=0.3253 \)), or for those in the “high noise” treatment compared with those in the “low noise” treatment (females, \( P=0.8809 \), could not run the analysis on males).

Hatch date was not correlated with the index of reactivity for either males (\( P=0.5341 \)) or females (\( P=0.2687 \)), and neither was nesting success (males, \( P=0.4059 \); females, \( P=0.2581 \)). Nestling survival was also not correlated with the index of reactivity for males (\( P=0.2428 \)), but was marginally correlated for females (\( P=0.0820 \)). Productivity (number of young fledged per nesting attempt) was negatively correlated, however, with index of reactivity for both males (\( F_{1,18}=5.68, P=0.0284, R=-0.4898 \)) and females (\( F_{1,20}=4.36, P=0.0497, R=-0.4232 \); Fig. 3.3). Index of reactivity explained a significant proportion of the variation in productivity for both males (\( R^2=0.3270 \)) and females (\( R^2=0.2416 \)). (Failed nests were not included in the analysis; when failed nests
Fig. 3.3. Productivity (number of young fledged per nesting attempt) vs. index of reactivity to low-altitude jet overflights for individual adult peregrine falcons.
were included in the analysis, $R^2=0.2399$ for males and $R^2=0.1791$ for females.) These results indicate that individuals that responded more intensely to overflights on average experienced lower productivity.

There was a trend toward a positive correlation between the indices of reactivity for individuals that were a mated pair (1-way ANOVA, $F_{1,18}=3.77$, $P=0.0680$; Fig. 3.4). This trend suggests that pairs tended to be similar in reactivity rather than compensatory. When the reactivity indices for the two individuals in a pair were added together, there was a negative correlation between productivity and the combined reactivity for the pair ($F_{1,18}=8.66$, $P=0.0086$, $R^2=0.3249$; Fig. 3.5). The combined reactivity did not differ for nests located in the upper stretch compared with those in the lower stretch of the study area (upper: reactivity= -0.4922, $n=11$; lower: reactivity= -0.0059, $n=9$; $F_{1,18}=1.20$, $P=0.2880$). Total reactivity for a pair also did not differ significantly between treatment groups (experimental: reactivity= -0.2310, $SE=0.2300$, $n=19$; reference: reactivity= -1.07, $n=1$; $F_{1,18}=0.66$, $P=0.4255$) (high noise: reactivity= -0.1399, $SE=0.2190$, $n=18$; low noise: reactivity= -1.475, $SE=0.6571$, $n=2$; $F_{1,18}=3.72$, $P=0.0698$) (many overflights: reactivity= 0.0137, $SE=0.2745$, $n=12$; few overflights: reactivity= -0.7040, $SE=0.2745$, $n=8$; $F_{1,18}=2.73$, $P=0.1156$). Mean reactivities tended to be higher in the high noise vs. the low noise treatments ($P=0.0698$).
Fig. 3.4. Index of reactivity for female peregrine falcons to jet aircraft overflights vs. index of reactivity for their mate
Fig. 3.5. Productivity (number of young fledged per nesting attempt) vs. index of reactivity to low-altitude jet overflights for peregrine falcon pairs
DISCUSSION

Individual reactivity of breeding peregrine falcons was negatively correlated with productivity, or the number of young fledged per nesting attempt. This indicates that the more reactive an individual was towards overflights, the less young it was likely to successfully fledge. This same negative correlation existed between productivity and the combined index of reactivity for mated pairs. These results are consistent with the hypothesis that the reduction in productivity of nesting peregrine falcons due to potentially-disturbing jet aircraft overflights is a result of the intensity of behavioral reactions. We predicted a negative correlation between reactivity and productivity, assuming that reactions represent a measurable cost to current reproductive output and the more intense the reaction, the greater the cost (Awbrey and Bowles 1990). The alternative hypothesis was not supported, namely that little or no response to jet aircraft overflights reflects a low investment in the current reproductive attempt and a tendency toward reproductive failure.

The index of reactivity was calculated as the average residual for reaction intensity of each individual peregrine falcon, based on the gender-specific regression of reaction intensity on slant distance. The trend toward a positive correlation in reaction index between members of a breeding pair was only marginally significant, but suggests that individuals tended to be similar in reactivity to their mate, rather than compensatory. The index of reactivity for pairs was not greater for those in treatment groups, such as experimental nests or “many overflights” nests. The index of reactivity for pairs in the
“high noise” treatment group, however, was marginally greater than the “low noise” treatment group, suggesting that lower reactivity was not a reflection of habituation to frequent loud overflights.

