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LONG-TERM REPRODUCTION (1984–2013), NESTLING DIET, AND EGGSHELL THICKNESS OF PEREGRINE FALCONS (*FALCO PEREGRINUS*) IN YELLOWSTONE NATIONAL PARK

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ABSTRACT.—Peregrine Falcons (*Falco peregrinus*) were extirpated from Yellowstone National Park (YNP) by 1970 as a result of widespread use of DDT (dichloro-diphenyl-trichloroethane) throughout North America from the late 1940s to the early 1970s. DDT, and its primary metabolite DDE (dichloro-diphenyl-dichloroethylene), caused eggshell thinning and impaired reproduction in Peregrine Falcons and other raptors. Restoration of Yellowstone's Peregrine Falcon population began with nationwide restrictions placed on the use of DDT in 1972, coupled with the release of 36 captive-raised juveniles in YNP and the dispersal of 644 captive-raised juvenile Peregrine Falcons released within 260 km of YNP. We monitored Peregrine Falcon reestablishment and reproductive success in YNP (nesting success, productivity, and brood size) from 1984–2013. Productivity was defined as the number of young reaching ≥28 d per territorial pair. Brood size referred to the number of young reaching ≥28 d per successful pair. From 2010–2013, we collected and analyzed prey remains and eggshell fragments from nine Peregrine Falcon territories across YNP. We documented a substantial increase in the number of occupied territories from one in 1984 to 32 by 2007, as well as high nesting success (74%), productivity (1.62 young/territorial pair), and brood size (2.18 young/successful pair) during 1984–2013. Nesting success, productivity, and brood size were at or above the target values identified by U.S.F.W.S. and those found for the Rocky Mountain/Great Plains region during the 2003 national survey. Peregrine Falcon eggshells collected at the nine eyries were 4% thinner than pre-1947 measurements (pre-DDT) and presumably indicate low DDE concentrations. Prey remains were dominated by birds (97% of individuals), mostly terrestrial species (63%) including American Robins (*Turdus migratorius*), Franklin's Gulls (*Leucophaeus pipixcan*), and Mountain Bluebirds (*Sialia currucoides*).

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *DDE*; *diet*; *eggshell thickness*; *nesting success*; *productivity*; *reproductive rates*; *Yellowstone National Park.*

REPRODUCCIÓN A LARGO PLAZO (1984–2013), DIETA DE POLLOS Y GROSOR DE LA CÁSCARA DEL HUEVO DE *FALCO PEREGRINUS* EN EL PARQUE NACIONAL YELLOWSTONE

RESUMEN.—*Falco peregrinus* desapareció del Parque Nacional Yellowstone (PNY) hacia 1970 como resultado del uso generalizado de DDT (dicloro-difenil-tricloroetano) a lo largo y ancho de América del Norte desde finales de los cuarenta hasta principios de los setenta. El DDT y su metabolito primario, el DDE (dicloro-difenil-dicloroetileno), provocaron un adelgazamiento de la cáscara del huevo y una disminución en la reproducción de *F. peregrinus* y de otras especies de aves rapaces. La restauración de la población de *F. peregrinus* en el PNY comenzó con una restricción nacional sobre el uso de DDT en 1972, junto con la liberación de 36 individuos criados en cautividad en el PNY y la dispersión de 644 individuos juveniles de

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F. peregrinus criados en cautividad, en un área que no se alejó a más de 260 km del PNY. Seguimos el restablecimiento y el éxito reproductor (éxito de nidificación, productividad y tamaño de la nidada) de *F. peregrinus* en el PNY desde 1984 hasta 2013. La productividad fue definida como el número de pollos que llegaron o superaron los 28 días de edad por pareja territorial. El tamaño de la nidada se refirió al número de pollos que llegaron o superaron los 28 días por pareja exitosa. Durante el periodo 2010–2013, recolectamos y analizamos restos de presa y fragmentos de cáscara de huevo en nueve territorios de *F. peregrinus* a través del PNY. Documentamos un incremento substancial en el número de territorios ocupados, de uno en 1984 a 32 en 2007, así como un elevado éxito de nidificación (74%), una elevada productividad (1.62 pollos/pareja territorial) y un elevado tamaño de la nidada (2.18 pollos/pareja exitosa) durante el periodo 1984–2013. El éxito de nidificación, la productividad y el tamaño de la nidada fueron igual o mayor que los valores objetivo identificados por el Servicio de Pesca y Vida Silvestre de los Estados Unidos (USFWS por sus siglas en inglés) y aquellos determinados para la región de las Montañas Rocosas/Grandes Planicies durante el censo nacional del 2003. Las cáscaras de huevo de *F. peregrinus* recolectadas en nueve nidos fueron más delgadas que las medidas antes de 1947 (pre-DDT) y probablemente indican bajas concentraciones de DDE. Los restos de presa estuvieron dominados por las aves (97% del total de individuos), la mayoría especies terrestres (63%), incluyendo a *Turdus migratorius*, *Leucophaeus pipixcan* y *Sialia currucoides*.

