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An Ecological study of peregrine falcons (*Falco peregrinus*) at Lake Mead National Recreation Area, 2006-2010

Joseph Graham Barnes
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AN ECOLOGICAL STUDY OF PEREGRINE FALCONS (*FALCO PEREGRINUS*)
AT LAKE MEAD NATIONAL RECREATION AREA, 2006-2010

by

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Bachelor of Science
Baldwin-Wallace College, Berea, Ohio
1997

A thesis submitted in partial fulfillment of
the requirements for the

Master of Science in Biological Sciences
School of Life Sciences
College of Science

Graduate College
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THE GRADUATE COLLEGE

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Joseph Graham Barnes

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May 2011

ABSTRACT

An Ecological Study of Peregrine Falcons (*Falco peregrinus*) at Lake Mead National Recreation Area, 2006-2010

by

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Peregrine Falcons (*Falco peregrinus*) represent an encouraging conservation biology success story in North America during the twentieth century. Their distribution and population size suffered major restrictions after the initiation of widespread application of the synthetic pesticide dichloro-diphenyl-trichloroethane (DDT) within the U.S. in the 1940s. The species was federally listed as endangered in the U.S. in 1969 and was then delisted in 1999 after DDT was banned in 1972. Herein, I present my ecological research of peregrines within Lake Mead National Recreation Area (LMNRA), concentrating on the years 2006-2010. This thesis is comprised of two chapters. In the first chapter, I describe the development, testing, and utilization of a novel call-broadcast survey protocol to quickly establish territorial occupancy of peregrines. The first chapter represents an article being prepared for publication in early 2011, co-authored with Jef R. Jaeger, and Daniel B. Thompson, therefore I use plural pronouns throughout this chapter to keep it consistent with the future publication work. In Chapter 2, I present results of my ecological studies of peregrines, focusing on known breeding population size, reproductive efforts, spatial distribution, foraging ecology, and competition. In the

second chapter, I also report on aquatic bird abundance data I collected during a separate inventory and monitoring project conducted within LMNRA from 2004-2009. The aquatic bird data indicates seasonal shifts of potential prey in relation to observed and collected peregrine diet composition. The ecological results presented in Chapter 2 are consistent with a healthy, still-increasing, breeding population of peregrines. The seemingly recent expansion of breeding peregrines in areas far from water, with their depressed level of reproductive success, indicate a likely habitat quality gradient that may act to limit future population growth in the region. Most compelling, are the abundant availability of aquatic birds, and the high dietary composition of those birds at peregrine territories in close proximity to permanent water. Additionally, I document an increased number of intraspecific agonistic interactions over time, which indicates density-dependent factors may begin regulating peregrine numbers in highly suitable breeding habitat.

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CHAPTER 1

A CALL-BROADCAST APPROACH FOR RAPIDLY ASSESSING
PEREGRINE FALCON TERRITORIAL OCCUPANCY

Introduction

Peregrine Falcons (*Falco peregrinus*) represent a success story for conservation biology (Ratcliffe 1993, White et al. 2002). This formerly endangered species was delisted in 1999 following increases in nesting success and population numbers in a wide variety of habitats across North America (USFWS 2003). Yet as numbers of this species continue to rise, monitoring population trends remains important because these top predators can be used as bio-indicators of regional ecosystem health. In Nevada, peregrines were considered extirpated as a breeding species from the 1950s through 1984 (Walton et al. 1988, Floyd et al. 2007). The first breeding pair in the state in well over two decades was documented in 1985 along the shoreline of Lake Mead within the Lake Mead National Recreation Area (LMNRA), near the border with Arizona. Monitoring of peregrines within the recreation area since 1985 has tracked a rapid increase in the number of occupied territories, reaching a maximum of 33 in 2010.

Over the years, monitoring of peregrines within LMNRA has varied with respect to objectives, intensity, and methodology. In 2006 we implemented on an annual basis the standard post-delisting protocol for monitoring peregrines as recommended by the U.S. Fish and Wildlife Service. This protocol calls for a minimum of three passive surveys, each up to 4 hr per site, to determine occupancy and document reproductive success (USFWS 2003). However, with the growing number of territories at LMNRA, the passive protocol became impractical given the time required to monitor a high percentage

of the known territories (an objective of resource managers at that time). Consequently, we developed and tested a call-broadcast survey protocol to efficiently monitor the increasing number of territories within the recreation area.

The use of call-broadcast methodology has been shown to increase the likelihood of detection and decrease the amount of time required to detect many bird species (Johnson et al. 1981, Anderson 2007). Specifically, broadcasting a conspecific or interspecific call can act to enhance detectability of the target species by triggering a vocal or behavioral response (e.g., territory advertisement or defense, mate acquisition, food procurement). The approach has been found especially effective when dealing with nocturnal species, species existing in low densities, and those that are otherwise secretive or difficult to detect (Johnson et al. 1981, Conway and Gibbs 2005). In particular, call-broadcasting has been useful as a survey tool for both diurnal (Kimmel and Yahner 1990, Mosher et al. 1990, McLeod and Anderson 1998) and nocturnal (Haug and Didiuk 1993, Flesch and Steidl 2006, Crowe and Longshore 2010) raptors, but has little documented use with diurnal raptors occupying non-forested habitats (Salvati et al. 2000).

Even in light of the documented usefulness of call-broadcasting, any survey method must account for imperfect detection of the target species or risk underestimating site occupancy and producing biased population estimates and trends (Rosenstock et al. 2002, MacKenzie et al. 2003, Johnson 2008). As such, a reliable survey and monitoring program requires a standardized sampling protocol with high detection probability, low detection variation, and low observer variability (Thompson 2002, Conway and Simon 2003). There are several factors that can affect the probability of detection, among which are: (1) the response rate, type, intensity, and duration; (2) the observer's ability to detect

a response; (3) weather conditions; (4) surrounding vegetation and topography; and (5) the potential of habituating birds over time (Richards 1981, Proudfoot et al. 2002, Rosenstock et al. 2002, Conway and Gibbs 2005, Barnes and Belthoff 2008). In addition, the responsiveness of birds to call-broadcasting can be related to the different stages of the breeding season (Cerasoli and Penteriani 1992, Haug and Didiuk 1993, Kennedy and Stahlecker 1993, Conway et al. 2004, Rehm and Baldassarre 2007), and when conducted at different times of day (McLeod and Anderson 1998, Rehm and Baldassarre 2007; but see Kimmel and Yahner 1990, DesRochers et al. 2008). There are also potential drawbacks to using call-broadcast surveys. From a methodological perspective, the approach may complicate discovery of territories or nests by drawing birds toward the surveyor and away from the breeding area (Conway and Gibbs 2005). More seriously, undue disturbance of breeding birds may result in increased predation risk, while prolonged exposure of eggs or young to the elements may negatively impact reproductive efforts.

In developing a fast and effective call-broadcast survey protocol for detecting Peregrine Falcons, we determined their response to conspecific call-broadcast surveys at territories known to be occupied, and measured the change in response rate and intensity of response over the course of the breeding season. To test the effectiveness of detecting territorial peregrines, we also conducted ‘blind’ surveys when the presence of resident peregrines had not been confirmed at the time of the survey, but at territories which we knew to be occupied. Additionally, we evaluated the usefulness of call-broadcasting for identifying nesting ledges early in the breeding season, and assessed potential impacts to reproduction, particularly during the incubation and brooding stages.

Methods

Study Area

We studied Peregrine Falcons in LMNRA (36°0.6'N, 114°47.8'W), within the eastern Mojave Desert. The recreation area consists of approximately 4025 km² of desert lands surrounding lakes Mead and Mohave, two large manmade reservoirs along the Colorado River. The landscape consists of open basins and sloping desert bajadas punctuated by numerous desert mountains with broken cliffs and canyons, with elevations ranging from 192 m to 1719 m. The area receives scant precipitation in the form of winter rains, with intermittent summer storms often contributing to annual totals. Vegetation within the region primarily consists of Mojave Desert scrub dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*), with brittlebush (*Encelia farinosa*) along slopes and canyons. Narrow intermittent strips of riparian vegetation line the shores of both lakes, consisting typically of salt cedar (*Tamarix* spp.), coyote willow (*Salix exigua*), and arrow weed (*Pluchea sericea*).

Call-broadcast Protocol

The call-broadcast surveys were initially planned for early morning (½ hr before sunrise to 4 hr after sunrise) and late afternoon (4 hr before sunset to sunset) when peregrines were thought to be the most active and in correspondence with the timing of the standard monitoring protocol (USFWS 2003). Our early results, however, showed this to be less of a constraint early in the breeding season and when temperatures were < 35° C, so when possible, surveys were also conducted throughout daylight hours to maximize efficiency. Our standard protocol consisted of a 3 min passive observation period, followed by a 30 sec broadcast period, a 1 min observation period, a second 30

sec broadcast period, and a final 5 min observation period. We used vocalizations from a commercially available recording (Stokes Field Guide to Bird Songs: Western Region; Time Warner Trade Publishing, New York, NY) which we converted to mp3 format and downloaded directly to a digital game caller (FoxPro XR6; FoxPro Inc., Lewiston, PA). The conspecific calls consisted of 5 sec of the ‘cack’ alarm call, immediately followed by 10 sec of the ‘eechup’ call from an adult female peregrine (White et al. 2002). We looped the cycle once for 30 sec of continuous calling, while rotating 360° in order to evenly project the sound around the broadcast point. The calls were broadcasted at a volume of 84-90 dB, as measured 1 m from the audio source by a sound-level meter set on slow response and C-weighting (Fuller and Mosher 1987). We did not conduct surveys during precipitation or when sustained wind speeds were ≥ 16 km/hr. In order to minimize disturbance, we ceased broadcasting immediately upon detecting a peregrine response (peregrine taking flight or vocalizing).

We conducted call-broadcast surveys at known occupied territories, considering them occupied if at least one territorial peregrine held the area during the breeding season (Steenhof and Newton 2007). During the first round of surveys (courtship), we based the broadcast points on eyrie locations from the previous year, whereas following surveys were based on eyrie locations as detected. The nature of the terrain surrounding nesting cliffs often dictated the distance of each broadcast point to an eyrie, but we determined a range of 200 to 600 m as a reliable distance from which responding peregrines could be detected. All distances were measured using a laser rangefinder with an accuracy of ± 0.3 m (TruPulse 200 B, Laser Technology Inc., Centennial, CO).

We considered a peregrine response to be any vocalization or flight-initiation observed from initial broadcasting through the standard survey period (Balding and Dibble 1984, McLeod and Anderson 1998), unless evidence led us to believe otherwise (e.g., an adult silently delivering prey to the eyrie mid-way through the survey session). At first detection, we estimated the distance of each peregrine to the broadcast point, and recorded each type of response (flight, vocal, flight and vocal). Whenever possible, we documented the sex and maturity (i.e., nestling, fledgling, subadult, adult) of the peregrines observed. During the survey session, we detailed peregrine behavior and interactions, as well as the presence and behavior of all other raptors, Turkey Vultures (*Cathartes aura*), Common Ravens (*Corvus corax*), and other species that may have interacted with the peregrines.

We recorded latency of response, which we defined as the time to response after the start of the first broadcast period, and duration of each response, recognizing that it was sometimes difficult to determine the exact time a response ended. We declared a response to have ended only after the responding birds remained silent or inactive for at least 2 min. We subjectively assessed the relative intensity (low, moderate, or high) of a response, based on the volume and frequency of vocalization, intensity of flight and display, and overall demeanor and level of aggression of the bird. Although subjective, these evaluations were all made by the same observer in order to standardize interpretations. The target of each bird's response was also estimated; that is, whether the bird aimed its actions toward the broadcast point, toward or from the eyrie ledge (e.g., departing from and returning to the eyrie, landing on or vocalizing from the eyrie, or concentrating the display within 30 m to either side of the eyrie), or toward some other

area. To address concerns over adverse effects to breeding success, we monitored closely the reaction of any incubating or brooding adults and recorded their time out of the eyrie.

Survey Periods

We conducted breeding season surveys from 18 February to 24 June in 2008 and from 25 February to 29 July in 2009, with additional surveys during the fledgling stage from 30 June to 2 July in 2010. We also conducted a single round of post-breeding season surveys from 23 September through 22 October in 2009. We began surveys during courtship in mid- to late-February, based on evidence we derived from monitoring breeding activity in previous years. During our monitoring efforts, we calculated a mean variation of 42 days between the first and last pairs to lay eggs. The earliest pairs typically began laying eggs by 13 March, eggs began hatching by late-April, and young began fledging by the end of May. When possible, we determined the breeding stage of each territory by using observed behavioral cues (e.g., aerial courtship displays, an adult in incubating posture, adults feeding young). We aged nestlings using binoculars and a spotting scope (usually from a distance of 150-450 m), while referencing a photographic aging guide (Cade et al. 1996). Published averages for each breeding stage (i.e., incubation = 31 days, nestling = 42 days) were then used to back-date reproductive timing. For the purposes of this study, we did not classify territories as ‘fledged’ until we confirmed the young had departed the eyrie and were still in the nesting area.

Our sample sizes during the various breeding stages varied over time, as we added new territories as discovered and dropped others from rotation after confirmation of breeding failure (McClaren et al. 2003). At times, inclement weather limited our ability to visit each territory during each stage, and we sometimes missed a breeding stage target

window at a territory because of uncertainties associated with estimating the timing of breeding using behavioral cues.

Response Surveys

As a test of peregrines' response to broadcasting, we conducted call-broadcast surveys at territories where we had confirmed the presence of at least one adult or subadult prior to broadcasting. For these response surveys, we modified our standard protocol by adjusting the length of the first passive monitoring period as needed to detect peregrine presence (range = 1-259 min) without creating a detectable disturbance to the birds. Our focus was on courtship through nesting periods during 2008. We focused on these stages because surveys later in the breeding season are of limited value when determining site occupancy or reproductive effort (Mayfield 1961, Steenhoff and Kochert 1982). As previously observed with peregrines, the frequency of nest defense, and therefore territorial vocalizations, is typically highest during courtship decreasing significantly as reproduction progresses (White et al. 2002). For comparison, we also conducted limited trials during the fledgling stage in 2008 and in the post-breeding period in 2009 (Fig. 1.1).

Detection Surveys

As a test of the use of call-broadcast surveys for detecting peregrines, we conducted standard 10-min blind surveys at occupied territories when the presence of resident peregrines was not known to the observer at the time of the survey. Detection surveys were conducted throughout the 2009 breeding season and during a post-breeding period, with additional surveys during the fledgling stage in 2010 (Fig. 1.2). We conducted

repeat visits at many territories within breeding stages to evaluate potential improvements in detection and to assess the potential for habituation to broadcasting (Table 1.1).

Statistical Analyses

We evaluated the success of the broadcast surveys to determine response rates and detection rates relative to breeding stage. Latency to response, response duration, response type, and response intensity by breeding stage were analyzed, while evaluating the effects of time of day and distance from eyrie on detection rates. We conducted bootstrap analyses and chi-square/Fisher exact tests in R 2.8.1 (R Core Development Team 2008), and the generalized linear models and survival analyses in SAS 9.1 (SAS Institute 2002-2008).

Response Rates – Peregrine response rates were calculated as the number of observed responses per number of response surveys during each stage. Our assessment of response rate was somewhat hampered by limited sample sizes (Fig. 1.1), which were insufficient to support a generalized linear model approach. Instead, we estimated 95% confidence intervals based on quantiles for each year, and year-stage combination, using 1000 bootstrap samples (Efron and Tibshirani 1998).

Detection Rates – Detection rates were calculated as the number of detected responses per number of detection surveys during each stage. We compared the detection rates between breeding stages for the first survey at each territory per breeding stage using a generalized linear model with binomial error (Sokal and Rohlf 1995). The model also included a random site effect to account for repeated measurements. We conducted Tukey post-hoc tests to assess significance ($\alpha = 0.05$), and report the least squares means.

The effect of breeding stage on detection rates in repeat visits was assessed using a Fisher's exact test by forming three categories (i.e., no response in either visit, response in at least one visit, or response in both visits) within each breeding stage and site (Table 1.1). To increase sample size, fledgling data from 2009 and 2010 were combined. We also looked at number of days after previous visit with a logistic regression analysis with random site effect. In order to look specifically for habituation to the broadcast surveys, we then limited our analysis to only those territories that had surveys repeated within a breeding stage ($N = 59$). We used a logistic regression test with detection as the dependent variable, the number of days after the previous visit (within territory and stage) as the independent variable, and a random site effect.

Latency and Duration of Response – We analyzed latency and duration of response during the first visits of all detection surveys in separate linear models of the detection surveys, which had breeding stage as the only fixed effect and a random repeated measures effect of site to avoid pseudoreplication. Latency was modeled as a Poisson variable, and a \log_{10} transformation of duration of response results was approximately normal and homoscedastic. Tukey post-hoc tests were performed to assess significance of stage effects ($\alpha = 0.05$). To further characterize latency (time to response), we ran a survival analysis with Kaplan-Meier estimates (SAS PROC LIFETEST) to obtain nonparametric estimates of the proportion of territories responding after broadcasting and the confidence envelope over time from 0-300 sec.

Other Response Variables – Our study design did not control for isolating peregrine detection rates by time of day or for distance from eyrie; however, we analyzed the results from first visits to look for effects of these two variables. In courtship, we also

looked at the number of days prior to laying eggs to model whether detection rates were affected by a potential drop in response as females approached egg-laying. Because the data were unbalanced within site (not all breeding stages were represented at each site) and sample sizes were not large within stages, we conducted separate logistic regression analyses (with random site effects) across all stages and by year to model the effects of time of day, distance from eyrie, and days prior to laying. We analyzed the type of response from peregrines (i.e., flight, vocal, or both) by stage and tested variation within breeding stages using a Fisher's exact test. We analyzed differences in response intensity during breeding stages by year (2009 and 2010) with a chi-square contingency test corrected with a Fisher's exact test for small sample sizes.

We analyzed the effect of gender and stage on likelihood of responding in a generalized linear model with binomial error. The dependence of male response on female response by stage was also examined in a similar model with main effects of male (response/no response), female (response/no response), and stage, along with two-way interactions. In both models, we used the Akaike Information Criterion for small sample size (AICC) to determine the minimum adequate model. Significant results were interpreted by comparing observed values to those expected under the hypothesis of independence.

Results

During our entire study period, we conducted a total of 217 call-broadcast surveys at peregrine territories in LMNRA. In 2008, we conducted 49 call-broadcast response surveys at 23 territories from the courtship through early fledgling period. Each of these

surveys was preceded by a passive observation period to determine that birds were present before broadcasting the call. All subsequent surveys were conducted under blind conditions without advance knowledge whether peregrines were present in the nesting area. In 2009, we conducted 131 call-broadcast surveys at 29 occupied territories throughout the breeding season. Fifty four of these surveys were repeat visits conducted within breeding stages. Additionally, we surveyed 24 territories (one visit per site) during the post-breeding period in 2009, and 13 surveys at eight territories during the fledgling stage in 2010.

Response and Detection

Across all stages of the breeding season, peregrines responded to our call-broadcasts during 83% of response surveys in 2008 ($N = 49$). Response rates showed a general decreasing trend from 100% during the courtship stage, to 73-80% later in the breeding season, and then down to 50% in during the post-breeding period (Fig. 1.1). Low sample sizes inhibited us from formally determining significant differences between breeding stages; however, differences from zero, and among groups, was inferred through non-overlapping bootstrapped confidence intervals.

Across all stages of the breeding season, we detected peregrine responses during 78% of the blind detection surveys used to test the methodology ($N = 77$). The detection rate was high during courtship (79%), peaked during incubation (90%), and then dropped during the later stages of the breeding season (Fig. 1.2). As a further indication of the lower tendency of peregrines to respond later in the breeding season, we detected responses in only three of eight (38%) initial surveys during the 2010 fledgling stage. While peregrines continued to respond to call-broadcast during the post-breeding season,

we detected responses at a significantly lower rate (42%) than during all other stages except fledgling ($F_{5,73} = 3.13$, $P = 0.013$; Fig. 1.2). During the courtship stage, the number of days prior to laying (surveys conducted from six to 56 d prior to laying) did not significantly affect response detection ($F_{1,52} = 0.18$; $P = 0.675$).

When surveys were repeated within breeding stages, we obtained lower detection rates in second visits than during first visits for courtship through nestling stages, but this pattern was reversed during the fledgling stage (Table 1.1). The overall detection rate of the second visit surveys was 56% ($N = 59$). Conducting second visit surveys, however, marginally increased the odds of detecting peregrines (during at least one of the two visits) in all breeding stages except fledgling ($P = 0.482$). We found that the number of days after the previous visit had a significant effect on detection of responses overall ($F_{1,53} = 6.60$; $P = 0.013$); however, there was no relationship between detection and the number of days since the previous visit within each breeding stage ($F_{1,34} = 0.54$; $P = 0.468$). The overall mean number of days between site visits within the same breeding stage was 7.8 d (Table 1.1).

Time of Day and Distance from Eyrie

Our ability to detect responses of peregrines was not significantly influenced by time of day ($F_{1,77} = 0.03$; $P = 0.863$) or distance from the eyrie ($F_{1,77} = 0.67$; $P = 0.417$). During the breeding season, we conducted surveys during daylight hours from 05:26 to 19:48. Morning surveys (sunrise to 10:00) accounted for 60.6% of all surveys, while we conducted 29.5% of all surveys in mid-day (10:01-15:00), and 9.8% in the evening hours (15:01 to sunset). While most surveys were conducted from between 200-600 m from the eyrie (82% of surveys), the maximum distance from an eyrie we detected a response

was approximately 1.6 km, which occurred during the courtship stage before we had determined the eyrie location for that year. While constrained by terrain features, the overall mean distance from our broadcast points to an eyrie was 382 m, and the average distance of the first responding peregrine to the broadcast point was 351 m (range = 70-1100 m).