Peregrine falcons nesting on the lower stretch of the study area had lower nesting success than those nesting on the upper stretch. There were more failed nests on the lower stretch, and successful nests fledged fewer young. This trend continued into 1998, after the field study had terminated and the close, intentional jet aircraft overflights had ended. During the 1998 breeding season, productivity in the upper stretch was 3.30 fledglings per nesting attempt ($sd=0.95, n=10, range=2-4$) and in the lower stretch was 1.83 fledglings per nesting attempt ($sd=1.60, n=6, range=0-4$; 1-tailed, 2-sample $t$-test, $P=0.0405, df=7$; Ritchie et al. 1998). While the lower stretch of the study area is closer to Eielson AFB, bombing ranges, the city of Fairbanks, and other human settlements, and thus was exposed to more background noise from jet aircraft and other potential sources of disturbance, there was no apparent relationship between peregrine falcon productivity and either number or intensity of overflights in this study. Also, the index of reactivity for pairs in the lower stretch did not differ from that of pairs in the upper stretch.

If disturbance is defined as a stimulus that lowers the probability of successful reproduction, then high doses of jet aircraft overflights apparently did not constitute a significant disturbance to most nesting peregrine falcons in this study. Murphy et al. (1998) found that while nesting success did not differ widely among overflight disturbance categories (low, moderate, or high) for nests along the Tanana River, it did for peregrine falcon nests at off-river sites. They reasoned that important differences
may exist in habitat quality and/or sensitivity to disturbance among sub-populations of peregrine falcons.

Response to potential disturbance apparently plays a role in limiting productivity of peregrine falcons. Because peregrine falcons differ in their reactivity to similar jet overflights, the actual dose of jet aircraft noise is apparently not as accurate a measure of disturbance as the reaction intensity elicited from breeding adults. The amount of disturbance perceived by peregrine falcons, as reflected in their reaction, is a better predictor of effects on nesting success. Additionally, jet aircraft overflights may represent only a fraction of the potential disturbances that nesting peregrine falcons are exposed to during the breeding season. The reactivity of breeding peregrine falcons to a wide variety of other disturbances may influence productivity as well.

Higher intensity reactions could interfere with parental duties, causing lower productivity among pairs that have had little previous exposure to overflights and are thus not habituated. Alternatively, factors other than disturbance may be responsible for low productivity (e.g., inexperience, young age, new mate), and these factors could also be associated with higher reaction intensity to disturbance. Parents with low probability of successfully fledging young may opt for their own survival over investment in raising young. The available data support the hypothesis that factors other than disturbance, such as age and experience, may be related to both high reaction indices and low productivity. Habituation apparently does not play a prominent role in determining reactivity, as neither reactivity nor productivity differed between experimental vs. reference nests or between nests in the “many overflights” treatment vs. the “few overflights” treatment.
CONCLUSIONS

1. Productivity (number of fledglings produced per nesting attempt) of peregrine falcons in the study area was within the normal range for Interior Alaska and the Tanana River.

2. There were no differences in productivity between experimental vs. reference nests, between nests exposed to many overflights vs. those exposed to few overflights, or between nests exposed to high levels of aircraft noise vs. those exposed to low levels.

3. Individual peregrine falcons differed in their reaction intensity to overflights, after controlling for slant distance and gender.

4. Productivity was negatively correlated with the reactivity of individual peregrine falcons and the combined reactivity of mated pairs to jet overflights.

5. Reactivity of individual peregrine falcons or mated pairs did not differ between nests located in an MTR vs. outside, nests exposed to many overflights vs. few overflights, or nests in the upper stretch vs. the lower stretch of the river. The reactivity of nesting peregrines in the “high noise” treatment was marginally higher than those in the “low noise” treatment.

6. The reaction intensity of breeding peregrine falcons to low-altitude jet overflights is a better indicator of subsequent productivity than actual dose of overflights. This is likely a reflection of lower parental investment among breeding pairs with high reactivity (i.e., younger, less experienced parents are less likely to be productive).
LITERATURE CITED


Murphy, S.M., R.J. Ritchie, M.D. Smith, and D.L. Nordmeyer. *Unpublished manuscript.* Effects of noise exposure from jet aircraft on nesting success and productivity of peregrine falcons in interior Alaska. ABR, Inc., Fairbanks, AK 99708 and Oregon Cooperative Fish and Wildlife Research Unit, USGS-BRD and Dept. of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331.


