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Source: Journal of Raptor Research, 42(1) : 13-19

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-07-16.1

*J. Raptor Res.* 42(1):13–19

# CROSS-CONTINENTAL PATTERNS IN THE TIMING OF SOUTHWARD PEREGRINE FALCON MIGRATION IN NORTH AMERICA

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ABSTRACT.—We analyzed the timing of southward migration of Peregrine Falcons (*Falco peregrinus*) across North America, based on passage data compiled by the Hawk Migration Association of North America, supplemented with two other similar datasets collected by individual observers at sites in western Canada. The results show two distinct continental-scale patterns. First, the north to south progression of peak peregrine passage down the continent is readily apparent, occurring primarily during September and October. Second, the movement of Peregrine Falcons is earlier by 4–6 wk on the west coast than on the eastern seaboard, and is intermediate at inland sites. The wavefront of Peregrine Falcons advancing southward is oriented from southwest to northeast across the North American continent. We hypothesize that these patterns have implications for the southward migrations of potential prey species, which may select routes or times to avoid places of high risk due to Peregrine Falcons.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *cross-continent*; *hawkwatch*; *migration*; *timing.*

## PATRONES TRANSCONTINENTALES EN EL MOMENTO EN QUE TIENE LUGAR LA MIGRACIÓN HACIA EL SUR DE *FALCO PEREGRINUS* EN NORTE AMÉRICA

RESUMEN.—Analizamos el momento en que tiene lugar la migración de *Falco peregrinus* hacia el sur a través de Norte América con base en datos del paso de individuos recopilados por la Hawk Migration Association de Norte América. Además complementamos estos datos con otros dos conjuntos de datos similares que fueron recolectados por observadores individuales en el oeste de Canadá. Los resultados muestran dos patrones distintos a escala continental. Primero, existe un patrón claro de progresión de norte a sur en el pico de pasada de individuos migratorios, que ocurre principalmente en septiembre y octubre. Segundo, el movimiento de *F. peregrinus* tiene lugar 4–6 semanas más temprano en la costa oeste que en la este, y es intermedio en sitios ubicados tierra adentro. El frente de la ola de individuos migratorios que se dirigen hacia el sur está orientado del suroeste al noreste a través del continente norteamericano. Proponemos la hipótesis de que estos patrones tienen implicaciones para la migración hacia el sur de especies de presas potenciales, las cuales pueden seleccionar rutas o momentos de migración para evitar lugares de alto riesgo debidos a la presencia de *F. peregrinus*.

[Traducción del equipo editorial]

Migration routes and migration timing of predators may possibly have coevolved with those of prey species, but this idea has been little studied (Alerstam et al. 2003). One of the first researchers to investigate this idea compared the migration timing of Peregrine Falcons (*Falco peregrinus*) and sandpipers (*Calidris mauri*, *C. alpina pacifica*) in southwestern British Columbia, demonstrating that sandpiper migrations avoided times and places of highest exposure to peregrines (Lank et al. 2003). The broader geographical applicability of these findings is still unknown, but investigating the continental-scale migratory passage pattern of peregrines and other raptors is an essential first step for addressing the coevolution hypothesis. The purposes of our study were: (1) to analyze the timing of Peregrine Falcon southward migration in North America; and (2) to determine whether easily-collected data on migratory passage are adequate to describe migration timing.

A variety of studies of migratory peregrines have been undertaken (Dekker 1980, Hunt et al. 1975,

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Mueller et al. 2000). Peregrines often soar during migration, but they also employ a significant amount of powered flight, and appear to hunt actively every day (Cochran 1975). Telemetry studies have followed the movements of individual birds and estimated the speed of migration (Chavez-Ramirez et al. 1994, Fuller et al. 1998, McGrady et al. 2002). Previous researchers (Beebe 1960, Enderson 1965, Heintzelman 1975, Dekker 1984, Ward et al. 1988) have reported passage dates for migrant peregrines, but these data have not been synthesized. Here we compare measures of Peregrine Falcon migration timing at 16 sites across North America.

