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Authors: Barnes, Joseph G., Haley, Ross D., Thompson, Daniel B., and Jaeger, Jef R.

Source: Journal of Raptor Research, 49(3) : 269-280

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-14-39.1

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J. Raptor Res. 49(3):269–280
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ATTRIBUTES OF A BREEDING POPULATION OF PEREGRINE FALCONS ASSOCIATED WITH RESERVOIRS ON THE COLORADO RIVER

JOSEPH G. BARNES[1]
Public Lands Institute, University of Nevada, Las Vegas, NV 89154 U.S.A.

ROSS D. HALEY
National Park Service, Resource Management, Lake Mead National Recreation Area, Boulder City, NV 89005 U.S.A.

DANIEL B. THOMPSON AND JEF R. JAEGER
School of Life Sciences, University of Nevada, Las Vegas, NV 89154 U.S.A.

ABSTRACT.—We describe results from a comprehensive effort to survey and monitor Peregrine Falcons (*Falco peregrinus*) breeding in Lake Mead National Recreation Area (LMNRA) from 2006–2010. We identified 37 breeding territories, and the annual occupancy rate averaged 94%. Pooled over time, breeding success was 72%, and average reproductive output was 1.8 young per nesting attempt. The closest distance between eyries from neighboring territories was 1.2 km; the lowest annual mean nearest-neighbor distance (NND) was 6.3 km. No relationship was apparent between NND and breeding success or reproductive output. Nesting attempts occurred twice as often in eyries with a north-facing (68%) aspect than in eyries with a south-facing (32%) aspect. Pairs using south-facing eyries began incubating 5 d earlier than those using north-facing eyries, although the difference was not statistically significant. On a finer scale, pairs most commonly selected northwest-facing eyries (45% of nesting attempts), despite experiencing a trend of lower mean breeding success (64%) than in eyries with aspects facing all other quadrants (83%). Within territories, peregrines used alternate eyries following 58% of nesting attempts; however, switching eyries between years did not influence breeding success. Peregrines appear to be largely year-round residents at LMNRA, based on monthly surveys at five territories during a nonbreeding season (August 2008 through January 2009). We also detected peregrines at 10 of 24 territories in September and October 2009 using 10-min call-broadcast surveys at eyrie cliffs. Our results contribute to knowledge of increasing populations of peregrines following the DDT era in the southwestern U.S., and provide insight about how reservoirs may influence local breeding populations.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *breeding*; *demographics*; *eyrie characteristics*; *Mojave Desert*; *reservoir*.

ATRIBUTOS DE UNA POBLACIÓN REPRODUCTIVA DE *FALCO PEREGRINUS* ASOCIADA A EMBALSES EN EL RÍO COLORADO

RESUMEN.—Describimos los resultados de un esfuerzo exhaustivo de censo y seguimiento de individuos de *Falco peregrinus* que se reproducen en el Área Recreativa Nacional del Lago Mead (ARNLM) entre los años 2006 y 2010. Identificamos 37 territorios de reproducción, con una tasa de ocupación anual del 94% en promedio. Teniendo en cuenta toda la serie temporal, el éxito reproductivo fue del 72% y la productividad promedio fue de 1.8 pollos por intento de cría. La distancia más cercana entre nidos de territorios colindantes fue de 1.2 km; y la distancia media anual con el vecino más cercano (DMVC) fue de 6.3 km. No hubo una relación aparente entre la DMVC y el éxito reproductivo o la productividad. Los intentos de nidificación ocurrieron con el doble de frecuencia en los nidos con orientación norte (68%) que con orientación sur (32%). Las parejas que utilizaron nidos con orientación sur comenzaron a incubar cinco días antes que

[1] Present address: Nevada Department of Wildlife, 4747 Vegas Dr., Las Vegas, NV 89108 U.S.A.; email address: jbarnes@ndow.org

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aquellas parejas que utilizaron nidos con orientación norte, aunque la diferencia no fue estadísticamente significativa. A una escala más pequeña, las parejas eligieron con mayor frecuencia los nidos con orientación noroeste (45% de los intentos de nidificación), a pesar de evidenciar una tendencia hacia un éxito reproductivo promedio menor (64%) que en los nidos orientados hacia todos los otros cuadrantes (83%). Dentro de los territorios, los halcones utilizaron nidos alternativos en el 58% de los intentos de cría; sin embargo, el cambio de nido entre años no tuvo influencia en el éxito reproductivo. Basados en censos mensuales en cinco territorios durante la época no reproductiva (agosto 2008 a enero 2009), *F. peregrinus* parece ser, en gran medida, residente en el ARNLM. También detectamos individuos de *F. peregrinus* en 10 de los 24 territorios en septiembre y octubre de 2009, utilizando censos de 10 minutos con reclamo en los roquedos con nidos. Nuestros resultados contribuyen al conocimiento de las poblaciones en crecimiento de *F. peregrinus* tras la era del DDT en el suroeste de los Estados Unidos y proporcionan valiosa información sobre cómo los embalses pueden influir en las poblaciones reproductivas locales.