CHAPTER 4
Comparison of Behavioral Responses by Nesting Peregrine Falcons to Several Types of Potential Disturbances

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ABSTRACT

Nesting peregrine falcons (*Falco peregrinus*) are well-known for their intense reactions to both natural predators of their progeny and anthropogenic disturbances such as aircraft, boats, and gunshots. We observed behavioral reactions to potential disturbances by peregrine falcons nesting along the Tanana River, Alaska during the 1995-1997 breeding seasons. As part of a study on the effects of Air Force jet overflights on peregrine falcons, military jet aircraft were scheduled to fly over a subsample of nests under observation (experimental nests). Close overflights (≤1000 m slant distance) by military jets at experimental nests accounted for 63% of all observed inanimate potential disturbances and 57% of all types of potential disturbances, but accounted for only 3.1% of potential inanimate disturbances, and 2.6% of all types of potential disturbances at reference nests. Other potential disturbances at reference nests included civilian fixed-wing aircraft (41%), boats (33%), avian predators (17%), helicopters (5.1%), and humans and other mammals (1.3%). Peregrine falcon responses were recorded for all types of potential disturbance, including animate and inanimate disturbances, as well as non-visual sources of noise. Peregrine falcons responded most intensely and most frequently to other raptors, particularly conspecifics. Forty-two percent of responses to other raptors were flight reactions, while 25% of responses to non-raptor avian predators were flight reactions. Humans and other mammals elicited extremely intense defense reactions when near the nest, but these interactions occurred infrequently. Among potential sources of disturbance from close (≤1000 m slant distance) mechanized vehicles, peregrine falcons...
responded most intensely to boats (6% of reactions involved flight) and least intensely to helicopters (3% flight reactions) and fixed-wing aircraft (2% flight reactions). Intensity of reactions to military jets was indistinguishable from intensity of reactions to boats or other aircraft. Peregrine falcons responded differently to animate and inanimate sources of disturbance. Flight reactions were a common response to animate potential disturbances, but not to inanimate potential disturbances. Using flight reactions to measure disturbance from inanimate objects may not be the most sensitive method, as number of flight reactions was not correlated with productivity of the nesting pair.

INTRODUCTION

Peregrine falcons respond strongly to intruders near their nests and have been known to attack a wide variety of potential predators of eggs and nestlings, as well as inanimate intruders such as fixed-wing aircraft and helicopters (White and Sherrod 1973, Monneret 1974, Cade and White 1976, Olsen and Olsen 1980). Startle and flight reactions by peregrine falcons have also been observed in response to close overflights by jet aircraft and other loud, sudden noises, such as sonic booms and log truck jake brakes. (see Chapt. 2; R. Ambrose, pers. comm.; J. Pagel, pers. comm). In order to examine the role of jet aircraft overflights as a potential disturbance affecting productivity of nesting peregrine falcons, we sought to measure the reaction intensity to other potential sources of disturbance and compare those reactions to responses elicited by jet overflights.
Bowles et al. (1990) postulated that an increase in flight responses induced by jet aircraft overflights could lead to a decrease in productivity. In my study of the relationship between acute behavioral responses to jet aircraft overflights and nesting success, we did not find a negative correlation between number of flight responses and productivity (see Chapt. 3), but we only observed a total of eight flight responses as a result of jet aircraft overflights, and all were by males (see Chapt. 2). By including flight responses induced by other potential sources of disturbance, including helicopters, fixed-wing aircraft, boats, thunder, animals, and humans, we can increase the sample size in order to more accurately assess the possible relationship between flight responses and productivity. Additionally, it would be helpful to place potential disturbance caused by jet aircraft overflights in the context of overall disturbance during the breeding season, as well as compare the intensity of reaction to jet aircraft overflights with reactions to other potential sources of disturbance.

The objective of this study was to determine the types of responses induced in peregrine falcons by a variety of potential disturbances, and then to compare the intensity of those responses to reactions caused by jet aircraft overflights. We predicted that jet aircraft would elicit more intense reactions than helicopters and fixed-wing aircraft, after controlling for slant distance (Awbrey and Bowles 1990). We also predicted that close jet overflights would elicit a greater proportion of intense startle responses than would any other type of potential disturbance.
STUDY AREA

The peregrine falcons that were the subjects of this study nested along a 300-km stretch of the Tanana River between Tok and Salcha, Alaska (from 63°8'N, 143°36'W to 64°18'N, 148°45'W). Nests were identified by river km, with the source at river km 0. Field observations were conducted during the breeding seasons of 1995-1997 and were initiated as soon as safely possible after ice break-up on the river (early May). Observations continued until the young had fledged and left the area of the nest (late August/early September).

Approximately half of the peregrine falcons under observation nested in Military Training Routes (MTRs), which are air corridors where low-altitude training flights by military jet aircraft can be conducted (see Chapt. 2). Nesting pairs within MTRs were considered “experimental.” The other pairs that we observed nested in areas where military jets are subject to altitude restrictions; these were considered “reference” pairs. During the 1995 field season, we recorded observations at five experimental nests and six reference nests. All of these nests were located along the Tanana River between Tanacross (km 155) and Sawmill Landing (km 305) (hereafter the “upper stretch”). In 1996 and 1997, the study area was expanded to include another stretch of the river between Delta Junction (km 385) and Salcha (km 472) (hereafter the “lower stretch”). We observed nine experimental nests and three reference nests in both 1996 and 1997. Six of these nests were located in the upper stretch of the study area, and six were located...
in the lower stretch. A more detailed description of the study area and the nesting habitat of peregrine falcons along the Tanana River is presented in Chapt. 2.