[Traducción del equipo editorial]

Peregrine Falcons (*Falco peregrinus*) were first noted in Yellowstone National Park (YNP) by naturalist Milton Skinner in 1914 (McEneaney et al. 1998). Although only six to eight territories were documented by the 1960s, Peregrine Falcons were probably more numerous in YNP than records indicate (Enderson and Burnham 1988, Oakleaf and Craig 2003). The lack of historical information in YNP is typical of the Rocky Mountains in general. Few historical data exist throughout the region primarily because of the remote and vast landscape over which Peregrine Falcons nest in the Rocky Mountains (Enderson 1965, Enderson and Craig 1974, Burnham et al. 1988).

Historical Peregrine Falcon territories were better known in the eastern U.S., and it was there that the first North American population declines were documented during the early 1950s (Hagar 1969, Rice 1969). Declines in eastern Peregrine Falcon numbers stimulated interest in western populations, including the largely unknown Rocky Mountain population. Enderson (1965) piloted the first widespread survey for Peregrine Falcons in the Rocky Mountains in 1964, but found only 13 of 47 known historical territories occupied from Colorado to Alberta. A second survey in 1973 (Enderson and Craig 1974) reported a similarly low occupancy rate in an area from northern New Mexico to southern Montana. In YNP, the last nesting territory became vacant in 1970 and the species was considered extirpated in the region by this time (Oakleaf and Craig 2003).

North America's Peregrine Falcon population reached its lowest point during the mid-1970s, with only 20% of all known historical territories occupied by a breeding pair (Enderson et al. 1995). Widespread use of DDT (dichloro-diphenyl-trichloroethane) from the late 1940s to the early 1970s was the principal factor responsible for the decline (Peakall and Kiff 1988). The accumulating effects of DDT's primary metabolite, DDE (dichloro-diphenyl-dichloroethylene), impaired reproduction by causing extreme thinning of eggshells (Ratcliffe 1967, Hickey and Anderson 1968). Because of these effects, the Peregrine Falcon was listed as endangered in 1970 under the Endangered Species Conservation Act of 1969, a precursor of the Endangered Species Act of 1973 (Peakall 1976).

Restrictions placed on the use of DDT in 1972, coupled with the reintroduction of more than 5000 captive-raised juvenile Peregrine Falcons in the U.S.A., led to their removal from the endangered species list in 1999 (U.S.F.W.S. 2003). YNP was the center for recovery efforts in Wyoming, Montana, and Idaho (Oakleaf and Craig 2003). Thirty-six captive-raised young were released in YNP at four sites (1983–1988). In addition, 644 captive-raised young were released within 260 km of YNP borders from 1980–1997 at 35 sites (W. Heinrich pers. comm.).

Oakleaf and Craig (2003) noted that in 1984 the last known occupied territory in YNP became reoccupied by a banded pair of Peregrine Falcons. The pair dispersed 80 km and 100 km, respectively, from their release sites to their new territory in YNP. The median distance between release sites and eventual nesting territories in Wyoming was 37 km for three males and 121 km for eight females that could be identified by reading leg bands in the field. The maximum distance was 75 km for males and 260 km for females (Oakleaf and Craig 2003).

Peregrine Falcon numbers in YNP continued to increase during 1988–1990 following reintroductions (Levine 1995), but the species' status in YNP has not been evaluated since that time. Furthermore, few data exist on eggshell thickness or nestling diet in YNP or for the northern Rocky Mountains in general, (but see Anderson and Hickey 1972, Enderson and Craig 1974, Enderson et al. 1988, Levine 1995). Because eggshell thickness is a proxy for DDE, it may be an important aid in the early detection of factors that may cause population declines.

The objectives of this study were to (1) determine trends in the number of nesting Peregrine Falcons, nesting success, productivity, and brood size during 1984–2013; (2) describe nestling diet during 2010–2013; and (3) compare eggshell thickness from samples collected in YNP during 2010–2013 to previously published measurements for the Rocky Mountains.

Methods

Study Area. YNP is an 8991-km^2 forested high plateau in northwestern Wyoming, southwestern Montana, and southeastern Idaho (Fig. 1). Elevation varies from 1605 m in the north to 3352 m along the eastern and northern boundaries (Despain 1990). Approximately 80% of YNP is forested and is dominated by lodgepole pine (*Pinus contorta*). Non-forested areas are dominated by big sagebrush (*Artemesia tridentata*) and Idaho fescue (*Festuca idahoensis*), particularly in the north (Despain 1990). YNP is characterized by long, cold winters and short, cool summers. Average temperature at Yellowstone Lake (south-central YNP) ranges from -11.8°C during winter (November–March) to 12.8°C during summer (July–August). Annual precipitation varies substantially park-wide depending on elevation. Lower-elevation areas in the north receive approximately 25–30 cm annually whereas southwestern YNP receives approximately 178 cm annually, most of which falls as snow (Despain 1990).

Nest Surveys. Park staff and volunteers searched for Peregrine Falcons in all historical territories and other potential, and reasonably accessible, nesting cliffs from 1984–2013. After a territory became occupied, we monitored it annually from 1984–2007. During 1984–2007, the expanding Peregrine Falcon population was documented by monitoring of occupied territories. In 2008, only five sites were monitored due to limited time and staff. From 2009–2013 we monitored a subset of all known territories. These included 10 randomly chosen territories selected by Wyoming Game and Fish as part of their monitoring effort and 13–19 additional territories selected for ease of access and to obtain broad coverage across YNP.

