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Source: Journal of Raptor Research, 49(4):359-366.
Published By: The Raptor Research Foundation
DOI: http://dx.doi.org/10.3356/rapt-49-04-359-366.1
URL: http://www.bioone.org/doi/full/10.3356/rapt-49-04-359-366.1

J. Raptor Res. 49(4):359–366

ESTABLISHMENT AND GROWTH OF THE PEREGRINE FALCON BREEDING POPULATION WITHIN THE MID-ATLANTIC COASTAL PLAIN

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ABSTRACT.—Between 1975 and 1985, 307 captive-reared Peregrine Falcons (*Falco peregrinus*) of mixed heritage were released within the mid-Atlantic Coastal Plain, a physiographic region with no historical breeding population, as part of the eastern peregrine recovery program. We have monitored the size, distribution, reproductive rate, and substrate use of the resulting breeding population (1979–2007). The population proceeded through an establishment phase (1979–1985) driven by releases with an average population doubling time of 1.3 yr to a consolidation phase (1986–2007) with an average doubling time of 23.4 yr. The region supported 55 breeding pairs by 2007. Reproductive rates have increased significantly over the study period from 1.18 young/occupied territory (1980–1987) to 1.87 young/occupied territory (1998–2007), and average nesting success increased from 66.3% to 79.9%. All breeding pairs nested on artificial substrates, including towers built for the peregrines (n = 37), bridges (n = 29), buildings (n = 7) and an assortment of other structures. Substrate use has diversified over time, with towers making up 100% of nesting structures in the early period of establishment and only 45% by 2007. The population appears to be self-sustaining, with reproductive rates exceeding 1.5 young/occupied territory every year since 1999.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *breeding*; *coastal plain*; *mid-Atlantic*; *population*.

ESTABLECIMIENTO Y CRECIMIENTO DE UNA POBLACIÓN REPRODUCTIVA DE *FALCO PEREGRINUS* DENTRO DE LA PLANICIE COSTERA DEL ATLÁNTICO MEDIO

RESUMEN.—Como parte de un programa de recuperación, entre 1975 y 1985, se liberaron 307 individuos de *Falco peregrinus* criados en cautividad y de herencia mixta dentro de la Planicie Costera del Atlántico Medio, una región fisiográfica sin poblaciones reproductoras históricas. Seguimos el tamaño, la distribución, la tasa reproductiva y el uso de substratos de cría de la población reproductora resultante (1979–2007). La población atravesó una fase de establecimiento (1979–1985) impulsada por las liberaciones, con un tiempo

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promedio de duplicación de la población de 1.3 años, hacia una fase de consolidación (1986–2007), con un tiempo promedio de duplicación de la población de 23.4 años. La región mantuvo 55 parejas reproductoras en 2007. Las tasas reproductivas se han incrementado significativamente a lo largo del periodo de estudio, de 1.18 pollos/territorio ocupado (1980–1987) a 1.87 pollos/territorio ocupado (1998–2007) y el éxito de nidificación promedio aumentó de 66.3% a 79.9%. Todas las parejas reproductoras nidificaron en substratos artificiales, incluyendo torres construidas para los halcones (n = 37), puentes (n = 29), edificios (n = 7) y una variedad de otras estructuras. El uso de substratos de cría se ha diversificado a lo largo del tiempo, pasando las torres del 100% de las estructuras de nidificación en el periodo temprano de establecimiento a sólo el 45% en 2007. La población parece ser sostenible por sí misma, con tasas reproductivas que superan 1.5 pollos/territorio ocupado cada año desde 1999.

[Traducción del equipo editorial]

The historical population of Peregrine Falcons (*Falco peregrinus*) in the eastern United States was estimated to be approximately 350 breeding pairs and was mostly confined to the Appalachian Mountains, relying on open cliff faces and cut-banks for nesting (Hickey 1942). The population experienced a precipitous decline throughout the 1950s (Hickey 1969) due to contaminant-induced reproductive suppression (Anderson and Hickey 1972) and was believed to have been extirpated by the early 1960s (Berger et al. 1969). The Peregrine Falcon was listed as endangered on the U.S. Federal List of Endangered and Threatened Wildlife (50 CFR 17.11–17.12) in June 1970. In 1975, the U.S. Fish and Wildlife Service appointed an Eastern Peregrine Falcon Recovery Team to develop and implement a recovery plan (Bollengier et al. 1979).