METHODS

Field crews conducted behavioral observations of breeding peregrine falcons and their young and collected data on characteristics of potential disturbances. Two field crews were present in the field in all three years. Field crews accessed the various nests using river boats (21-foot or 24-foot Alwelds with 150-hp jet outboards). We made observations from across at least one channel of the river, between 300 and 750 m from each nest. Observation distance also depended on the sensitivity of each pair of peregrines to observer presence.

The nesting cycle was divided into four phases: 1) pre-incubation (including arrival, courtship, and egg-laying), 2) incubation, 3) nestling-rearing (including hatching), and 4) fledging (from the first observed flight by a nestling until all fledglings had left the nest area). In addition, we treated failed nests as a separate phase of the nesting cycle for purposes of data analysis. Most data were collected during the incubation, nestling-rearing, and fledging phases due to the inaccessibility of nests during ice break-up on the Tanana River, which generally occurs around the peak of laying.

We observed behavioral responses of peregrine falcons to potential disturbances with the aid of 10x binoculars, 15-45x spotting scopes, and Questar telescopes. We also recorded responses using two Canon L2 Hi-8 mm video cameras. These cameras
recorded continuously during observation periods in order to have a video record of responses to potential disturbances (see Chapt. 2).

We measured behavioral responses to potential disturbances in the same way, regardless of the type of stimulus. We recorded responses to disturbance as one of the following categories, in order of increasing intensity: unknown reaction, no reaction (0), attentive (1), alert/alarmed (2), flight intention movement (3), stand up (3), crouch/cower (4), unknown flying (5), defensive flying (6), or evasive flying (7). Detailed definitions of response categories are presented in Chapt. 2. Response categories 0 and 1 were classified as “minimal.” Response categories 3 and 4 were classified as “intense” whereas response categories 5, 6, and 7 were classified as “flight”.

Overflights of nests in the MTRs were coordinated with existing missions of the 11th Air Force from Eielson and Elmendorf Air Force Bases (see Chapt. 2). Air Force personnel (Forward Air Controllers, or FACs) were present in the field during much of the 1996 and 1997 field seasons to direct military jet overflights and help with data collection. Type III Standard and Compact Animal Noise Monitors (ANMs) were deployed near the nests for the duration of the breeding season and were used for monitoring noise levels during jet overflights. A more detailed description of the ANMs is given in Chapt. 2.

For overflights by jets, helicopters, or fixed-wing aircraft, we recorded the type of aircraft, altitude above nest (usually estimated, sometimes obtained directly from pilots), and estimated lateral distance from nest. Slant distances were calculated for each overflight by combining altitude with lateral distance. Close jet overflights, defined as
≤1000 m slant distance from a nest, were used to examine the effects of jet overflight parameters on behavior of peregrine falcons (see Chapt. 2). Accordingly, reactions of breeding peregrine falcons to other close (≤1000 m slant distance) potential disturbances (helicopters, fixed-wing aircraft, boats, and animal intruders) were compared with reactions to close overflights by jet aircraft. For all other disturbances (thunder, gunshots, highway noise, sonic booms), slant distance was not an appropriate measure of intensity, and the ANMs did not record these types of noise events. Comparison with other types of potential disturbance is problematic due to a lack of quantifiable data to use as criteria for intensity (i.e., closeness, loudness). Therefore, we provide descriptions of the intensity of reaction to these noises without including them in statistical analyses of reaction intensity.

STATISTICAL ANALYSIS

Graphical displays were used for preliminary examination of the data. We used the NCSS97 statistical package to perform statistical analyses, including descriptives for means, standard deviations, ranges, and frequencies; regression analyses; one-way ANOVAs; and Duncan’s multiple comparison tests (Hintze 1997). We used multiple regression to explore the relationship between type of disturbance (jets, helicopters, fixed-wing aircraft, boats, birds, mammals, and people) and intensity of falcon reaction. We assumed that potential disturbances that did not elicit more than minimal responses were not likely to be disturbances (i.e., were not likely to have a detrimental effect on productivity).
We chose slant distance as the primary selection criterion for inclusion of overflights in the reaction analysis because slant distance explained a significant proportion of the variation in peregrine falcon response to jet aircraft overflights (see Chapt. 2). Also, we lacked noise measurements for most noise events that were not due to military jet overflights. A total of 878 verified above-threshold ANM measurements were recorded during the three years of the study, but only four noise events (0.5%) were the result of boats, helicopters, or fixed-wing aircraft.