Latency and Duration of Response

We found that latency to response did not vary by breeding stage ($F_{5,27} = 2.05$, $P = 0.103$). Approximately 89% of responses were noted within 3 min of the call-broadcast, and 100% of responses within 5 min (Fig. 1.3). Mean latencies by stage ranged from 65 ± 16 sec ($N = 21$) in courtship, peaked during the nestling stage at 146 ± 36 sec ($N = 9$), before dropping later in the breeding season. We calculated a significant change in duration of response across stages ($F_{5,27} = 4.2$, $P = 0.006$; Fig. 1.4), with fledgling responses being shorter than all stages except nestling. In general, response durations became shorter with each successive breeding stage, before lengthening in the post-breeding period. We recorded an overall mean duration of response throughout our entire study period of about 3.5 min ($N = 133$, range = 0.08-19 min).

Response Type and Intensity

The type of response did not differ among breeding stages ($X^2 = 7.51$, $df = 8$, $P = 0.482$); although the proportion of responses involving both flight and vocal elements dropped by a third from courtship to fledgling (Table 1.2). Our measure of response intensity was significantly greater early in the breeding season in comparison to the nestling and fledgling stages, showing a significant effect by stage (chi-square contingency test corrected with a Fisher's exact test for small sample sizes; $X^2 = 7.51$, df

= 8, $P = 0.001$; Table 1.2). Overall, the intensity of responses were higher than expected from random early in the breeding season, later shifting to lower than expected by the nestling and fledgling stages.

Response by Gender and Breeding Stage

Adult males were generally involved in less responses overall (44.9%) than adult females (69.3%; Table 1.3), but this difference was not significant ($F_{1,3} = 0.81$, $P = 0.433$). We also did not observe a significant effect of stage ($F_{3,3} = 5.29$, $P = 0.102$), although power to detect differences may have been hampered by small sample size in the latter stages. Males responded alone infrequently (12 of 127 total responses), but male response was positively related to the female response (45 mutual responses; $F_{1,12} = 8.15$, $P = 0.015$). Overall gender response rates were similar, and in cases when at least one individual was confirmed present, males responded 32 of 53 times (60.4%), while females responded in 45 of 68 surveys (66.2%). Individual gender response rates dropped from courtship to nestling stages; males from 70.8% to 23.1%, and females from 85.2% to 42.1%. We recorded a rebound in the fledgling stage but the sample size for both sexes was rather low ($N = 4$).

We noted peregrines seldom or never responded in certain situations involving young. Adults generally did not respond to the broadcast during the nestling stage when provisioning young just prior to, or during, the first broadcast period ($N = 7$ surveys, with only one response). The one active response in these cases was a 10 sec vocalization, 7 min after the broadcast by an adult feeding two 25-30 day old nestlings. We documented only a single response from nestlings during 53 nestling surveys and, on three occasions, nestlings which had been vocalizing became quiet immediately after the broadcast was

initiated. During the fledgling stage, young responded during five of 26 surveys (19%); however, during two of these surveys vocalizing fledglings quickly became quiet at the onset of call-broadcast. During six surveys, fledglings that had been detected passively prior to broadcasting, did not respond to the call-broadcast.

During the incubation and early nestling stages, we confirmed on 27 occasions (23 female, four male) the presence of an adult peregrine in the eyrie and in low incubating or brooding posture prior to call-broadcast. The incubating adult responded 19 times (70.4% response rate), and in 17 of these responses the adult ceased incubating or brooding and departed the eyrie. In two instances, neither adult returned to tend to the young during the remaining survey period (> 15 min and 17 min), but during each of the other 15 responses an adult returned after an average of 2.1 min (range = 1-4 min). In many cases during incubation, the adult did not begin vocalizing until shortly after departing the eyrie and perching 20-50 m away. After vocalizing 1-3 min they tended to become quiet briefly before returning directly to the eyrie. We found this predictable behavior to be greatly instrumental when attempting to confirm the location of actual eyrie ledges.

We found that peregrines focused 72% of their responses toward the eyrie during the first three breeding stages (courtship 30 of 46, incubation 30 of 35, nestling 19 of 28 responses, respectively). Only rarely ($< 4\%$ of responses) did these birds focus a response toward the call-broadcast point. We conducted 26 surveys at sites in which the peregrines went on to use alternate eyrie ledges from the previous year, and detected responses during 19 of these surveys. Four of the response displays were directed in

front of the previous year's eyrie, five in front of the ledge later used as a nesting site, and eight were split between the previous eyrie site and the new site.

Discussion

Peregrine Falcons tend to forage across large home ranges and nest at relatively low densities within rugged and sometimes inaccessible terrain. These characteristics can present problems when considering a survey method for these birds, ideally having a high detection rate and low variation in detection probability. In our efforts to monitor an increasing number of peregrines in LMNRA, we found that territorial birds responded readily and consistently to a call-broadcast survey approach. Response and detection rates were particularly high during courtship and incubation and remained high through the nestling stage. While our efforts were focused on earlier breeding stages, we found that peregrines remained responsive during the fledgling and post-breeding stages, although at lower rates. We found the high responsiveness and detection rates early in the breeding season favorable for studying territory occupancy and reproductive effort because it allowed us to pick up breeding attempts early and minimized the risk of missing breeding attempts that failed early (Mayfield 1961, Steenhoff and Kochert 1982).

The use of call-broadcast allowed us to greatly reduce the time spent at each territory documenting the presence of peregrines when compared with the standard passive monitoring protocol currently in use (USFWS 2003). Our 10-min call-broadcast protocol compared favorably with the 4-hr passive methodology in terms of detection rates and did not appear to have an impact on breeding success. We recognize that the passive surveys were designed to collect eyrie location and reproductive success data, in addition

to occupancy, whereas our call-broadcast surveys were primarily intended to obtain presence data (Conway and Gibbs 2005, Anderson 2007). Nevertheless, we found that by eliciting responses from resident peregrines, our method was useful for detecting breeding pairs, as both members of resident pairs often responded together. Also of high value, was the observation that resident peregrines often focused responses in front of the eyrie ledge which greatly simplified pinpointing eyries.

Prior to initiating our call-broadcast trials in 2008, we took into account a concern that females may be extra sensitive to disturbance during the laying and incubation stages (Fuller and Mosher 1981, Kennedy and Stahlecker 1993, McClaren et al 2003). We assessed early results to determine whether to continue testing during these sensitive periods. While incubating peregrines (mostly females) had a relatively high response rate (70.4%), in all cases in which the adult responded, the bird simply stood up and walked away from the eyrie scrape without noticeably disturbing eggs or brooding young. Those birds that did not respond simply remained in incubating posture. The short amount of time in which eggs or young were left untended led us to believe that breeding attempts were not adversely affected. In addition, we also did not observe a drop in apparent breeding success (success/breeding attempt) in either of the two test years versus those from earlier years (unpublished data).

We found that conducting repeat detection surveys within each breeding stage only marginally increased detectability (5-6% increase over the first visit). The fledgling period was the exception with a doubling of detection rate (33% to 67%) in territories with repeat visits; however, we revisited very few fledged territories ($N = 6$). In all stages other than fledgling, we recorded a drop in detection rates ranging from 15% to 22%

during second visits (Table 1.1), but we were not able to detect a relationship between detection and number of days after the previous visit within stages. One possibility is that peregrines may habituate somewhat to broadcasts; however, detection rates generally increased again during subsequent breeding stages except between nestling and fledgling stages. This apparent paradox may be explained in that the average time between the first and second visits within the same stage was 7 days, while the average time between the second visit of the previous stage and the first visit of the following stage was 32 days. Peregrines may lose any habituation effects during the longer interval of time between different stage visits.

Although we did not observe detection differences by the number of days before egg-laying, it is possible peregrines become less responsive as females approach this critical time. Peregrines may also become less responsive as eggs approach hatching and as nestlings become more capable of defending themselves in the eyrie. These biological and physiological changes may in part explain the drop in detection rates during the second round of visits of the courtship through nestling stages, but we cannot rule out habituation as a factor. Even so, detection rates increased during the first visit of the following stage so it is possible some level of balance is found between habituation, differing parental care strategies, and variable hormone levels.

Many studies implementing a call-broadcast method report lower response rates at greater distances from the nest site (e.g., Kimmel and Yahner 1990, Kennedy and Stahlecker 1993, Roberson et al. 2005) and from individual birds (Proudfoot et al. 2002, Conway et al. 2004, Crowe and Longshore 2010). We, however, did not detect a significant difference in response and detection rates across the range of distances from

which we conducted our call-broadcast surveys. Albeit, our study design was not developed to control for distance to eyrie, and access was limited in many cases by difficult terrain. While we detected responses from as much as 1.6 km from an eyrie and 1.1 km from an individual peregrine, it was difficult at distances of greater than 600 m from an eyrie to be certain of detecting a response.

Several environmental conditions can impact peregrines' response to broadcasting as well as researchers' ability to detect responses. We attempted to minimize effects of wind by not conducting broadcast surveys with sustained winds ≥ 16 km/hr. However, even lower wind speeds increased background noise when surveys were conducted near water which hampered the ability of the observer to make aural detections. Much of the potential breeding habitat for peregrines within LMNRA (i.e., open canyons and cliff faces, large amounts of standing water, and sparse desert-scrub vegetation) is ideal for conducting call-broadcast surveys, although it is always important to consider local conditions when implementing call-broadcast surveys. Attenuation of sound, which reduces the intensity of sound with increasing distance from the source, is minimized in environments with low humidity, scarce foliage, scant topsoil, and stretches of open water (Marten and Marler 1977, Richards 1981). These favorable conditions minimize sound absorption and scattering, and aid in sound transmission over great distances (from the broadcast point and from responding birds), while the open canyons and lack of significant vegetative structure facilitate long-distance visual detection of birds.

We found the duration, type, and intensity of responses all affected peregrine detectability. Likely because of small sample sizes, we did not find latency to vary significantly during the breeding season, although in the nestling stage latency was more

than double that of the other breeding stages. However, the mean duration of response during the fledgling stage was less than 10% of that during courtship. Also, as response and detection rates remained relatively high during the later stages of the breeding season, response intensity shifted to lower levels during nestling and fledgling stages. Furthermore, the number of responses combining flight and vocal attributes dropped by nearly a third as the season progressed. Taken together, these diminished and less-intense responses acted to compound the lower response and detection rates later in the breeding season and reduced the overall effectiveness of call-broadcasting at this time.

Detection probability is also potentially affected by gender and age (Joy et al. 1994, Anderson 2007), with gender a particularly significant factor in species like peregrines which divide hunting and incubation tasks during the breeding season (Rosenfield et al. 1988). In our study, male peregrines were involved in far fewer responses than females (45% vs. 69.3%) and were much less likely to respond when only one adult was involved (9% vs. 34%). This was mostly a result of males being away from the nesting area more frequently. When both members of the pair were confirmed present, males responded at a similar rate as did females (60.4% vs. 66.2%), excluding courtship (70.8% vs. 85.2%). Our broadcasted call consisted of a female 'eechup' and likely a female 'cack' vocalization, although the gender of the latter was not specified. Possibly, the sex-biased broadcasts may have elicited higher responses from females and lower responses from males. Both genders responded with the lowest frequency during the nestling stage, possibly to avoid drawing attention to their young (Roberson et al. 2005).

In some species, young may be easier to detect than adults when they are begging for food (Anderson 2007, McClaren et al. 2003), but in others young apparently do not

respond to taped calls (Salvati et al. 2000). Peregrine young in our study were not very responsive to call-broadcasting. It is possible young may respond more readily to calls associated with prey delivery ('wail' or 'beg'), as opposed to our broadcasted calls which are usually given in an agonistic context of territorial defense (Wrege and Cade 1977).

Our surveys during the post-breeding season, well after fledglings apparently disperse from their natal territory, indicate at least a portion of adults within LMNRA continue with territorial defense well outside the breeding period. Although they tended to respond at a lower rate than during the breeding season, we detected peregrines at a moderate rate later in the year. It appears that call-broadcast surveys in the non-breeding season have the potential to give an idea of site occupancy at territories of non-migratory peregrines.

Rapid Site-assessment

In order to identify previously undocumented peregrine territories we developed a habitat suitability model using a maximum entropy approach in the program Maxent v. 3.2.19 (Phillips et al. 2006). Our intent was to high-grade areas for potential breeding based on previously identified territories. The model was based on the slope, solar insolation (watt hours/m², from 08:00 to 16:00 on 7 June), and distance to river or lake of all previously known eyrie locations ($N = 28$). We visualized the model using Geographic Information System (GIS) software (ArcGIS v. 9.3, Environmental Systems Research Institute, Redlands, CA 2008) and targeted our standard 10-min call-broadcast surveys in areas with highly predicted habitat for breeding.

We conducted these rapid assessment surveys at 111 locations from 25 February through 13 April (courtship through incubation) with some follow up visits in late May,

2009. Of these survey points, 101 (91%) were located within 700 m (a reasonable range for the call-broadcast approach) of highly suitable habitat predicted from the final model. We detected peregrines at 12 of the 111 survey points, resulting in the confirmation of 10 previously undocumented territories. The average distance from the broadcast point to nearest detected peregrine was 429 m ($N = 10$, range = 113-860 m), and the average distance to the eyrie was 613 m ($N = 7$, range = 156-1446 m).

There is a possibility that non-breeding floaters may respond to call-broadcast surveys in addition to breeding birds (Yahner and Ross 1995), although Mosher et al. (1990) believed the technique was selective for territorial adults with the six species of raptor they studied. We never detected a response from birds that did not seem to be holding a territory. At two of the newly confirmed territories we initially detected an unmated second-year peregrine and neither responded to the initial call-broadcast visit, nor follow-up call-broadcast events. We heard both birds at different times vocalizing and aerially displaying on their territories, but neither responded when we broadcasted. One of the young birds remained on its territory throughout the winter months and bred with an adult the following year. Although more research is needed, it appears that non-breeding peregrines do not tend to respond to broadcast surveys.

Several studies have shown that observer experience can influence detection probability to various degrees (Rosenstock et al. 2002, Conway et al. 2004, Booms et al. 2010). We minimized problems with variability in observer skill by ensuring the same primary observer led each survey throughout our study period. This approach likely acted to control fluctuations in detection rates driven by different observers, but probably enhanced detection probability as a result of high familiarity with territories and resident

pairs. Any observer advantage we encountered was likely reduced in our rapid assessment exploratory surveys. Even so, our primary observer was very familiar with conducting nest searches and monitoring peregrines in the area, so we may have obtained elevated detection rates in relation to trained but naïve observers.

We recommend further testing of call-broadcast methodology with peregrines be conducted in addition to our first assessment. Due to increased sound attenuation, it's likely that the effective range of this method may be cut down substantially in areas with dense vegetation or canopied forest surrounding nesting areas (Marten and Marler 1977, Richards 1981). McClaren et al. (2003) speculated that lower goshawk detection rates in the dense forests of the Pacific Northwest, in relation to the arid open forests of the southwest U.S.A (Kennedy and Stahlecker 1993), may be attributed at least partially to increased degradation of sound from high tree density. Areas in which snow persists well into the breeding season may exhibit different distances of accurate sound transmission, as may coastal areas with high levels of background noise due to crashing surf. Additionally, visual detection of flight responses will likely be hindered in forested areas in comparison to the wide open desert lands we encountered in our study area. Before implementing any wildlife surveys, it is advisable to account for the method's detection probability and variability under local conditions in order not to bias results.

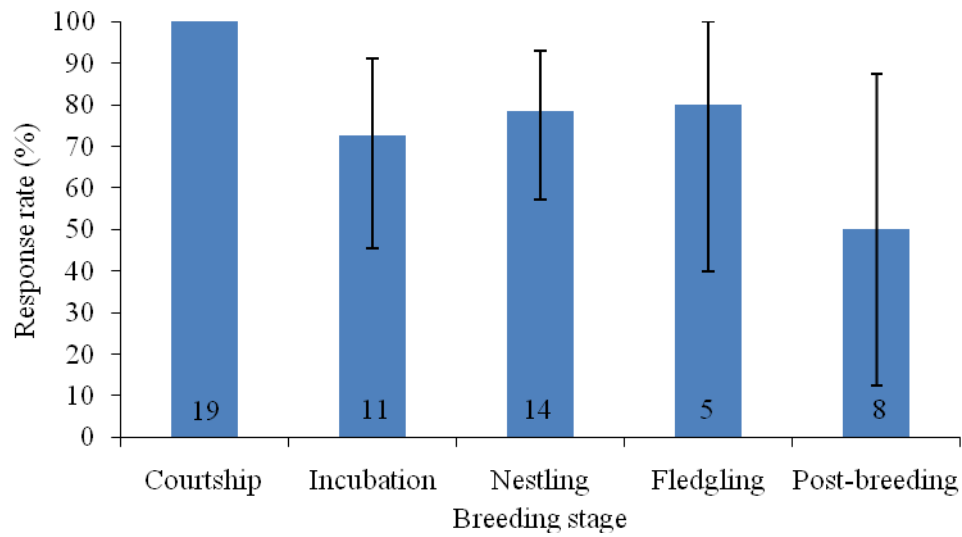


Figure 1.1. Response rates of resident Peregrine Falcons to call-broadcast surveys in Lake Mead National Recreation Area during the 2008 breeding season and post-breeding in 2009. Error bars represent bootstrapped 95% confidence intervals. Numbers at the base of each bar represent sample size.

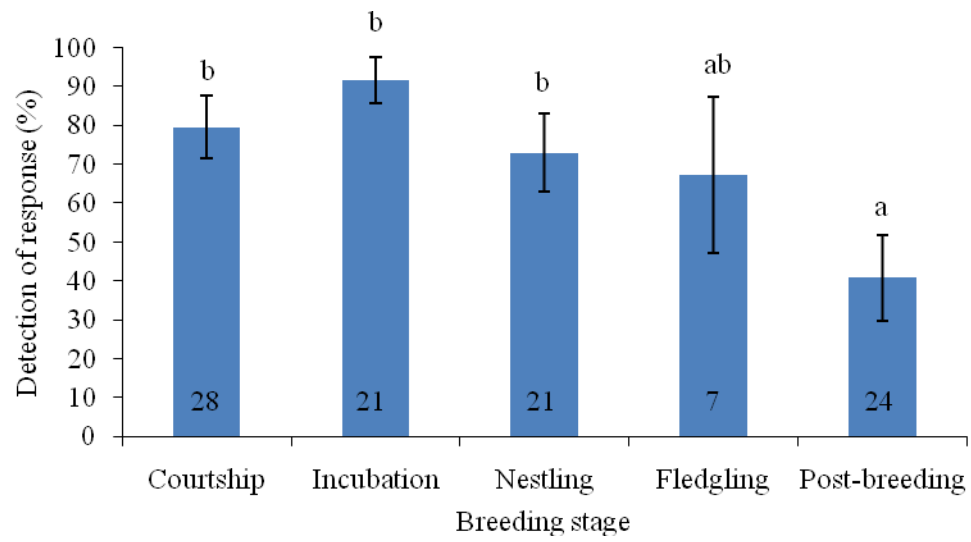


Figure 1.2. Detection rates of Peregrine Falcons to call-broadcast surveys in Lake Mead National Recreation Area during the 2009 breeding and post-breeding seasons. Results reported are the back-transformed least squares means and 95% confidence intervals for the first survey at each territory in each stage. Letters above each bar indicate means that are significantly different from other letters (Tukey test, $P < 0.05$), and numbers at the base of each bar represent sample size.

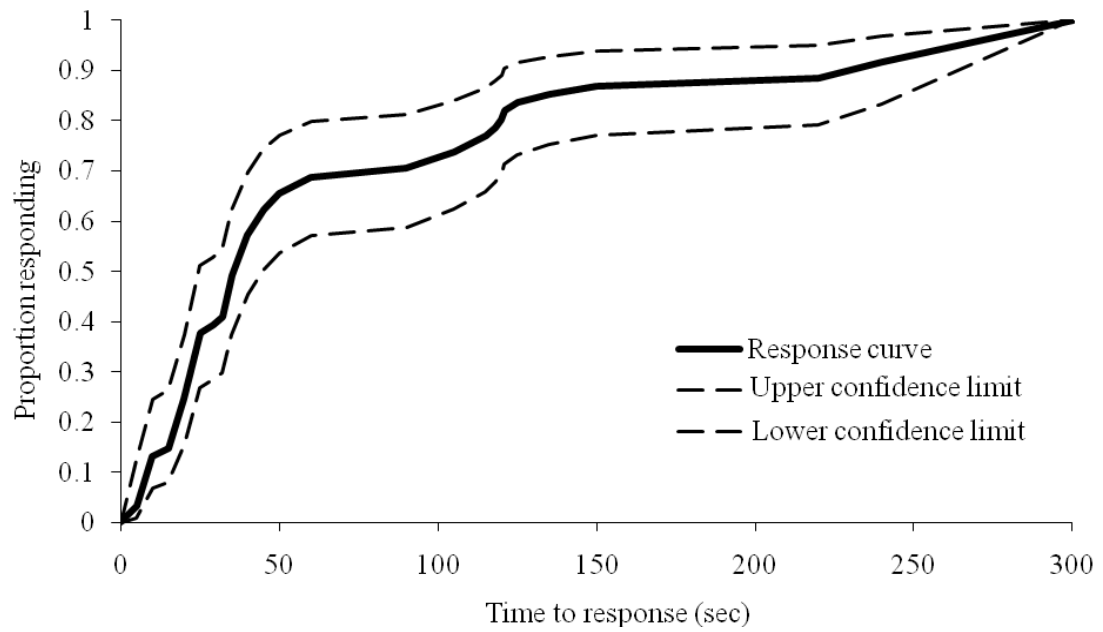


Figure 1.3. Kaplan-Meier estimates of the time to response after the start of the first broadcast in Lake Mead National Recreation Area in 2009. Results are from detection surveys pooled across all stages. The dashed lines represent a 95% confidence envelope.

