

## Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's Hawks *Buteo swainsoni* in the Western Hemisphere

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We describe and compare the migration routes, length of migration, and duration of migration of Peregrine Falcons *Falco peregrinus tundrius* and Swainson's Hawks *Buteo swainsoni* in the Western Hemisphere. We radio tracked migrants using the Argos satellite system. Our initial samples were 34 Swainson's Hawks from representative areas of their breeding range, and 61 Peregrine Falcons captured at nest sites across the North American boreal forest and low Arctic or on the migration routes along the mid-Atlantic and Gulf of Mexico coasts. The average distance of migration for Peregrines was 8,624 km southward, and 8,247 km northward. Peregrines travelled at an average rate of 172 km/d southward and 198 km/d going north. Peregrine Falcons used at least three broad, general routes south from the breeding areas, and individuals stopped migrating as far north as the U.S.A. mid-Atlantic coast and as far south as central Argentina. The radiomarked Peregrine Falcons used coastal routes, mid-continental routes, and water-crossing routes: the Davis Strait and Caribbean Sea. During northward migration, Peregrines migrating through at Padre Island, Texas diverged for destinations from central Alaska across the continent to central West Greenland. Swainson's Hawks migrated an average of about 13,504 km southward and 11,952 km northward, and travelled 188 km/d southward and 150 km/d northward. Swainson's Hawks converged in eastern Mexico on the Gulf of Mexico coast. Southward, these hawks followed a narrow, well-defined path through Central America, across the Andes Mountains in Columbia, and east of the Andes to central Argentina where they all spent the austral summer. Swainson's Hawks northward migration largely retraced their southward route.

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In this paper we describe the difference in migration patterns of two species of raptor with different flight behavior; predominately soaring flight by Swainson's Hawks *Buteo swainsoni* and predominately flapping flight by Peregrine Falcons *Falco peregrinus tundrius*. Members of both species make regular, long, inter-continental migrations between North America and South America. We relate our results to some concepts found in the bird migration literature (Kerlinger 1989, Berthold 1993) and to general information about Peregrine Falcon (Palmer 1988)

and Swainson's Hawk migration (England et al. 1997).

Our results are based on radio tracking individuals either through complete migration, or incomplete tracks of migration from a "midpoint" stop over to the end of migration. Regular tracking of birds during their migration is possible because of the development of small radio transmitters (Fuller et al. 1984, Mita and Kanmuri 1994, Strikwerda et al. 1986), whose signals can be received and located via the Argos satellite system (Fancy et al. 1988, Taillade

lade 1992). This technology has been used to study movements of large raptors (e.g., Meyburg et al. 1995a, b, Brodeur et al. 1996, Kjellén et al. 1997) and other types of birds (e.g., Nowak et al. 1990, Priede and Swift 1992, Fuller et al. 1995, Pennycuik et al. 1996). Our goal was to obtain location estimates, about once every three days, and use them to map individual migration routes and to estimate distances and rates of travel.

## Methods

Individual birds were captured and radio marked from autumn 1993 through the summer 1997. The method of capture varied by location and species. Among the methods used were bal-chatri with bait, noose carpets, harnessed pigeons, and dho-gaza with bait or lure animal (Bloom 1987). Satellite-received transmitters (Microwave PTT 100) weighing 20 g or 30 g were attached with backpack harness methods (Snyder et al. 1989). Transmission cycles generally were 8 h on and the off-periods ranged from 1 to 6 days.