RESULTS

Inanimate Potential Disturbances

A total of 676 close (≤1000 m slant distance) aircraft overflights and other inanimate potential disturbances occurred when breeding peregrine falcons were in sight of observers during the course of the three-year study. These consisted of military jet aircraft (393 events, 58% of close inanimate potential disturbances), helicopters (34 events, 5%), large military fixed-wing aircraft (6 events, 1%), small civilian fixed-wing aircraft (142 events, 21%), and motor boats (100 events, 15%; Fig. 4.1).

Animate Potential Disturbances

Only 83 (11%) of all potential disturbances during observation periods were not noise-producing, but were instead due to natural nest predators (Fig. 4.1). The most frequently observed potential disturbance from nest predators was other birds (87%, 72
Experimental Nests
(n=24)

Mammalian
1%
Avian
9%
Boats
11%
Fixed-wing
17%
Helicopters
4%
Jets
58%

Reference Nests
(n=11)

Mammalian
1%
Avian
17%
Boats
33%
Helicopters
5%
Fixed-wing
41%
Jets
3%

Fig. 4.1. Proportion of each type of close (≤1000 m slant distance) potential disturbance observed for nesting peregrine falcons during the 1995-1997 breeding seasons along the Tanana River, Alaska.
instances). Birds accounted for 10% of total potential disturbance events. The relative frequency of potential disturbances by each bird species observed is given in Figure 4.2. Other peregrine falcons and bald eagles were the most frequent species of avian intruder observed near active peregrine falcon nests. Mammalian predators accounted for only 4% (3 instances) of the total animate potential disturbances occurring during observation sessions. Potentially disturbing human intrusions, exclusive of researcher activities, occurred only twice at 2 different nests.

Non-visual Potential Noise Disturbances

Non-visual potential noise disturbances, such as thunder, gunshots, highway noise, and sonic booms, were not recorded by the ANMs. This was problematic because there was no quantifiable data that could be used as a criterion for inclusion in the data set for analysis (i.e., closeness, loudness). Observers did, however, record the times of each potentially disturbing noise, as well as the reaction of any visible peregrine falcons to that noise. We recorded 52 instances of non-visual noises when peregrine falcons were in sight (compared to 83 animate and 676 inanimate potential disturbances). Only minimal responses (no reaction or attentive) were elicited by thunder, road noises, or sonic booms (all were quite distant). One episode of gunshots (at least 1 km away) elicited a flight reaction by a female, and another instance elicited an alert response.
Fig. 4.2. Proportion of each species of avian nest predator \( n=72 \) observed within 1000 m of peregrine falcon nests during the 1995-1997 breeding seasons along the Tanana River, Alaska. Species included: AMKE (American kestrel, *Falco sparverius*), BAEA (Bald eagle, *Haliaeetus leucocephalus*), SSHA (Sharp-shinned hawk, *Accipiter striatus*), RLHA (Rough-legged hawk, *Buteo lagopus*), PEFA (Peregrine falcon, *Falco peregrinus*), OSPR (Osprey, *Pandion haliaetus*), RTHA (Red-tailed hawk, *Buteo jamaicensis*), GOEA (Golden eagle, *Aquila chrysaetos*), NOHA (Northern harrier, *Circus cyaneus*), HEGU (Herring gull, *Larus argentatus*), CORA (Common raven, *Corvus corax*), and other (1 each Goshawk (*Accipiter gentilis*), Gyrfalcon (*Falco rusticolus*), and unidentified).
Peregrine Falcon Reactions to Inanimate Potential Disturbances

A total of 40% of all known responses by peregrine falcons to potential inanimate disturbances were listed as "no reaction." An additional 51% were categorized as attentive, suggesting that the nesting peregrines were aware of the noise, but not disturbed. Alert reactions accounted for 5% of all known responses to potential inanimate disturbances; 98% of these alert reactions were induced by military jet overflights. Less than 1% of all known reactions to potential inanimate disturbances were classified as intense (stand, crouch/cower, flight intention movement); all intense reactions to inanimate potential disturbances were induced by military jet overflights. Only 3% of responses were classified as flight reactions; 35% of these were due to military jet overflights.

Peregrine falcons reacted differently to different types of inanimate disturbance, even after accounting for slant distance (1-way ANOVA; female, $F_{3,428}=5.75$, $P=0.0007$; male, $F_{3,334}=5.31$, $P=0.0014$). Only minimal responses (no reaction or attentive) were elicited by large fixed-wing aircraft. All but one alert response were due to military jet aircraft overflights. Flight reactions were induced by boats (41%, 9 reactions), military jets (36%, 8), fixed-wing aircraft (18%, 4), and helicopters (5%, 1) (Fig. 4.3).