[Traducción del equipo editorial]

Peregrine Falcons (*Falco peregrinus*) were not known to breed in large numbers along the Arizona, Nevada, and California portions of the Colorado River prior to the latter half of the twentieth century (Bond 1946, Ellis and Monson 1989), although details of that time are poorly known. The lack of breeding records is somewhat surprising, considering the abundance of suitable nest cliffs, although few formal studies were conducted in the region before 1975 (Ellis and Monson 1989). Grinnell (1914) did not record peregrines along the lower Colorado River from southern Nevada to the Mexico border during a zoological expedition in 1910, nor did Bond (1946) cite evidence of them breeding upriver in the Grand Canyon during his western North American species assessment. A historical review by Ellis and Monson (1989) indicated there may have been four breeding sites along the lower Colorado River below the Grand Canyon before 1975, with six more probable breeding sites throughout northern Arizona. Ellis and Monson (1989) documented 41 confirmed or probable breeding sites throughout Arizona during surveys from 1975–1985, and they did not detect peregrines breeding downriver below the Grand Canyon. Correspondingly, little was known about peregrines in Nevada; only five breeding pairs were known throughout the state before the mid-1950s, after which they were thought to be extirpated statewide as a breeding species (Alcorn 1988).

Breeding populations of peregrines began recovering in North America after organochlorine pesticides, used prevalently from the 1940s to the early 1970s, were restricted in Canada and the U.S. (Mesta 1999). By the mid-1980s, the number of known breeding peregrines had increased dramatically throughout Arizona and southern Utah, including very high densities found within the Grand Canyon by 1989 (Brown et al. 1992, Enderson 2003). Lake Mead National Recreation Area (LMNRA) is just downriver of the Grand Canyon and comprises arid lands surrounding the impounded waters of Lake Mead and Lake Mohave, which cover 225 km of river channel along the Colorado and Virgin rivers (Turner et al. 2012; Fig. 1). The first known breeding pair of peregrines in LMNRA was discovered in 1985, representing the return of peregrines as a breeding species in Nevada (Alcorn 1988). Subsequent monitoring within LMNRA documented an increase to 16 known breeding territories by 2005 (Barnes 2011). Before 2005, monitoring largely focused on determining occupancy at breeding territories as they were discovered.

We studied Peregrine Falcons within LMNRA from 2006–2010. Our primary objectives were to provide an estimate of the breeding population size and to assess territory occupancy and reproductive output. We also describe eyrie characteristics, breeding chronology, and the year-round status of peregrines at LMNRA. This was the first comprehensive, large-scale study of peregrines breeding downriver of the Grand Canyon and, as such, the results are instrumental in understanding the extraordinary regional population increase documented since the mid-1980s, which was presumably facilitated by a regime shift in the avian assemblage from passerines to aquatic birds since the mid-1900s (Rosenberg et al. 1991).

METHODS

Study Area. The LMNRA (36°0.6'N, 114°47.8'W) consists of 4025 km^2 of land surrounding Lakes Mead and Mohave, and overlaps the state border between southern Nevada and northwest Arizona (Fig. 1). The lakes are large reservoirs along the Colorado and Virgin rivers, created in 1935 (Lake Mead) and 1951 (Lake Mohave; Turner et al. 2012). This area is located within the eastern Mojave Desert of the Basin and Range Province, an arid physiographic region characterized by narrow mountain ranges separated

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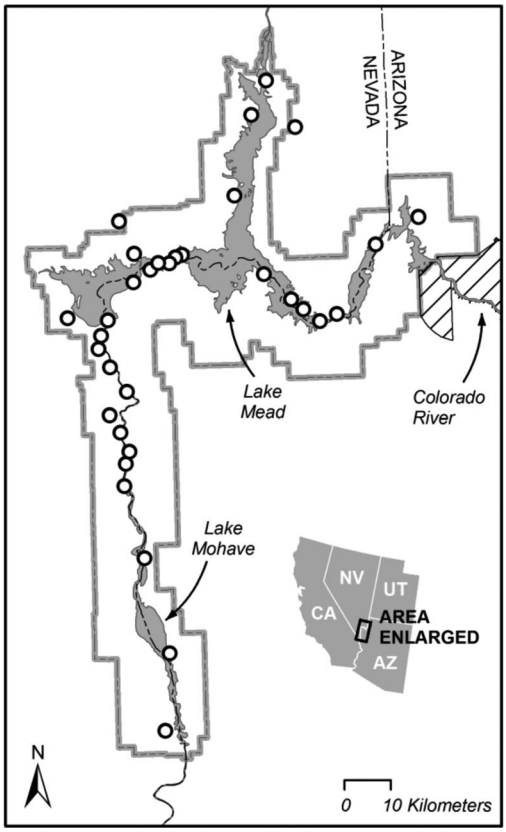


Figure 1. Distribution of Peregrine Falcon breeding territories in Lake Mead National Recreation Area (LMNRA), Nevada and Arizona, during the 2010 breeding season. The LMNRA boundary is shown by the dashed gray line. Open circles indicate occupied territories. The western extent of Grand Canyon National Park is designated by diagonal lines.

by broad basins with north–south orientation (Eaton 1982). Cliffs are widely distributed across LMNRA and are abundant in three tightly constricted canyons overlooking water (i.e., Black, Boulder, and Virgin canyons). Outside these rugged canyons, the topography tends to taper into open, sloping basins, with less frequent and generally lower cliffs. Elevations range from 192 to 1719 m. The area receives an average of <14 cm/yr of precipitation (Hereford et al. 2004), with extreme summer temperatures (July mean daily high = 45°C) and mild winters (January mean daily low = 1°C). Vegetation along slopes and canyons primarily consists of Mojave Desert scrub dominated by creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and brittlebush (*Encelia farinosa*). Narrow, intermittent strips of riparian vegetation line the shores of both lakes, represented typically by salt cedar (*Tamarix* spp.), coyote willow (*Salix exigua*), and arrowweed (*Pluchea sericea*).