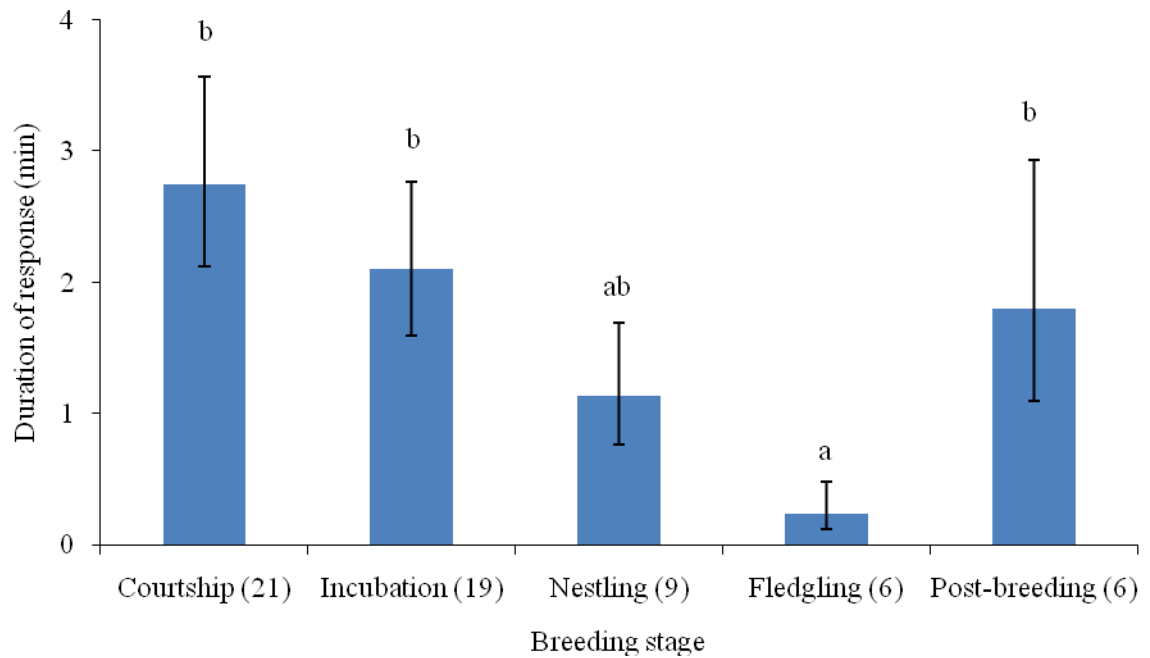


Figure 1.4. Duration of all peregrine responses during first visit surveys in 2009 and first visit surveys during the fledgling stage in 2010 within Lake Mead National Recreation Area. The back-transformed least squares means and standard error are reported. Letters above each bar indicate means that are significantly different from other letters ($P < 0.05$). Numbers in parentheses after each stage name indicate sample size ($N = 3$ per year for Fledgling).

Table 1.1. Detection rate of Peregrine Falcons to call-broadcast surveys in Lake Mead National Recreation Area, for those territories with repeat visits in each breeding stage. The fledgling stage includes surveys conducted in 2009 and 2010.

Breeding stage	<i>N</i>	Mean time between visits (d)	1 st visit	2 nd visit	≥ 1 detection	2 detections
Courtship	20	6.8	0.80	0.65	0.85	0.60
Incubation	15	5.5	0.87	0.60	0.93	0.53
Nestling	18	12.4	0.72	0.50	0.78	0.44
Fledgling	6	3.2	0.33	0.50	0.67	0.17

N = number of responses

Table 1.2. Intensity and type of response exhibited by Peregrine Falcons during call-broadcast surveys by breeding stage within Lake Mead National Recreation Area. Numbers reported for response intensity are the observed and expected (in parentheses) number of responses. Numbers in bold indicate results with higher values than expected.

Breeding Stage	Response Type (%)				Response Intensity			
	<i>N</i>	Flight	Vocal	Both	<i>N</i>	Low	Medium	High
Courtship	52	23.1	13.5	63.5	33	8 (14)	16 (14)	8 (3)
Incubation	35	14.3	17.1	68.6	27	10 (12)	15 (12)	1 (3)
Nestling	28	28.6	28.6	42.9	17	11 (8)	6 (8)	0 (2)
Fledgling	12	33.3	25.0	41.7	8	8 (3)	0 (3)	0 (1)
Post-breeding	6	33.3	16.7	50.0	6	3 (3)	3 (3)	0 (0)

N = number of responses

Table 1.3. Composition of Peregrine Falcon responses by gender to call-broadcast surveys within Lake Mead National Recreation Area. Responses include all flight and vocal detections.

Breeding Stage	<i>N</i>	Involvement in Response				
		Male Only	Female Only	Pair	Unk Adult Only	Young
Courtship	52	4	16	23	9	0
Incubation	35	3	13	15	4	0
Nestling	28	2	12	6	8	1
Fledgling	12	3	2	1	2	5
Total	127	12	43	45	23	6
% Composition		9.4	33.9	35.4	18.1	4.7

N = number of responses

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CHAPTER 2
THE ECOLOGY OF PEREGRINE FALCONS WITHIN
LAKE MEAD NATIONAL RECREATION AREA

Introduction

The causes of population limitation are fundamental to ecological studies of living organisms, with birds being no exception (Lack 1966, Brown 1969, Newton 1998). To understand population dynamics, requires evaluating both intrinsic (demographic) as well as external (environmental) factors (Newton 1998). Intrinsic factors (e.g., reproductive success, mortality, immigration, emigration) mediate external factors (e.g., food-supply, interspecific interactions, disease) to determine local population trends, the latter ‘causing’ population changes in a proximate role while the former assumes an ultimate role. For example, food scarcity (the ultimate cause) reduces breeding success (the proximate cause) and drives population decline, or relegates a population segment to a ‘sink’ at a metapopulation scale (Pulliam 1988, Newton 1998).

With many species of birds, territory sizes are smaller and population densities are higher when food is abundant near nests (Schoener 1968, Newton 1976, Peery 2000). The theory of density-dependent habitat selection assumes that an individual should choose to occupy that habitat in which its evolutionary fitness is maximized (Morris 1989). Morris (1989) postulated that under Ideal Despotic Distribution (see Fretwell and Lucas 1970) habitat selection is constrained by the activities of territorial individuals. For territorial species, population density in a habitat reflects the additional effect of dominance behavior in addition to intrinsic differences between habitats. Myers et al. (1979) found territory size was as large as possible given food limitation, but the size of

the defended area was limited by increased competition in areas with higher density of food. For example, core defended territories of Golden Eagles (*Aquila chrysaetos*) were generally smaller in areas with the highest breeding density (McGrady et al. 2002). Similarly, other raptors tend to maximize territory size when competitor pressure is low (Temeles 1987, Schmutz 1989).

As with most predatory birds, the basic resource requirements of breeding Peregrine Falcons (*Falco peregrinus*) are suitable nesting sites and availability of prey (Ratcliffe 1993). When considering an area with relatively continuously suitable nesting habitat, the observation of regularity of spacing of nests is consistent with the theory that density is limited by territorial behavior (Newton 1979). Territoriality serves as a process limiting density and local population size, where resident birds secure and defend ideal nesting habitat with an adequate prey-base (Newton 1998). While peregrines vigorously defend and exclude conspecifics from focal areas around nesting cliffs (territory), they often overlap with neighboring pairs to varying degrees in utilizing foraging areas (home range). In addition to defending the nest site itself, peregrines defend a surrounding area, the size of which depends on what is feasible given suitable habitat and food availability in addition to pressure from intruders (Cade 1960, Ratcliffe 1993). While peregrines defend their territories from conspecific individuals, they also appear to exclude other species with similar foraging ecology and nesting requirements (potential competitors), as well as those that may prey upon their young.

Peregrines are primarily cliff-nesting raptors that prey mainly on other avian species. This species is highly territorial, and shows a high degree of mate and site fidelity between years (Ratcliffe 1993, White et al. 2002). Often the use of specific nesting cliffs

can span generations, as individuals and pairs replace each other, with nearly continuous occupancy of a nesting area over decades or centuries (Newton 1979, Ratcliffe 1993).

Although peregrines can employ several hunting techniques depending on the prey type and surrounding terrain, they tend to be most successful hunting from above and using speed and surprise to their advantage. For this reason, and to protect eggs and nestlings from terrestrial predators, peregrines tend to breed in areas with high topographical relief preferably adjacent to open areas that may enhance foraging by presumably limiting escape options for their prey.

Peregrines are not restricted to cliff-nesting and in the absence of terrestrial predators have been known to nest freely on the ground or on gradual slopes (Newton 1979, Ratcliffe 1993, White et al. 2002). Nesting on cliffs to avoid predators, thus limits spatial distribution, and a lack of cliff sites may limit density and population size in areas where prey is abundant. In addition to predator avoidance, nesting on cliff faces, and in cracks and overhung ledges, has the added benefit of shading nesting birds and young. This could be a critical factor for nesting success within areas like that in the Lower Colorado River Valley where daytime air temperatures are extremely high by late spring before young have fledged.

Peregrines are versatile, opportunistic predators that have been shown to select prey in relation to prey-species density (Porter and White 1973, Hunt 1988, Ratcliffe 1993, Stevens et al. 2009). A reliance on a wide range of avian prey species is believed to lead to stability in peregrine breeding populations (Newton 1979, Ratcliffe 1993). Indeed, because peregrines prey on so many species of birds, it is not likely that variations in

individual species abundance would have a great impact on peregrine breeding and population size (Hickey 1942, Newton 1979, Hunt 1988, Ratcliffe 1993).

Reservoirs created by river impoundments have been shown to greatly impact avian species composition and enhance aquatic bird abundance and diversity (Pandey 1993, Stevens et al. 1997). Along the Colorado River, the creation of large reservoirs (e.g., lakes Mead, Mohave, and Powell) has created conditions that allow for increased numbers of migrating and wintering aquatic birds and has enhanced the region's value as a migratory route for both terrestrial and aquatic birds (Rosenberg 1991, Stevens et al. 1997, Spence 1998). Regionally, these reservoirs have increased the abundance and diversity of potential prey species for peregrines, as well as concentrating prey in some areas along shorelines directly below large cliff faces. At least 94 species of shorebirds, waterfowl, and other open water birds use lakes Mead and Mohave seasonally and are often found in large numbers (Barnes 2006). This situation has likely been a major force behind the successful colonization and subsequent population increases of peregrines within this region (see below; Grebence and White 1989).

Peregrines at Lake Mead National Recreation Area

Peregrines have a worldwide distribution that is larger than any other species of bird. In North America, peregrines historically occurred from subarctic boreal forests of Canada and Alaska south through the high volcanic mountains of south-central Mexico (Cade 1982, Ratcliffe 1993). By the 1950s, peregrines had begun a serious decline within industrialized countries primarily in Europe and North America. Populations had dropped by over 90 percent in portions of northern Europe by 1963 and in North America were eliminated as a breeding species east of the Mississippi River by 1964, with 80-90

percent declines in western states by the mid-1970s. Sparking this decline was heavy exposure to the persistent pesticide dichloro-diphenyl-trichloroethane (DDT) and other chlorinated hydrocarbons (White et al. 2002). Within the U.S., peregrines were listed as endangered under the Endangered Species Conservation Act of 1969 and subsequently under the Endangered Species Act (ESA) of 1973. The species began recovering following restrictions on DDT use, and was subsequently delisted by the U.S. Fish & Wildlife Service (USFWS) in 1999 (Mesta 1999). Nevertheless, as primary predators, peregrines remain vulnerable to persistent environmental contaminants, and localized populations have not always recovered successfully (Mora et al. 2002, Elliott et al. 2005). As part of a recovery strategy (USFWS 2003), continued monitoring to determine the stability of regional populations has been recommended through 2015.

Peregrines were never recorded commonly in Nevada (Bond 1946), but were considered extirpated as a breeding species in Nevada from the 1950s until 1985 (Walton et al. 1988, Floyd et al. 2007), at which time a breeding pair was documented along the shoreline of Lake Mead within Lake Mead National Recreation Area (LMNRA). Since that time, efforts have been made to monitor peregrines within LMNRA and a sustained increase in the number of known nesting territories has been documented (Table 2.1). Currently, the steep cliffs adjacent to the shorelines of lakes Mead and Mohave within LMNRA contain the core breeding population of peregrine falcons in Nevada, and contribute substantially to a broader distribution of breeding peregrines in Arizona.

The National Park Service (NPS) has actively supported monitoring of peregrines within LMNRA, with assistance and additional monitoring from the Nevada Department of Wildlife, Arizona Game and Fish Department, and more recently University of

Nevada, Las Vegas. Monitoring approaches, intensity, and objectives have varied widely over the years, but surveys mostly have focused on determining occupancy at known breeding territories with much less effort on searching for additional breeding areas. In the early 1990s, a more intensive effort by Glinski and Garrison (1992) was focused on Black Canyon, predominately along the stretch of the Colorado River below Hoover Dam. During that two year study, these researchers attempted to locate all peregrine falcon breeding territories in the canyon, identify important foraging habitats, and document occupancy during the nonbreeding season. During that study, these researchers documented occupied eyries roughly every 5 river km within Black Canyon, which was consistent with documented densities of breeding peregrines in other favorable habitats (Brown et al. 1992, Ratcliffe 1993). Building upon previous efforts in LMNRA, my research has sought to monitor annual occupancy and reproductive effort at all known breeding territories, while providing a more accurate estimate of active territories within the park.

Methods

Study Area

This research was conducted on a breeding population of Peregrine Falcons in LMNRA. See Chapter 1 for a detailed description of the study area.

Survey and Monitoring Methods

For purposes of tracking reproductive effort and productivity, I monitored all known territories within LMNRA throughout the 2006 through 2010 breeding seasons (Table 2.2). Sample size and survey hours varied annually and seasonally, adding new

territories as they were discovered, dropping others after breeding failure was confirmed and conducting exploratory surveys at new sites to evaluate occupancy. I employed several survey approaches (see below) to various degrees throughout the study period; initiating passive surveys in 2006, call-broadcast in 2008, and conducting an exploratory rapid site assessment in 2009 (see Chapter 1). In 2010, I combined the call-broadcast and passive survey approaches, typically beginning each survey session with call-broadcasting to quickly establish occupancy and then passively monitoring the area for as long as necessary to obtain information on reproductive effort.

Active Surveys – Historically, surveys at LMNRA often included flying Rock Pigeons (*Columba livia*) near eyries to elicit responses from resident peregrines. These ‘active’ surveys were conducted by boat with at least two trained observers, and generally occurred at least once per breeding season (usually April through June) at all known peregrine territories. Each survey generally lasted around 30 min at a site, but varied according to peregrine presence and behavior at the time of the survey. To minimize double counting, the active surveys at known territories and other potential sites along each lake were completed during the same day, beginning as soon as possible after sunrise to survey falcons during their most active time of the day. Over the years, the number of sites monitored increased as new territories were discovered. The primary objectives of these active surveys were to establish presence of territorial peregrines and determine their breeding status. Eyrie locations and presence of young were noted when observed, but these were not primary objectives. The use of Rock Pigeons was phased out beginning in 2006 in favor of more standardized survey methodology and alternative approaches.

Passive Surveys – Beginning in 2006, I implemented a standard survey protocol following USFWS (2003) guidelines. This method consists of spot surveys conducted throughout the breeding season to determine occupancy, breeding attempts, and reproductive success. Initially, I used this survey method at selected territories (three in Nevada, eight in Arizona), selected as part of each state's random sub-sample of known breeding territories. These sites were scheduled to be monitored once every three years through 2015. I initiated surveys in January 2006 in order to document the onset of courtship activities, and as a result I began surveys by mid- to late-February in the following years. From 2007-2009, I expanded the number of passively surveyed sites within LMNRA to include all known territories within the park. In addition, I used this method at promising sites in 2007 and 2008 in an attempt to discover previously undocumented peregrine territories.

The 'passive' surveys consisted of one 4-hr monitoring session at each selected territory during peak diurnal activity periods, using 10 X 50 binoculars and 20-60 power spotting scope. Depending on the breeding stage, I did not remain at the site the entire 4-hr period if I could obtain the desired information more expediently. I conducted the passive surveys as needed to determine occupancy, breeding attempts, and breeding results throughout the courtship and breeding season (March–July in 2006; February–July after 2006). After initial observations, I determined that surveys could be conducted throughout daylight hours early in the season and then gradually shifted to focus on early morning and late afternoon periods by mid-May as temperatures rose and peregrine activity levels during mid-day declined. I followed up evening surveys the next morning if needed to clarify territory status.

During each of the passive surveys, I recorded the coordinates of the observation point, the temperature, approximate wind speed, percent cloud cover, and time of the effective survey period. When applicable, I recorded the nesting cliff coordinates, estimated distance to the nest cliff from the observation point, the bearing to the nesting location, and the aspect of the eyrie. I made an attempt to record the number of individuals, age, and sex of all peregrines encountered during the survey period. When it was possible to see into the eyrie, I aged the young by visually comparing nestlings to a standard photographic guide (Cade et al. 1996). I took detailed behavioral and general observation notes, as well as documenting all observations of potential interspecific competitors (i.e., large predatory birds and cliff-nesting species).

Site Occupancy during the Non-breeding Season – I selected five territories as a subset of known breeding territories within LMNRA for which to conduct monthly non-breeding season passive surveys from August, 2008 through January, 2009. I implemented these surveys in an effort to gain insight into whether breeding peregrines at LMNRA were migratory or year-round residents, and to better understand whether incidental sightings of peregrines during fall and winter months were local residents or migrants from elsewhere. I initiated these surveys shortly after sunrise and followed the same passive methodology as described above (see Passive Surveys), but used a shortened, 2-hr survey period centered on eyrie locations identified during the 2008 breeding season. Attention was spent to determine whether territorial behavior, or behavior that would indicate the presence of a pair-bond between resident adults (i.e., territorial display or defense, cooperative hunting, prey sharing, or affinity for the nesting area), was exhibited which might indicate whether the birds were the resident breeders,

dispersing birds, or nonresident migrants. It was necessary to rely on behavioral cues to determine residency because no peregrines have been marked in this region since Glinski and Garrison's (1992) effort in the early 1990s, and it is extremely difficult to accurately determine the identity of unmarked peregrines in the field.

Call-broadcast Surveys – In conjunction with this project, I developed a call-broadcast survey technique in 2008 in order to reduce the time necessary to establish presence of territorial peregrines from that required using the passive method (see Chapter 1). Research I conducted within LMNRA during the 2008 and 2009 breeding seasons was used to establish response and detection rates of peregrines to broadcasted conspecific calls throughout the breeding season, as well as general usefulness of the methodology, and the demographic data acquired during that effort was also used for this study.

Rapid Site-assessment – In order to efficiently identify previously undocumented peregrine territories, I collaborated with a Geographic Information System (GIS) specialist (Ms. Stacy Crowe) to develop a predictive habitat suitability model using a maximum entropy approach in the program Maxent v. 3.2.19 (Phillips et al. 2006; see Chapter 1). Our intent was to high-grade areas for potential breeding based on previously identified territories. The model was based on the slope, solar insolation (watt hours/m², from 08:00 to 16:00 on 7 June), and distance to river or lake of all previously known eyrie locations ($N = 28$). We visualized the model using GIS software (ArcGIS v. 9.3, Environmental Systems Research Institute, Redlands, CA 2008) and targeted call-broadcast surveys in areas with highly predicted habitat for breeding (Fig. 2.2).

Specific survey points were located in areas predicted as having high peregrine breeding habitat potential from the model, or where previous incidental sightings of peregrines were observed (e.g., Fig. 2.3). I used the call-broadcast method to conduct a rapid assessment of peregrine occupancy at these points. Since peregrines are known to be highly territorial, I conducted surveys outside previously known territories (i.e., generally > 2 km from the nearest known eyrie or territory center). Additional call-broadcast or passive surveys (as needed) were repeated at all sites where peregrines were detected in order to determine territorial occupancy, breeding status, and to locate the eyrie if possible.

Occupancy and Reproductive Assessment

Site Occupancy – I defined an occupied site as an area containing at least one adult or subadult (second-year plumage) territorial peregrine during a portion of the breeding season. Occupancy rate is the proportion of monitored years a territory was occupied after the first year it was discovered. I defined a peregrine territory as an area that contained, or historically contained, one or more alternate eyries within the home range of a mated pair (Steenhoff and Newton 2007). An eyrie, as defined herein, consists of a peregrine nesting surface contained within or on a crack, hole, or ledge on the face of a cliff. A territory will usually contain alternate eyries over succeeding years (sometimes on separate eyrie cliffs), but is an area where no more than one pair is known to have bred in the same year. I analyzed whether there was independence of reproductive success for previous and current year with a Fisher's exact test (2008-2010). I also tested the independence of the decision to move an eyrie with the previous year's success using

a chi-squared test with all years pooled to obtain sufficient sample size (Sokal and Rohlf 1995).