Mean reaction intensity of females was significantly higher for motor boats than for either helicopters or fixed-wing aircraft. The mean reaction intensity of female peregrine falcons towards military jets did not differ from that towards boats or other types of aircraft (Duncan’s Multiple-Comparison Test, $P<0.05$). Male peregrine falcons,
Fig. 4.3. Proportion of total flight reactions observed for nesting female (n=29) and male (n=44) peregrine falcons in response to each type of close (≤1000 m slant distance) potential disturbance during the 1995-1997 breeding seasons along the Tanana River, Alaska.
on the other hand, reacted with similar intensities to all types of inanimate potential disturbance (Duncan’s Multiple-Comparison Test, P>0.05).

Peregrine Falcon Reactions to Animate Potential Disturbances

A total of 27% of all known responses to animate potential disturbances (natural predators) were recorded as "no reaction." An additional 31% were categorized as attentive, suggesting that the peregrines were aware of the presence of the intruder, but were not disturbed. Alert reactions accounted for 3% of all known responses to animate intruders, while 1% of all known reactions to animate intruders were classified as intense (stand, crouch/cower, flight intention movement). A total of 37.5% (50) of known reactions to animate intruders were classified as flight reactions (Fig 4.2), a much higher incidence of flight reactions than any other category of potential disturbance.

Peregrine falcons reacted differently to the proximity of different types of potential predators. Peregrines responded most intensely to other raptors within 500 m of the nest (Fig 4.3). A total of 42% of all reactions to other raptors were flight reactions. Peregrines responded nearly as intensely to humans on the cliffs (31% of reactions were flight), followed by potential avian nest predators other than raptors (25% flight reactions).

We witnessed only 3 encounters with mammals near the nest (mink (*Mustela vison*), black bear (*Ursus americanus*), and red fox (*Vulpes vulpes*)); these all involved only the female and ranged from no reaction to defensive flight. One of these instances, which we recorded on video tape, involved a mink that came into the nest after a young
nestling while it was being brooded by the female. The female reacted violently, flying off the nest scrape and knocking the mink off the nest cliff at the same time. We also observed a black bear with two cubs and a fox near nest cliffs. The female reacted violently to the bear and cubs, flying off the nest scrape, vocalizing, diving, and pulling out chunks of fur until the intruders left the area. The red fox was on an outcropping above the nest ledge and apparently went undetected.

Comparison of Peregrine Falcon Reactions Among Types of Potential Disturbance

Individual peregrine falcons reacted differently to different types of close (≤1000 m slant distance from the nest) potential disturbance (1-way ANOVA, females: $F_{5,489}=19.65$, $P<0.00001$; males: $F_{4,390}=30.13$, $P<0.00001$, respectively; Fig 4.4). Reaction intensity of both male and female peregrine falcons was significantly higher towards potential avian predators than towards inanimate potential disturbances (Duncan’s Multiple-Comparison Test, $P<0.05$). Males reacted with similar intensities to all animate potential disturbances (Duncan’s Multiple-Comparison Test, $P>0.05$). Unlike males, however, females exhibited significantly lower mean reaction intensities against non-raptor avian species in comparison to other raptors and mammalian predators (Duncan’s Multiple-Comparison, $P<0.05$).

Relationship Between Flight Responses and Productivity

The proportion of flight responses to all known responses to close potential disturbances (by males, by females, or pairs combined) was not related to any of our
Fig. 4.4. Mean reaction intensity of peregrine falcons, separately by sex, to each type of close (slant distance ≤ 1000 m from the nest) potential disturbance (military jets, civilian fixed-wing aircraft, helicopters, boats, avian intruders, and mammals).
measures associated with overall productivity (hatch date, nestling survival, productivity) (Table 4.1).

DISCUSSION

Several previous studies on behavioral reactions of raptors to disturbance have shown that raptors are more sensitive to humans on foot and other raptors near their nests than they are to potential disturbances by machinery (White and Sherrod 1973, Johnson 1988, Grubb et al. 1992). The results of this study agree with these previous studies. Perhaps peregrine falcons do not always perceive boats, aircraft, and other machines as potential predators. Additionally, visual cues may influence raptors more than noise stimuli (Delaney et al. 1997, Trimper et al. 1998). Peregrine falcons have extremely acute eyesight and are highly dependent on visual cues for prey detection and capture (Monneret 1978).