## METHODS

Data on Peregrine Falcon passage timing were obtained from Hawk Migration Studies Flyway Reports published biannually by the Hawk Migration Association of North America (Byland 1998, Hoffman 2000, Hoffman 2001; www.hmana.org). The HMANA is a nonprofit volunteer organization that monitors raptor migrations across North America. Using standard reporting forms and procedures, migration data are collected by experienced observers from established strategic lookout points spread across the continent. Inzunza (2005) provides an overview, and discusses the use of these data to estimate population trends and status of North American raptors in the Raptor Population Index Project. We followed policies governing HMANA data use described at http://hmana.org/data policies/.

For the following analysis we selected data from 1998, 2000, and 2001, because these years had the greatest number of hawkwatch sites that reported in all 3 yr. Sites were included in our analysis if at least 19 peregrine sightings were recorded there in each year and if the site was monitored at least 1 wk of near-consecutive days during the peak southward passage period (as we estimated it, based on comparison with nearby sites). Most sites were continuously monitored for much longer periods.

'Peak migration date' was defined as the day with the greatest number of observed Peregrine Falcons, and the '50% passage date' was defined as the date by which half the total number of birds recorded at that site over the observation period had been observed. We also recorded for each year and site the number of peregrine sightings, the number of observation days, and the number of missed observation days between the first and last reported day (Table 1).

To test how missed observation days affected the estimation of the 50% passage date, we built a computer simulation of the passage of peregrines ($N = 394$) past an observation site over 50 d, with the cumulative number of migrants following a logistic curve. In our simulation, the true date of 50% passage was reached on day 25. We varied the probability that each observation day was missed from 0.1 to 0.9 in increments of 0.1, simulated the number of migrants that would have been counted, and calculated the resultant 50% passage date. We repeated the exercise 20 times at each probability level, and calculated the error about the mean 50% passage estimate.

HMANA sites are concentrated in the eastern portion of the continental U.S.A. We were able to supplement passage date estimates for the western part of the continent with two additional data sets. Lank et al. (2003) described data collected on the George C. Reifel Migratory Bird Sanctuary, located on the Fraser River estuary, adjacent to Vancouver, British Columbia. These data differed somewhat from the HMANA data, in that they were based on the average daily number of peregrines sighted during near-daily 1 h surveys made since 1986 by the refuge manager (John Ireland; see Ydenberg et al. 2004). A graphical summary of the seasonal pattern was provided by Lank et al. 2003 (see their Fig. 3). Although the methodology differed from that used in the HMANA studies, these data were suitable to permit an estimate of peregrine migration timing (see Niehaus and Ydenberg 2006). Passage timing varies widely between years on the west coast, and we used the 2001 data in our basic analysis as representative of an average year. However, we fully describe and discuss the interannual variation and its effects.

A second dataset was collected at Beaverhills Lake, near Edmonton, Alberta by Dick Dekker, who has since 1969 spent hundreds of field days at this site between late August and October. Peregrine sightings made between 1969 and 1983 were reported by Dekker (1984). The data used herein are previously unpublished data of 45 sightings made over 52 d in 2000–2005, spanning the period 1 September to 15 October in each year. Peregrines are rarely seen here prior to 1 September (Dekker 1984; D. Dekker unpubl. data).

## RESULTS

Migration data from some hawkwatch sites in close proximity that recorded low numbers of peregrines were grouped to meet the minimum criteria

Table 1. Summary data for the 14 North American hawkwatch sites in the study. The two remaining sites were the Fraser River estuary in SW British Columbia and Beaverhills Lake, Alberta. (Locations of hawkwatch sites shown in Fig. 2).