In the absence of any residual breeding stock, one of the key components of the recovery strategy for the eastern population was the production and release of captive-reared falcons (Cade and Fyfe 1978, Cade 2003). The breeding stock used for the captive program was of mixed heritage and contained individuals from nonindigenous subspecies (*F. p. cassini*, *F. p. brookei*, *F. p. pealei*, *F. p. peregrinus*, *F. p. tundrius*, and *F. p. macropus*), as well as native *F. p. anatum* (Barclay and Cade 1983). Within a relatively short period, a captive breeding program was established with enough capacity to sustain an aggressive release program (Barclay and Cade 1983, Barclay 1988). Experimental releases included both natural cliff sites and artificial towers constructed in coastal marshes. However, early results quickly focused release efforts on coastal towers because they were placed in areas with abundant prey, low predation pressure, and low human disturbance, resulting in both higher fledging rates and higher rates of return to the release area as breeders (Barclay 1988). Twenty coastal towers were established during the early release phase within the mid-Atlantic Coastal Plain (Barclay and Cade 1983). Tower design included four corner posts connected by a wooden platform that supported a hack box. As birds began to return to towers in subsequent years, hack boxes were replaced with nest boxes. Between 1975 and 1985, 307 captive-reared birds were released from sites on the Coastal Plain of Virginia, Maryland, Delaware, and New Jersey, with an additional 13 in Washington, DC, and five in coastal North Carolina.

The successful establishment of a breeding population of Peregrine Falcons within the mid-Atlantic Coastal Plain has clearly contributed to the recovery of the broader eastern population (Enderson et al. 1995, Millsap et al. 1998) and to the eventual removal of the species from the U.S. Federal List of Endangered and Threatened Wildlife (Mesta 1999). However, due to the paucity of historical breeding evidence and to the importance of this area to breeding and migratory waterbirds that serve as prey, the decision to establish the population was not without controversy (Barclay 1988). Nonetheless, the current breeding population is well established and expanding. Here, we describe the establishment, growth, and nesting substrate use of this coastal population.

METHODS

The study area includes the Coastal Plain of Virginia, Maryland, Delaware, and New Jersey. The boundaries of the area are formed by the Atlantic Ocean to the east and the fall line to the west (Fig. 1). The fall line is an erosional scarp where the metamorphic rocks of the Piedmont meet the sedimentary rocks of the Coastal Plain. Between these two boundaries, the land slopes gently toward the fall line, where it generally reaches an elevation of less than 80 m. The surface of the land has been reworked considerably by fluvial processes over the past 2–3 million yr. Although there are a number of terraces and scarps in the region that are