We used the Argos satellite system (Argos 1996, Taillade 1992) to radio track the birds. Argos is a polar orbiting-based system that collects and processes environmental data, including location estimates, from autonomous platform transmitter terminals (PTTs) and distributes the data to users. Argos sends processed data from the satellites to the distribution centers for additional computing of the location estimate of the PTT, using principles of the Doppler shift. Computed locations and sensor data (e.g., battery voltage, activity) are then distributed to users. Each location estimate is associated with a measure of accuracy; location accuracy (designated by location class, LC) is assigned by Argos and is determined using parameters of the satellite overpass and PTT position relative to the overpass. Standard locations are: LC 3, with an estimated accuracy  $\leq 150$  m; LC 2, with an estimated accuracy of 150–350 m; LC 1, with an estimated accuracy of 350–1000 m; and LC 0, with an estimated accuracy  $> 1000$  m. LC 0, LC A, LC B, and LC Z location estimates have failed certain quality control checks; consequently, there is no upper limit on their accuracy (Argos 1996). However, these location estimates are available upon request and we used them because data with estimated accuracy  $< 1000$  m can be sparse, and the scale at which we were working (the Western Hemisphere) is compatible with the additional possible error.

We categorized each location estimate as having been obtained during a northward (outward) migration, a southward (return) migration, or on a breeding area or a "winter" (goal) area (austral summer south of the equator). We defined the start of a migration as the first location after which all subsequent locations occurred away from the breeding, wintering, or migration cap-

ture site (a relatively uni-directional movement). Likewise, we defined the end of migration as the point after which all subsequent points were localized (non-directional movement). Typically there was a lapse of at least 48 h between transmitting cycles, therefore the first or last location estimate during migration usually was easily discernible because of the relatively long distance moved during migration compared to the proximity of locations in the breeding or wintering area. If we ceased to obtain location estimates before we received multiple days of localized location estimates from a PTT, we categorized that migration data set as incomplete. Likewise, if a migration ended with a PTT activity sensor indicating that the PTT had ceased all motion, we presumed that the PTT had fallen off or that the bird had died, and thus categorized the migration as incomplete.

Our analyses of rates of migration are based on one location estimate selected from each transmission cycle for each bird (during some cycles, no location estimates were obtained). Within each transmission cycle for each bird, we selected a "representative" location estimate based on the LC (in order of preference: 3, 2, 1, 0, A, B, Z). If there was more than one location estimate with the preferred LC within the cycle, the first one acquired was selected. Visual inspection of the estimates was the basis for removing obvious outliers from the data.

We calculated the distance travelled (km) from a representative location estimate to the subsequent representative location estimate as the orthodromes (great circle distance) between positions, thereby obtaining a distance travelled between successive pairs of representative location estimates for each bird. Rates of travel between pairs of representative location estimates (km/d) were calculated from time and distance between representative successive location estimates.

The total number of days from the last day that a bird's location was recorded at the departure point (breeding, wintering, migration capture location) to the day it was first recorded at the destination at the other end of the migration was divided into three segments for full migration data sets (breeding to wintering or vice versa) and into two segments for incomplete tracks (migration capture location to wintering or breeding area).

We compared the cumulative distance travelled (the sum of the two or three segments) for each individual with the shortest distance between the beginning and the end of the migration (the straight line distance between the first and last representative migration location estimates) for all complete migrations using paired T-tests. We analysed the following seven subsets of the data: each species' northward and southward migration separately (4 tests), each species' combined northward and southward migrations (2 tests), and the entire data set (species combined).

We used the rate of travel data that are associated with the segments of the migrations to describe the pattern of the rate of travel, as well as to compare rates of travel *per se*. By pattern, we mean the general tendency for the rate of travel through all the segments. We tested for differences of patterns between species or between northward and southward migration. Rates of travel for complete migrations were compared among species (Peregrine Falcon, Swainson's Hawk) and direction of travel (north, south) using two-factor repeated measures ANOVA with migration segment as the repeated measure.

We then compared rates between direction of travel for the two species separately and rates between the species for the two directions of travel separately using one-factor repeated measures ANOVAs; the segment of the migration was the repeated measure for both analyses. We used orthogonal contrasts to test for differences among the three segments of migration for each of the four species-direction combinations. Rates of travel for incomplete migration tracks were compared for Peregrine Falcons only (no Swainson's Hawks were captured on migration). For incomplete migration tracks, rates were compared between directions of travel (north, south) using one-factor repeated measures ANOVA with the segment of the migration (first half or early, second half or late) as the repeated measure (Systat 1992).