Distance and Measures of Density – I used a laser rangefinder with an accuracy of +/- 0.3 m (TruPulse 200 B, Laser Technology Inc., Centennial, CO) for all distance measurements in the field and to determine cliff and eyrie height. Eyrie locations were plotted on ArcMap to the nearest meter after taking field measurements and superimposing coordinates on digital topographic maps and aerial photographic layers. Accuracy of eyrie points varied by site, but was generally +/- 2.5 m. I determined the nearest neighbor distance (NND) as the distance in meters from one occupied eyrie or territory center to the eyrie or territory center of the nearest neighboring territorial peregrines (measured with GIS software). In some cases I could not locate the eyrie, or territorial peregrines persisted at a site for a portion of the breeding period without laying eggs or selecting a nest. In those cases, to calculate NND I used the territory center, which is the center of most activity observed throughout the course of the breeding season. I restricted relative territory size estimates to localized areas with continuous habitat for breeding (e.g., Black Canyon, Boulder Canyon, and Virgin Canyon), using half the mean NND as a circular buffer around each eyrie (Calef and Heard 1979, Newton 1979). When considering possible effects of density on breeding, I used a cutoff of < 5 km NND to define ‘high’ density sites, with all territories ≥ 5 km NND existing in ‘low’ densities. Low density sites included territories spaced farther apart than the median NND and were assumed to receive lower intruder pressure from neighboring pairs than in the high density areas. I measured the nearest distance to water (i.e., lake, or permanent river) of all eyries with GIS, and categorically pooled them into ‘near’ (< 640

m) and 'far' (≥ 640 m) for purposes of comparing reproductive output, and evaluating prey composition. I used general linear regression models to analyze effects of distance to water on breeding indices and found no significant difference. However, a trend among years indicated there may be some discernable impacts of distance to water, so I conducted further categorical analyses. Initially, I considered eyries as either near (≤ 750 m) or far (>750 m) because there appeared to be a break in spacing at that point; 72% of all eyries were ≤ 750 m from water and there was a gap of nearly 400 m to the next nearest eyrie (1142 m). However, I reduced the cutoff point to 640 m because I was not able to collect prey from any eyries > 640 m from water. Categorical levels of reproductive success were similar when setting the cutoff at 640 m or 750 m (near = 85.9% at ≤ 750 m, and 84.8% at < 640 m vs. far = 50% at > 750 m, and 59.3% at ≥ 640 m).

Reproduction – I monitored all known breeding attempts throughout the duration of each breeding season or until confirmed breeding failure. I considered observations of copulation, prolonged courtship, or evidence of reproduction (i.e., incubation posture, nestlings or fledglings present, adults delivering prey to the nest) confirmation of a breeding attempt. I visually determined nestling ages (as describe above), and then back-dated using the average number of days required for each stage of the breeding cycle (i.e., Laying = 7 days, Incubation = 31 days, Nestling = 42 days) in order to assign laying and hatching dates. My definition of breeding success followed the USFWS (2003) definition for peregrines in which a nest was considered to be successful if at least one nestling reached the age of 28 days old, otherwise stated as $> 65\%$ of their age at first flight (Steenhoff and Newton 2007). I considered a breeding attempt to have been

unsuccessful when a pair of adults previously observed engaged in prolonged courting or copulating did not produce eggs or produced infertile eggs, when nestlings were documented dead prior to attaining 28 days of age, or when the eyrie was verified empty by visual inspection prior to nestlings surviving to 28 days with no surviving young discovered nearby.

Only those breeding attempts I was able to detect in the early stages of the reproductive cycle (i.e., courtship or incubation) have been included when calculating breeding success rates and when determining productivity. The apparent breeding success rate (success rate) was calculated as the proportion of successful nesting pairs to the total number of breeding attempts in the population (Newton 1979, Steenhoff and Newton 2007). Productivity was the number of young that reached 28 days of age, reported as the number of young per breeding attempt. I modeled two continuous independent variables (NND, and distance to permanent water) using a generalized linear model with a binomial error term for reproductive success and multinomial error for reproductive output (Sokal and Rohlf 1995). These calculations were restricted to the years 2008-2010 when adequate sampling provided data for sites far from water. Models were produced within years in order to avoid pseudoreplication for territories sampled more than one year. Generalized linear models and analyses were conducted in SAS 9.1 (SAS Institute 2002-2008).

Prey Assessments

To evaluate prey composition, I recorded observations of direct prey attempts during standard monitoring and survey efforts and opportunistically during other times. A prey attempt was any hunting effort involving at least one full dive on a given prey item (Bird

and Aubry 1982). Only those attempts in which I was able to observe the interaction from start to finish were used to calculate hunting success rates. I determined the identity of the intended prey to the lowest taxonomical unit possible. When possible, I recorded the gender and age (i.e., fledgling, subadult, adult) of the foraging peregrines and whether the attempt was a tandem attempt involving two individuals. The number of observations per month varied from nine to 52 January through November (mean = 19.8 observations/month), with only two observations during the month of December.

As a second, independent assessment of prey use, I collected prey from five territories following three breeding seasons (2008-2010). These collections were conducted after fledging had occurred in order to avoid disturbing breeding attempts. I brought back all prey remains for laboratory analysis, which involved identifying diagnostic structural and plumage characteristics of feathers and skeletal remains. I collaborated with a regional expert (Mr. N. John Schmitt) to identify prey remains and to determine the minimum number of individuals for each prey type by counting body parts such as beaks, legs, and diagnostic flight feathers (Olsen et al. 2004).

I conducted five years of Aquatic Bird Count surveys on lakes Mead and Mohave during a separate inventory and monitoring project within LMNRA designed to assess aquatic bird numbers and timing of migration (March 2004 through July 2009). For that project, I defined aquatic birds as the members of all families from Gaviidae through Anatidae and from Rallidae through Laridae (1998 AOU sequence). I selected intensive monitoring locations in which to conduct monthly surveys, representing local areas of high aquatic bird activity (three permanent sites on each lake). Two of the three Lake Mead locations were within 4 km of three peregrine territories, while one of the Lake

Mohave locations was within close proximity to a single peregrine territory. Beginning in January 2008, I also conducted monthly surveys along a 19.5 km stretch of Black Canyon on the north end of Lake Mohave, a stretch of flowing water immediately in front of four peregrine nesting cliffs. These surveys were conducted by traveling the targeted shoreline by boat or kayak and counting all aquatic birds and raptors within the designated survey areas. Herein, I reference the results of the inventory and monitoring in order to obtain an idea of aquatic bird availability as potential prey for resident peregrines.

I determined avian prey mass by referencing published values (Dunning 1993) of average adult mass for each species, and calculated prey biomass from the proportion of each prey type. I differentiated by gender as many sexually-dimorphic species as possible for a more accurate assessment of prey selection by mass. In order to analyze prey composition at territories 'near' (< 640 m) versus 'far' (≥ 640 m) from permanent water, and to track monthly change in diet, I categorized birds as 'aquatic' or 'terrestrial.' I defined aquatic birds as an informal and diverse group of birds tied ecologically to bodies of water for a significant portion of their lives. Aquatic birds include all waterfowl and coots (Anseriformes, Rallidae), diving birds (Gaviiformes, Podicipediformes, Pelecaniformes), shorebirds (Charadriiformes), gulls and terns (Laridae, Sternidae), as well as riparian obligate species in our area. Terrestrial birds include all birds regularly found away from open water, which were most species of Passeriformes, Apodiformes, Falconiformes, and Galliformes. Only prey attempts that were initiated within 600 m of an eyrie were considered during analysis of prey attempts at territories near and far from water. I collected prey remains after three breeding

seasons (2008-2010) from one eyrie considered far from water (640 m), and collected remains from eight eyries near water for a total of 11 collection years.

Agonistic Interactions

I documented all intraspecific and interspecific agonistic interactions involving peregrines which escalated at least to a chase during the years 2004-2010. Whenever possible, I identified the species, gender, and number of individuals involved, peregrine breeding stage, and other circumstances associated with the event. Additionally, I recorded breeding activities of nearby large predatory birds (i.e., Falconiformes) and Common Ravens (*Corvus corax*); species with the ability to alter peregrines' behavioral patterns, and which are potential competitors for prey and nest-sites and also a predatory threat to peregrine adults and young (White and Cade 1971). I determined all inter-nest distances for these species if they were within an area of influence around the eyrie in which peregrines routinely patrol and defend (Cade 1960). I extended this for all known Prairie Falcon (*Falco mexicanus*) breeding attempts, a congener with a high likelihood of influencing territory dispersion in areas of sympatry with peregrines and with strong ecological overlap (Porter and White 1973, Dekker and Corrigan 2006).

Results

The number of known peregrine territories within LMNRA increased from a single territory in 1985 to a total of 37 by the end of the current study, of which a maximum of 33 were occupied in a single year (Table 2.1, Fig. 2.1). During the course of the present study (2006-2010), I documented a 136% increase in known occupied peregrine territories (Table 2.1, Appendix 1). Some of this increase likely was a result of increased

exploratory efforts to identify previously undocumented territories and a large increase in the number of survey hours per breeding season (Table 2.3).

I recorded a maximum of 65 territorial peregrines in 2010, up from a total of 34 in 2006; this includes single adults or subadults holding a territory for at least part of a breeding season. I had no way of distinguishing between territorial residents and nonbreeding ‘floaters,’ so the total number of territorial peregrines does not include the many incidental observations recorded away from breeding areas, nor does it include occasions in which I documented more than two adults at a territory.

Nesting Chronology

The estimated mean annual date peregrines began laying ranged from 27 March in 2010 to 6 April in 2006 and the earliest annual laying date averaged 13 March (earliest laying = 8 March; Table 2.3). During individual years, an average of 42 days passed between the earliest nesting pair to that of the last pair to lay eggs. Over the study period, peregrines initiated egg laying progressively earlier in subsequent years, with the earliest laying date 8 days earlier in 2010 than in 2006 (Table 2.3). The earliest hatching began on 15 April (mean = 20 April), and earliest fledging date on 27 May (mean = 1 June). The latest confirmed successful fledging date was 14 July. Low sample size and a lack of local and regional climatic data preclude further analysis at this time of changes in the timing of breeding initiation. I recorded a total of 42 acts of copulation, primarily between mid-February and mid-April, and usually during the courtship (71%) and laying (12%) stages. However, I also observed copulation during the incubation (7%) and nestling (5%) stages, and as late as mid-May on four occasions.

Eyrie Characteristics

Over the course of this study, I identified 64 individual eyries at 32 distinct territories. Eyries were placed on cliffs averaging 100 m (range = 12-270 m) in total height, about two thirds of the way up the cliff face (mean = 66.4 m, range = 8-238 m). All identified eyrie scrapes (actual nesting platform) were placed directly on bare substrate (rock with fine gravel) on the face of the eyrie cliff, split nearly evenly between three primary structural types (ledge = 24, crack = 20, hole = 20). Ledges (horizontal rock shelf with no direct overhang) were the most exposed to the elements, while cracks (horizontal shelf with overhang) and holes (approximately circular opening recessed into cliff) both were overhung to various degrees. Eyrie dimensions ($N = 7$; 2 ledge, 4 crack, 1 hole) were an average of 301 cm wide (median = 227 cm, range = 59-831 cm), 45 cm high (range = 32-58 cm), and 114 cm deep (range = 39-175 cm). The directional aspect of eyries was not distributed evenly (Fig. 2.4); with 23 facing north to east (36%), 7 facing east to south (11%), 11 facing south to west (17%), and 23 facing west to north (36%). By contrast, randomly selected points within each territory (600 points on cliffs $> 42^\circ$ slope randomly selected within a 300 m buffer of each eyrie) were distributed such that 33% faced north to east, 26% faced east to south, 17% faced south to west, and 23% faced west to north (Fig. 2.5).

Alternate Eyries – During the study period, individual eyries were used an average of 1.5 years. At territories monitored during consecutive years ($N = 57$), eyrie locations were relocated the following year on 57.9% of occasions with an average distance moved of 200 m. Reproductive success (81.8% success before eyrie relocation, 72.7% success after eyrie relocation, $N = 33$, $P = 0.219$) and productivity (2.0 young/attempt before and

after eyrie relocation, $N = 33$, $P = 0.363$) both showed independence at territories from one year to the next. The decision to move an eyrie was independent of the previous year's success ($X^2 = 0.063$, $df = 1$, $P = 0.198$), with relocation occurring after 27 of 46 (59%) previously successful breeding attempts, and after 6 of 11 (55%) failed attempts. In two territories, the same eyrie was used in four consecutive years with successful breeding each year. At other territories, peregrines never used the same eyrie in consecutive years ($N = 9$) yet still attained a high rate of breeding success. After a failed breeding attempt, peregrines that selected a different eyrie the following year moved an average of 319 m ($N = 6$, range = 81-630 m), while alternate eyries after successful breeding the previous year were only 174 m ($N = 27$, range = 3-647 m) distant.

Population Parameters

Occupancy – Peregrine Falcon territories within LMNRA have a high rate of annual occupancy. From 2006-2010, the overall annual occupancy rate was 94.3%. In comparison, territories monitored for ≥ 5 years since 1985 ($N = 20$) had an overall occupancy rate of 93.2% (occupied 219 out of 235 territory years), with the individual site occupancies ranging from 80-100%. Nine territories were occupied ≥ 10 consecutive years, and one territory (Promontory Point) has been occupied for 26 continuous years (1985-2010).

Distance to Water – Eyries were located an average of 886 m from water ($N = 64$, median = 161 m, range = 1-9318 m). Including the reuse of individual eyrie sites, I recorded 93 confirmed breeding attempts (94 eyrie years including one site without reproductive output verified). Of these breeding attempts, 72 (71%) of the eyries were

located 'near' permanent water (< 640 m), while all others (29%) were 'far' from water (640-9318 m).

Density – The overall mean annual NND within LMNRA varied from a high of 6.78 km in 2006 (range = 1.64-27.43 km) to a low of 6.3 km in 2009 (range = 1.51-32.71 km), while the median annual NND varied from 4.93 km in 2007 to 4.07 km in 2008 (Table 2.4). The recorded densities were much higher in localized canyons with an abundance of available high cliffs near water for nesting. This was particularly evident within Boulder Canyon, a 7.81 km stretch of broken cliffs and deeply incised coves (Fig. 2.6). This stretch of canyon harbored five successful breeding pairs in 2010 (mean NND = 1.9 km, minimum NND = 1.52 km), with an average territory size of just 2.7 km². Two pairs on the east end of the canyon nested just 1.21 km from one another in 2009, the closest nesting distance documented. The density in 2010 was one territory/122 km² within the entire land area of LMNRA (approximately 4025 km² with a Lake Mead water level of 335 m asl), although the meaningfulness of such statistics is questionable given that density clearly drops as one moves away from the lake shores and preferred canyons.

Reproduction – The overall breeding success rate for 2006-2010 was 70.6%, with yearly rates fluctuating from 61.5% to 75.9%, respectively (Table 2.5). I documented a total of 177 successful young produced at LMNRA during the study period (185 young including those discovered late in the breeding season). The cumulative mean number of successful young/occupied territory was 1.28, with 1.74 successful young/breeding attempt, and 2.46 successful young/successful attempt. Neither NND nor distance to permanent water had a significant effect on reproductive success or productivity from 2008-2010 (Tables 2.6 & 2.7). Although distance to water did not have a significant

effect on breeding by year, a pooled categorical analysis of reproductive attempts near permanent water ($N = 66$) yielded a success rate of 84.8% and 2.23 young/attempt, while attempts far from water ($N = 27$) had a success rate of 59.3% and 1.0 young/attempt (Table 2.8). Territories existing in high density (< 5 km NND, $N = 54$) had a success rate of 75.0% with 1.9 young/attempt, which compared to low density territories ($N = 39$) with a 66.7% success rate and 1.73 young/attempt (Table 2.9).

Non-breeding Season

My assessments of peregrine activity during the 2008-2009 non-breeding season provide evidence that many peregrines within LMNRA do not migrate and maintain a high level of year round site fidelity (Table 2.10). Four of five sites showed relatively consistent occupancy of at least one adult present throughout the non-breeding season, with pairs regularly present at three of the four territories. These birds appear to have been residents, as they showed a strong affinity for perching on the eyrie cliff (usually within 100 m of the eyrie). In addition, I often detected cooperative hunting, food sharing, and mutual demonstrations of territory advertisement or defense, indicating evidence of pair-bonding throughout the year. I was not able to detect peregrines at one site from November through mid-February, after which time courtship activities commenced. These findings were supplemented with 44 incidental observations of peregrines on territories during non-breeding periods in previous and subsequent years at a total of 18 different territories.

Prey Composition

I observed 220 prey attempts and collected remains of 217 individual prey items (Appendix 3). Results of prey attempt observations ($N = 220$) indicated a 27.6% success

rate and 37 distinct prey types targeted (58 successful attempts on 13 prey types). The collection of prey remains ($N = 217$) resulted in the identification of 56 distinct prey types, 23 prey types were shared between the two methods (Tables 2.11 & 2.12). Pooled results of observations and prey remains indicated peregrines at LMNRA took 70 types of prey, including 58 avian species, nine avian genera that could not be identified to species, one genus of bat (*Chiroptera* sp.), a single desert spiny lizard (*Sceloporus magister*), and an observed attempt on unidentified invertebrates. One common carp (*Cyprinus carpio*) was collected from a plucking perch immediately below an eyrie, which possibly may represent pirated prey from a wintering Osprey (*Pandion haliaetus*).

Taken together, the order Passeriformes (also including single species from Caprimulgiformes, Apodiformes, and Coraciiformes) and open water birds (Anseriformes, Podicepediformes, and Pelecaniformes) were the two most abundant overall prey categories by observed attempts (40% and 23.6%) and remains (34.6% and 22.6%). After breaking the results into species and family groups, composition of the most common prey groups of birds were similar between attempts observed and collection of remains (Tables 2.11 & 2.12). Columbids (pigeons and doves) were the most numerous when considering attempts (10%) and remains (21.2%), but were surpassed by icterids (e.g., grackles and blackbirds) and ducks in biomass of successful attempts and by biomass of collected individuals of Eared Grebes (*Podiceps nigricollis*) and American Coots (*Fulica americana*). After combining methods, the three most common groups of prey items were doves ($N = 68$), Eared Grebes ($N = 43$), and icterids ($N = 39$).

Prey Availability – The abundance of aquatic birds undergoes dramatic, but seasonally and annually predictable, variations throughout the year within LMNRA (Fig. 2.7). The period with the lowest numbers of aquatic birds on either lake, and within the Black Canyon corridor, occurs late in the peregrine breeding cycle at LMNRA (Fig. 2.7). Aquatic bird numbers peaked in April on Lake Mead, experiencing a precipitous 84% drop by June. The peak coincided with the local peregrines' incubation stage, while the low period in June and July coincided with when most territories were either late in the nestling stage or recently fledged. Overall numbers of aquatic birds at the three permanent sites on Lake Mohave were much lower than on Lake Mead, but they also became scarce by early summer, a more gradual 92% drop in abundance from January through June. I recorded a large number of birds in Black Canyon and Lake Mohave in 2008, primarily American Coots (82% of all records), in January before the count dropped 91% by May, not beginning to rebound until September-October.

Variation in Diet Composition – Prey attempt observations indicate the proportion of aquatic versus terrestrial birds taken by peregrines at LMNRA shifts markedly throughout the year (Fig. 2.8), reflected also in a change of monthly mean prey weight (Fig. 2.9). The proportion of attempts on aquatic birds ($N = 76$) dropped from nearly 82% in January to just over 14% in March, not increasing to above 50% of the overall composition until September and later. Terrestrial birds ($N = 111$) showed an opposite trend, reaching a peak composition of 72% in May and dropping quickly after August. The monthly mean weight of prey attempts mirrored the monthly change in aquatic bird composition of prey attempts. The large categorical difference in mean weight of all aquatic and riparian obligate bird types in the sample ($N = 35$, mean = 413.4 g), as compared with terrestrial

bird types in the sample ($N = 32$, mean = 89.2 g), was mainly responsible for driving this pattern (Appendix 3). Interestingly, the lowest mean prey weight was in September (68.4 g, Fig. 2.9), which coincides with the southern migration of shorebirds, typically a rather small aquatic bird type as found in LMNRA (number of prey species = 12, mean weight = 164.8 g) and making up 46.2% of the month's total prey attempts. The mean prey weight of attempts in April-June ($N = 126$, mean = 153.5 g) was less than a third of that in November-January ($N = 22$, mean = 516.6 g).

Prey selected at territories far from water (≥ 640 m) differed from those territories near water (< 640 m) in both observations of prey attempts and collected prey remains (Table 2.13). The proportion of aquatic birds targeted by peregrines during observed prey attempts were much greater in those territories near water (47%) than those far from water (17%), and correspondingly the mean prey weight was over three times greater at territories near water. In comparison, prey collection data indicated near parity (46% versus 43%) in territories near and far from water; however, the mean collected prey weight at far territories was still just two thirds of that recorded at near territories (far = 147.4 g, near = 228.9 g).

Agonistic Interactions

I observed an increase in numbers of aggressive agonistic interactions between peregrines during the years 2006-2009, before dropping in 2010 (Table 2.14). Over three times as many interactions were observed in 2008 and 2009 as compared with the previous two years and the number of observation hours between bouts in 2009 was just 23% of that in 2006. I observed peregrines engaged in agonistic interactions with 10 different species ($N = 113$; Table 2.15). Red-tailed Hawk (*Buteo jamaicensis*) was the

species most commonly interacted with ($N = 39$). The four most common species accounted for 88% of all interactions. Mean inter-nest distances to breeding peregrines varied by species, although Common Ravens (minimum distance = 50 m) and Red-tailed Hawks (minimum distance = 87 m) both successfully bred surprisingly close to active peregrine eyries (Table 2.16). Overall aggression of peregrines toward other species was highest from March through May, peaking at various times for each species throughout the breeding season (Table 2.17). Intraspecific interactions between peregrines peaked in April ($N = 9$).