We visited most selected territories a minimum of three times during the breeding season: once in April to determine site occupancy, once in May to determine nesting location, and once in July to determine productivity. Because of the inaccessibility of some territories during April–June (i.e., deep snow or unfordable rivers) we made only one visit to these territories during late July or early August, after fledging. Field protocols were consistent with those outlined in the 2003 U.S. Fish and Wildlife Service monitoring plan (U.S.F.W.S. 2003).

We use reproductive terminology defined in Steenhof and Newton (2007) as follows; territorial pairs refers to the total number of mated pairs defending nesting territories within YNP. A nesting territory is an area that contains, or has historically contained, one or more nesting ledges within the home range of a mated pair. Nesting success was defined (U.S.F.W.S. 2003) per breeding season regardless of the number of breeding attempts made by that pair; productivity was defined as the average number of young reaching $\geq$28 d per territorial pair per breeding season, and brood size refers to the number of young reaching $\geq$28 d per successful pair per breeding season, where a successful pair is one that raises at least one young to $\geq$28 d. We were unable to calculate daily nest survival because prior to 2008 only the fate of each territorial pair was documented.

Statistical Analysis of Reproductive Rate. To test for trends in nesting success, productivity, and brood size we used generalized least squares regression with autocorrelated errors (Kutner et al. 2005). We tested for autocorrelation in all reproductive variables using the Durbin–Watson test and by examining plots of autocorrelation and plots of partial autocorrelation in the residuals (Kutner et al. 2005). We excluded the years 1984–1987 from analyses of nesting success, productivity, and brood size because only one territory was occupied during these years; however, we plot the full dataset (1984–2013) for all variables.

Prey Remains and Eggshell Thickness. We collected eggshell fragments, prey remains, and pellets from one to three ledges at each of nine Peregrine Falcon territories post-fledging during August–October of

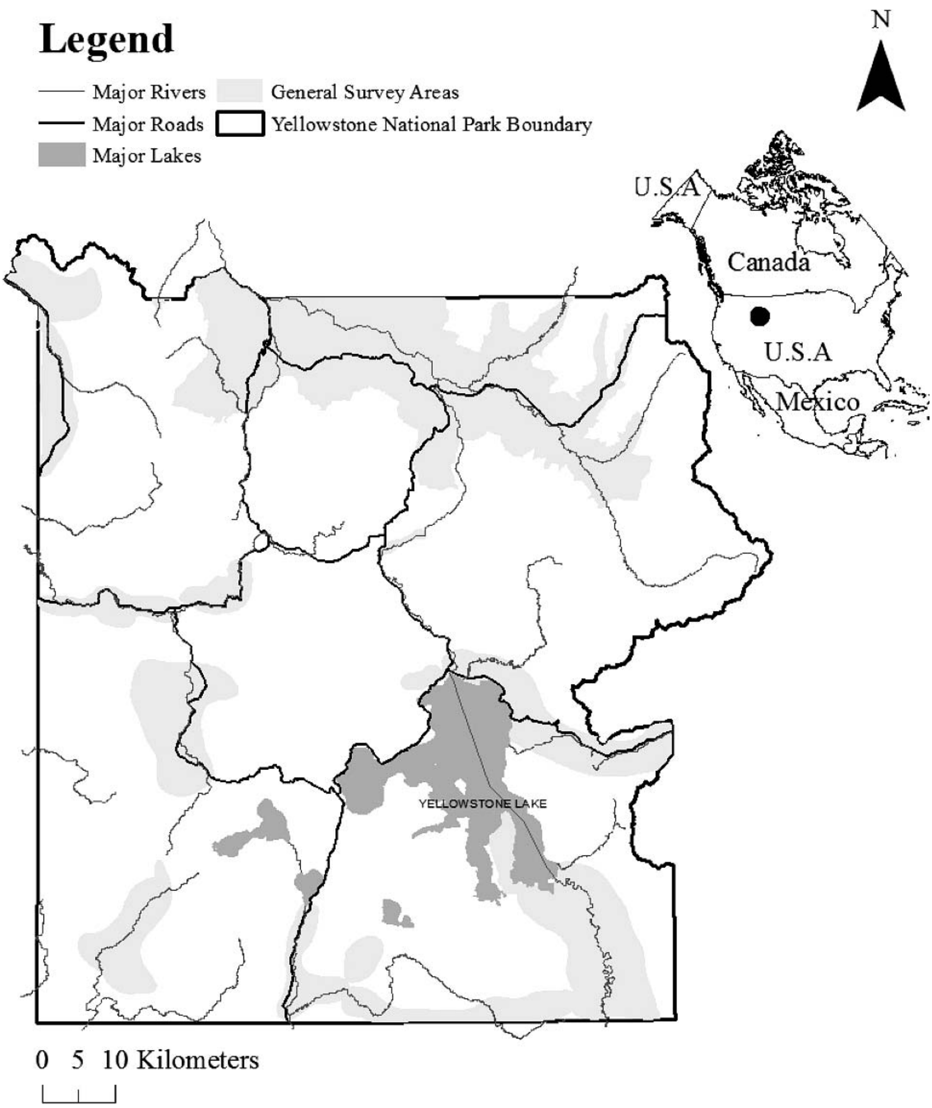

Figure 1. Location of areas in Yellowstone National Park, Wyoming, U.S.A. where trends in Peregrine Falcon reproduction (territorial pairs, nesting success, productivity, and brood size) were examined from 1984–2013.