Survey Methods. We attempted to search all suitable nesting habitat (i.e., continuous cliffs and sizable rock outcrops) within LMNRA for peregrine territories to estimate the breeding population. We monitored each known territory a minimum of once per breeding stage (i.e., courtship, incubation, nestling, fledgling) until we confirmed breeding success or failure. We determined breeding stage by observing behavioral cues (e.g., aerial courtship displays, incubating posture, and feeding young), but also assigned breeding stage to previous surveys by backdating after estimating the age of young. We generally conducted our surveys at distances of 150–800 m from the eyries (i.e., far enough to avoid eliciting territorial behavior from attendant individuals) using 10 × 42 binoculars or a 20–60× spotting scope. Most surveys were ground-based, but some involved boats. Surveys within the breeding season occurred from 16 March to 13 July in 2006, 29 January to 13 July in 2007, 6 February to 9 July in 2008, 10 February to 15 July in 2009, and 14 February to 2 July in 2010. We conducted exploratory surveys in areas we considered suitable for breeding peregrines (e.g., cliffs outside of known territories), while continuing to monitor suitable nesting habitat identified in previous years. We reached our maximum survey area by 2009.

We used a mix of passive and call-broadcast survey methods to determine territory occupancy and monitor breeding effort. Passive surveys followed recommendations presented in the U.S. Fish and Wildlife Service post-delisting monitoring plan (U.S.F.W.S. 2003), and consisted of at least one survey per breeding stage at each territory during peak daily activity periods (4 hr after sunrise and 4 hr prior to sunset). We used the 4-hr period as a guideline, and observed for at least 4 hr when we did not detect any peregrines. We sometimes extended surveys to collect additional reproductive and behavioral observations, and we ended surveys early when we had obtained the needed information. Our call-broadcast protocol consisted of two 30-sec broadcast periods within 10 min. We used conspecific vocalizations to facilitate detection of peregrines (Barnes et al. 2012), followed by passive monitoring to collect the necessary reproductive and behavioral observations. We ceased broadcasting immediately

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after detecting a peregrine response to minimize disturbance.

We evaluated the migratory status of peregrines nesting in LMNRA by conducting additional surveys at five territories during the nonbreeding season from 11 August 2008 to 21 January 2009. These monthly surveys consisted of 2-hr passive observations at eyrie cliffs. To further assess territory occupancy outside the breeding season, we conducted single, 10-min call-broadcast surveys at 24 territories from 23 September to 22 October 2009. To help distinguish resident territory holders from nonresident migrants during these surveys, we looked for behavior such as territorial displays or defense, cooperative hunting, and sharing prey as indicative of pair bonds between resident peregrines.

Occupancy and Reproduction. We monitored all known territories throughout the 2006–2010 breeding seasons to determine occupancy, breeding success, and reproductive output. We defined a territory as an area that contained ≥1 eyrie over time, in which only a single pair of peregrines was known to breed each year (Postupalsky 1974, Steenhof and Newton 2007), or that contained ≥1 adult (after second-year plumage) or subadult (second-year plumage) territorial peregrine during ≥2 surveys in a breeding season. We defined a territorial peregrine as one we observed defending an area against intruding conspecifics, other raptor species, or Common Ravens (*Corvus corax*), or one that exhibited defensive behaviors in response to the broadcast of conspecific calls (Barnes et al. 2012). During a given year, we considered a territory occupied when it contained at least one territorial peregrine during a portion of the breeding season (Ratcliffe 1993). In calculating the annual occupancy rate (the proportion of known territories that were occupied in a given year) we excluded territories in their first year of discovery.

When possible, we recorded the sex and age class (i.e., adult, subadult, fledgling, nestling) of each peregrine. We designated a nesting attempt when we observed a pair of peregrines (adult or subadult) copulating or exhibiting courtship or pair-bonding behavior during more than one survey (i.e., aerial or ledge courtship displays, cooperative hunting, or prey exchanges), or when we detected other evidence of reproduction (i.e., incubation posture, nestlings or fledglings present, or prey delivery to the eyrie). We estimated the age of nestlings based on a photographic guide (Clum et al. 1996), and then used published lengths of breeding stages (i.e., incubation = 30 d, nestling = 42 d) to calculate incubation, hatch, and fledge dates (Ratcliffe 1993). We considered nesting attempts successful when ≥1 nestling was ≥28 d old (U.S.F.W.S. 2003, Steenhof and Newton 2007). We considered nesting attempts to have failed when a pair previously observed engaged in a breeding attempt did not produce eggs, the eggs did not hatch, all nestlings were confirmed dead without reaching 28 d, or when eyries were verified empty by visual inspection prior to nestlings surviving to 28 d.

We included only nesting attempts detected in the early stages of the reproductive cycle (i.e., courtship or incubation) in calculations of breeding success and reproductive output, because nesting attempts discovered late are inherently biased toward successful pairs (Steenhof and Kochert 1982). We calculated apparent breeding success as the proportion of nesting attempts that were successful (Newton 1979, Steenhof and Newton 2007). We equated reproductive output ("productivity" in Steenhof and Newton 2007) with the number of young that reached ≥28 d, reported as the average number of young per nesting attempt.