## Results

We captured 57 Peregrine Falcons and 34 Swainson's Hawks. Of the Peregrine Falcons, three individuals were radio marked with 20 g PTTs and 54 were radio marked with 30 g PTTs; two were after hatch year (AHY) males, 55 were AHY females; 31 were marked on migration at Padre Island or Assateague Island; 26 were marked on breeding grounds in Greenland, Quebec, or the Northwest Territories (Table 1). We marked all of the Swainson's Hawks with 30 g PTTs within the

breeding range in nine states and provinces; all were AHY and the sex distribution was unknown (Table 1). We omitted 17 Peregrine Falcons and seven Swainson's Hawks from analyses because we did not obtain a migration track from an origin (breeding area, migration capture site) to a destination (breeding area, winter area).

### Peregrine Falcons

We obtained 22 complete and 12 incomplete southward migration tracks and seven complete and 11 incomplete northward migration tracks of Peregrine Falcons (Table 2). The average southward migration covered 8,624 km, and the rate over this distance was 172 km/d. Southward tracks occurred over a broad front, including coastal and inland routes over large landmasses, with frequent use of water crossings over the Gulf of Mexico and Caribbean Sea (Fig. 1). Winter destinations ranged from 40°N to 40°S and 36° to 98°W. Northward routes tended to be inland until the Texas Gulf Coast, from which the Peregrines headed toward various northern destinations; north routes rarely included water crossings. The average northward migration was 8,247 km, and the rate over this distance was 198 km/d.

### Swainson's Hawks

We obtained 27 complete southward and 19 complete northward migration tracks of Swainson's Hawks (Table 2). Southward and northward tracks followed a similar route, almost entirely inland except through Central America where some tracks were coastal. There were no crossings of large bodies of water. The rates over this distance were 188 km/d and 150 km/d for southward and northward migrations respectively (Fig. 2). Swainson's Hawks converged on a general region during the winter (30° to 40°S, 61° to 64°W).

Table 1. Locations and year of capture and radio marking of Peregrine Falcons (PEFA) and Swainson's Hawks (SWHA).

Species	Location	1993	1994	1995	1996	1997
PEFA	Kangerlussuaq, Greenland		8		2	6
	Assateague Island, MD/VA	2	5	2	3	
	Padre island, TX		12	2	3	2
	Rankin inlet, NT		4			
	Leaf pass, PQ		4			
	Koksoak, PQ		2			
SWHA	Idaho			4	6	
	Utah				3	
	Canada				7	
	Arizona				2	
	Oregon				6	
	California				1	
	Colorado				3	
	Minnesota				2	

Table 2. Sample sizes (n), mean distance travelled (km) and mean rates of travel (km per day) for Peregrine Falcons (PEFA) and Swainson's Hawks (SWHA).

	PEFA	SWHA
Individuals tagged (n)	57	34
Individuals used in analyses (n)	40	27
None-way origin to destination (N or S) (n)	72	46
Incomplete track S (n)	12	
Incomplete N (n)	11	
Distance total mig S (n)	22	27
Distance total mig N (n)	7	19
Mean total complete distances S	8,624.40	13,503.70
Mean total complete distances N	8,247.31	11,951.63
Mean total incomplete track distances S	6,450.26	
Mean total incomplete track distances N	5,583.26	
Mean segment distance S	755.92	540.95
Mean segment distance N	962.19	946.01
Mean rate complete distance S	171.93	188.00
Mean rate complete distance N	197.50	149.59
Full migration		
Rate 1st segment S	143.54	142.67
Rate 2nd segment S	184.94	219.77
Rate 3rd segment S	187.31	201.58
Rate 1st segment N	220.56	111.18
Rate 2nd segment N	227.03	186.87
Rate 3rd segment N	193.63	150.68
Incomplete track migration		
Rate 1st segment S	172.53	
Rate 2nd segment S	181.07	
Rate 1st segment N	152.20	
Rate 2nd segment N	140.59	