| | 1998 | | | | | 2000 | | | | | 2001 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site Location | Peak Migration Date | 50% Date | # Birds sighted | # Obs. Days | # Missed Obs. Days | Peak Migration Date | 50% Date | # Birds sighted | # Obs. Days | # Missed Obs. Days | Peak Migration Date | 50% Date | # Birds sighted | # Obs. Days | # Missed Obs. Days |
| Manzano Mountains, NM, U.S.A. | 20-Sep | 23-Sep | 46 | 70 | 5 | 23-Sep | 23-Sep | 25 | 63 | 6 | 1-Oct | 23-Sep | 28 | 70 | 0 |
| Hawk Ridge, MN, U.S.A. | 19-Sep | 22-Sep | 16 | 116 | 2 | 29-Sep | 28-Sep | 24 | 91 | 7 | 20-Sep | 22-Sep | 18 | 119 | 0 |
| Goshute Mountains, NV, U.S.A. | 28-Sep | 28-Sep | 17 | 17 | 6 | 1-Oct | 21-Sep | 12 | 81 | 3 | 25-Sep | 18-Sep | 16 | 85 | 2 |
| Cranberry Marsh, ON, CAN. | 10-Oct | 3-Oct | 16 | 95 | 14 | 28-Sep | 22-Sep | 16 | 98 | 12 | 7-Nov | 30-Sep | 18 | 108 | 0 |
| Hawk Cliff/Holiday Beach, ON CAN. | 27-Sep | 27-Sep | 44 | 216 | 19 | 9-Oct | 1-Oct | 33 | 94 | 8 | 9-Oct | 3-Oct | 33 | 163 | 38 |
| Hazel Bazemore/Corpus Christi, TX, U.S.A. | 26-Sep | 28-Sep | 34 | 92 | 18 | 25-Sep | 1-Oct | 28 | 92 | 1 | 6-Oct | 30-Sep | 38 | 93 | 0 |
| Montclair/Little Gap/Hawk Mtn., PA/NJ, U.S.A. | 4-Oct | 4-Oct | 84 | 324 | 85 | 2-Oct | 5-Oct | 85 | 391 | 87 | 2-Oct | 4-Oct | 61 | 355 | 13 |
| S. Harpswell, ME, U.S.A. | 5-Oct | 3-Oct | 16 | 58 | 7 | 11-Oct | 11-Oct | 14 | 64 | 10 | 18-Oct | 18-Oct | 11 | 61 | 7 |
| Waggoner's Gap, PA, U.S.A. | 6-Oct | 6-Oct | 15 | 151 | 13 | 4-Oct | 4-Oct | 15 | 151 | 13 | 5-Oct | 5-Oct | 27 | 112 | 6 |
| Cape May, NJ, U.S.A. | 1-Oct | 1-Oct | 55 | 90 | 0 | 6-Oct | 6-Oct | 62 | 91 | 0 | 6-Oct | 4-Oct | 61 | 91 | 0 |
| Kiptopeke, VA, U.S.A. | 5-Oct | 5-Oct | 64 | 92 | 2 | 6-Oct | 6-Oct | 64 | 92 | 2 | 23-Sep | 4-Oct | 58 | 97 | 5 |
| Fire Island, NY, U.S.A. | 1-Oct | 2-Oct | 40 | 72 | 7 | 7-Oct | 7-Oct | 40 | 72 | 7 | 7-Oct | 11-Oct | 45 | 73 | 5 |
| Guano River, FL, U.S.A. | 2-Oct | 5-Oct | 16 | 16 | 0 | 30-Aug | 30-Aug | 9 | 9 | 0 | 9-Oct | 8-Oct | 15 | 16 | 0 |
| Veracruz, MX | 8-Oct | 6-Oct | 67 | 93 | 0 | 27-Sep | 3-Oct | 65 | 83 | 0 | 9-Oct | 6-Oct | 46 | 94 | 2 |