Eyrie Characteristics and Density. We recorded survey points near eyries using a Global Positioning System (GPS), and estimated eyrie locations based on distance, height, and bearing from the survey points. We used a laser rangefinder (TruPulse 200 B, Laser Technology Inc., Centennial, Colorado, U.S.A.) with an accuracy of +/− 0.3 m for all distance and height measurements in the field. Whenever possible, we verified eyrie locations using a GPS while accessing eyries after each breeding season. We determined the aspect of eyries (corrected for declination) using a compass, directly from the eyrie rim, or by estimating the direction each eyrie faced from the base of the eyrie cliff. We grouped eyries by orientation into four quadrants: northeast (1–90°), southeast (91–180°), southwest (181–270°), and northwest (271–360°). For each eyrie, we determined if the scrape was sheltered by an overhang, and we estimated eyrie height from the cliff base and the total height of the eyrie cliff to the nearest m using the laser rangefinder's height calculation feature. We measured the shortest distance from each eyrie to the nearest permanent water (shoreline), and calculated nearest-neighbor distances (NND) between occupied eyries of adjacent territories, using Geographic Information System tools (ArcGIS v. 9.3, Environmental Systems Research Institute, Redlands, California, U.S.A.). When we did not detect

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an actual eyrie (i.e., cases with nonbreeding pairs, single territory holders, or where no eyrie was found), for measurement purposes we approximated a territory center as the area where we observed most peregrine activity throughout the breeding season.

Statistical Analysis. We evaluated variation in breeding success among years using a generalized linear model (GLM), with a binomial error term, year as a fixed effect, and territory as a random effect. In an effort to isolate reproductive output of successful breeding pairs from overall breeding success, we assessed variation in reproductive output among years using a mixed-model analysis of variance (ANOVA), with year as a fixed effect and territory as a random effect. We excluded unsuccessful territories from this analysis of reproductive output to avoid confounding the effects of breeding success and number of successful young. We permuted the number of young within each territory across years (999 permutations) to determine significance (Efron and Tibshirani 1993).

We produced additional models to assess physical characteristics of eyries relative to reproductive effort. We used GLMs to evaluate the influence of NND and distance to permanent water (continuous predictors), with a binomial error term for breeding success (yes or no response) and a multinomial error term for reproductive output (i.e., 0, 1, 2, etc., representing the number of young produced; Sokal and Rohlf 1995). We restricted these analyses to data from 2008–2010, the period during which adequate sampling provided data for territories far from water, and produced year-specific models to avoid pseudoreplication of territories surveyed in more than one year. We used independent GLMs to model the influence of overhang and eyrie aspect (categorical predictors) on breeding success and reproductive output. These models included presence/absence of an overhang, eyrie aspect (north-facing = 271–90° or south-facing = 91–270°), and the interaction between overhang and aspect as fixed effects, and territory as a random effect. For these analyses, we pooled eyrie aspect into north and south categories, instead of quadrants, to increase sample size and statistical power. We ran all GLMs using PROC MIXED in SAS 9.1 (SAS Institute, Cary, North Carolina, U.S.A.).

We used a chi-square goodness-of-fit test to determine if the distribution of peregrine eyries was nonrandom with respect to eyrie aspect by quadrant. We used Fisher's exact test to determine if use of eyries with an overhang varied depending on the eyrie aspect (quadrants). We used a complete, mixed-model ANOVA to determine if the presence of an overhang or eyrie aspect influenced when peregrines began incubating (hereafter ''incubation date''). For this analysis, we converted incubation dates to Julian dates for each nesting attempt, analyzed each year separately, and collapsed quadrants into north- or south-facing orientation to increase statistical power. We used a one-way ANOVA to evaluate interannual variation in estimated incubation dates. We ran these analyses using R 2.14.2 (R Development Core Team, Vienna, Austria).

We used a three-way chi-square analysis (Zar 1999) to evaluate whether the probability of breeding success in a given year depended on the previous year's breeding success and whether or not a change in eyrie location occurred between the two years. We also used a chi-square test to determine if the odds of an eyrie being moved depended on the reproductive output from the previous year. We used independent-samples *t*-tests to compare reproductive output at territories which did, or did not, move their eyrie in consecutive years, and to compare the mean distance eyries were moved within territories the following year after breeding success or failure.

We report means ± SD, unless otherwise indicated. We considered results significant at $P \leq 0.05$.

RESULTS

We conducted 238 exploratory surveys at 156 locations throughout LMNRA. The number of known peregrine territories increased from 16 to 37 between the 2006 and 2010 breeding seasons, an increase that was attributable, at least in part, to our finding previously unknown territories. The maximum number of occupied territories in a year was 33 in 2010 (Table 1; Fig. 1). The occupancy rate of known territories averaged 94% over the 5-yr study period (annual range 90–100%; Table 1). Pooled across years, subadults were present at only 3% of the occupied territories. Single subadults held territories throughout the breeding season on two occasions, and two adult/subadult mixed pairs nested but failed to fledge young.