2010, 2011, and 2013 using standard nest entry and collection techniques (Pagel and Thorstrom 2007). Prey remains (e.g., feathers, bones) and pellets were placed in zipper bags and labeled for later identification and quantification (by N. John Schmitt of the Western Foundation of Vertebrate Zoology [WFVZ], Camarillo, California, U.S.A.).

We determined the minimum number of individuals taken by duplication of remiges, rectrices, and body parts (e.g., feet, bills, bones) from the same species. For example, if two left wings and one right wing of the same species were collected from an eyrie, then we counted it as two individuals. Pellets were not included in our analysis.

Eggshell fragments and addled eggs were collected in the surface of the eyrie or sieved from the substrate and then placed in glass I-chem™ jars and labeled. Fragments were sent to the WFVZ for thickness measurements and storage. Fragments were measured using a Starrett™ digital gauge mounted to a Federal™ "35" micrometer. To account for variability in thickness within a sample

(Burnham et al. 1984), 10 fragments were selected randomly from each sample jar, recorded to the nearest 0.001 mm, and averaged. We added an average membrane thickness of 0.078 mm for all samples that did not contain a membrane (Burnham et al. 1984).

We compared samples collected in 2010, 2011, and 2013 to published data from four time periods throughout the Rocky Mountains: (1) pre-1947 or baseline (Anderson and Hickey 1972); (2) 1968–1973 or decline (Enderson and Craig 1974); (3) 1973–1976 or decline (Enderson et al. 1988); and (4) 1988–1989 or recovery (Levine 1995). We calculated percent thinning against pre-1947 eggshell thickness of 0.359 mm for eggshells collected in Alberta, Saskatchewan, and Montana because this time period represented eggshell thickness prior to the effects of DDE (Anderson and Hickey 1972).

Anderson and Hickey (1972) measured Peregrine Falcon eggshells to the nearest 0.001 mm using a hand micrometer. Enderson and Craig (1974), Enderson et al. (1988) and Levine (1995) used an ocular scale calibrated with a stage micrometer with an accuracy of 0.004 mm. Although less sophisticated than our measurements, they nevertheless provided a useful comparison.

Results

The number of territorial pairs of Peregrine Falcons in YNP increased from one pair in 1984 to 32 pairs by 2007, reaching a density in YNP of 1 pair/278 km^2, and there was no indication that the population had stabilized by 2007 (Fig. 2). Beginning in 2008, we monitored a subset (five in 2008 and 23–29 from 2009–2013) of all known regular territories (i.e., known territories that are occupied in most years; Steenhof and Newton 2007); therefore, the apparent decline in the number of territorial pairs was the result of less intensive monitoring post-2007. Occupancy rate for individual territories monitored $\geq$10 yr averaged 95% and ranged from 55–100%. From 1983–2013 annual occupancy ranged from 33% to 100% with an average of 87%. Most (64%) territories were occupied for 10 or more years.

We located an average of two newly occupied territories per year from 1984–2007, and the average number of territories located increased until 2005. Once a territory became occupied it usually remained occupied for the duration of the study; however, seven territories were abandoned between 2008 and 2013. All recently abandoned territories were occupied between three and 10 consecutive years and were first discovered during the last 12 years. Three territories were last occupied in 2007 and were occupied for three, four, and six consecutive years. An additional three territories were last occupied in 2009 and were occupied for four, seven, and 10 consecutive years. The remaining territory was occupied by a pair of Peregrine Falcons from 2006–2010, then a single adult in 2011 and 2012, and none in 2013. We observed partnering of an adult peregrine with a subadult peregrine in each of two years: 2010 and 2013. In 2013, a single subadult peregrine occupied a territory that had been vacant for the previous three years.

Trends in Reproduction. Nesting success and productivity were highly variable from 1988–2004, but were less variable post-2004. Brood size increased in variability post-2003. The Durbin–Watson test for trends in nesting success, productivity, and brood size indicated a significant autocorrelation at lag 1 ($P < 0.05$); therefore, we included a lag 1 autocorrelation in our trend analyses. There were no trends in annual nesting success from 1988–2013 ($T = -1.35$, $n = 26$, $P = 0.19$). Nesting success from 1988–2013 averaged 74% with a range of 40% in 1989 to 96% in 2003 ($n = 26$, SE = 0.54; Fig. 2). There were no significant trends in productivity from 1988–2013 ($T = 0.38$, $n = 26$, $P > 0.05$). Productivity (1988–2013) ranged from 0.60 young/territorial pair in 1989 to 2.18 young/territorial pair in 1996 with a mean of 1.62 ($n = 26$, SE = 0.02). No trend in brood size was apparent from 1988–2013 ($T = 1.04$, $n = 26$, $P > 0.05$). Brood size ranged from 1.33 young/successful pair in 1988 to 2.50 young/successful pair in 2008 with a mean of 2.18 ($n = 26$, SE = 0.32).