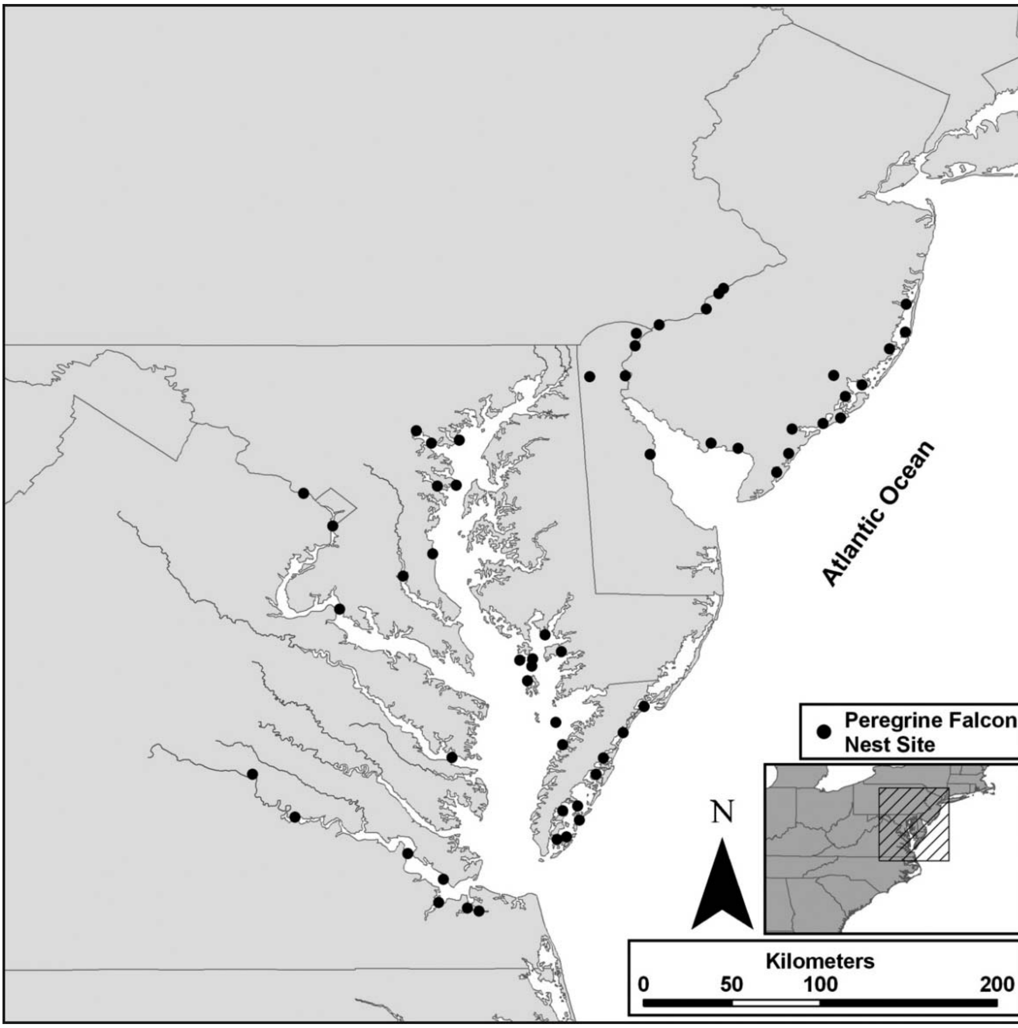

Figure 1. Map of mid-Atlantic Coastal Plain study area, with Peregrine Falcon breeding territories (black dots) that were active (eggs laid) in 2007. Breeding density generally declines moving from the outer coast west to the fall line.

considered "high-water marks" formed by shifts in sea level during the Pleistocene (Cooke 1931), there are no exposed rock surfaces available for nesting peregrines. The only documented breeding record prior to the introduction program was on an Osprey (*Pandion haliaetus*) nest (Jones 1946). However, the region supports a large and growing human population with associated human-made structures that are attractive to breeding pairs.

We determined numbers of nesting pairs, productivity, and nesting success by regular monitoring. A large number of artificial structures have been established within the region specifically for use by breeding peregrines. In addition, the area supports many human-made structures that may be suitable for nesting. Nesting structures were surveyed early in the season to determine occupancy by falcons. Although some prominent human-made structures have been monitored by biologists over the years for peregrine activity, many of these nesting sites were initially reported by the public. We monitored sites known to be occupied during a given year 2–5 times from March through July to document breeding activity, to band young, and to document fledging success. Field activities were consistent with the National

Monitoring Protocol (United States Fish and Wildlife Service 2003). Many of the human-made structures used for nesting were enhanced to improve nesting success before or after pairs were established. Enhancements included the addition of pea gravel or the installation of nesting trays or boxes.