We documented 117 nesting attempts, resulting in at least 197 young (≥28 d). We excluded 12 nesting attempts from calculations of breeding success and reproductive output, because we either discovered them late in the breeding season or we could not determine their fate. Annual breeding success ranged from 64–82%, averaged 72.4 ±

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Table 1. Occupancy, breeding success, and reproductive output at Peregrine Falcon breeding territories in Lake Mead National Recreation Area, Nevada and Arizona, 2006–2010. Numbers in parentheses indicate occupied territories and nesting attempts discovered late in the breeding season (i.e., late-incubation through fledgling stages); we excluded these cases from calculations of breeding success and reproductive output.

PARAMETER	2006	2007	2008	2009	2010	TOTAL
Occupancy rate (%)[a]	93.8	100	100	89.7	91.2	94.4
Occupied territories[b]	12 (8)	17 (8)	26 (2)	32	30 (3)	117 (21)
Nesting attempts[c]	11 (4)	14 (4)	24 (1)	28	28 (3)	105 (12)
Successful attempts[d]	9 (3)	9	16 (1)	20	22 (2)	76 (6)
Breeding success (%)[e]	81.8	64.3	66.7	71.4	78.6	72.4
Young/nesting attempt	1.4	1.6	1.5	2.0	2.0	1.8
Young/successful attempt	1.7	2.4	2.3	2.8	2.6	2.4
Successful young[f]	15 (6)	22	36 (3)	55	57 (3)	185 (12)

[a] Percentage of territories occupied each year, excluding those in their first year of discovery.
[b] Number of territories containing at least one territorial peregrine during the breeding season.
[c] Number of pairs observed copulating or courting during more than one survey, or when incubation or young were confirmed in the eyrie.
[d] Number of pairs that raised at least one young to 28 d or older.
[e] Percentage of nesting attempts with at least one young raised to 28 d or older.
[f] Total number of young raised to 28 d or older.

6.7% (Table 1), and did not vary significantly among years ($F_{4,68} = 0.39$, $P = 0.81$). Reproductive output averaged 1.8 ± 0.3 young per nesting attempt (range 1.4–2.0) and 2.4 ± 0.4 young per successful nesting attempt (range 1.7–2.8; Table 1). The number of young fledged per successful attempt was lower in 2006 than in 2009 and 2010 ($F_{4,42} = 3.30$, $P = 0.03$), with no other significant interannual differences.

Density. We found peregrine territory densities as high as one per 2.7 km^2 in localized canyons with abundant cliffs; however, such calculations are highly dependent on the extent of the area considered (i.e., it was unknown how far territories extended from the canyon walls). The minimum NND was 1.2 km (range 1.2–32.7 km). The mean annual NND for LMNRA varied little among years, from a high of 6.8 ± 7 km in 2006 to a low of 6.3 ± 6.4 km in 2008, and had no influence on breeding success or reproductive output from 2008–2010 (Table 2). The highest densities of Peregrine Falcon breeding territories occurred in canyons overlooking water, where cliffs suitable for nesting were not limiting. For example, five territories were occupied along a 7.8-km stretch of Boulder Canyon in 2010 (mean NND = 1.9 km); five territories were occupied along a 15.7 km stretch of Virgin Canyon in 2008 (mean NND = 2.6 km); and nine territories were occupied along a 40.4 km stretch of Black Canyon, between Lakes Mead and Mohave, in 2009 and 2010 (mean NND in 2010 = 3.9 km).

Eyrie Attributes. We detected 64 eyries within 32 territories at elevations ranging from 211–864 m (mean elevation = 503 m). All eyries were scrapes on ledges or in potholes. The height of eyrie cliffs averaged 100.2 ± 61.7 m (range 12–270 m), and the height of eyries above the cliff base averaged 66.4 ± 50.9 m (range 8–238 m). Eyries were an average of 886 m from permanent water (median = 161 m, range 1–9318 m); distance to permanent water had no effect on breeding success or reproductive output from 2008–2010 (Table 2).

A higher than expected proportion of eyries faced northward (70%, $n = 45$; 30% southward, $n = 19$; $\chi^2_3 = 19.12$, $P < 0.001$; Table 3). Nesting attempts were distributed similarly: 68% ($n = 63$) in north-facing eyries and 32% ($n = 30$) in south-facing eyries. Breeding success and reproductive output did not vary significantly between north-facing and south-facing eyries (Table 4). Most eyries (73%) had an overhang over the scrape. Peregrines did not appear to preferentially choose eyries with overhangs depending on the eyrie aspect (Table 4).

Alternate Eyries. We identified an average of two eyries per territory (range = 1–4), and recorded peregrines using individual eyries for up to 4 years during the five breeding seasons of our study (mean = 1.5 yr/eyrie). The greatest distance between alternate eyries within a territory was 1.5 km. Within territories, peregrines used an alternate eyrie the next year following 58% of nesting attempts. Alternate eyries were located an average of 200 m from

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Table 2. Effects of nearest-neighbor distance and distance to permanent water on the breeding success and reproductive output of Peregrine Falcons in Lake Mead National Recreation Area, Nevada and Arizona, 2008–2010. Results are from generalized linear model outputs with binomial error for breeding success and multinomial error for reproductive output. Each variable and year was analyzed independently.