Prey Remains. Prey remains collected in 2010, 2011, and 2013 included 186 individuals representing at least 40 species (Table 1). Approximately 80% of the individuals could be identified to species with the remaining 20% identified to genus, family, or groups (e.g., passerines, shorebirds, fish). Nearly all (97%) prey remains were birds and more than half (53%) of the samples identified to species were represented in at least two of the three sample years, and most were terrestrial birds (63%) or shorebirds (22%).

The most frequently detected prey item identified to species was the American Robin (*Turdus migratorius*) representing 11% of the total individuals, followed by Franklin's Gull (*Leucophaeus pipixcan*) at 8%, Mountain Bluebird (*Sialia currucoides*) at 6%,

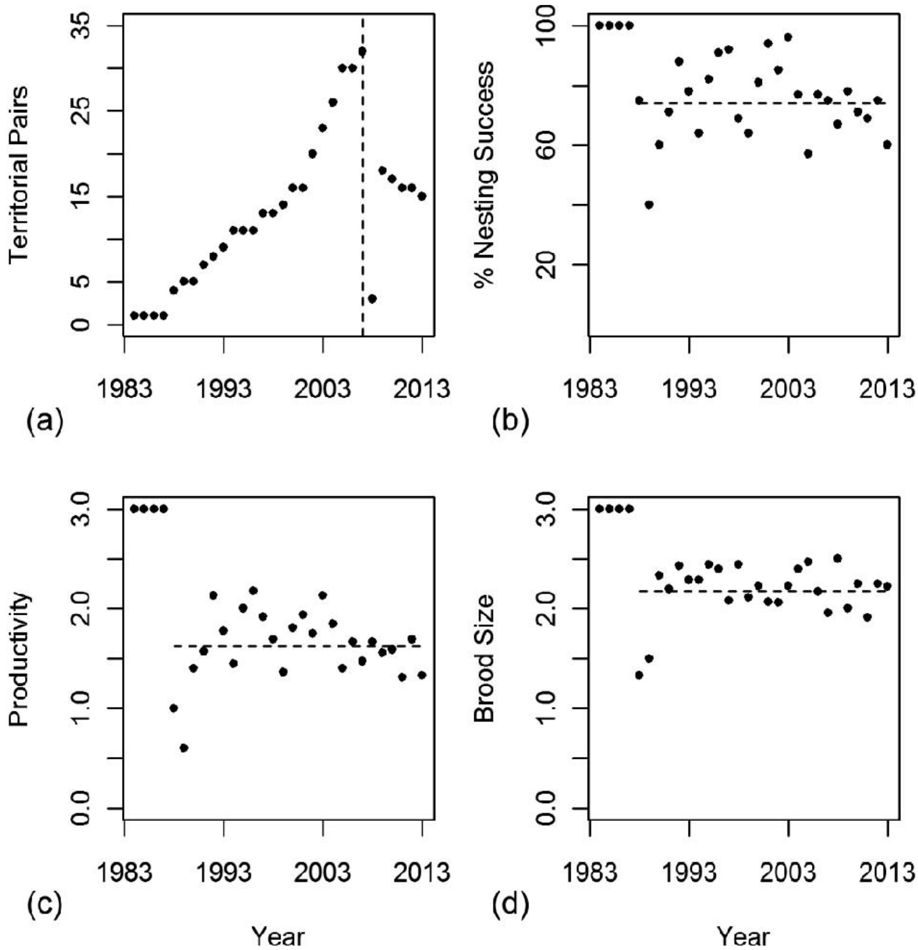

Figure 2. Trends in Peregrine Falcon (a) territorial pairs, (b) nesting success, (c) productivity, and (d) brood size in Yellowstone National Park, Wyoming, U.S.A. from 1984–2013. For nesting success, productivity, and brood size, the mean shown excludes 1984–1987 because only one pair of Peregrine Falcons occupied a nesting territory during this time. Only a subset (five in 2008 and 23–29 from 2009–2013) of all known territories was monitored post-2007, as indicated by the vertical dashed line in "a".

and Red-necked Phalarope (*Phalaropus fulicarius*) at 6%, Northern Flicker (*Colaptes auratus*) at 5%, and Wilson's Phalarope (*Phalaropus tricolor*) at 5% of the total. All other species were represented by six or fewer individuals and are grouped by family.

Ten prey species, representing 24% of the total individuals, are nonbreeders in YNP and are rarely observed during migration according to the YNP species checklist. Red Phalarope (*P. fulicarius*), for example, has no reported records in YNP. Notable prey included four individual fish collected from two territories as well as the remains of a pine marten (*Martes americana*) from one territory (Pagel and Schmitt 2013).

Eggshell Thickness. During 2010, 2011, and 2013 we collected eggshell fragments from nine territories in YNP (Table 2). Mean thickness for eggshell fragments collected during 2010, 2011, and 2013 was 0.347 mm ± 0.017 SD (Table 2). When compared with the pre-1947 mean thickness (Enderson and Craig 1974), YNP eggshells were 4% thinner. Eggshell thickness in YNP ranged from 0.310 mm to 0.378 mm, with thinning ranging from 14% thinner to 5% thicker than pre-1947 thickness. In 2011,

Table 1. Total individuals and percent frequency of prey remains by category collected from nine Peregrine Falcon eyries in Yellowstone National Park, Wyoming, U.S.A. from 2010–2013.