We defined several simple and composite population parameters. We considered a breeding territory to be occupied (occupied territory) if a pair of adult peregrines was resident during the breeding season. The number of occupied territories was used as an estimate of population size. We considered nests to be active (active nest) if eggs or young were detected and successful (successful nest) if ≥1 nestling survived to fledging (Postupalsky 1974). Reproductive output for the population was the number of young (young produced) surviving to fledging age. We defined breeding success as the percentage of active nests that contained ≥ one young (successful nests/active nests × 100), reproductive rate as the number of young produced per pair (young produced/occupied territory), and average brood size as the number of young produced per successful nest. We also calculated the average young produced per breeding attempt (young produced/active nest). It should be noted that the population is under management that includes the rescue and/or rehabilitation of young birds that are reported to be on the ground or in other dangerous situations in some cases.

Colonization rates were expressed using the average time (yr) required for the nesting population to double in size (t_{double}). Doubling time was calculated using the growth equation $N_t = N_0e^{rt}$ where N_t is the population size in 2007, N_0 is the population size in 1980, e is the base of the natural logarithm, r is the intrinsic rate of increase, and t is the time interval between population estimates. With this configuration, $t_{double} = \ln(2)/r$.

RESULTS

Within the study area, Peregrine Falcons have become well established as a breeding species over the past 30 yr. From a single pair in 1979, the population has grown to 55 pairs by 2007 with an average doubling time of 5.0 yr (Table 1). The establishment phase through 1985 (year when releases were discontinued in the region) was particularly dramatic with an average doubling time of 1.3 yr. Remarkably, the release of just over 300 birds resulted in the establishment of 27 territories in less than 10 yr. Since 1985 the average doubling time has increased to 23.4 yr as the population has become self-sustaining.

During the study period, we documented 820 breeding attempts that produced 1552 young. Average, annualized breeding success was 71.8 ± 1.73%, average reproductive rate was 1.82 ± 0.059 young/occupied territory, and average brood size was 2.53 ± 0.054 young/successful nest. The population has exhibited tremendous forward momentum such that more than 50% of young produced over the 29-yr period have been produced since 1999. Reproductive rates have exceeded 1.5 young/occupied territory every year since 1999.

Reproductive rates increased significantly over the study period ($r^2 = 0.68$, $F_{1,26} = 56.4$, $P < 0.001$). Reproductive rates averaged 1.18 ± 0.088 young/occupied territory for the period 1980 to 1987 compared to 1.87 ± 0.033 young/occupied territory for the period 1998 to 2007. The overall increase in reproductive rate appears to have resulted from a significant increase in success rate ($r^2 = 0.24$, $F_{1,26} = 8.1$, $P < 0.01$) rather than average brood size ($r^2 = 0.18$, $F_{1,26} = 4.2$, $P > 0.05$). Average success rate increased from 66.3% for the period 1980 to 1987 to 79.9% for the period 1999 to 2007. The variance in these parameters also declined over the study period, possibly due to an increase in sample sizes. Coefficient of variation declined between the two time periods from 22.5% to 5.4% and from 15.8% to 6.8% for reproductive rate and success rate, respectively.

We identified 88 structures used for nesting within the study area. The most common structures were peregrine towers ($n = 37$), bridges ($n = 29$), and buildings ($n = 7$) that collectively represent 82.9% of the total. Less common structures have included three abandoned shacks, two water towers, two military ships, and two active smokestacks at coal-fired power plants. One of the most unusual structures was the smoke box of a derelict brick chimney isolated in a marsh. The smoke box was only 1 m above the marsh surface. Another pair was resident on a duck blind for two years but nesting was never confirmed. Three pairs have nested on Osprey stick nests, all of which were on artificial substrates.

Substrates used for nesting have diversified through time. Birds released from towers returned to establish nests on towers during the early colonization period. The first bridge and building were not used until 1983 and 1984, respectively. In 1990, 69% of known pairs were still nesting on

Table 1. Summary statistics for Peregrine Falcon breeding population within the mid-Atlantic Coastal Plain (1979–2007).