Ward and Stehn (1989) determined that geese were more sensitive to helicopter overflights than to overflights by fixed-wing aircraft; Grubb and Bowerman (1997) observed similar results for bald eagles. White and Sherrod (1973), on the other hand, noticed that raptor attacks were more frequent on fixed-wing aircraft than on helicopters. Slow-moving potential disturbances (like helicopters) could be more harmful, or at least cause more intense behavioral reactions, than higher velocity ones. Owens (1977) found that slow, noisy aircraft, especially helicopters, caused more intense behavioral reactions in geese than did high velocity, low noise ones. Slower airspeed may enhance the visual
Table 4.1. Peregrine falcon nesting success and productivity in relation to flight reactions (proportion of all reactions observed) by males, females, or pairs combined to all types of close potential disturbance.

<table>
<thead>
<tr>
<th></th>
<th>Hatch Date</th>
<th>Nestling Survival</th>
<th>Overall Productivity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Male Flight Reactions</strong></td>
<td>$F_{1,30}=0.9050$, $P=0.3490$</td>
<td>$F_{1,27}=0.8409$, $P=0.3673$</td>
<td>$F_{1,32}=1.67$, $P=0.2054$</td>
</tr>
<tr>
<td><strong>Female Flight Reactions</strong></td>
<td>$F_{1,29}=0.9953$, $P=0.3267$</td>
<td>$F_{1,26}=0.7384$, $P=0.3980$</td>
<td>$F_{1,32}=0.0963$, $P=0.7584$</td>
</tr>
<tr>
<td><strong>Total Flight Reactions per Nesting Pair</strong></td>
<td>$F_{1,30}=1.33$, $P=0.2577$</td>
<td>$F_{1,27}=1.42$, $P=0.2443$</td>
<td>$F_{1,32}=0.9409$, $P=0.3393$</td>
</tr>
</tbody>
</table>
stimulus associated with an overflight and thus elicit a more intense behavioral reaction (Trimper et al. 1998).

Among mechanized disturbances, we found that boats induced a higher mean intensity of reaction in females than did fixed-wing aircraft or helicopters. Ritchie (1997) found similar results with peregrine falcons nesting along the Trans-Alaska Pipeline System. Stalmaster and Kaiser (1997) obtained similar results when studying the effects of military activity on bald eagles. Olsen and Olsen (1980) found that high-speed boats elicited little reaction from peregrine falcons, while fishermen caused more intense reactions because fishermen tended to move through the nest area slowly and were often directly beneath nests. The close boats observed in our study area were always located in the river channel directly under the nests, and the peregrine falcons along the Tanana River may also associate boats with people who come to the nest to band young. Stalmaster and Kaiser (1997) also found that bald eagles responded more to boats, and less intensely to noise stimuli that were unaccompanied by visual stimuli.

We found a definite gender difference in reaction intensity among different types of potential disturbances. Males reacted more intensely than did females, in general, but also did not appear to distinguish types of disturbance beyond the broad categories of animate and inanimate. Females, on the other hand, seemed to reserve their most intense reactions for raptors and mammalian predators as opposed to gulls and ravens, and for boats as opposed to aircraft. Because gulls and ravens are opportunistic nest predators (i.e., are a threat only when the nest is not being attended) and aircraft are not associated with visits to the nest, perhaps the benefit from helping the male defend the nest from
these types of threats does not outweigh the cost of leaving the nest and exposing eggs or young. Females may assist their mate in defending the nest only when they perceive an imminent threat of attack on the nest.

CONCLUSIONS

1. Adult peregrine falcons responded differently to animate and inanimate potential disturbances.

2. Reaction intensity for both males and females was higher in response to natural nest predators than it was to inanimate potential disturbances (including military jets). Peregrines exhibited a higher proportion of flight reactions in response to avian intruders than to any other type of potential disturbance.

3. Among inanimate potential disturbances, peregrine falcons exhibited the highest mean reaction intensities in response to motor boats, and the lowest mean reaction intensities to helicopters and fixed-wing aircraft. Reaction intensities to military jets did not differ from that to either boats or other aircraft.

4. Unseen noises (excepting gunshots) elicited only minimal responses. Responses to loud sonic booms were not observed in this study.

5. Flight reactions were rare in response to inanimate potential disturbances, and this type of reaction may be a poor gauge of disturbance by inanimate objects.

6. The proportion of all reactions to potential disturbance that were flight reactions was not correlated with productivity of the nesting pair.
LITERATURE CITED


CHAPTER 5: Synopsis

Low-altitude military jet overflights did not appear to adversely affect the productivity of peregrine falcons nesting along the Tanana River, Alaska. Dose of military jet disturbance (i.e., number of overflights, noise level) was not correlated with productivity during the course of this three-year study. Additionally, peregrine falcons were rarely observed exhibiting intense behavioral responses (including flight responses) to military jet overflights, even at slant distances <500 m.

Individual peregrine falcons did, however, react differently to similar jet overflights, and this difference in reactivity was associated with differing productivity. Those peregrine falcons (either individuals or mated pairs) that were most reactive (i.e., exhibited more intense reactions than average to similar overflights) were also the least productive. This means that the effect of military jet overflights on productivity of peregrine falcons can not be predicted based solely on military jet activity, but must take into account individual differences in sensitivity to overflights.