Prey Category	Individuals (%)
American Robin (*Turdus migratorius*)	20 (11)
Franklin's Gull (*Leucophaeus pipixcan*)	14 (8)
Mountain Bluebird (*Sialia currucoides*)	12 (6)
Red-necked Phalarope (*Phalaropus fulicarius*)	12 (6)
Northern Flicker (*Colaptes auratus*)	9 (5)
Wilson's Phalarope (*Phalaropus tricolor*)	9 (5)
Other Scolopacidae spp.[a]	13 (7)
Icteridae spp.[b]	13 (7)
Other Picidae spp.[c]	11 (6)
Fringillidae spp.[d]	9 (5)
Other birds[e]	59 (32)
Other animals[f]	5 (3)
Total	**186 (100)**

[a] Includes Red Phalarope (*Phalaropus fulicarius*; $n = 2$), Marbled Godwit (*Limosa fedoa*; $n = 2$), Lesser Yellowlegs (*Tringa flavipes*; $n = 1$), *Limnodromus* spp. ($n = 5$), *Tringa* sp. ($n = 1$), *Phalaropus* sp. ($n = 1$), *Limosa* sp. ($n = 1$).

[b] Includes Red-winged Blackbird (*Agelaius phoeniceus*; $n = 6$), Common Grackle (*Quiscalus quiscula*; $n = 2$), Brewer's Blackbird (*Euphagus cyanocephalus*; $n = 2$), Western Meadowlark (*Sturnella neglecta*; $n = 2$), Brown-headed Cowbird (*Molothrus ater*; $n = 1$).

[c] Includes Hairy Woodpecker (*Picoides villosus*; $n = 3$), Williamson's Sapsucker (*Sphyrapicus thyroideus*; $n = 2$), Three-toed Woodpecker (*Picoides dorsalis*; $n = 1$), *Sphyrapicus* sp. ($n = 1$), *Picoides* spp. ($n = 4$).

[d] Includes Pine Siskin (*Carduelis pinus*; $n = 2$), Red Crossbill (*Loxia curvirostra*; $n = 2$), Evening Grosbeak (*Coccothraustes vespertinus*; $n = 1$), Cassin's Finch (*Carpodacus cassinii*; $n = 1$), *Carpodacus* sp. ($n = 1$), Fringillidae sp. ($n = 1$).

[e] Includes *Aythya* spp. ($n = 2$), *Bucephala* sp. ($n = 1$), Green-winged Teal (*Anas crecca*; $n = 1$), American Kestrel (*Falco sparverius*; $n = 4$), American Coot (*Fulica americana*; $n = 1$), Virginia Rail (*Rallus limicola*; $n = 1$), Killdeer (*Charadrius vociferous*; $n = 2$), American Avocet (*Recurvirostra americana*; $n = 1$), Shorebird spp. ($n = 3$), Ring-billed Gull (*Larus delawarensis*; $n = 2$), Common Nighthawk (*Chordeiles minor*; $n = 1$), Eastern Kingbird (*Tyrannus tyrannus*; $n = 2$), Unidentified *Tyrannus* sp. ($n = 1$), Clark's Nutcracker (*Nucifraga columbiana*; $n = 7$), Horned Lark (*Eremophila alpestris*; $n = 2$), Tree Swallow (*Tachycineta bicolor*, $n = 4$), Barn Swallow (*Hirundo rustica*; $n = 2$), Unidentified Hirundinidae spp. ($n = 2$), Townsend's Solitaire (*Myadestes townsendi*; $n = 3$), Unidentified Turdidae ($n = 1$), Cedar Waxwing (*Bombycilla cedrorum*; $n = 1$), European Starling (*Sturnus vulgaris*; $n = 5$), Western Tanager (*Piranga ludoviciana*; $n = 2$), Unidentified Emerizidae ($n = 1$), Unidentified Passerine ($n = 5$).

[f] Includes Pine Marten (*Martes americana*; $n = 1$), Unidentified Salmonidae ($n = 1$), Unidentified fish ($n = 3$).

Table 2. Peregrine Falcon eggshell thickness in Yellowstone National Park (YNP), Wyoming, U.S.A. from 2010–2013 compared with previous studies in the Rocky Mountains. GYA (Greater Yellowstone Area) refers to the tri-state region of Montana, Idaho, and Wyoming centered on Yellowstone and Grand Teton National Parks.

Location	Year	Mean Thickness (mm ± SD)	% Thinning
YNP	2010–2013 ($n = 24$)	0.347 ± 0.017	4%
GYE[a]	1988–1989 ($n = 15$)	0.317 ± 0.027	12%
Southern Rockies, U.S.A.[b]	1973–1976 ($n = 34$)	0.301[e]	16%
Central Rockies, U.S.A.[c]	1968–1973 ($n = 9$)	0.292 ± 0.016	19%
Alberta, CA; Saskatchewan, CA; Montana, U.S.A.[d]	Pre-1947	0.359 ± 0.005[f]	baseline

[a] Levine (1995).

[b] Enderson et al. (1988).

[c] Enderson and Craig (1974).

[d] Anderson and Hickey (1972).

[e] Variability not reported.