Call-broadcast and Rapid Site-assessment

I used the call-broadcast technique extensively to evaluate territory occupancy early in the season from 2008-2010 (method testing 2008 and 2009), and in an attempt to rapidly assess areas for undocumented territories in 2009. In 2009, I used an exploratory rapid site-assessment approach at 111 individual locations, primarily from February 25 through April 13 (courtship through incubation) with some follow-up visits in late May (132 total call-broadcast events). These locations were based on a preliminary habitat suitability model that highlighted about 2.5% of the area of LMNRA. Peregrines were detected at 12 of the 111 rapid assessment survey points, resulting in the discovery of six previously unknown territories and verification of four additional territories that were suspected but previously unconfirmed; two of the positive detections were duplicate observations of birds from territories previously discovered at earlier rapid assessment points. In the case of one of the newly verified territories, I traced the eyrie nearly 2.8 km from the primary activity center as identified during 3 previous years of surveys.

This eyrie had not previously been pinpointed due to rugged terrain and the vast amount of suitable breeding habitat in the area.

Discussion

Whether the known territories documented each year at LMNRA has reflected the actual number of territories present is not clear since numbers have continued to increase with increased search effort (Table 2.1). Nevertheless, the number of breeding peregrines at LMNRA has increased substantially after the first detection of breeding in 1985 and now represents an important regional breeding area (Appendix 2). With the exception of the intense search effort along the length of Black Canyon in the early 1990s, the historical survey efforts were focused on monitoring areas with known peregrine presence, with new territories added as they were detected. Given this scenario, the detection of territories (Table 2.1, Appendix 1) likely lagged behind that of the true rate of expansion of the breeding population. Furthermore, the detection of territories was likely biased toward those areas along the lakes where breeding territories were already known and survey crews spent significant time travelling to and from monitored sites, this is especially likely in areas with high density within Black Canyon, Boulder Canyon, and Virgin Canyon.

Beginning in 2006, a more focused effort with drastically increased survey time was initiated to search for additional (undocumented) peregrine territories (Table 2.2). The result was a rapid increase in the number of known breeding territories each year to the present. I documented large increases in the number of known territories from 2006-2008, as I began using the passive survey method in areas previously not surveyed in

conjunction with monitoring traditional sites. A second large increase occurred in 2009 as I combined the newly developed call-broadcast method with a habitat suitability map to rapidly assess many more areas of predicted high quality habitat in a short period of time (Figs. 2.2 & 2.3). The increases continued in 2010, as three new territories were confirmed while combining the call-broadcast and passive survey approaches.

Population Dynamics

High overall breeding success rates and productivity throughout the study period are likely indicators that the breeding population at LMNRA is still expanding. Mean productivity within LMNRA from 2006-2010 was 1.7 young/breeding attempt, but had increased to 2.0 in both 2009 and 2010 (Table 2.5). This compares favorably with expanding populations in Colorado from 1989-2001 (1.7 young/breeding pair; Craig et al. 2004) and California from 1993-1997 (1.6 young/breeding pair; Mesta 1999). By contrast, the Rocky Mountain/Southwest Peregrine Recovery Plan established 1.25 young/territorial pair as the threshold productivity level that would result in a self-sustaining population (USFWS 1984). Additionally, stable resident peregrine populations elsewhere in North America typically experience productivity of 1.0-2.0 young/pair. The size and stability of breeding populations are commonly buffered by floater-to-breeder ratios commonly in the range of 1:1 to 2:1 (White et al. 2002). Without marked individuals I could not evaluate parameters important for establishing population dynamics; such as, size of a non-breeding floater population, mortality rates, age of breeding (but see below), natal dispersal, turnover of breeders, and emigration from outside sources. Nonetheless, I have observed no evidence to suggest mortality and

turnover rates are outside expected values for healthy populations, and I did not observe any banded individuals from outside breeding areas.

While the overall rate and timing of the increased numbers of breeding peregrines at LMNRA is difficult to determine with accuracy, there are indications that particular locations have increased markedly in recent years. Black Canyon was thoroughly surveyed by an experienced crew during the 1990 and 1991 breeding seasons, and after surveying 49 sites, only four occupied territories were documented along the 35 km river channel – an average of one pair/8.75 river km with a mean NND of 8.01 km (Glinski and Garrison 1992; Fig. 2.10). Survey efforts in recent years were of similar intensity, and during the 2010 breeding season I documented seven occupied territories along the same river stretch, resulting in an average of one pair/5.0 river km with a mean NND of 4.2 km. Additionally, breeding territories along the canyon have expanded southward with two new territories identified in a 6 km stretch of canyon south of the original study area; one discovered in 1995 and one in 2007. Thus, by 2010, a total of nine territories were active along the 40.3 km stretch of canyon with about one pair/4.5 river km (mean NND 3.9 km), roughly twice the linear breeding density detected in 1991. Assuming an average territory size of half the local mean NND (Newton 1979), the average territory size in 2010 was 11.8 km², down from 50.4 km² in 1991.

The reproductive success of territories discovered in later years, combined with territory acquisition and attempted breeding by young peregrines, provides another indication that the local population may still be increasing. I was not able to detect any signs of accumulated musing under eyrie ledges or associated perches, at four of the 10 newly discovered territories in 2009; suggesting the possibility of only recent site

occupancy. Importantly, none of the four sites were successful and only three of the remaining new sites fledged young (30% success rate at newly discovered territories). These observations fit with known patterns that indicate younger breeding pairs generally have low breeding success (Newton 1979, Ratcliffe 1993). Eight of these 10 territories were reoccupied in 2010, and overall seven were successful; producing an average of 1.88 young/successful attempt, as compared with 2.59 young/successful attempt for all territories in 2010. The increased success rate (but with lower productivity) observed in 2010 may not be definitive but, even if 2009 was not the first year of occupancy for several of these territories, it appears as though these sites may only recently have been established. Complicating the issue, however, is the fact that five of the territories were also far from the lakes (1459-9318 m from major water bodies), in which case breeding success may possibly be lower regardless of the age of breeding individuals because of the lack of abundant aquatic prey in close proximity to the nesting site.

Within LMNRA, the presence of recent territory holders and breeding attempts from young peregrines (subadult) with second-year plumage is a further indication that this population is still growing. A similar pattern of breeding age skewed towards younger individuals was documented in an expanding population of peregrines in the Midwest that was not density limited (Tordoff and Redig 1997). Within LMNRA, a subadult was observed during the breeding season at a territory on Lake Mohave in 2004, but it was unclear if this bird was a member of the breeding pair. This was followed by an unsuccessful breeding attempt at a newly discovered territory by a subadult female paired with an adult male in 2007. Also, two of the newly confirmed territories in 2009 were held throughout the breeding season by single, unmated subadults (one male, one

female). One of the young birds remained on its territory throughout the winter months and successfully produced one fledgling in 2010. Also in 2010, I observed the first confirmed mate-switch during the breeding season within LMNRA with a subadult for an adult breeder. An adult male was observed with its mate during the laying and incubation stages, but was observed to have been replaced by a subadult male mid-way through the nestling stage (nestlings about 23 days old). I observed the young male feeding nestlings in the presence of the adult female and later perched within 1 m of the female for ≥ 1 hr. On a subsequent visit, the juvenile male delivered prey to two successful nestlings (71% of fledging age).

Density Considerations

Regularity of spacing, at various densities and relative to local habitat and prey availability, is a result of territoriality and peregrines appear to have a minimum interspecific compression distance or tolerance threshold (Cade 1960, Newton 1979, White et al. 2002). Territorial spacing in this species can be seen as a repulsion or avoidance of one territory to the next, so half the distance between two territories can be roughly considered the area of influence of each territory and will generally be defended by the resident falcons (Ratcliffe 1993). The minimum and average NND can then inform as to the minimum territory requirements in a given area. The mean NND across the LMNRA region has held relatively stable over the past five years (2006 mean NND = 6.71 km, 2010 mean NND = 6.43 km), even as the number of known territories appears to have increased by nearly 60% in the same period (Table 2.4). However, the minimum NND has dropped over 26% (1.64 km-1.21 km), which is a result of increased crowding

in localized canyons along the lake shores that provide high quality foraging and contain abundant potential nesting sites.

The high densities of peregrines within LMNRA now rival those of some of the highest concentrated breeding areas known globally (Appendix 2). Within North America, local breeding density has been shown to reach one territory/10 to 20 km² or higher, but one territory/100 to >1,000 km² tends to be more typical (Ratcliffe 1993). Within LMNRA, the overall density in 2010 was roughly one territory/122 km², but density in three localized canyons not limited by available nesting habitat, and in close proximity to water, have been documented at much higher densities (1 territory/2.7 km², $N = 5$; 1 territory/10.8 km², $N = 4$; 1 territory/11.8 km², $N = 9$). At what point density begins limiting breeding success and population size within the highly preferred canyons at LMNRA remains to be seen.

Population Limitation

Habitat quality can be measured by its ability to sustain a population over time, without immigration; that is, the quality of a territory can be measured by the duration and rate of occupation, contribution to reproductive output, and the predictability of breeding success (Newton 1991, Sergio and Newton 2003). As predicted for territorial species, the highest quality individuals, or first to arrive, tend to monopolize the highest quality sites (Fretwell and Lucas 1970). This model predicts more low quality territories will be occupied over time as localized density increases in highly suitable habitat and as energetic and defense costs accrue in the high quality sites. The increase in occupancy of low quality territories lowers the mean per capita productivity which, in turn, results in density-dependent reproduction that can regulate population size (Sergio and Newton

2003). The situation is somewhat complicated in that it is not always possible to separate whether high breeding success is due to habitat quality or of the quality of the occupying birds (Newton 1979). Besides considerations of quality of individuals, it is also possible that the first birds to arrive in an area occupy the highest quality sites and following birds are relegated to lower quality areas regardless of the individual's fitness (Newton 1979).

Highly productive individual territories may be thought of as 'sources' within a local population when compared to 'sink' territories not productive enough to sustain population levels long-term (Newton 1991). From 2004-2010, the top five peregrine territories (12.8% of all territories) within LMNRA produced 37% of the total number of successful young (2.69 young/breeding attempt), and the top 12 territories (30.8% of all territories) produced 66.7% of all young (2.38 young/breeding attempt). In contrast, the 27 territories with the lowest overall number of young (69.2% of all territories) only accounted for 33.3% of all young (1.17 young/breeding attempt). Depending on mortality, the top territories will each have twice the recruitment potential than the low-grade territories. The low-grade territories may act as sinks that may not be able to remain occupied without steady immigration from more productive areas.

By analyzing productivity in relation to distance to water, it may be possible to more precisely define territories that act as population sinks within LMNRA. Territories far from water have been shown to reproduce at levels theoretically unable to sustain themselves over time (1 young/breeding attempt). New breeding pairs are constrained by existing territory holders, so an increasing number of low-grade territories far from water will be occupied as the territories near water reach a density threshold, either from insufficient prey or intensified territorial aggression as density increases. According to

the theory behind density-dependent population limitation, at some point the growing proportion of sink territories will provide enough negative feedback that will act to limit the overall population size and thus establish a maximum sustainable population size.

Access to prey near eyries lowers the energy demands of foraging, especially when individuals are forced to return great distances to the eyrie while carrying prey (Newton 1979, White et al. 2002). A prominent eyrie cliff and presence of surrounding cliffs allows resident peregrines to employ a sit-and-wait hunting method, and the proximity of eyrie cliffs to open water within LMNRA provides peregrines with wide open hunting areas with limited cover and escape options for prey. Through 2010, territories near water, even those in extremely dense concentrations (e.g., Boulder Canyon = 1 territory/2.7 km², and Black Canyon = 1 territory/11.8 km²), continue to reproduce presumably at a rate sufficient for sustainability and likely continued expansion (1.9 young/breeding attempt). This indicates the population within LMNRA has not yet reached its upper limit. However, as the frequency and intensity of territorial interactions increase reproductive success may begin decreasing from interference competition and possibly also increasing mortality rates, thus capping future population growth.

Individuals residing at territories far from water experience higher energy demands if they forage for aquatic birds over permanent water. Long-distance foraging bouts increase time away from the eyrie, which then reduces parental care and nest-defense capabilities. Proportionately, these peregrines do not feed on aquatic birds to as great an extent as those in territories near water, thus they must conduct more hunting attempts on much smaller terrestrial birds to make up dietary demands. Although I was not able to quantify terrestrial prey availability, birds living in open desert scrub (primarily small

passerines and Galliformes) tend to exist in much lower density and biomass across the landscape than aquatic and terrestrial birds concentrated around a water source (Szaro and Jakle 1985). Presumably peregrines nesting away from water must rely on a much larger foraging area in order to meet their nutritional needs.

Prey Considerations

Assessing diet is not always straightforward, and each method of evaluating raptor dietary composition has its advantages and disadvantages (Collopy 1983, Mersmann et al. 1992, Marchesi and Pedrini 2002, Ellis et al. 2002). Ellis et al. (2002) found that the collection of peregrine prey remains tends to overestimate rare prey, and under represent common prey, since many items are plucked before delivery to the eyrie or are removed prior to collection. Feathers of small birds also do not remain in eyries as long as many larger prey items because feathers are fewer in number and smaller in size, thus biasing prey collection results towards larger avian prey types (Oro and Tella 1995). Prey observations have often been cited as the least biased approach to evaluating diet, but this is a very time consuming method (Mersmann et al. 1992) and in particular can create identification problems for small prey.

When comparing my observations of prey attempts with prey collection, I found the two methods possessed separate strong and weak points, while yielding similarities with respect to categorical prey composition. Compiling prey observations throughout the breeding season was far more time consuming in comparison with single visits to eyries after the breeding season to collect prey remains. However, observations could be conducted opportunistically during standard surveys and they allowed prey to be assessed temporally. In most cases (except occasionally at plucking perches) it was not possible to

evaluate shifts in diet composition throughout the breeding season; however, prey collection allowed for much more accurate identification of prey items. Only two of 217 (0.9%) of collected items could not be identified below the level of Order, while 73 of 220 attempts (33.2%) and 24 of 58 (41.4%) of successful attempts were thus limited. Primarily the distances (up to 600 m or more) at which attempts were observed resulted in imperfect identification, especially a problem with small prey items. Even so, prey observations allowed for an assessment of hunting success and the documentation of very small and large prey items that were likely to be consumed away from the eyrie. While prey collection likely missed a sizable proportion of small prey (many swifts, swallows, and bats were consumed on the wing immediately after capture), it allowed for the documentation of many small and uncommon items in which at least one identifiable feather was collected from a site (e.g., many small passerines and shorebirds, American Kestrel *Falco sparverius*, Lesser Nighthawk *Chordeiles acutipennis*, etc.), and occasionally from very large species as well (i.e., Double-crested Cormorant *Phalacrocorax auritus*, and Common Raven). Considering these strengths and weaknesses, the two methods complemented each other well to provide a more accurate measure of species impacted by hunting peregrines.

Within LMNRA, it appears that peregrines may select prey at least partly based on overall abundance and availability. The observed proportion of attempts on aquatic birds (Fig. 2.8), as well as the calculated mean prey mass by month (Fig. 2.9), show similar trends as aquatic bird abundance tallied on lakes Mead and Mohave (Fig. 2.7). Aquatic birds were shown to decrease nearly 95% in the first half of the year, while their proportional composition in prey attempts dropped over 83% from January-March and

mean monthly prey weight dropped almost 70% by April. The proportional drop in aquatic bird prey composition in March predates the local drop in aquatic bird abundance, but corresponds with a predictable major increase in northbound passerine migrants at that time. These analyses, however, remain incomplete, and how these patterns play out with regards to prey selection remains unknown. No abundance assessment of terrestrial birds within LMRNA (migration or resident) exists for comparison, and I was unable to obtain enough prey data at individual territories to determine if individual birds preferentially selected certain prey types over others, regardless of availability. Nor was I able to evaluate potential prey composition, abundance, or vulnerability within proximity to individual peregrine eyries or at primary foraging areas within individual peregrine home ranges.

Synchronization of hatching dates of peregrines with the hatching dates of their primary prey species has been documented in a breeding population of peregrines in northern Alaska (White and Cade 1971). In opposition to this pattern, hatching and rearing of peregrine young at LMNRA occurs after a major portion of aquatic birds and shorebirds have departed (Fig. 2.7). Shorebirds, waterfowl and coots, gulls, terns, and wading birds predictably are present on lakes Mead and Mohave in large numbers throughout the fall and winter months, and account for 77.1% of the total prey biomass and 36.6% of all individual prey items. These birds are available in abundance from January-March (peregrine courtship and pre-laying stages), which is an important period for female peregrines as they develop eggs (a clutch of 4 eggs can equal almost 20% of the female's body weight), but also for males who must expend great amounts of energy foraging for the female and nestlings. The caloric intake of females at this time has been

shown to influence the number of eggs laid and date of laying (Newton 1979). However, the abundance of aquatic birds on the lakes drops precipitously by May (Lake Mead = 40.1% decrease, Lake Mohave and Black Canyon = 91.1% decrease) as migratory species leave for breeding grounds. This appears to be a critical time, possibly the most limiting to peregrine breeding success at LMNRA, as the adults must forage for young in addition to themselves at a time of decreasing prey abundance. Adequate estimates of resident and breeding terrestrial bird numbers are lacking at LMNRA; however, the size disparity between these types of birds (mean weight = 473.9 g vs. mean terrestrial and riparian bird weight = 90 g) indicates peregrines must compensate with many more prey captures per day as their diet shifts primarily from aquatic birds to terrestrial or riparian birds. Indeed, the estimated food intake for a single nestling from hatching to fledging is nearly 35% greater than that required of an adult over the same period (Weir 1978).

Agonistic Interactions

Agonistic interactions with peregrines, as in many other animals, is a mechanism by which territories are established and defended, including foraging areas (Newton 1979, Ratcliffe 1993). These interactions can be expressed on an intra- or interspecific level, and can involve communicative (vocal and behavioral) and physical interactions. Many, if not most, agonistic interactions are resolved without contact, thus limiting the risk to both parties involved. My treatment of the topic is reserved for the more serious interactions involving chasing, diving, or grappling with other individuals. The number, intensity, and change over time of such interactions with the same, or other, species can be informative as to the degree of competition for resources (e.g., nest sites, perching and roosting sites, foraging areas and prey), or predation risk, between individuals or species.

In particular, agonistic interactions are generally more intense between more closely related species and those with high ecological overlap (Porter and White 1973).

Intraspecific Interactions – While an available prey-base regulates the maximum number of peregrines that can be supported in a given area, the realizable density of a population is limited by territoriality (Cade 1960). If the number of available nest sites has become limited, it will be expected that the number of interspecific encounters near eyrie sites will increase. Indeed, I recorded an increase of agonistic interactions between peregrines during the years 2006-2009 (Table 2.14). Notably, the number of interactions in 2008 and 2009 were more than three times greater than the number observed in the previous two years. I observed fewer interactions in 2010, but the number of observation hours was just 41% of that in 2009 and the focus of survey effort was streamlined to primarily determine occupancy and breeding data. My number of yearly survey hours varied each year; however, the average interval of time between interactions in 2009 was just under 23% of that observed in 2006 (Table 2.14).

Although many of the intraspecific interactions I observed did not escalate beyond a chase, consequences can be severe when interactions lead to direct physical contact. Four of the observed interactions progressed to grappling, becoming very violent and prolonged and easily may have resulted in injury to the combatants. Two interactions near an eyrie site involved females and lasted over 30 min, with intense grappling, biting, and several falls of 6-30 m from cliff ledges. The resident male became involved in one of these fights and was engaged with the interloping female for ≥ 16 min while the resident female patrolled in front of the eyrie.

Interspecific Interactions – I observed interspecific agonistic interactions between several species and peregrines, from rare interactions with coyotes (*Canis latrans*) and Great Blue Herons (*Ardea herodias*) to much more frequent encounters with Common Ravens, Turkey Vultures (*Cathartes aura*), and Red-tailed Hawks (Table 2.15). Indicative of their highly aggressive and territorial nature, I only observed peregrines forced to retreat or break off hostilities on two occasions (once with a female Northern Harrier, *Circus cyaneus*, and once with a nest-building male Bald Eagle, *Haliaeetus leucocephalus*). I was often not able to determine the causal factor at the onset of aggressive interactions; however, 22 of the 113 interspecific interactions were just prior to, or just following, peregrine prey interactions, food delivery by either species, or either species provisioning young in the nest. Specifically, interactions with ravens most commonly involved food or tending to nests by one or both species (12 of 24 interactions).

While competition for food and nesting sites with other species may be contributing factors to peregrines' spatial pattern of dispersion within LMNRA (Porter and White 1973, Newton 1979, Ratcliffe 1993), it is difficult to separate interspecific territoriality from pressure exerted in predation and predator defense interactions (White et al. 2002). The observed distance at which breeding peregrines tolerated interspecific nesting of potential competitors or predators varied widely (Table 2.16). All of these species are cliff-nesters in this region (as are Golden Eagles, and Great Horned Owls *Bubo virginianus*, but with no nesting data to compare), and potentially come into competition for nest-sites with peregrines, although several authors indicate varying levels of microhabitat preference and tolerance levels (White and Cade 1971, Porter and White

1973, Newton 1979). The observed minimum distances the birds nest to one another appears to correlate to some degree with how closely the species are related phylogenetically, with the exception of Red-tailed Hawks and Bald Eagles (Wink and Saur-Gürth 2004). The degree of dietary overlap strongly shapes the ecological niche of birds (Newton 1998), and the degree of diet overlap with these species and peregrines also seems to be somewhat inversely correlated with observed inter-nest distances. More research is needed to resolve interspecific interactions on an ecological level; however, these species do seem to impact peregrines' use of time and energy and may impact breeding success and spatial distribution (more time spent driving away competitors translates to less time available for foraging and tending to young).