Behavioral response to disturbance differed more among types of disturbance than among disturbances of a single type. Although behavioral response to jet overflights was more closely related to productivity than was dose of jet overflight disturbance, we do not know whether this same relationship holds for potential disturbances that elicit a more intense response (i.e., other raptors, mammalian predators).

Gender differences in behavioral reactions to disturbance were obvious throughout the study. Males tended to react more than females to jet overflights,
regardless of extrinsic factors. Females did not react as strongly or as often as males, and there was more variation among individual females in reaction intensity than among males. Males reacted intensely to potential disturbances of all types, whereas females tended to react more toward particular types of disturbance. Females reacted most intensely toward raptors and mammalian predators that pose a significant potential threat of nest predation (as opposed to gulls and ravens) and toward boats (as opposed to aircraft). Males also responded intensely to overflights at all measurable SELa levels (>85 dB), while females reacted more intensely to the loudest overflights. These differences are probably related to the pronounced sexual dimorphism in peregrine falcons and differences in the roles of the two sexes during reproduction (Monneret 1974).

The greater average reaction intensity of males may be related to their greater role in nest defense throughout most of the breeding season. Perhaps females react most intensely when their mate needs assistance (or when the male is not present) because the cost of flight reactions can be high in terms of exposing eggs or young. The cost of flight reactions by males is comparatively low and so they may react more intensely to a wider range of disturbance types or intensities. Because gulls and ravens are opportunistic nest predators (i.e., are a threat only when the nest is not being attended) and aircraft are not associated with visits to the nest, perhaps the benefit from helping the male defend the nest from these types of threats does not outweigh the cost of leaving the nest. The mean reaction intensity of females was significantly greater both when their mates were out of
sight of the observers and when a threat of imminent attack on the nest could have been perceived.

The significant, negative correlation between the reactivity of nesting peregrine falcons and their subsequent productivity is a major finding of this study. Two possible explanations exist: 1) those falcons that have little or no previous exposure to jet overflights may react more intensely and as a consequence have lowered productivity (the “habituation hypothesis”), or 2) younger, less experienced parents that normally have lower productivity may tend toward higher reactivity (the “parental investment hypothesis”). In the latter case, older breeding peregrines would do better than younger breeders, whether or not they had been exposed to jet aircraft overflights in the past. A companion study (Murphy et al. 1998) found that dose of jet disturbance was negatively correlated with productivity of peregrines nesting off of major river drainages, a relationship that we did not find in our study of peregrines nesting along the Tanana River. Off-river areas are presumably sub-optimal breeding habitat, likely to be occupied by younger, less experienced breeding pairs.

Habituation was not adequately addressed in this study because we did not have a sufficiently large sample of banded adults with known nesting histories. Future studies should focus on banded populations of peregrines in order to more adequately address differences in response related to previous exposure to disturbance. Future studies should also attempt to produce higher doses of aircraft disturbance so that the relationship between dose of disturbance and nesting success/productivity can be more thoroughly explored. Ground-to-air communication (i.e., participation of Forward Air Controllers) is
critical for meeting this objective. Noise monitoring of overflights should be an integral part of future studies of the effects of aircraft disturbance, but we recommend that noise monitors be set at a lower threshold (<85 dB) in order to have a more complete record of noise exposure at each nest site.

Peregrine falcons are an appropriate study species for investigation of behavioral reactions to disturbance because they exhibit strong reactions to a variety of disturbances. The results from this study, however, apply only to this population of peregrine falcons. As we have demonstrated, results can vary among subpopulations of peregrine falcons (i.e., upper stretch vs. lower stretch, Tanana River vs. off-river). Generalizing our results to other raptor species is inadvisable.

Jet aircraft overflights did not constitute a disturbance (i.e., did not ultimately have a measurable effect on the survival or productivity) for nesting peregrine falcons along the Tanana River, except when pairs of falcons exhibited a higher-than-average reactivity to jet overflights. We found no evidence of 1) abandonment of nest sites, 2) decreased hatchability, 3) damage to eggs/chicks due to startle responses of parents, or 4) premature fledging as a result of jet aircraft overflights. The Awbrey and Bowles (1990) model predicting the effects of jet aircraft overflights on nesting raptors should be modified to reflect the results of this study. The model is correct in using raptor behavioral response, rather than magnitude of disturbance, to predict the effects of disturbance on productivity. Frequency of flight responses, however, was not the best indicator of effects of disturbance on productivity. Reactivity of individual peregrine
falcons to military jet overflights was the best indicator of the reduction in productivity
from jet overflight disturbance.
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