[f] Mean ± 95% confidence limits.

eggshells ($n = 6$) were the least thin, with a mean thickness of 0.358 mm, only 0.3% thinner than pre-1947 levels. Percent thinning declined by 15 percentage points from pre-1947 measurements to eggshells sampled during 2010–2013, with the greatest declines in thinning occurring between 1988–1989 and 2010–2013.

DISCUSSION

The number of occupied Peregrine Falcon territories in YNP increased from one territory in 1984 to 32 territories by 2007. Peregrine Falcons increased in YNP in response to restrictions placed on the use of DDT in 1972, the release of 36 juvenile Peregrine Falcons in YNP, and dispersal of 644 captive-raised young released within 260 km of the borders of YNP from 1980–1997 (W. Heinrich pers. comm.). The reintroductions of Peregrine Falcons in and around YNP were the primary source for recovery because most Peregrine Falcons in newly occupied territories were banded (Levine 1995); however, as the number of territorial pairs grew, recruitment from unbanded birds contributed to growth in the region (Oakleaf and Craig 2003).

Similar trends occurred throughout the Rocky Mountains as Peregrine Falcons responded to recovery efforts. In Colorado, the number of occupied territories increased from fewer than 25 territories in 1985 to 115 territories by 2001 (Craig and Enderson 2004, Enderson et al. 2012) and in Montana the number of occupied territories increased from 28 territories in 1999 to 147 by 2013 (J. Sumner pers. comm.). In Wyoming, 90 Peregrine Falcon territories were on record by 2009, 30 of which are in YNP (Enderson et al. 2012).

Overall, occupancy of known Peregrine Falcon territories in YNP averaged 87% during 1984–2013, slightly above the target value of 84% identified by U.S.F.W.S. (2003). In Colorado, Montana, and Wyoming, occupancy varied between 75% and 100% during 2005–2009, but varied widely within years and among states (Enderson et al. 2012). In this study, occupancy also varied widely, probably due to small sample size, and declined slightly in recent years. Seven previously occupied territories were abandoned by 2012 and only one additional territory was located post-2007 despite extensive surveys for other cliff-nesting raptors (i.e., Golden Eagles [*Aquila chrysaetos*]) and Prairie Falcons [*F. mexicanus*]) throughout YNP during 2011–2013. However, three Peregrine Falcon territories were discovered in 2014 (data not included in this study).

In two of the seven abandoned Peregrine Falcon territories, Golden Eagles began nesting on the main cliff the year of abandonment or post-abandonment. One of these territories was occupied by a pair of Peregrine Falcons from 2006–2009 and the other from 2005–2007. In a third territory (occupied from 2004–2007), Peregrine Falcons nested within 2.8 km and within direct view of an established Golden Eagle territory that has been occupied since at least 1999 (J. Sumner pers. comm.). The Peregrine Falcon pair abandoned this territory after 4 yr despite successfully fledging young annually. Peregrine Falcons tend to avoid areas occupied by Golden Eagles as a means of predator avoidance and this may explain abandonment of these three territories (Poole and Bromley 1988, Gainzarain et al. 2000).

In two territories, human disturbance may have caused abandonment. Both territories are at the base of a popular waterfall with thousands of tourists visiting annually from June through August. One pair successfully fledged young from 2002–2004, but failed the last 3 yr. The other was occupied from 2000–2009 and successfully fledged young in all but 2 yr. Another abandoned territory, occupied from 2003–2009 and successful in all but 1 yr, is a small rocky outcropping accessible to ground predators, which may explain abandonment there. There was no obvious explanation for why the remaining Peregrine Falcon territory was abandoned. It is a large cliff that was occupied by a pair of Peregrine Falcons for 5 yr (2006–2010), then by only one adult for the next 2 yr before it became unoccupied.

Attrition of some nesting territories is expected as some become unsuitable or pairs relocate to nearby cliffs (Craig and Enderson 2004). Attrition also can occur, at least temporarily, as a result of normal mortality of adults (Craig and Enderson 2004). Despite the loss of some territories, a previously unknown territory was discovered in 2011 and three new territories were discovered in 2014 (data not included in this study). Overall, we observed a net loss of three territories since surveys began in 1984 which, given the length of occupancy for most territories (64% occupied at least 10 yr), is probably not significant. The discovery of new territories highlights the importance of revisiting previously surveyed, but vacant, cliffs and searching for new territories, as well as revisiting territories apparently abandoned, to avoid misinterpreting the significance of abandoned territories.

Partnering of an adult peregrine with a subadult peregrine may be a cause for concern, as it may indicate a small adult floating population. We observed this in at least two cases and we also recorded a third case in which a single subadult peregrine colonized a vacated territory for two consecutive years. Prior to 2008, the age of territorial pairs was not recorded, so it is difficult to interpret these data over the short-term; however, the observation warrants continued monitoring.

We found no trend in nesting success, productivity, or brood size from 1988–2013 and all reproductive measures remained at or above the target values identified by U.S.F.W.S. and those found for the Rocky Mountain/Great Plains region during the 2003 national survey (U.S.F.W.S. 2003). Productivity of 1.5 young/pair is thought to be necessary to maintain a stable or increasing population (Craig and Enderson 2004). Productivity for Peregrine Falcons in YNP averaged 1.62 from 1988–2013. We found similar results for nesting success and brood size.