Although commonly overlapping in breeding areas, Common Ravens are frequently observed conflicting with resident peregrines, and nesting on the same cliff face by the two species has been shown to depress peregrine breeding success and productivity (Ratcliffe 1993, Brambilla et al. 2004). Regardless, there was a wide range of tolerance levels between peregrines and ravens at LMNRA. The two species nested successfully in close proximity to one another on several occasions (Table 2.16), sometimes on the same nesting cliff, and without observed hostility in several situations. However, at two territories intense and persistent aggression of peregrines (mainly by the adult male late in the raven nesting cycle) on the ravens may have contributed to the ravens abandoning their nesting area the following year. I also observed an unsuccessful nest-robbery attempt by a pair of ravens on a peregrine eyrie in which the female peregrine had recently departed with prey and the male was left behind to incubate. Additionally, I

collected remains of two late-stage nestling, or recently fledged, ravens as peregrine prey in an eyrie and on a nearby plucking perch.

At least four interactions with both Red-tailed Hawks and Turkey Vultures seemed to be driven mainly by defense of newly acquired prey on the part of peregrines; however, interactions during most other occasions, and with other species, seemed to be mainly territorial in nature, or preemptive defense of nestlings. Interactions with Red-tailed Hawks were generally brief, but became very intense at times, with peregrines occasionally making contact on aggressive dives and driving red-tails to the ground on several occasions. This could possibly impact the breeding success of either species, but all of the nearby nesting attempts that I documented ended successfully for both breeding pairs ($N = 9$).

Notably in 2009, intense interactions during the peregrine courtship stage with a newly resident male Bald Eagle resulted in the pair of peregrines relocating their eyrie roughly 650 m away from the eagle nest. Even so, the peregrines still successfully raised young that year at an eyrie 860 m from the eagle nest. The eagle acquired a mate the following year and raised a nestling almost to fledging (likely dying from exposure to exceptionally high temperatures), while the peregrines successfully raised four young in a new eyrie 590 m away.

Breeding Prairie and Peregrine Falcons have been shown to impact one another when breeding areas overlap with mixed results, but peregrines have been shown to displace Prairie Falcons in several instances, especially near water (Porter and White 1973). In central Alberta, Prairie Falcons were found to be limited by competition with peregrines for nest sites, not by prey availability (Dekker and Corrigan 2006). Although thought to

be much more common historically (Ross Haley NPS, pers. comm.), I was only able to locate two Prairie Falcon territories during my research; one of them occupied for only a single year (2006), while the other used the same eyrie four consecutive years (2007-2010) and produced young during at least three years. I did not observe interactions between the two falcon species but the closest pair of peregrines to the Prairie Falcons was 4.6 km away, even though much of the intervening area consisted of abundant nesting cliffs seemingly suitable for either species. It seems quite possible that the expanding population of peregrines at LMNRA may be impacting Prairie Falcons locally. Interestingly, on two occasions Prairie Falcons took to the ground and became quiet after I broadcasted a peregrine call in front of their eyrie cliff.

Temporal Variation – The seasonal variation of interactions seemed to be influenced by the breeding cycle of the local peregrines, as well as that of the interacting species. Interactions between peregrines peaked in April, a time early enough in the breeding season when it is quite possible non-breeding floaters may take over a breeding attempt and assume a permanent role as a breeding individual in the future (Ratcliffe 1993, White et al. 2002). This also corresponds with when peregrines are usually incubating or with relatively young nestlings, and is a period in which young may be most vulnerable to potential predators (Ratcliffe 1993).

The timing of interactions varied between species and, particularly with Red-tailed Hawks and Common Ravens, the peak number of interactions seemed to coincide with the periods when each had late-stage nestlings or young were fledging. Peregrines usually being the aggressors, these interactions likely were a result of increased activity at nearby nests as parents were provisioning growing young. Interactions with Bald Eagles

were highest in January and February, a time in which many wintering eagles are still in the area. Also, this was when the single resident pair of Bald Eagles would be most likely to encounter the neighboring pair of peregrines while engaged in frequent courtship displays. I did not document any Turkey Vulture nesting areas, but these birds usually began migrating back into the area by March. Observations of copulation events and the presence of juveniles in the summer months indicate Turkey Vultures likely breed within LMNRA which may bring them into conflict with peregrines as they forage to feed their young.

Future Direction

As an apex predator, peregrines remain vulnerable to bioaccumulation of persistent environmental contaminants and have proven to be an indicator of contamination within regional ecosystems (Mora et al. 2002, Elliot et al. 2005). Many of the persistent organic pollutants that contributed so greatly to the drastic population declines of peregrines in the mid-1900s (e.g., chlorinated hydrocarbon insecticides and polychlorinated biphenyls) have been banned in the U.S., however many new chemicals are introduced each year in addition to thousands of commercial chemicals currently in use (Henny et al. 2009). Lakes Mead and Mohave are downstream repositories for urban and industrial waste waters from the Las Vegas Valley, as well as from expanding residential, and agricultural areas along the Virgin and Muddy river drainages. Aquatic and shoreline birds are particularly susceptible to absorbing, and potentially biomagnifying, any number of the many potentially harmful compounds present in the aquatic system. The high aquatic bird prey composition in peregrine diets documented in this study indicates that there is

an ongoing need to monitor this resident population as an indicator of environmental health and emerging water quality issues (Henny and Elliot 2007) within the park.

Historically, monitoring within the park has been very important in establishing the high long-term occupancy rates, as well as steadily adding to the minimum number of known territories. This has provided a framework from which the more comprehensive research described herein was based. It is not yet known whether the current number of territories accurately represents the true local breeding population, or to what degree emigration and natal dispersal impact population size, much less whether outside immigration (possibly from the Grand Canyon) plays a significant role. Addressing these questions will require a more hands-on approach than what was possible in my study. My study provides a valuable population and ecological baseline from which to guide future research for years to come.

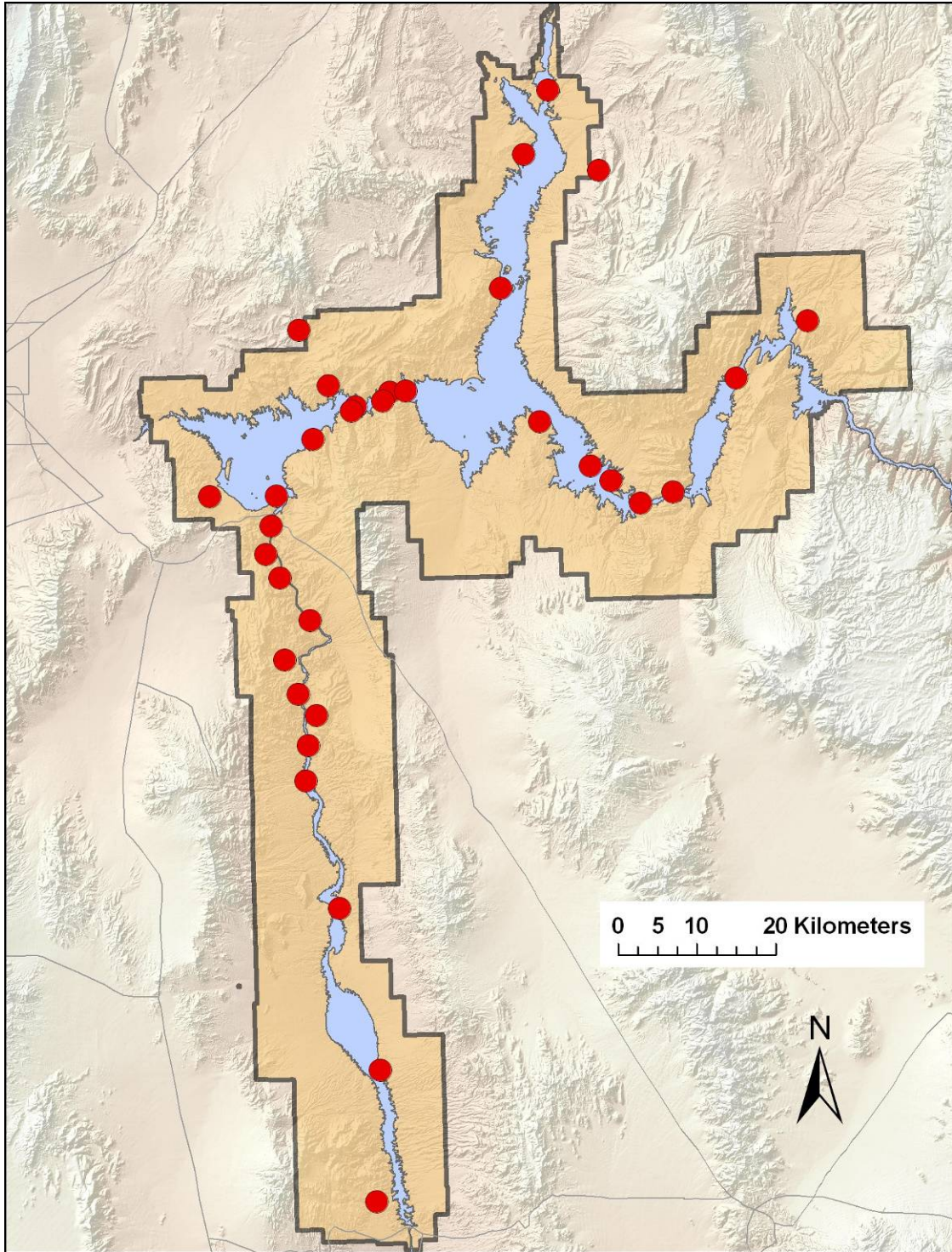


Figure 2.1. Occupied Peregrine Falcon territories (red dots) within Lake Mead National Recreation Area in 2010. An occupied territory was defined as a site containing ≥ 1 territorial peregrine present during a portion of the breeding season.

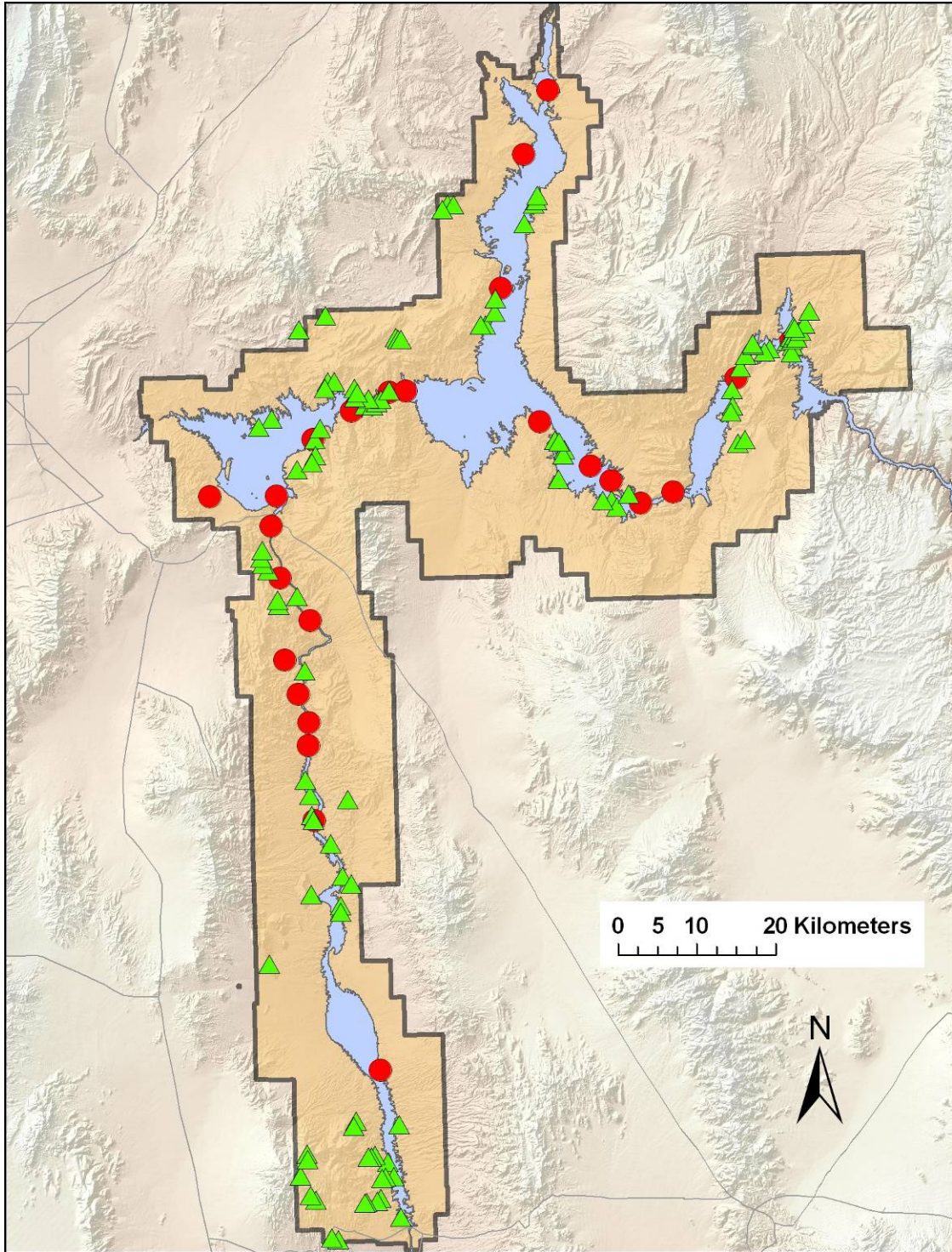


Figure 2.2. Occupied Peregrine Falcon territories in 2008 (red dots) and survey locations (green triangles) for rapid exploratory site-assessments in early 2009 at Lake Mead National Recreation Area. An occupied territory was defined as a site containing ≥ 1 territorial peregrine present during a portion of the breeding season.

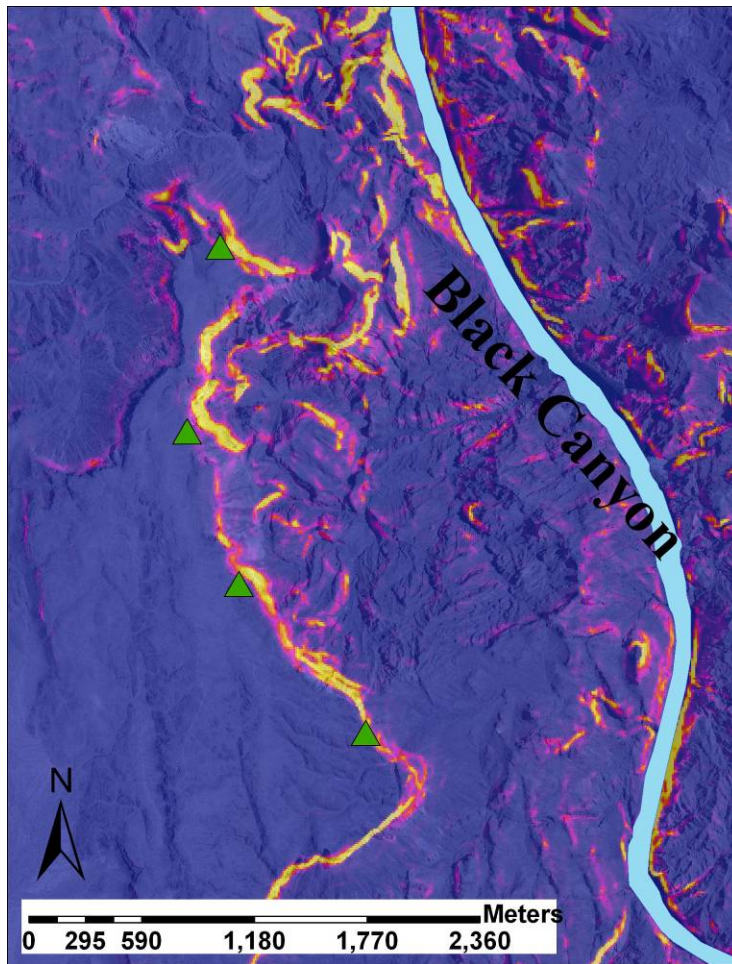


Figure 2.3. Example of rapid site-assessment survey locations based on a draft predictive habitat model in an area of Black Canyon, Lake Mead National Recreation Area. Survey points are indicated by green triangles. The draft predictive habitat model was generated using known eyrie locations prior to 2009 and was based predominately on slope and solar radiation variables. Red predicts areas of high suitability and yellow depicts areas of highest predicted suitability for breeding locations.

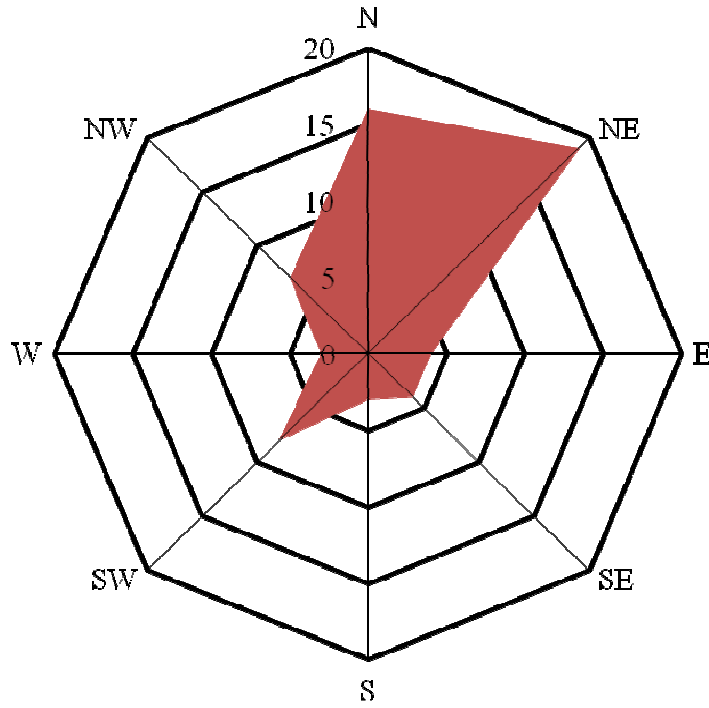


Figure 2.4. Distribution of the aspect of Peregrine Falcon eyries by categorical direction at Lake Mead National Recreation Area ($N = 64$). Aspect is divided into 45° incremental units. Verticle numbers (0-20) indicate number of eyries, and the point of intersect of the polygon on each spoke signifies the number of eyries oriented within each category.

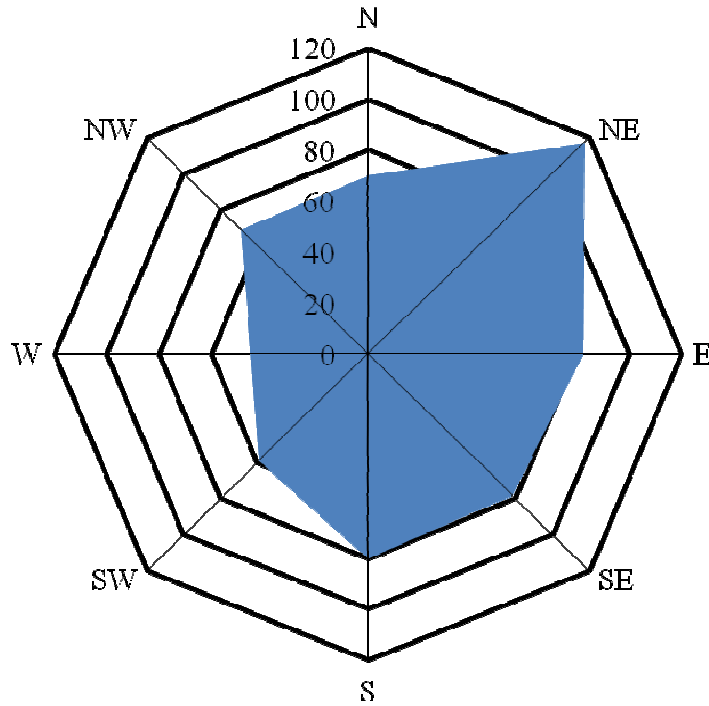


Figure 2.5. Distribution of the aspect of random points selected around of Peregrine Falcon eyries by categorical direction at Lake Mead National Recreation Area ($N = 600$). Points were restricted to cliffs with $\geq 42^\circ$ slope and within a 300 m buffer surrounding all known peregrine eyries. Aspect is divided into 45° incremental units. Verticle numbers (0-120) indicate number of points, and the point of intersect of the polygon on each spoke signifies the number of points oriented within each category.

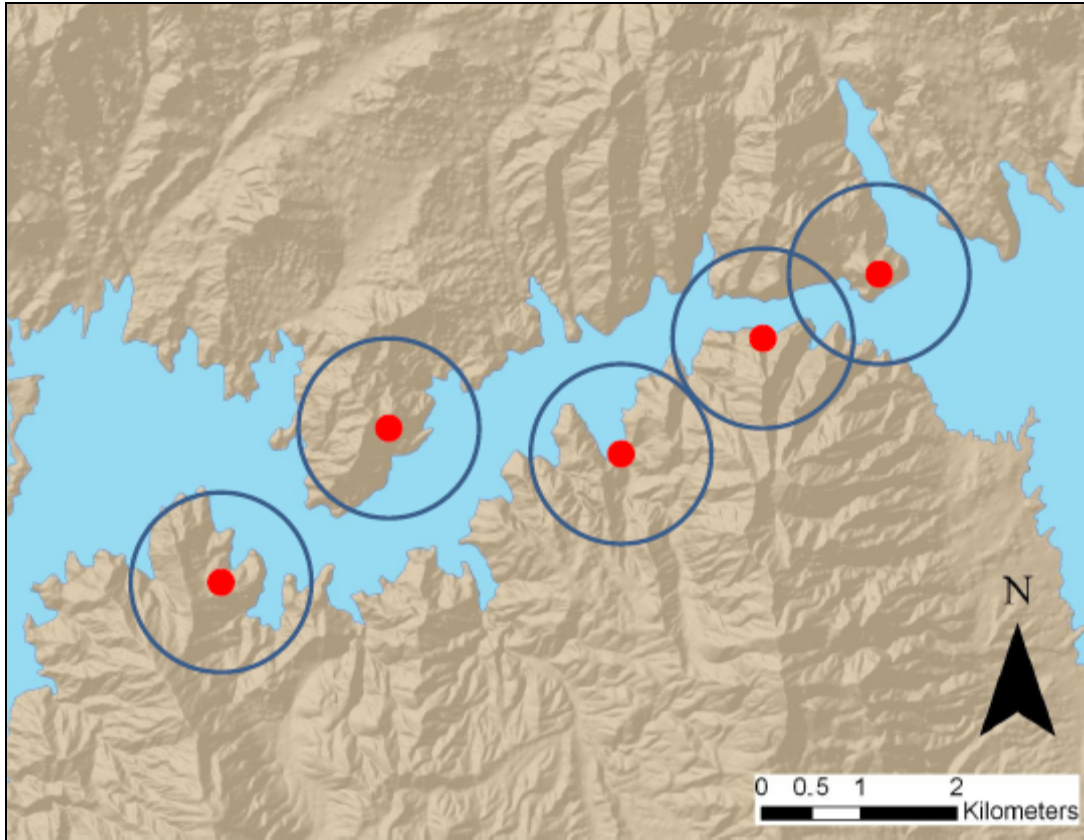


Figure 2.6. Spatial distribution of Peregrine Falcon eyries within Boulder Canyon at Lake Mead National Recreation Area. Red dots indicate 2010 eyrie locations and blue circles are 0.9 km buffers representing approximate local territory sizes (radius of half the local NND).