		Breeding Success[a]			Reproductive Output[b]		
Effect	Year	df	*F*	*P*	df	*F*	*P*
Nearest-neighbor distance	2008	1, 23	0.02	0.893	1, 19	0.13	0.727
	2009	1, 26	1.02	0.322	1, 22	1.30	0.267
	2010	1, 29	0.22	0.640	1, 26	0.04	0.842
Distance to permanent water	2008	1, 20	2.53	0.127	1, 17	3.40	0.083
	2009	1, 25	1.42	0.245	1, 22	2.24	0.148
	2010	1, 22	<0.01	0.988	1, 19	0.10	0.759

[a] Percentage of pairs that raised at least one young to 28 d or older.
[b] Number of young raised to 28 d or older per nesting attempt.

the previous year's eyrie (range 3–647 m, $n = 33$). Alternate eyries were located farther away from the previous year's eyrie in territories that failed the previous year (mean = 319.2 m, SE = 93.7, $n = 6$) than in territories that were successful the first year (mean = 173.8 m, SE = 34.1, $n = 27$), but the difference was not significant ($t_{31} = 1.73$, $P = 0.09$). There were no significant associations among breeding success in one year, the movement of an eyrie, and success in the following year ($\chi^2_4 = 4.18$, $P = 0.38$). The likelihood that a pair shifted eyries also did not vary based on the number of young fledged the previous year ($\chi^2_3 = 2.44$, $P = 0.48$), and reproductive output did not vary depending on whether pairs did (mean = 2.19 ± 0.27 SE young per breeding attempt) or did not (mean = 2.39 ± 0.30 SE) move their eyrie ($t_{44} = 0.45$, $P = 0.66$).

Breeding Chronology and Annual Status. The estimated incubation dates for 73 breeding attempts where we were able to age the nestlings ranged from 15 March to 5 May, and averaged 5 April ± 12 d. The average incubation date did not vary among years ($F_{4,68} = 0.48$, $P = 0.75$), incubation date was not influenced by the presence of an overhang over the eyrie ($F_{1,39} = 0.002$, $P = 0.96$) or whether the eyrie faced north or south ($F_{1,39} = 1.31$, $P = 0.26$), and there was no interactive influence of overhang and aspect on incubation date ($F_{1,39} = 0.001$, $P = 0.98$). The difference between when the first and last pairs began incubating ranged from 33–52 d, depending on the year, and averaged 42 ± 8 d. Estimated hatch dates ranged from 15 April to 2 June, and averaged 6 May ± 12 d ($n = 73$). Assuming an average nestling period of 42 d (Ratcliffe 1993), estimated fledging dates ranged from 27 May to

Table 3. Peregrine Falcon reproductive characteristics in relation to the aspect of eyries used for breeding in Lake Mead National Recreation Area, Nevada and Arizona, 2006–2010. The number of nesting attempts and estimates of breeding success, reproductive output, and mean incubation dates were calculated based on data aggregated over the entire study period.

Eyrie Aspect	Eyries	Nesting Attempts[a]	Breeding Success (%)[b]	Young per Nesting Attempt (Mean ± SD)[c]	Incubation Date (Mean ± SD)[d]
Northeast	15	21	95.2	2.1 ± 1.0	5 April ± 10 d
Northwest	30	42	64.3	1.5 ± 1.4	7 April ± 11 d
Southeast	6	7	71.4	2.0 ± 1.7	2 April ± 13 d
Southwest	13	23	82.6	2.0 ± 1.3	1 April ± 14 d

[a] Number of pairs observed copulating or courting during more than one survey, or when incubation or young were confirmed in the eyrie.
[b] Percentage of pairs that raised at least one young to 28 d or older.
[c] Mean number of young raised to 28 d or older per nesting attempt.
[d] Mean date pairs began incubating.

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Table 4. Peregrine Falcon breeding success and reproductive output in relation to the presence/absence of an overhang over the eyrie and eyrie aspect (i.e., north-facing or south-facing) in Lake Mead National Recreation Area, Nevada and Arizona, 2006–2010. Results are from generalized linear model outputs with binomial error for breeding success, multinomial error for reproductive output, and territory as a random effect.

	Breeding Success[a]			Reproductive Output[b]		
Effect	df	*F*	*P*	df	*F*	*P*
Overhang	1, 16	0.03	0.869	1, 28	1.17	0.288
Aspect	1, 16	0.29	0.599	1, 28	0.63	0.435
Overhang×Aspect	1, 16	0.12	0.739	1, 28	0.16	0.690

[a] Percentage of pairs that raised at least one young to 28 d or older.
[b] Number of young raised to 28 d or older per nesting attempt.

14 July, and averaged 16 June ± 11 d (n = 70). We observed copulation throughout the breeding season (January–June, n = 43 events), with most instances (86%) occurring from February through April. Copulation occurred during courtship (n = 29), egg-laying (n = 6), incubation (n = 2), nestling (n = 2), and fledgling (n = 2) stages, and during periods when breeding stage was undetermined (n = 2).

Outside of the breeding season, we detected at least one peregrine during 26 of 30 monthly surveys conducted at five targeted territories from August 2008 to January 2009. We did not detect hatch-year peregrines at territories during this period. Four of the five territories were consistently occupied each month throughout the nonbreeding season, whereas at the fifth territory we failed to detect peregrines from November through January. Overall, pairs were present during 16 of 26 surveys in which we detected peregrines. The occupying peregrines appeared to have been residents, as they tended to perch within 100 m of the 2008 eyrie locations (25 of 26 surveys with peregrines detected), were vocal (n = 12), or engaged in territorial displays or defense of the eyrie cliff (n = 5). Pairs were often perched or flying together when present (n = 16), and we documented cooperative hunting (n = 5) and a single instance of food-sharing after a successful cooperative foraging attempt. We also detected adult peregrines near eyrie cliffs in 10 of 24 (42%) 10-min call-broadcast surveys conducted during the post-breeding period in 2009. When present, adults responded by taking flight or vocalizing during 6 of 10 broadcast surveys, which we interpreted as territorial defense elicited by our conspecific broadcasts.