### Analyses of full migration

Regardless of migration direction, routes taken by migrating Peregrine Falcons and Swainson's Hawks did not correspond to the shortest distance between breeding and wintering areas (Table 3). Overall, the pattern in rates of travel across the three segments of full migration (early, mid, late; Table 2) on northward migration compared to southward migration did not differ depending on the species (3-way interaction among direction of travel, species, and segment of migration:  $F_{2,70} = 1.67$ ,  $P = 0.20$ ). However, patterns of rates in segments did vary depending upon species (2-way interaction between species and segment of travel, combining north and south migrations:  $F_{2,70} = 3.20$ ,  $P = 0.04$ ) and upon whether the birds travelled north or south (2-way interaction between direction and segment of travel, species:  $F_{2,70} = 3.37$ ,  $P = 0.04$ ). Generally, both Peregrine Falcons and Swainson's Hawks started and finished migration at slower rates than they travelled during the middle of migration; however, Peregrines travel faster than Swainson's Hawks at the beginning of a migration, whereas they travelled more slowly than Swainson's Hawks towards



Fig. 1. Peregrine Falcon migration as recorded by satellite telemetry.

the end of a migration. Likewise, for the two species combined, rates of travel for northward and southward migrations were similar at the beginning and in the middle of migration, but travel rates were different at the end of migration; birds slowed northward as they approached the breeding area, whereas the rate of travel remained constant from the middle to the end of southward migration.

Given these interactions, we examined species and direction of travel separately to isolate differences in patterns of rate of travel among segments of migration.

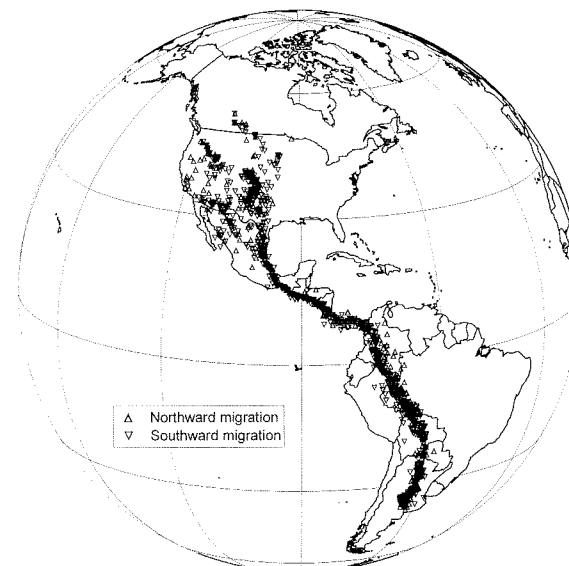


Fig. 2. Swainson's Hawk migration as recorded by satellite telemetry.

Table 3. Results of paired T-tests comparing the cumulative distance travelled (the sum of all segments of travel) with the direct (or shortest possible) distance travelled (the straight-line distance between origin and destination) for Swainson's Hawks (SWHA) and Peregrine Falcons (PEFA).

	N	Mean cumulative distance	Mean direct distance	Mean difference (SD)	95% confidence interval	t	d.f.	P
All	74	11,188.65	8,896.61	2,292.04 (1,178.88)	2,020.81–2,563.28	16.84	73	<0.000
SWHA	All	46	12,862.63	10,151.77 (1,025.90)	2,710.86–3,015.51	17.92	45	<0.000
	North	19	11,951.63	10,170.57 (588.75)	1,497.29–2,064.83	13.19	18	<0.000
	South	27	13,503.70	10,138.55 (710.82)	3,083.97–3,646.35	24.60	26	<0.000
PEFA	All	29	8,533.37	6,905.65 (1,111.84)	1,204.80–2,050.64	7.88	28	<0.000
	North	7	8,247.31	6,930.93 (681.29)	686.30–1,946.50	5.11	6	= 0.002
	South	22	8,624.39	6,897.61 (1,213.69)	1,726.78–2,264.90	6.67	21	<0.000