YEAR	OCCUPIED TERRITORIES	ACTIVE NESTS	SUCCESSFUL NESTS	YOUNG PRODUCED	BREEDING SUCCESS	YOUNG/ACTIVE NEST	YOUNG/OCCUPIED TERRITORY	BROOD SIZE (YOUNG/SUCCESSFUL NEST)
1979	1	0	0	0	–	–	–	–
1980	5	3	2	4	0.67	1.33	0.80	2.00
1981	6	3	2	5	0.67	1.67	0.83	2.50
1982	8	5	4	9	0.80	1.80	1.13	2.25
1983	10	8	6	15	0.75	1.88	1.50	2.50
1984	17	15	9	22	0.60	1.47	1.29	2.44
1985	27	21	10	30	0.48	1.43	1.11	3.00
1986	25	22	15	33	0.68	1.50	1.32	2.20
1987	29	25	18	39	0.72	1.56	1.34	2.17
1988	29	23	16	50	0.70	2.17	1.72	3.13
1989	31	22	16	36	0.73	1.64	1.16	2.25
1990	28	23	19	46	0.83	2.00	1.64	2.42
1991	33	26	19	48	0.73	1.85	1.45	2.53
1992	36	31	20	44	0.65	1.42	1.22	2.20
1993	36	32	18	49	0.56	1.53	1.36	2.72
1994	38	34	22	52	0.65	1.53	1.37	2.36
1995	40	35	25	71	0.71	2.03	1.78	2.84
1996	43	38	24	59	0.63	1.55	1.37	2.46
1997	39	34	24	54	0.71	1.59	1.38	2.25
1998	46	39	26	64	0.67	1.64	1.39	2.46
1999	43	36	30	83	0.83	2.31	1.93	2.77
2000	43	41	30	76	0.73	1.85	1.77	2.53
2001	44	37	30	81	0.81	2.19	1.84	2.70
2002	47	41	35	83	0.85	2.02	1.77	2.37
2003	48	46	32	95	0.70	2.07	1.98	2.97
2004	50	42	33	89	0.79	2.12	1.78	2.70
2005	52	43	36	96	0.84	2.23	1.85	2.67
2006	56	47	40	106	0.85	2.26	1.89	2.65
2007	55	48	38	113	0.79	2.35	2.05	2.97

towers. By 2007, towers accounted for less than 45% of substrates.

DISCUSSION

The captive breeding and release program outlined in the federal recovery plan (Bollengier et al. 1979) and implemented by the Peregrine Fund and partners has been successful in establishing a breeding population of Peregrine Falcons within the mid-Atlantic Coastal Plain. First modern breeding records were recorded in all four states between 1980 and 1987 (Byrd 1989, Steidl et al. 1991, Therres et al. 1993, Hess et al. 1999). The growth rate of this population is comparable to those in other regions of North America that have included intensive reintroduction efforts (Enderson et al. 1995, Mesta 1999, Kauffman et al. 2003), with a clear establishment phase driven by releases and a more gradual consolidation phase driven by internal productivity. All the early breeding pairs resulted from released birds returning to hack towers, and the conclusion of the reintroduction program within the region reflected the successful colonization of these towers. In recent years, identification of marked breeders has documented considerable dispersal throughout the Coastal Plain and a relatively small (<3%) amount of exchange with the New England breeding population (Clark et al. 2013, Mojica et al. 2014).

Although we have not performed a population viability analysis (Wootton and Bell 1992), both reproductive performance and the population trajectory suggest the population is self-sustaining. Reproductive rates have become more stable over the past decade and have been maintained well above 1.25–1.50 young per occupied territory, generally believed to support positive population growth rates (Grier and Barclay 1988, Wootton and Bell 1992). Releases during the establishment phase averaged just under 30 birds/yr. The population has exceeded this production every year since the last year of releases and in 2007 produced more than three times this number. Elevation in reproductive rates over the study period has resulted from increases in breeding success rather than in brood size. The underlying cause of this improvement is unclear but may be an artifact of a shifting age structure as the population became established. Both clutch and brood size increased with female age in Scotland (Mearns and Newton 1988), and nestling survival increased throughout the lifespan of peregrines breeding in captivity (Clum 1995).