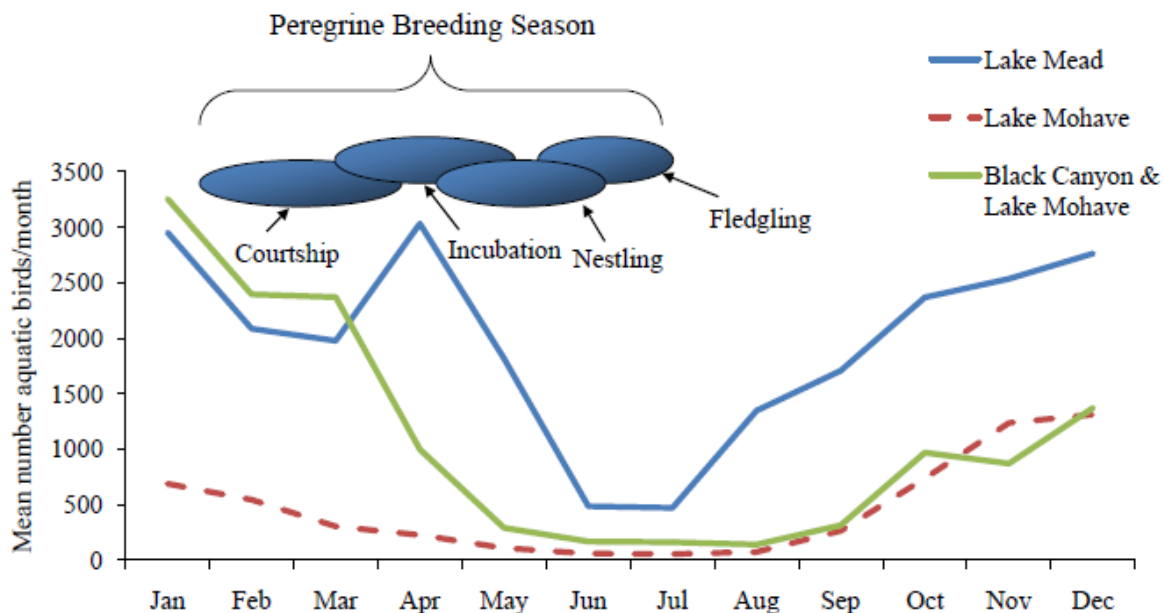


Figure 2.7. Peregrine Falcon breeding season and aquatic bird abundances recorded at Lake Mead National Recreation Area. Aquatic birds include waterfowl (Anseriformes, Rallidae), diving birds (Gaviiformes, Podicipediformes, Pelecaniformes), shorebirds (Charadriiformes), and aerialists (Laridae, Sternidae). Data collected during a five-year monthly inventory and monitoring project on lakes Mead and Mohave (2004-2008). Survey sites focused on areas of high importance to aquatic birds. Monitored sites located on Lake Mead (2004-2008; 3 sites), Lake Mohave (2004-2007; 3 sites), and along the Black Canyon corridor and Lake Mohave (2008). Blue ovals above indicate average duration of each of the peregrine breeding season stages (2006-2010).

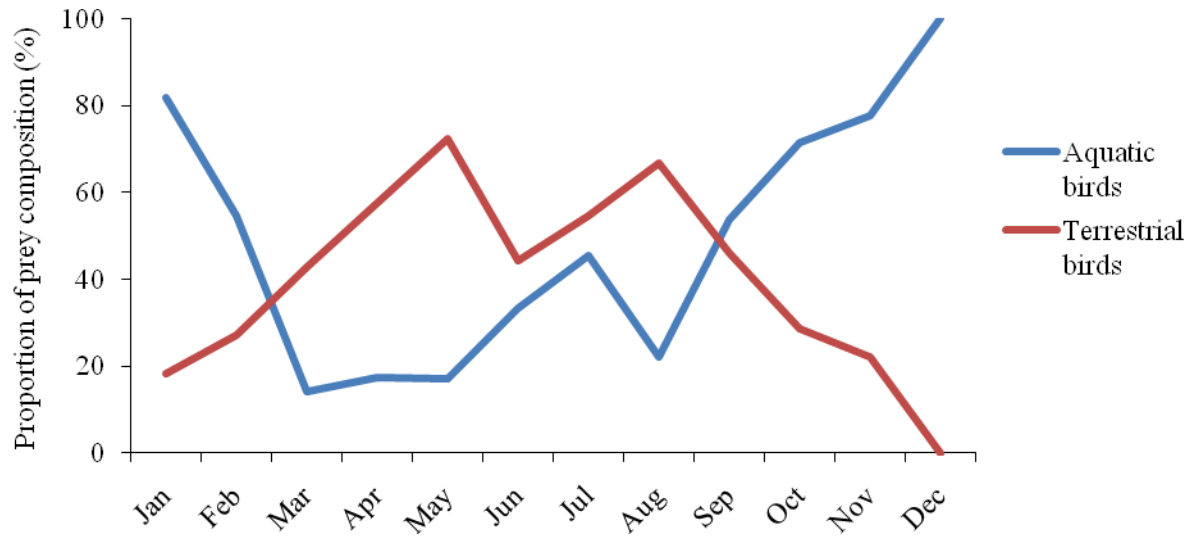


Figure 2.8. Categorical proportion of prey composition by month of Peregrine Falcons at Lake Mead National Recreation Area (aquatic and terrestrial birds). Data compiled from number of individually observed prey attempts that were identified to category (2004-2010). Aquatic birds ($N = 75$) include all waterfowl, diving birds, shorebirds, waders, and riparian obligates. Terrestrial birds ($N = 111$) includes all birds that are regularly found away from water, includes most species of Passeriformes, Apodiformes, Falconiformes, and Galliformes.

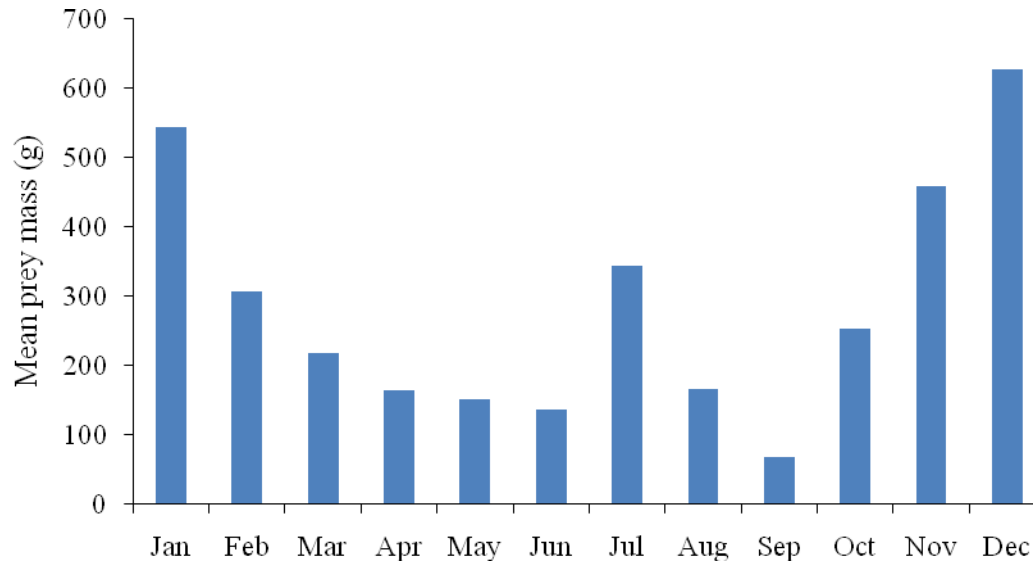


Figure 2.9. Mean mass of prey by month of Peregrine Falcons at Lake Mead National Recreation Area ($N = 220$). Data compiled from number of individually observed prey attempts that were identified to category (2004-2010). Data from prey attempt observations were compiled during peregrine surveys, aquatic bird count observations, and incidental observations.

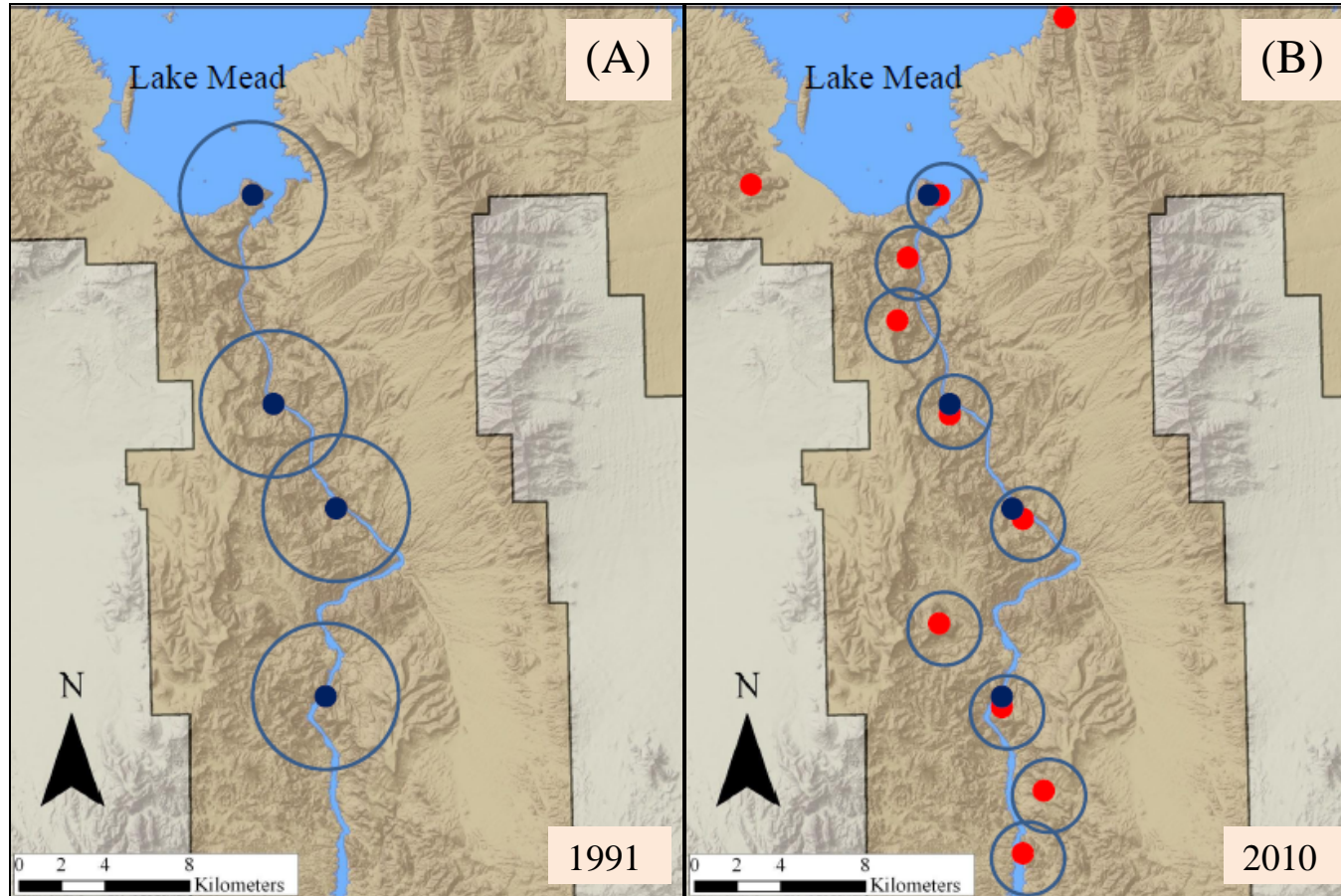


Figure 2.10. Spatial distribution of Peregrine Falcon eyries within Black Canyon at Lake Mead National Recreation Area. (A) Blue dots are approximate eyrie locations (1991) and blue circles are 3.6 km buffers representing approximate local territory sizes (radius of half the local NND in 1991). (B) Blue dots are historical eyrie locations (1991), while red dots indicate 2010 eyrie locations and blue circles are 2.0 km buffers representing approximate local territory sizes (radius of half the local NND in 2010).

Table 2.1. Number of known occupied Peregrine Falcon territories within Lake Mead National Recreation Area (1985-2010). An occupied territory was defined as a site containing ≥ 1 territorial peregrine present during a portion of the breeding season.

Date	Territories on or near Lake Mead	Territories on or near Lake Mohave	LMNRA Total Occupied Territories
1985§	1	0	1
1986§	1	0	2
1987§	1	0	1
1988§	1	2	3
1989§	1	3	4
1990*	1	3	4
1991*	1	3	4
1992	1	4	5
1993	1	5	6
1994	1	4	5
1995**	2	5	7
1996	3	5	8
1997	2	5	7
1998	4	4	8
1999	4	4	8
2000	5	4	9
2001	5	4	9
2002	5	3	8
2003+	7	6	13
2004+	7	7	14
2005+	9	5	14
2006	14	6	20
2007	16	9	25
2008	19	9	28
2009	21	11	32
2010	21	12	33

§ Monitoring conducted exclusively by NDOW.

* Includes territories identified in AGFD research.

** Includes territories verified by AGFD.

+ Includes Burro Wash surveys conducted by NDOW.

Table 2.2. Summary of survey efforts for Peregrine Falcons within Lake Mead National Recreation Area throughout the 2004-2010 breeding seasons. Survey effort reflects surveys conducted by NPS and UNLV personnel only.

	2004	2005	2006	2007	2008	2009	2010
Total no. of surveys	49	58	118	146	247	376	183
Total sites surveyed	15	25	30	39	49	139	41
Exploratory surveys	2	16	32	36	26	132	6
Exploratory sites	2	10	14	17	21	111	8
Occupied territories	14	14	20	25	28	32	33
Survey hours	21.8	25.7	192.4	227.8	308.3	260.6	107.8

Table 2.3. Variation in laying and fledging dates of Peregrine Falcons within Lake Mead National Recreation Area (2006-2010). Dates have been calculated by estimating nestling ages from a photographic guide, using published averages for duration of breeding stages (i.e., 7 days laying, 31 days incubation, 42 days nestling) to determine estimated laying and fledging dates. *N* is the number of eyries used for estimation.

Year	Laying Date			Fledging Date		
	<i>N</i>	Earliest	Mean	<i>N</i>	Earliest	Mean
2006	12	17 March	6 April	12	5 June	25 June
2007	8	21 March	31 March	7	9 June	21 June
2008	17	12 March	29 March	16	29 May	17 June
2009	22	8 March	28 March	20	27 May	14 June
2010	24	9 March	27 March	24	28 May	15 June

Table 2.4. Summary of Peregrine Falcon territory density within Lake Mead National Recreation Area (2006-2010). An occupied territory was defined as a site containing ≥ 1 territorial peregrine present during a portion of the breeding season.

Category	2006	2007	2008	2009	2010
Total occupied territories	20	25	28	32	33
Mean NND (m)	6781	6645	6277	6298	6434
Median NND (m)	4332	4930	4065	4577	4585
Minimum NND (m)	1640	1640	1509	1211	1522

Table 2.5. Summary of Peregrine Falcon productivity at Lake Mead National Recreation Area (2006-2010). An occupied territory was defined as a site containing ≥ 1 territorial peregrine present during a portion of the breeding season. A breeding attempt was designated for a territorial pair when copulation, prolonged courtship, or evidence of reproduction was observed (i.e., incubation posture, nestlings or fledglings present, adults delivering prey to the nest). Only those breeding attempts detected in the early stages of the reproductive cycle (i.e., courtship or incubation) have been included. A successful breeding pair was defined as having produced at least one offspring ≥ 28 days old, and a successful young was any nestling or fledgling ≥ 28 days old.

Categories	2006	2007	2008	2009	2010	Total§
Occupied territories	20	25	28	32	33	138
Breeding attempts	15*	13	24	28	29	102
Successful attempts	13*	8	16	20	22	72
Breeding success rate (%)	75.0	61.5	66.7	71.4	75.9	70.6
Successful young/occupied territory	1.05*	0.84	1.29	1.72	1.73	1.28
Successful young/breeding attempt	1.00	1.62	1.50	1.96	1.97	1.74
Successful young/successful attempt	1.62*	2.63	2.25	2.75	2.59	2.46
Total successful young detected	21*	21	36	55	57	177
Total adults detected	34	46	55	61	65	NA

§ Total calculations only include breeding attempts discovered early in the breeding season.

*Includes results from 7 breeding attempts discovered late in the breeding season, resulting in 13 successful young.

Table 2.6. Effects of nearest neighbor distance and distance to permanent water on Peregrine Falcon reproductive success at Lake Mead National Recreation Area (2008-2010). Output from general linear models with binomial error for reproductive success. Each variable and year was analyzed alone.

Effect	Year	df	<i>F</i>	<i>P</i>
Nearest neighbor distance	2008	1,23	0.02	0.893
	2009	1,26	1.02	0.322
	2010	1,29	0.22	0.64
Distance to permanent water	2008	1,20	2.53	0.127
	2009	1,25	1.42	0.245
	2010	1,22	0.00	0.988

Table 2.7. Effects of nearest neighbor distance and distance to permanent water on Peregrine Falcon productivity at Lake Mead National Recreation Area (2008-2010). Output from general linear models with multinomial error for productivity (reproductive output). Each variable and year was analyzed alone.

Effect	Year	df	<i>F</i>	<i>P</i>
Nearest neighbor distance	2008	1,19	0.13	0.727
	2009	1,22	1.30	0.267
	2010	1,26	0.04	0.842
Distance to permanent water	2008	1,17	3.40	0.083
	2009	1,22	2.24	0.148
	2010	1,19	0.10	0.759

Table 2.8. Reproductive success by distance to water of Peregrine Falcon territories within Lake Mead National Recreation Area (2005-2010). Only those territories with eyrie location pinpointed are included. Distance to water was analyzed categorically (near < 640 m; far \geq 640 m), and indicates distance of eyrie to nearest major source of permanent surface water (i.e., Lake Mead, Lake Mohave, Colorado River).

Reproductive Effort	Overall	Distance to Water	
		Near	Far
Breeding attempts	93	66	27
Successful attempts	72	56	16
Success rate (%)	77.4	84.8	59.3
Young/attempt	1.87	2.23	1.0
Young/successful attempt	2.42	2.63	1.69
Total young	174	147	27

Table 2.9. Reproductive success by relative density of Peregrine Falcon territories within Lake Mead National Recreation Area (2008-2010). High density territories are those with a nearest neighbor (NND) distance of < 5 km, low density with NND \geq 5 km.

Reproductive Effort	Overall	Relative Density	
		High	Low
Occupied territories	93	54	39
Breeding attempts	81	48	33
Successful attempts	58	36	22
Success rate (%)	71.6	75	66.7
Young/attempt	1.83	1.9	1.73
Young/successful attempt	2.55	2.53	2.59
Total young	148	91	57

Table 2.10. Summary of monthly survey results at five Peregrine Falcon territories at Lake Mead National Recreation Area during the 2008-2009 nonbreeding season (August–January). Results indicate peregrine presence and behavioral observations.

Territory	August	September	October	November	December	January
Engine Beach	♂♀, TD, E, V	♂, E	U, PA*3	♂, PA, E, V	♀, E	♂, E
Grebe Bay	♂♀, TA, PA, E, V	♂♀, PA*3, E, V	♂, E	Unoccupied (2 surveys)	Unoccupied	Unoccupied
Promontory Point	♂, TD, E, V	U, E, V	♂♀, TD, E	♂♀, TD, E, V	♂♀, E, V	♂♀, C, TA*2, E
Chalk Cliffs	♂♀, TA, PA*2, E	♂♀, PA*2, E, V	♂♀, PA*2, FS, V, E	♂♀, TA*2, PA, E, V	♂♀, E, V	♂, PA*3, TD*2, E
South Basin Cove	♀, PA, E	Unoccupied	♂♀, TA*2, PA, E	♂♀, E	♂♀, E	♂♀, C, E

♂♀ = pair; ♂ = single male; ♀ = single female; U = unknown peregrine; C = courtship; TD = territorial display or defense; TA = tandem prey attempt; PA = single adult prey attempt; FS = food sharing; E = perched ≤ 100 m from eyrie; V = vocalizing

Table 2.11. Predominant prey items of Peregrine Falcons at Lake Mead National Recreation Area, determined by prey attempt observations ($N = 220$). Percentage of successful attempts calculated from the number of successful attempts on each prey type divided by the total successful attempts, and only including those attempts observed from start to finish. Mean mass is the average mass of prey items within each prey type. Biomass calculated by mean mass of prey item multiplied by successful attempts.