Discussion

The attributes we describe of breeding Peregrine Falcons within LMNRA improve our understanding of their status and spatial distribution in the Mojave Desert of southern Nevada and northwest Arizona. Our results parallel increases in the number of occupied territories upriver on the Colorado River, documented since the mid-1980s as populations rebounded from lows attributed to the effects of DDE, the persistent metabolite of DDT (Brown et al. 1992, White et al. 2002, Enderson 2003). We are uncertain, however, about how much this current expansion of peregrines in LMNRA has resulted from anthropogenic habitat manipulation associated with the impoundment of water along the Colorado River since the 1930s (Glinski 1998, Stevens et al. 2009). As previously stated, peregrines had not been documented as breeders along the Colorado River downstream of the Grand Canyon in the early 1900s, before several large reservoirs were built in the area (Grinnell 1914). The creation of Lakes Mead and Mohave substantially altered faunal assemblages along the old river channel (Rosenberg et al. 1991), changes which appear to have favored breeding peregrines. These alterations provided open-water habitat that now supports vast numbers of wintering and migrating aquatic birds (Barnes and Jaeger 2012), which were not documented in earlier times (Rosenberg et al. 1991). In light of these changes, it is difficult to estimate the eventual size that the peregrine population may reach within LMNRA, and at what point density-dependent factors, including availability of nest cliffs, may limit population size.

Population Trend. The number of known peregrine territories within LMNRA increased from 16 in 2005 to 37 by 2010. Because our study was the first comprehensive survey conducted throughout LMNRA, it is difficult to determine to what extent the increase in territories we documented reflects an ongoing population increase versus discovery of

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previously overlooked territories. Nonetheless, on a more localized level, the nine occupied peregrine territories we documented in Black Canyon by 2009 was more than double the four territories known in 1991 (Glinski and Garrison 1992), and indicates a nearly 5% annual rate of increase over 18 yr.

We did not observe previously banded peregrines during our study, nor have any been observed since peregrines were first documented breeding in the area in 1985. Therefore, the role of immigration in our system is unknown. The large number of peregrines breeding in the Grand Canyon by the mid-to-late 1980s (Brown et al. 1992), and scarcity of other known breeding peregrines nearby, suggests dispersal from the Grand Canyon may have contributed to colonization in LMNRA. Because we did not mark individuals, we could not estimate demographic measures such as mortality rate, immigration, or age at first breeding. Thus, we are uncertain to what degree local reproduction drove the observed increase in the breeding population and, similarly, whether peregrines at LMNRA represent a source or sink in the context of a regional metapopulation. Nonetheless, the high levels of occupancy, breeding success, and reproductive output we documented likely represent an increasing population that may contribute to continued population growth in the region.

Lakes Mead and Mohave provide critical habitat for tens of thousands of migrating and wintering aquatic birds in an otherwise extremely arid region (Barnes and Jaeger 2012). These resources now provide resident peregrines with a nearly limitless and predictable prey base during much of the year; however, this food source is largely absent during the critical late-spring and summer months (i.e., May–July) when young peregrines are fledging and starting to forage independently. This temporal variation of prey availability may ultimately be a limiting factor controlling the size of the peregrine breeding population at LMNRA. Peregrines can also be limited by lack of suitable cliffs for nesting (Newton 1979, Ratcliffe 1993). As with other expanding or recovering populations (Ratcliffe 1993), peregrines in LMNRA are now nesting on ''marginal'' cliffs that previously were not selected for breeding (e.g., low cliffs with eroded and unstable structure).

The limited number of peregrines breeding away from water in LMNRA (only 28% of the documented breeding pairs used eyries >750 m from a shoreline) was likely influenced by the abundance of aquatic birds available as potential prey on the lakes, as well as the relative scarcity of terrestrial birds in the adjacent desert landscapes. Researchers in Arizona found significantly lower species richness and overall abundance of birds in desert uplands compared to adjacent riparian areas (Kirkpatrick et al. 2009). A low density of terrestrial prey near eyrie cliffs, together with energy demands associated with traveling from eyrie cliffs to forage at distant patches of open water, may restrict the number and density of peregrine territories that can be supported away from water in LMNRA and surrounding areas of the Mojave Desert.

Breeding Success and Reproductive Output. Peregrine breeding success and reproductive output in LMNRA did not differ by NND, suggesting density-dependent factors were not yet limiting breeding even in the densely populated canyons. The mean annual breeding success (72%) and relatively high reproductive output (1.8 young/pair) of LMNRA peregrines compare favorably to levels reported for expanding populations elsewhere in North America (White et al. 2002). An annual growth rate of 16%, average breeding success of 66%, and average reproductive output of 1.6 young per pair were reported in the Yukon-Tanana uplands in Alaska (Ritchie and Shook 2011). Similarly, average breeding success of 77% and reproductive output of 1.8 young per pair were reported for an expanding population in Montana, Wyoming, and Colorado (Enderson et al. 2012). In Colorado, a peregrine population was predicted to increase 3% per year with an average reproductive output of 1.7 young per pair, assuming no breeding by subadults and reasonable mortality rates in adults and subadults (Craig et al. 2004). Although we know little about mortality rates, age at first breeding, and dispersal in LMNRA, we can infer positive population status based on sustained high territory occupancy (94%), low incidence of subadult territory holders (3%), and high annual reproductive output.