Neither Peregrines nor Swainson's Hawks differed in their patterns of travel between north and south migrations (2-way interaction between segment of migration and direction of travel: Peregrine Falcon:  $F_{2,25} = 2.85$ ,  $P = 0.08$ ; Swainson's Hawk:  $F_{2,43} = 0.44$ ,  $P = 0.65$ ). Additionally, neither Peregrine Falcons nor Swainson's Hawks travelled at different rates on southward and northward migration (effect of direction of travel: Peregrine Falcons:  $F_{1,26} = 2.20$ ,  $P = 0.15$ ; Swainson's Hawks:  $F_{1,43} = 1.54$ ,  $P = 0.22$ ).

Examining northward and southward migrations separately, we can compare patterns of rate of travel between species. On southward migration, there was no difference between species in pattern of their rates of travel across segments of the migration (2-way interaction between segment of migration and species:  $F_{2,46} = 0.97$ ,  $P = 0.39$ ) or in the rates of travel (effect of species:  $F_{1,47} = 1.68$ ,  $P = 0.20$ ). Conversely, on northward migration, Peregrine Falcons travelled faster than did Swainson's Hawks ( $F_{1,24} = 5.94$ ,  $P = 0.02$ ). Specifically, Peregrines started travelling at a faster rate than did Swainson's Hawks, but Swainson's Hawks' rates increased to nearly match Peregrine Falcons' rates during the middle of migration, and both decreased again towards the end of migration (2-way interaction between segment of migration and species:  $F_{2,23} = 4.50$ ,  $P = 0.02$ ).

Considering each direction of travel for each species separately, comparisons among segments of travel reveal that there were no differences in rates of travel among segments for either north or south migration of Peregrine Falcons. However, over all segments there was a tendency for an increasing rate as Peregrines approached the winter areas (linear contrast:  $F_{1,20} = 5.91$ ,  $P = 0.03$ ), but not for their northward migration (Table 4). Swainson's Hawks travelled more slowly at the beginning of their southward migrations, whereas the rates of travel in the middle and end segments of migration were similar (Table 4). On northward migration, they travelled more

slowly at the beginning of the migration than in the middle segment, but then reduced their rate of travel as they neared their breeding grounds to a rate similar to those in the first segment.

#### Analyses of incomplete tracks of Peregrine Falcons

The travelling pattern of Peregrine Falcons from capture locations on Padre Island and Assateague Island to breeding or wintering areas did not differ depending on whether the birds were travelling north towards a breeding area or south to a wintering area (2-way interaction between direction of travel and segment of migration:  $F_{1,20} = 0.39$ ,  $P = 0.54$ ). Likewise, the overall rate of travel on northward migrations did not differ from rates on southward migrations (effect of direction of travel:  $F_{1,20} = 1.01$ ,  $P = 0.33$ ). Within migrations of a given direction, there was no difference in rates of travel (north:  $F_{1,9} = 0.03$ ,  $P = 0.86$ ; south:  $F_{1,10} = 0.78$ ,  $P = 0.40$ ).

#### Discussion

Most of the information about avian migration routes and migratory movements is based on observation of visible migration from a few locations along routes, or on an initial and a final location of ringed individuals. Radar and radio telemetry (from the ground or aircraft) have provided data about continuous movements over longer distances (tens to thousands of km). Radio tracking via satellites is a method that can provide samples of a bird's location over the entire course of its migration. This type of data should be useful for study of migration. Our sample of 57 Peregrine Falcons and 34 Swainson's Hawks provides a basis for comparing results from tracking via satellites with characterizations,

conclusions, and concepts derived from other techniques used to study avian migration.