Prey type	Number Attempts	Successful (%)	Mean Mass (g)	Biomass (%)
Columbidae spp.	22	8.6	194	16.2
American Coot	19	0	642	0
Shorebirds & waders	19	6.9	181	4.0
Icteridae spp.	16	10.3	71	20.5
Swift/swallow spp.	16	15.5	22	4.0
Eared Grebe	13	3.4	292	13.4
Anatidae spp.	12	3.4	790	20.8
% of Total	53.2	48.1	NA	78.9

Table 2.12. Predominant prey items of Peregrine Falcons at Lake Mead National Recreation Area, determined by prey remains collected at eyries and plucking perches ($N = 217$). Mean mass is the average mass of prey items within each prey type. Biomass calculated by mean mass of prey item multiplied by successful attempts.

Prey type*	Number Individuals	Mean Mass (g)	Biomass (%)
Columbidae spp.	46	194	12.6
Eared Grebe	30	292	18.8
Icteridae spp.	23	71	4.6
Shorebirds & waders	22	181	9.4
Swift/swallow spp.	12	22	0.6
Gull/tern spp.	12	388	12.3
American Coot	11	642	15.2
% of Total	71.8	NA	73.5

* Prey remains identified by N. John Schmitt.

Table 2.13. Comparison of prey composition by distance to water at Peregrine Falcon territories within Lake Mead National Recreation Area (2004-2010). Distance to water was analyzed categorically (near < 640 m; far \geq 640 m), and indicates distance of eyrie to nearest major source of permanent surface water (i.e., Lake Mead, Lake Mohave, Colorado River).

Prey Composition	Distance to Water	
	Near	Far
Prey Attempt Observations		
Number of attempts	127	41
Proportion aquatic birds	0.47	0.17
Mean prey weight (g)	231.3	74.4
Prey Remains Collection		
Number of items	169	44
Proportion aquatic birds	0.46	0.43
Mean prey weight (g)	228.9	147.4

Table 2.14. Summary of observed intraspecific agonistic interactions with Peregrine Falcons at Lake Mead National Recreation Area (2006-2010). The numbers of territories are only those territories within the study area that were occupied by ≥ 1 territorial peregrine. Observation hours are the total number of survey hours conducted during each peregrine breeding season.

	2006	2007	2008	2009	2010
No. Territories	20	25	28	32	33
No. Interaction	1	3	8	6	2
Observation hours	192.4	227.8	308.3	260.6	107.8
Mean interval between interactions (hr)	192.4	75.9	38.5	43.4	53.9

Table 2.15. Summary of agonistic interactions with Peregrine Falcons at Lake National Recreation Area (2004-2010). Only those interactions escalating to at least a chase are reported.

Species	Total Interactions
Red-tailed Hawk <i>Buteo jamaicensis</i>	39
Turkey Vulture <i>Cathartes aura</i>	25
Common Raven <i>Corvus corax</i>	24
Peregrine Falcon <i>Falco peregrinus</i>	20
Bald Eagle <i>Haliaeetus leucocephalis</i>	12
Northern Harrier <i>Circus cyaneus</i>	3
Great Horned Owl <i>Bubo virginianus</i>	2
Great Blue Heron <i>Ardea herodias</i>	2
Coyote <i>Canis latrans</i>	2
Osprey <i>Pandion haliaetus</i>	1
Cooper's Hawk <i>Accipiter cooperii</i>	1
Eagle/raptor Unid.	2
Total	133

Table 2.16. Summary of interspecific nesting attempts and distances to the nearest Peregrine Falcon eyrie at Lake Mead National Recreation Area (2006-2010). Nesting attempts include all known occupied territories with active nest sites. Only the nesting attempts of cliff-nesting species near enough to influence neighboring peregrines are included. Reported species are restricted to the families Accipitridae, Falconidae, and Corvidae.

Species	Nesting attempts	Mean distance (m)	Minimum distance (m)
Common Raven <i>Corvus corax</i>	10	274	50
Red-tailed Hawk <i>Buteo jamaicensis</i>	9	351	87
Prairie Falcon <i>Falco mexicanus</i>	5	5823	4579
Bald Eagle <i>Haliaeetus leucocephalis</i>	2	725	590

Table 2.17. Summary of monthly agonistic interactions with Peregrine Falcons at Lake Mead National Recreation Area (2004-2010). Reported interactions include all intraspecific interactions, as well as and the four most commonly interacting species.

Species	Jan	Feb	Mar	Apr	May	Jun
Peregrine Falcon <i>Falco peregrinus</i>		2	5	9	1	3
Red-tailed Hawk <i>Buteo jamaicensis</i>		6	7	13	5	6
Turkey Vulture <i>Cathartes aura</i>			3	6	9	6
Common Raven <i>Corvus corax</i>		2	4	2	14	
Bald Eagle <i>Haliaeetus leucocephalis</i>	5	4	1	1		
Total	5	14	20	31	29	15

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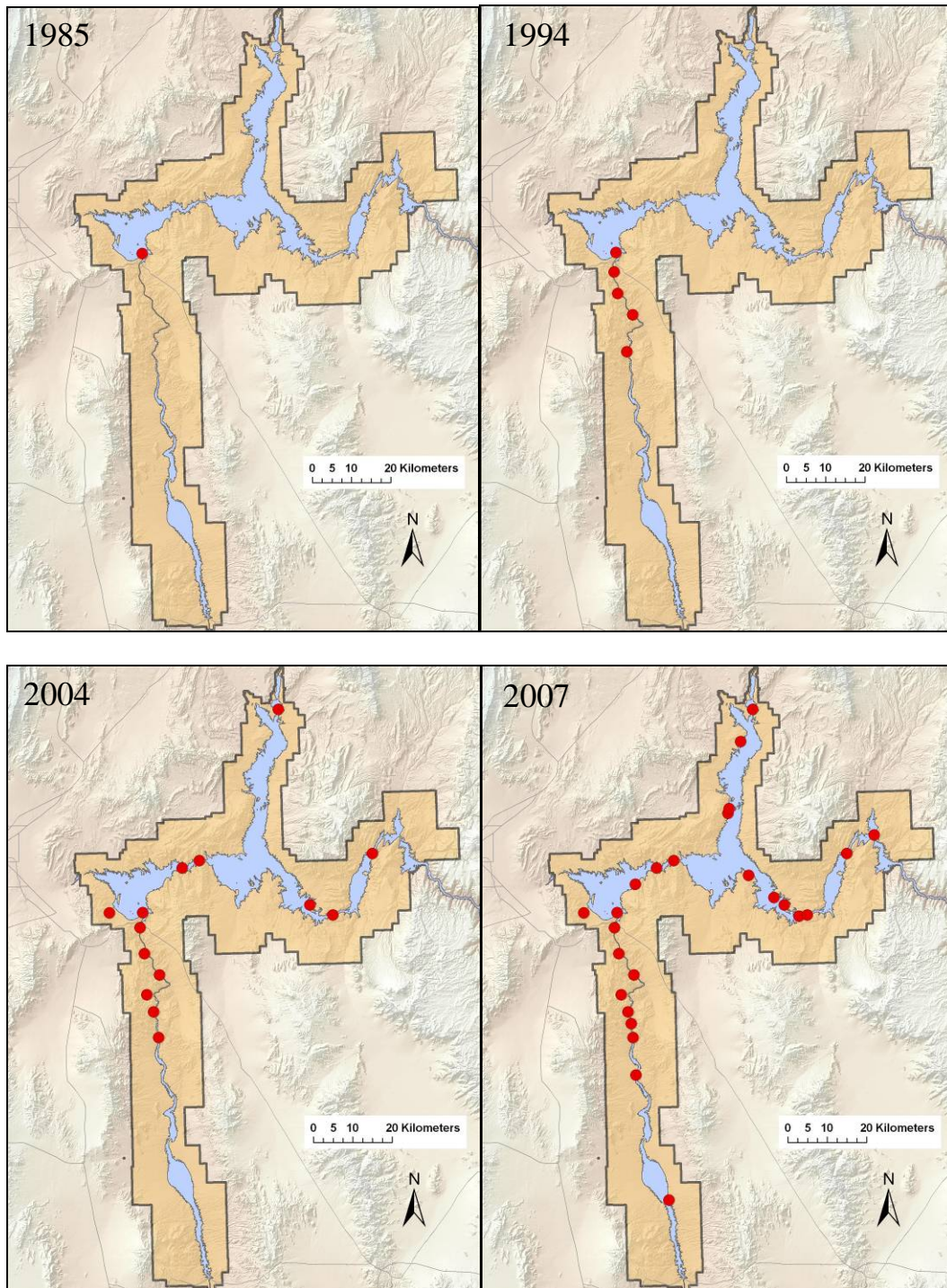
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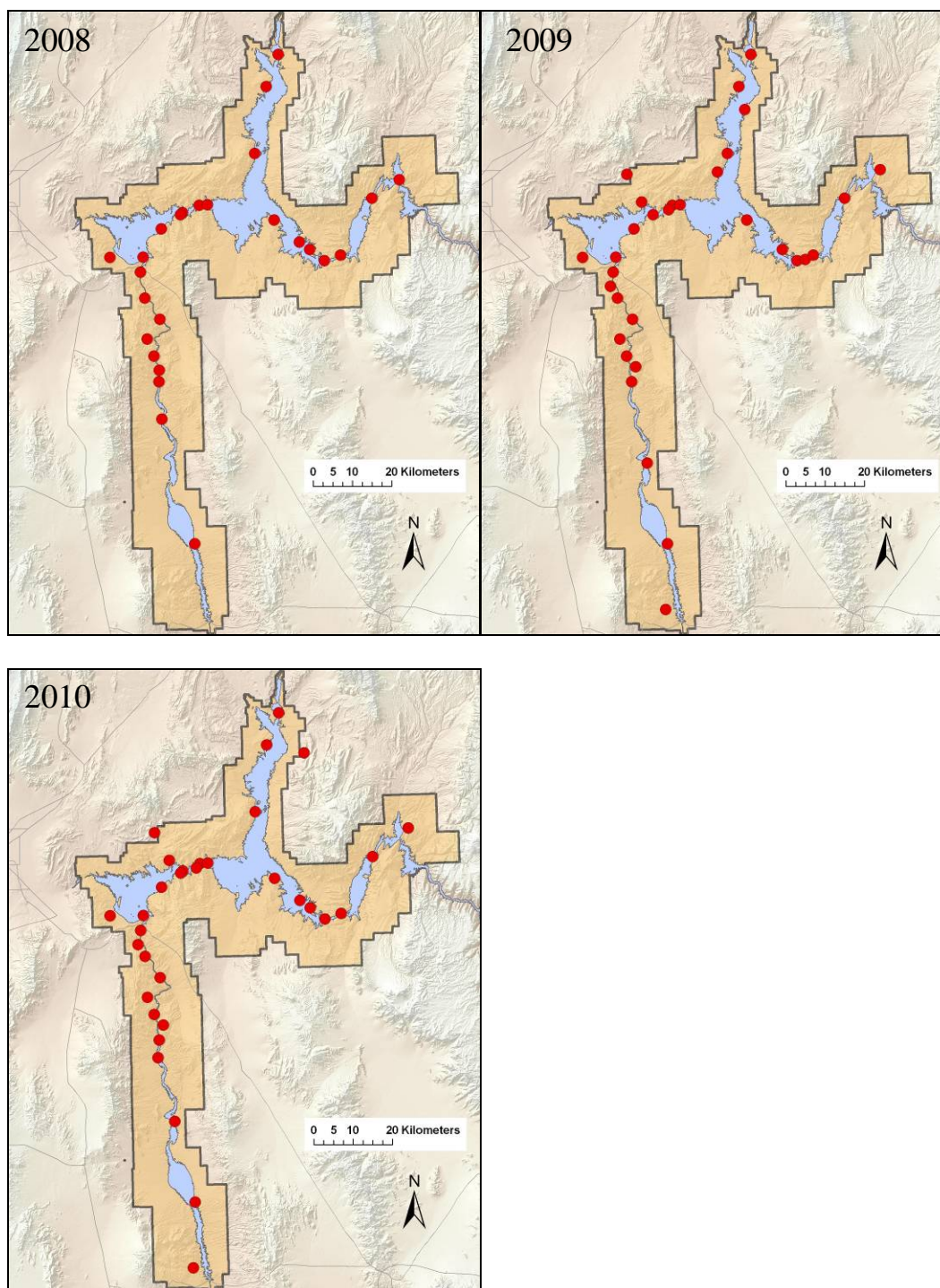
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APPENDIX 1. Dispersion, by year, of known Peregrine Falcon occupied territories at Lake Mead National Recreation Area. Red dots indicate occupied territories with ≥ 1 peregrine present during a portion of the breeding season.



APPENDIX 1 (continued). Dispersion, by year, of known Peregrine Falcon occupied territories at Lake Mead National Recreation Area. Red dots indicate occupied territories with ≥ 1 peregrine present during a portion of the breeding season.



APPENDIX 2. Selected studies of Peregrine Falcon breeding populations.

Location (years)	Successful young/breeding attempt	Successful young/successful breeding pair	Breeding success rate	Density (pair/km ²)	Mean nearest neighbor distance	Reference
LMNRA (2006-10)	1.74	2.46	71%	*1/122	6.3 km	This study
Arizona (1976-85)	1.7	2.27	73%			Ellis 1988
Utah (1984-85)	1.3	2.1				Enderson et al. 1988
Colorado (1984-85)	1.4	2.1				Enderson et al. 1988
Pennsylvania (1939-46)	1.3	2.3	80%			Rice 1969
Northwest Territories (1977)	2.2	2.95	84%	1/50		Calef & Heard 1979
Greenland (1981-85)	2.4	3.0		1/192	7.7 km	Mattox & Seeger 1988
Southern Greenland (1981-85)	1.8	2.7	73%	1/240		Falk & Moller 1988
Southern Alps (2002)	1.24	2.4	51.7%			Brambilla et al. 2004
Southern Alps (2002-04)				1/69.9	5.4 ± 0.609 km	Brambilla et al. 2005
Northern Spain (1996)	1.45	2.23	65%			Gainzarain et al. 2000
Northern Spain (1997)	1.44	2.12	68%			Gainzarain et al. 2000
Grand Canyon, Arizona (1988-89)				1/16.3		White et al. 2002
Britain (1945-61)				1/52.1	4.83 km	Ratcliffe 1962

*This number represents the number of known occupied territories/available land area in LMNRA (4025 km²) as of the 2010 breeding season. It likely does not account for an accurate density of the entire breeding population of peregrines within LMNRA, including some areas not surveyed as of 2010, nor from peregrines in neighboring regions.

APPENDIX 3. Frequency of prey taken by Peregrine Falcons within Lake Mead National Recreation Area from 2004-2010. Prey remains and observations were identified to the lowest possible taxa.

Prey	Weight (g)	Remains		Observations		
		Collected	Biomass (g)	Attempts	Successful	Biomass (g)
Canada Goose <i>Branta canadensis</i>	1978			1		
Mallard <i>Anas platyrhynchos</i>	1082			2		
Cinnamon Teal <i>Anas cyanoptera</i>	408			1	1	408
Teal spp. <i>Anas discors/cyanoptera</i>	386	3	1158	1		
Northern Shoveler <i>Anas clypeata</i>	613			1		
Green-winged Teal <i>Anas crecca</i>	341	1	341	2		
Ring-necked Duck <i>Aythya collaris</i>	730			1		
Merganser spp. <i>Mergus serrator/merganser</i>	1070	1	1070	1		
Ruddy Duck <i>Oxyura jamaicensis</i>	499			1	1	499
Duck (Anatidae) spp.				1		
Gambel's Quail <i>Callipepla gambelii</i>	166	4	664			
Eared Grebe <i>Podiceps nigricollis</i>	292	30	8760	13	2	584
Clark's/Western Grebe <i>Aechmophorus clarkii/occidentalis</i>	1477			1		
Double-crested Cormorant <i>Phalacrocorax auritus</i>	1674	3	5022	3		
Green Heron <i>Butorides virescens</i>	212	1	212			
White-faced Ibis <i>Plegadis chihi</i>	622	1	622	1		
American Kestrel <i>Falco sparverius</i>	116	3	348			
American Coot <i>Fulica Americana</i>	642	11	7062	19		
Killdeer <i>Charadrius vociferous</i>	97	1	97	1		
Black-necked Stilt <i>Himantopus mexicanus</i>	161	5	805			
American Avocet <i>Recurvirostra Americana</i>	316	2	632	1		
Spotted Sandpiper <i>Actitis macularius</i>	40			1		
Yellowlegs spp. <i>Tringa melanoleuca/flavipes</i>	126	1	126			

Long-billed Curlew <i>Numenius americanus</i>	587	2	1174	1		
Marbled Godwit <i>Limosa fedoa</i>	371	1	371			
Sanderling <i>Calidris alba</i>	57			1	1	57
Least Sandpiper <i>Calidris minutilla</i>	23	2	46			
Sandpiper spp. <i>Calidris minutilla/mauri/alba</i>	34			10	2	68
Dowitcher spp. <i>Limnodromus scolopaceus/griseus</i>	109	1	109			
Red-necked Phalarope <i>Phalaropus lobatus</i>	34	1	34			
Red Phalarope <i>Phalaropus fulicarius</i>	56	1	56			
Phalarope spp. <i>Phalaropus tricolor/lobatus/fulicarius</i>	50	2	100	1	1	50
Shorebird (Charadriiformes) spp.		1		2		
Ring-billed Gull <i>Larus delawarensis</i>	519	8	4152	3		
Gull spp. <i>Larus delawarensis/californicus</i>	563	2	1126	2		
Forster's Tern <i>Sterna forsteri</i>	158	1	158			
Tern spp. <i>Sterna hirundo/forsteri</i>	311	1	311	1		
Aquatic bird spp.				4		
Rock Pigeon <i>Columba livia</i>	355	1	355			
Eurasian Collared-Dove <i>Streptopelia decaocto</i>	149			5		
White-winged Dove <i>Zenaida asiatica</i>	153	3	459	7	2	306
Mourning Dove <i>Zenaida macroura</i>	119	39	4641	5	1	119
Dove (Columbidae) spp.	140	3	420	5	2	280
Lesser Nighthawk <i>Chordeiles acutipennis</i>	50	1	50	1		
White-throated Swift <i>Aeronautes saxatalis</i>	32	4	128	2	1	32
Belted Kingfisher <i>Megaceryle alcyon</i>	317			1		
Say's Phoebe <i>Sayornis saya</i>	21			3	1	21
Kingbird spp. <i>Tyrannus verticalis/vociferans</i>	43	4	172			
Loggerhead Shrike <i>Lanius ludovicianus</i>	47	3	141			
Common Raven <i>Corvus corax</i>	1199	2	2398			
Horned Lark <i>Eremophila alpestris</i>	31	1	31			
Northern Rough-winged Swallow <i>Stelgidopteryx serripennis</i>	16			2		
Cliff Swallow <i>Petrochelidon pyrrhonota</i>	22	6	132			

Swallow (Hirundinidae) spp.	17	1	17	10	6	102
Hirundinidae/Apodidae spp.	21	1	21	2	2	42
Cactus Wren <i>Campylorhynchus brunneicapillus</i>	39	1	39			
Rock Wren <i>Salpinctes obsoletus</i>	17	1	17	1	1	17
Canyon Wren <i>Catherpes mexicanus</i>	13	2	26			
Wren (Troglodytidae) spp.	23			3	1	23
Gnatcatcher unidentified <i>Poliophtila melanura/caerulea</i>	6	1	6			
Northern Mockingbird <i>Mimus polyglottos</i>	49	1	49	1		
Thrasher spp. <i>Toxostoma lecontei/crissale</i>	63	2	126			
European Starling <i>Sturnus vulgaris</i>	83	2	166			
Yellow Warbler <i>Dendroica petechia</i>	10	1	10			
<i>Oporornis</i> spp.	10	1	10			
Warbler (Parulidae) spp.	9	1	9			
Green-tailed Towhee <i>Pipilo chlorurus</i>	29	1	29			
Abert's Towhee <i>Melozone aberti</i>	46	1	46			
Black-throated Sparrow <i>Amphispiza bilineata</i>	14	1	14			
White-crowned Sparrow <i>Zonotrichia leucophrys</i>	28	1	28			
Western Tanager <i>Piranga ludoviciana</i>	28	4	112			
Red-winged Blackbird <i>Agelaius phoeniceus</i>	53	3	159	3		
Western Meadowlark <i>Sturnella neglecta</i>	101	1	101			
Yellow-headed Blackbird <i>Xanthocephalus xanthocephalus</i>	65			2		
Brewer's Blackbird <i>Euphagus cyanocephalus</i>	63	5	315			
Blackbird (Icteridae) spp.	60	2	120			
Great-tailed Grackle <i>Quiscalus mexicanus</i>	149	9	1341	11	6	894
Brown-headed Cowbird <i>Molothrus ater</i>	44	1	44			
Oriole spp. <i>Icterus parisorum/bullockii</i>	36	2	72			
House Finch <i>Carpodacus mexicanus</i>	21	3	63	1		
House Sparrow <i>Passer domesticus</i>	28	4	112			
Passeriformes spp.	38	1	38	45	22	836
Bird unidentified				22	2	

Bat spp. <i>Chiroptera</i> spp.	5	4	20	9	3	15
Desert spiny lizard <i>Sceloporus magister</i>		1				
Invertebrate unid.				1		
Common carp <i>Cyprinus carpio</i>		1				
Prey unid.				1		
Totals		217	46593	220	58	4353

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An Ecological Study of Peregrine Falcons (*Falco peregrinus*) at Lake Mead National Recreation Area, 2006-2010

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