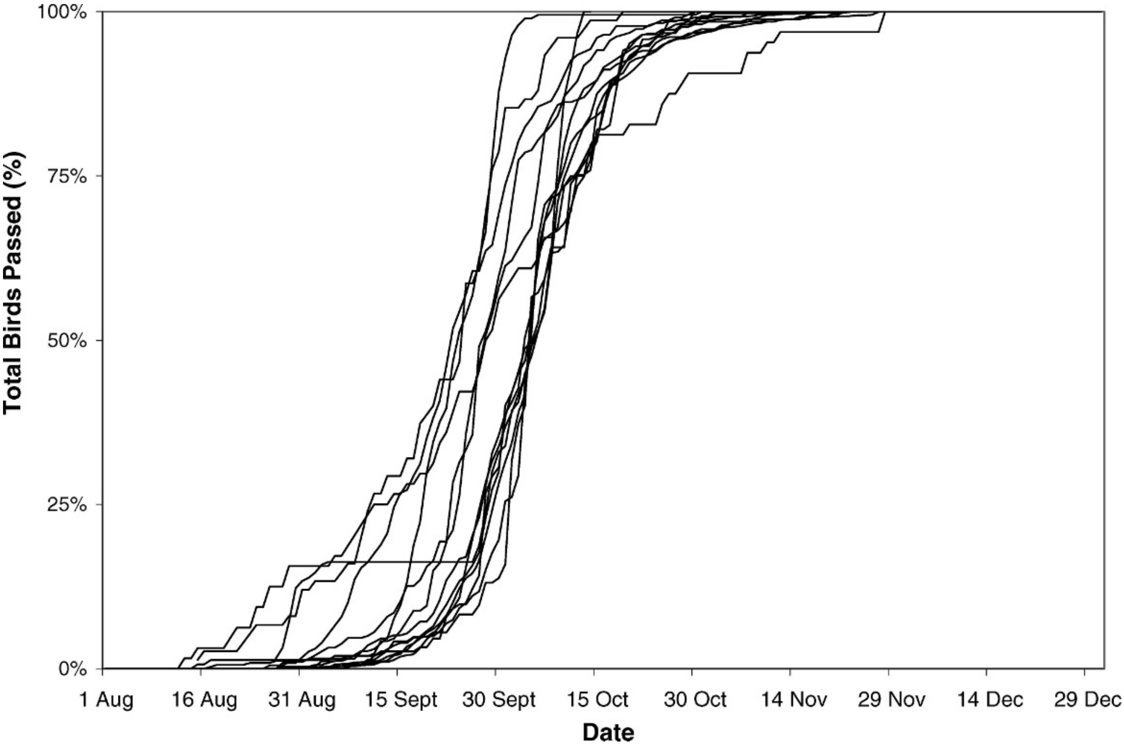

Figure 1. Cumulative percent frequency of Peregrine Falcons passing the 14 hawkwatch sites in North America (Table 1), pooled across years for each site.

for inclusion in our analyses (Holiday Beach and Hawk Cliff, ON, Canada, were grouped; and Montclair, NJ, Little Gap, PA and Hawk Mountain, PA, were grouped). The absolute difference in 50% passage dates for these sites was always small, averaging 3.5 d, and never more than 9 d. Including these grouped sites, we obtained sufficient HMANA data for a total of 14 sites (Table 1).

The general pattern of peregrine passage was broadly similar at most sites (Fig. 1). The cumulative number of birds passing rises slowly at first, accelerates steeply, and then tapers off. The traces do not rise equally steeply, but all are roughly symmetrical, indicating that the periods of observation bracket the main migratory period. A plot of the daily tallies rather than the cumulative passage shows a waveform, with the height and sharpness of the peak varying between sites.

Two lines of evidence suggest that these curves allow for a reasonable assignment of a date to represent the timing of passage at a site. First, 'Peak' and '50% passage' dates are nearly identical within years, with the 50% date occurring on average only 0.3 d earlier than and not differing significantly from the peak passage date (paired *t*-test, $t = 0.79$, $P > 0.05$, $N = 36$).We judged that the 50% passage date was less subject to random variation due to occasional days with relatively many or few peregrine sightings (e.g., due to viewing conditions) and we used this measure here. Second, our computer simulation showed even when most observation days were missed, the estimate of the 50% passage date was close to the true value. The precision of the estimate decreased (the 95% confidence interval grew as the probability of missing an observation day increased), but there was no systematic bias above or below the true value (Fig. 2).