The map of Peregrine Falcon locations reveals a scatter of paths across the North and South American continents with some concentrations of locations along the Atlantic coast of North America, the Caribbean Islands, and Central American coasts (Fig. 1). These concentrations might in part be due to our radio marking at the Assateague Island and Padre Island sites. However, these are documented as stopover areas for relatively large numbers of Peregrines (Yates et al. 1988). Therefore, we consider our samples from these sites, in conjunction with samples from breeding areas, to be representative of a large portion of the tundra Peregrine migration. Apart from these coastal concentrations, the map of locations suggests breeding Peregrines from North America migrate over a relatively broad front, and that their migration is dispersive (Berthold 1993). Further evidence that these Peregrines fit the dispersive characterization is the large area within which they settle for the winter or austral summer period. This range of latitudes spanning boreal winter and austral summer areas is greater than previously expected for *Falco peregrinus tundrius* (Palmer 1988, Kerlinger 1989). We suggest that the shape of the Peregrine migration is more like that resulting from a sieve, than like the funnel- and fan-shaped migration of many species (Berthold 1993).

Migrating Swainson's Hawks location estimates produce a map of movement that is broad front at the onset (Berthold 1993), but changes to a funnel shape during the southward (outward) migration. The northward (return) migration is of the fan shape (Berthold 1993). Swainson's Hawk migration can be characterized as concentration migration (Berthold 1993). The adult birds we sampled from throughout most of the breeding range spent the austral summer in central Argentina, an area known to be part of the species' goal or resting area (England et al. 1997). None of our radio marked birds went to Florida or central California where wintering Swainson's Hawks occur regularly in relatively small numbers.

The routes taken by Peregrines appear to be influenced by coastlines that might act as ecological barriers that can influence migration direction (Berthold 1993). The Appalachian Mountains seem to create a migratory divide between birds flying along the coast or coastal plain, and those flying west of the mountains

over the mid-continent. However, the tracks of the radio marked birds also confirm Kerlinger's (1989) characterization of Peregrines as a species that can undertake long distance water crossings. Our sample illustrates relatively long non-stop flights over the Davis Strait between West Greenland and Canada, and over Hudson Bay. Our map of Peregrine tracks also illustrates island hopping (Kerlinger 1989) along the northeastern coast of Canada, the U.S.A. Atlantic coast, among the Caribbean Islands, along the eastern Mexico and Central American coasts, and northern South American coasts.

Swainson's Hawks became concentrated at the Central Mexican coast of the Gulf of Mexico, and remained concentrated along the other ecological barriers of the Pacific coast of Central America, through Panama, and along the eastern flanks of the Andes Mountains. The Isthmus of Tehuantepec and the Isthmus of Panama are areas of extreme canalization of the Swainson's Hawks' migratory routes. Kerlinger (1989) used a variety of empirical data and models to make general predictions about which species, under certain circumstances, would be likely to make water crossings or detour around water. Based largely on data for Red-tailed Hawks *Buteo jamaicensis* and Broad-winged Hawks *B. platypterus*, he predicted that *Buteo* hawks will be less likely to make water crossings than many other raptors. Our tracks along the Swainson's Hawks' migration route, and Smith's (1985) observations in Panama indicate Swainson's Hawks conform with the prediction. The map of the Swainson's Hawks movements reveals that this species performs an arched migration, making gradual turns to detour ecological barriers (Berthold 1993).

The average distances covered by Peregrines, 8,624 km southward and 8,247 km northward, lack any basis of comparison in the literature. We suspect that the ranges of latitudes from which, and to which Peregrines migrate complicates any efforts to estimate migration distance. The average migration distances of 13,504 km (southward) and 11,952 km (northward) for our sample of Swainson's Hawks greatly exceed the 8,000 km value Kerlinger (1989) used to estimate daily flight distances.

In addition to the routes taken by migrants, another important component of the migration strategy is the rate of travel. We calculated rates of travel based on location estimates obtained about one day out of three during the migration. We used pattern as another mea-

Table 4. Results of contrasts among segments of complete migration. Analyses were done separately for each direction of travel for each species.