Due to the large number of human-made structures, it is difficult to estimate the carrying capacity of the region. However, pairs have already been established on many of the prominent bridges available. Breeding density within the outer coastal marshes is among the highest in North America (approaching 1 pair/20 km^2 in some areas), reflecting the very high density of available prey. Nesting substrate is likely limiting within these systems. Early in the establishment phase as towers became saturated, pairs established territories on almost any structure that was elevated above the marsh surface. Newly constructed towers were rapidly colonized. Contests for existing territories have been frequent and lost adults have been rapidly replaced, suggesting an adequate pool of floaters and a high draw to the coastal territories. Buildings represent the most numerous potential nest substrates but still support a relatively small portion of the population. Continued growth of the population will likely require further colonization of available buildings or some novel substrate such as Osprey nests. The use of Osprey nests by three pairs might prefigure a shift toward such structures. Several thousand Osprey nests are present within the region (Watts et al. 2004) and even moderate use of these nests would be difficult to monitor.

Despite the fact that the ancestry of the introduced population reflects a very large portion of the global range, the breeding population has successfully adapted to the region. Breeding phenology is comparable to what is known from the historical mountain population (Therres 1996). Migratory status is mixed. Of 61 hatch-year birds tracked with satellite transmitters from Virginia (Watts et al. 2011), half migrated south to establish winter territories ranging from North Carolina to Colombia, South America. Remaining birds established winter territories within the mid-Atlantic region from Virginia through New York. Diet during the breeding season generally reflects the availability of bird species. Pairs nesting within inland locations feed primarily on Rock Pigeons (*Columba livia*) and migratory passerines (Barber and Barber 1983, 1988, Long 2009). In contrast, migratory shorebirds are the dominant prey used by pairs nesting on the outer coast, representing 55% and 52% of the prey documented in New Jersey (Steidl et al. 1997) and Virginia (Long 2009), respectively. In both locations, Willets (*Tringa semipalmata*) and Short-billed Dowitchers (*Limnodromus griseus*) were taken in the highest numbers.

The population continues to be subjected to hazards. Approximately half of the breeding pairs nest on bridges and buildings and are vulnerable to the array of factors associated with living in an urban landscape (Cade and Bird 1990, Cade et al. 1996). Collisions with urban structures such as buildings, guy wires, and transmission lines represented 40% of mortality identified during a tracking study in the region (Watts et al. 2011). Similar observations have been made in Maryland (Therres et al. 1993). Young from bridge nests frequently drown around fledging time when they are unable to fly back up to eyries due to the lack of updrafts. Exposure to some classes of contaminants such as flame retardants are believed to be higher within urban settings compared to the coastal areas, as indicated by higher concentrations within addled eggs (Potter et al. 2009, Chen et al. 2010). By contrast, pairs along the outer coast appear to have higher exposure to legacy contaminants such as DDT and its metabolites, possibly due to their higher consumption of migratory shorebirds that winter in the tropics (Clark et al. 2008, Potter et al. 2009). However, eggshell-thinning rates relative to pre-DDT estimates have varied through time and space, making the general connection between contaminant exposure levels and spatial variation in reproductive rates difficult to assess within the region (Steidl et al. 1991, Burns et al. 1994, Clark et al. 2008, Potter et al. 2009, Chen et al. 2010).

ACKNOWLEDGMENTS

We thank the New Jersey Division of Fish and Wildlife, Delaware Division of Fish and Wildlife, Maryland Department of Natural Resources, Virginia Department of Game and Inland Fisheries, and the U.S. Fish and Wildlife Service for financial and logistical support over the years. We thank the many landowners who have allowed access to their properties for peregrine management and monitoring. We thank the many biologists and citizens who have contributed to monitoring activities over the years, including M. Barrow, D. Bradshaw, D. Brauning, R. Cashwell, K. Cline, S. Dawson, B. Halla, S. Padgett, G. Taylor, and B. Wurst. D. Bell, J.B. Buchanan, C. Dykstra, and an anonymous reviewer made helpful comments on an earlier draft of this report. Peregrine falcons were banded in New Jersey, Delaware and Maryland, and Virginia under federal permits 22803, 21769, and 21567, respectively.

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Received 26 September 2014; accepted 16 April 2015
Associate Editor: Joseph B. Buchanan