When the data were pooled, the 50% passage dates for peregrines ranged from 22 August to 6 October, with a strong and distinct progression from west to east across the continent. The latest dates occurred at the east coast sites, all of which were between 4–6 October. The earliest 50% passage date was 22 August, recorded on the Fraser estuary in British Columbia. The 50% passage dates at inland sites were between these two extremes. These data indicated that there

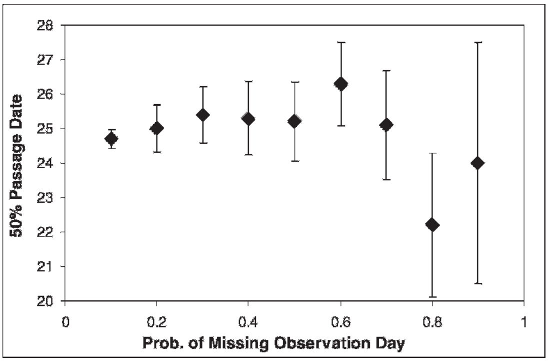

Figure 2. Results of a computer simulation investigating the influence of missed observation days on the accuracy of estimating the 50% passage date of 394 peregrines passing an observation post over 50 d with a mean 50% passage date on day 25. We calculated the mean and 95% confidence intervals about the 50% passage date estimates based on 20 replicates. There was no systematic relationship between the frequency of missed observation days and the bias in the estimate (correlation coefficient $r = 0.41$, $N = 9$, $P > 0.05$).

were both north-south and west-east components in the aggregate progression of peregrine migration.

The southward progression of the 50% passage date was used to estimate the speed of migration. For example, the 50% passage dates in the data presented here for Goshute Mountains, Nevada, and Veracruz, Mexico differed by 12 d in 2000 and 17 d in 2001 (mean = 14 d). Using great circle distance (the shortest distance between two points on the surface of a sphere) we estimated the distance from Goshute Mountains, to Veracruz, Mexico as 3017 km, and thus the calculated migration speed as 3017 km/14 d = 215 km d$^{-1}$.

To measure the west-east component of peregrine passage, we estimated the position of the 1 October isophene, which is defined as the position of the migratory front on October 1st (see Byrkjedal and Thompson 1998). We used Fuller et al.'s (1998) estimate of 172 km d$^{-1}$ as representative of migration speed, and added or subtracted the expected progression of the observed 50% passage date at each site to 1 October. For example, the 50% passage point occurred in New Mexico (Goshute Mountains) on 23 September, meaning that on 1 October (i.e., 8 d later) it should have progressed southward by 1376 km (= 8 d × 172 km d$^{-1}$). As peregrines move on a broad front, we indicate these calculated positions by arcs of 20° centered on the main direction of migration, which was taken from figure 5 of Schmutz et al. (1991). The resulting plot showed that, on 1 October, the position of peak peregrine passage was oriented across the continent, from southwest to northeast (Fig. 3).

Figure 3. The 1 October migration isophene (i.e., the calculated positions of Peregrine Falcon migrants on 1 October, based on the 50% passage dates). Estimation method described in the text. The arcs indicate positions that peregrines are estimated to have reached on 1 October by traveling in the typical migration direction past the hawkwatch sites studied (Table 1). The line segment on each arc points to its corresponding hawkwatch site, which is located to the north of the arc if October 1 is after the 50% passage date at that site, and to the south if October 1 precedes the 50% passage date. Peregrines at the west coast Fraser estuary site were likely not all long distance migrants, and hence no migration is indicated.

## Discussion

The data revealed clear patterns in the southward migration of Peregrine Falcons. As viewed from a single location, peregrine migration occurred as a wave, with a distinct peak and timing that was revealed even by simple census data. The north-to-south sweep of this 'predator tsunami' (Butler et al. 2003) down the continent was readily apparent, and its speed (215 km d$^{-1}$) was roughly similar to that of individual migrant peregrines tracked via satellite telemetry (172 km d$^{-1}$, Fuller et al. 1998; 141 km d$^{-1}$, McGrady et al. 2002 ). The arrival and advance of peregrines was much earlier on the west coast than on the eastern seaboard, and was intermediate at inland sites.