Eyrie Attributes. Among other considerations, eyrie orientation varies by latitude, elevation, and prevailing weather conditions (Cade 1960, Ratcliffe 1993). Much of the variation in aspect can be interpreted as a means to ameliorate thermal extremes from sun exposure, or to avoid prevailing winds or weather patterns that can desiccate or chill eggs and young (Cade 1960, Grebence and White 1989, Craig and Enderson 2004). Our results indicate a preference for north-facing eyries, which was not surprising given the high-heat environment of our study area in the Mojave Desert. This observation supports the premise that extremes in solar insolation influence eyrie aspect (Grebence and White 1989).

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Although not a significant difference, we noted that peregrines using south-facing eyries began incubating on average nearly a week earlier than those using north-facing eyries, which could help offset the high temperatures experienced by nestlings. We did not, however, observe a discernible difference in the presence or degree of overhang above eyrie scrapes by aspect, nor was there a difference in reproduction by aspect. Curiously, peregrines in LMNRA exhibited a pattern of the lowest breeding success (64%) in eyries with the most frequently selected aspect by quadrant (i.e., 45% of all breeding attempts faced northwest). Clearly, additional research on microhabitat is needed to determine actual conditions experienced within eyries and to determine the importance of aspect in eyrie selection in a high-heat environment.

Our results agreed with those of other researchers, who found that breeding success one year did not influence the probability of peregrines returning to the same eyrie the following year (Ratcliffe 1993, Craig and Enderson 2004). Alternate eyries tended to be farther from the previous year's eyrie following a breeding failure (mean = 319 m) than when following a breeding success (mean = 174 m), but the pattern was not statistically significant. Clark and Shutler (1999) interpreted longer dispersal between breeding attempts by ducks after nest failure as an adaptive avoidance of sites associated with breeding failure. Because we did not mark individuals, we were unable to determine if the same individuals were involved in breeding attempts from one year to the next within territories. Barring elevated turnover or mortality rates, however, it is likely that at least one member of the pair remained.

Annual Status. Some peregrines are highly migratory, particularly those breeding at high latitudes, but they are markedly less migratory in temperate regions (Ratcliffe 1993, White et al. 2002). Whether birds migrate or remain sedentary during winter appears to be largely influenced by prey availability, and year-round residency is common when conditions allow (Newton 1979). Results from our nonbreeding season surveys suggest that breeding adults in LMNRA may be quite sedentary. Radio-tracking of peregrines in Black Canyon during the winters of 1990–1991 and 1991–1992 also indicated year-round residency (Glinski and Garrison 1992). Mild winters and the annual influx of large numbers of aquatic birds migrating and wintering on the lakes (Barnes and Jaeger 2012) likely provide the impetus for year-round peregrine residency in LMNRA.

Historical Context. The first known peregrine breeding territory within LMNRA was discovered in 1985, corresponding roughly with the discovery of large numbers of breeding pairs upriver in the Grand Canyon (Ellis and Monson 1989, Brown et al. 1992). The patchy nature of available nesting cliffs and extensive areas of open surface water found in LMNRA provide an interesting contrast to the near continuous presence of suitable peregrine nesting habitat found in the Grand Canyon, where tight canyon walls overlook the swift waters of the Colorado River and large terraced cliffs rise up to 1.5 km above the river (Brown et al. 1992). The relatively recent creation of Lakes Mead and Mohave in the otherwise arid environment of the Mojave Desert has enhanced the region's value as a migratory route for both terrestrial and aquatic birds (Rosenberg et al. 1991, Barnes and Jaeger 2012). This has increased the abundance and diversity of potential prey species, while rendering these birds vulnerable to predation by concentrating many of them along shorelines below eyrie cliffs. Peregrines have taken advantage of the human-influenced environment in LMNRA, which provides new insight into the mechanisms that have contributed to widespread population increases in the southwestern U.S. following the DDT era.

ACKNOWLEDGMENTS

We thank K. Turner for his support through the duration of this project. We are thankful for the five years of valuable field assistance from M. Urban. Assistance with statistical analyses was gratefully received from C. Vanier, and M. Sappington assisted with map preparation. Additionally, we thank E. Barnes, G. Jacobs, and J. Johnson for their insight and assistance with various aspects of our research. We are grateful for the constructive comments from three anonymous reviewers and J. Smith, which substantially improved this manuscript. This study was conducted under task agreement between the Public Lands Institute at the University of Nevada, Las Vegas (UNLV) and the National Park Service, and administered through the Great Basin Cooperative Ecosystem Studies Unit. Partial support for this project was provided by the Clark County Desert Conservation Program, with funding from the Southern Nevada Public Lands Management Act to further implement or develop the Clark County Multiple Species Habitat Conservation Plan. Methods were approved by the Animal Care and Use Committee, UNLV.

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Received 11 April 2014; accepted 16 December 2014
Associate Editor: Jeff P. Smith

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