Peregrine Falcons in YNP appeared not to prey particularly on any one species, at least while feeding nestlings. Prey remains collected from territories in YNP from 2010–2013 indicate a nestling diet composed largely of terrestrial bird species (63%) and shorebirds (22%). American Robins, the most common prey item, represented just 11% of the total individuals. The remaining individuals identified to species each represented less than 5% of the total and most represented <1%. Our results were similar to those found in other studies (Hunter et al. 1988, Craig and Enderson 2004). The presence of Red Phalarope feathers in one of the eyries revealed a species not previously documented in YNP, but perhaps most surprising were the pine marten leg (Pagel and Schmitt 2013) and the fish remains, probably stolen from nearby nesting Ospreys (*Pandion haliaetus*).

The relatively high percentage (8%) of Franklin's Gulls found on at least one ledge in 2010, 2011, and 2013 in eight of the nine territories where prey remains were collected was somewhat surprising, because it is considered a rare summer resident in YNP, but prey behavior plays a role in susceptibility to predation (Hunter et al. 1988). Franklin's Gulls are relatively large, white birds that flock together and would be easily visible to a hunting Peregrine Falcon. Pellets collected from eyries have yet to be analyzed, but combining prey remains and pellets may be more representative of diet and may reveal species not found in the prey remains alone (Marti et al. 2007, Oro and Tella 1995). Nevertheless, prey remains collected from nesting ledges provide an initial list of species Peregrine Falcons in YNP are feeding nestlings.

Eggshell thinning of 17% has been described as the threshold at or below which Peregrine Falcon populations are unaffected (Peakall and Kiff 1988). Eggshell fragments collected from YNP Peregrine Falcon eyries from 2010–2013 averaged 0.347 mm, or 4% thinner than pre-1947 values, indicating low exposure to DDT. Throughout the northern Rocky Mountains, eggshells showed a steady decline in percent thinning from 19% thinner from 1968–1973 (Anderson and Hickey 1972) to 4% thinner in this study. By the late 1980s, eggshell thinning in the northern Rocky Mountains was 12%, less than the minimum threshold (17%) at which population declines may occur (Levine 1995).

In 1953, 1955, and 1957, 62 tons of DDT were applied to more than 50,000 ha in northern YNP to control a spruce budworm infestation (Cope 1961, Furniss and Renken 2003). In 1958 and 1959, DDT was found in fish sampled from Pelican Creek, a tributary to Yellowstone Lake, more than 50 km from any known application site (Cope 1961). More than 40 yr after the last application, DDT and its metabolites were found in cutthroat trout sampled from the Yellowstone River at the northern end of Yellowstone Lake (Peterson and Boughton 2000). These studies indicate that DDT has a large geographic and temporal spread; however, its persistence in YNP appears not to affect productivity of Peregrine Falcons in the region.

Compounds within the family of brominated flame retardants (BFRs), particularly polybrominated diphenyl ethers (PBDEs), may also threaten raptors (Law et al. 2003, Herzk et al. 2005). PBDEs, developed in the 1970s and used in electronics, textiles, paints, carpets, clothing, and other common products, easily leach into the environment (Alaee et al. 2003). From 1986–2003, PBDE concentrations increased threefold in Peregrine Falcon eggshells from Greenland (Vorkamp et al. 2005) and even higher concentrations were found in Peregrine Falcon eggs from the northeastern U.S. (Chen et al. 2008) and California (Park et al. 2009). PBDEs were also found in the eggshells of Ospreys, Golden Eagles, Merlins (*Falco columbarius*), and White-tailed Eagles (*Haliaeetus albicilla*) in Norway (Herzke et al. 2005). We are unaware of any studies linking PBDEs to Peregrine Falcon reproduction and eggshell thickness, but an experimental study revealed that environmentally relevant

PBDE concentrations in the tissues of American Kestrels (*Falco sparverius*) caused thinner eggshells, reduced and inappropriately timed copulations, poorer egg quality, lower fertility, and reduced fledging success (Fernie et al. 2009). These smaller falcons may exhibit the effects of PBDEs before their larger counterparts. Therefore, continuing to analyze eggshell fragments and to monitor Peregrine Falcon occupancy and reproduction at known nesting territories, in addition to searching for new nesting pairs, will aid in the early detection of a declining population as a result of contaminants or other factors.

Conclusions. In this report, we present 29 yr of data on Peregrine Falcon reproduction in Yellowstone National Park. During that time, the first breeding pair of Peregrine Falcons was discovered in 1984, 15 yr after the last known pair fledged three young from the same location. The number of occupied territories increased substantially from one in 1984 to 32 by 2007. We also documented high average nesting success (74%), productivity (1.62 young/territorial pair), and brood size (2.18 young/successful nest) during 1984–2013. Peregrine Falcon eggshells collected during 2010–2013 indicated low DDT and DDE concentrations and minimal eggshell thinning (4%). Analysis of prey remains indicated a wide variety of songbirds, shorebirds, blackbirds, woodpeckers, and other species, including a pine marten and fish, were consumed by adult peregrines and their nestlings. The U.S.F.W.S. is concluding its 15-yr post-delisting monitoring effort in 2015 provided there is no evidence of immediate threats to Peregrine Falcons in the U.S. This study, along with numerous long-term data available on peregrines in North America, will aid U.S.F.W.S. in their evaluation.

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