The total number of birds recorded during a migration season varied between locales, and the relation of these tallies to total numbers of peregrines can be complicated by a number of factors (Inzunza 2005). However, measuring the timing of migration from these data appeared to be less prone to complications. Compilations of the timing estimates from a number of different stations enabled us to assemble a coherent broad-scale picture. Previous studies (Beebe 1960 for coastal British Columbia; Enderson 1965 for Great Lakes; Heintzelman 1975 for Hawk Mountain, Pennsylvania; Dekker 1984 for Alberta; Ward et al. 1988 for Maryland) were consistent with the timing estimates made here, supporting our contention that good timing measures could be readily derived from these hawkwatch data.

The causes of the difference in timing between the east and west likely involve several factors. The study of satellite-tracked peregrines (Fuller et al. 1998) showed that the southbound routes of individuals from similar breeding locales spread out widely over North America, and that individuals traveling through or to the same nonbreeding locales may come from very different breeding sites (McGrady et al. 2002). Peregrines traveling along the eastern seaboard had flown from breeding areas in the western and eastern Arctic, Greenland, and northern Canada.

On the Pacific coast, the measurement of migration timing is further complicated by the presence of local resident peregrines, as well as wintering birds, short-distance migrants, and long-distance migrants. These birds together comprise a danger to prey species that increases in early autumn along the Pacific coast and remains relatively high almost until spring.

A second factor affecting the west coast is significant annual variation in the timing of arrival. Niehaus and Ydenberg (2006) report that the arrival (equivalent to the 50% passage statistic used here) of peregrines in southwest British Columbia varied by 54 d in the period 1986–2001, with the overall mean arrival on Julian day 220 (8 August). Over the same period, passage timing at Hawk Mountain in Pennsylvania varied by only 7 d (mean arrival on Julian day 276 [3 October]). In the 3 yr analysed here (1998, 2000, 2001), 50% passage dates at the 14 HMANA sites had a median range of 6.5 d, while the range observed on the Fraser estuary over these same 3 yr was 54 d. The larger variation observed in the west may result from strong annual variation in the timing of breeding of the birds along the northern Pacific coast. This difference is unlikely to be methodological because Niehaus and Ydenberg (2006) showed that annual variation in the date of peregrine arrival on the Fraser estuary was strongly related to the date of snowmelt in Alaska, and suggested that there may be an underlying climatic cause.

Additional data on peregrine migration timing would improve our understanding of migration patterns and factors influencing annual variation in migration movements. For example, there are relatively few HMANA sites reporting data from the central portions of the continent, whereas it is clear from satellite telemetry studies that many peregrines travel through the continental interior. As we have shown, simple repeated census data may be sufficient to reveal the basic pattern, and many such data already exist.

These continental-scale patterns in peregrine migration may have implications for the timing and routing of migrations and molt of potential prey species by making certain times and places more dangerous than others (Ydenberg et al. in press). Further evaluation of this idea will require more detailed knowledge of the predator landscape than is yet available.

## ACKNOWLEDGMENTS

Use of the Hawk Migration Association of North America data in this paper is governed by the data use policy at http://hmana.org/data policies/. HawkWatch International is the source of the Goshute NV, Manzano NM, and Corpus Christi TX datasets. Hawk Mountain Sanctuary, HWI, and Pronatura Veracruz MX are the sources of the Veracruz dataset. The data collected by the Guano River FL, Hawk Ridge MN, Cranberry Marsh ON, South Harpswell ME, Hawk Cliff ON, Holiday Beach ON, Fire Island NY, Cape May NJ, Kiptopeke VA, Montclair NJ, Waggoner's Gap PA, Hawk Mountain Sanctuary PA and Little Gap PA watchsites were provided by HawkWatch International and the Hawk Migration Association of North America (www.hmana.org) through its publication and online HawkCount database (www.hawkcount.org). We thank these organizations and the many volunteers who collected and collated the data for their efforts. We also thank Dick Dekker and John Ireland for so generously sharing with us their data on peregrine sightings at Beaverhills Lake, Alberta, and the George C. Reifel Migratory Bird Sanctuary, British Columbia, respectively. Comments made by Ian G. Warkentin, Will Cresswell, and Josef Schmutz improved earlier versions of this manuscript.

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Received 22 March 2007; accepted 9 October 2007
Associate Editor: Ian G. Warkentin