Species	Direction	Early vs Mid	Mid vs Late	Early vs Late
Peregrine Falcon	South	$F_{2,20} = 2.27, P = 0.13$	$F_{2,20} = 0.65, P = 0.58$	$F_{2,20} = 3.16, P = 0.06$
	North	$F_{2,5} = 0.01, P = 0.99$	$F_{2,5} = 1.87, P = 0.25$	$F_{2,5} = 4.28, P = 0.08$
Swainson's Hawk	South	$F_{2,25} = 12.04, P < 0.01$	$F_{2,25} = 1.12, P = 0.32$	$F_{2,25} = 5.67, P = 0.01$
	North	$F_{2,17} = 7.04, P = 0.01$	$F_{2,17} = 1.06, P = 0.23$	$F_{2,17} = 1.82, P = 0.19$

sure to study migration strategy. The pattern of migration is the relationship among the rates of travel of the segments. Regardless of species or direction of migration the pattern of the rates of travel were statistically similar. Generally birds travelled faster during the middle third of migration than at the start, then maintained or slowed their rate of travel during the last third. This result is not especially interesting, but some comparisons of the actual travel rates, rather than the pattern, reveal other aspects of the strategies.

We detected no difference in rates of travel on northward versus southward migrations for either Peregrine Falcons or Swainson's Hawks; both travelled at about the same rate whether they were flying to or from breeding areas. Further, although the two species travelled at similar rates during their southward migration, Peregrine Falcons moved at a faster travel rate than Swainson's Hawks on the northward migration. The average rate of travel by Peregrines was about 172 km/day going south, and 198 km/day going north. Those travel rates fall in the range of predicted rates Kerlinger (1989) derived for Peregrines flying in opposing and following winds ( $-9$  to  $+9$  m/s; about 80–450 km/d), and in a 6 m/s wind from various directions relative to flight direction (120–450 km/d). The observed rates of migration in Peregrines and Swainson's Hawks are similar to those of other large raptors studied by satellite telemetry (e.g. Meyburg et al. 1995a, b, Kjellén et al. 1997).

By using thermal soaring large birds can achieve much higher migration speeds than had they used flapping flight (Hedenström 1993). By using the soaring flight strategy they can even reach overall travel rates in excess of what small passerines can achieve (Hedenström and Alerstam 1998). However, the Peregrine might actually use flapping flight to a significant extent, which makes this species less dependent on thermals and which can explain the very high migration speed observed (especially during spring migration). Cochran and Applegate (1986) reported flight speeds of a few radio-tracked Peregrines of on average 12.1 m/s (about 1045 km/d) during migration, which would result in an overall rate of migration five times that reported here. This means that on average during migration Peregrines are stopping over four days for every day of flight. This comparison refers to flapping flight. When Peregrines use soaring flight their cross-country speed is reduced and the true relationship between stopover and flight time therefore is probably smaller than 4:1.

For birds migrating by thermal soaring the cross-country speed is partly determined by the rate at which the bird gains altitude while circling in thermals; that is, the higher climb rate the higher migration speed (Pennycuik 1972, Hedenström 1993). An interesting observation was that the birds of this study showed the highest speeds during the middle third of their journey. This coincides with the passage of the equatorial re-

gion, where thermals are stronger than in more temperate regions.

Location estimates of migrant birds obtained by radio tracking via satellites are available regularly and frequently compared to those based on observation of passing migrants, or a few radar or radio tracking sites. These location estimates are less likely to be biased by our inability to gather data in remote areas or during inclement weather. Data obtained via satellite telemetry contribute to more complete maps of migration routes, and more accurate estimates of the distance and duration of migration. Our initial analyses of radio tracking comparatively large samples of Peregrine Falcons and Swainson's Hawks suggest the migrations of these two species conform with some general characterizations of avian migration and with some general strategies, but more continuous data also reveal some differences. This is to be expected as greater amounts of data become available. Thus, we are not so bold as to claim that our data describe the optimal migration of Peregrines and Swainson's Hawks, but we do believe they are representative of the migratory movements of after hatching year birds (largely females) in North America.

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## References

- Argos 1996. User's Manual 1.0. – CLS/Service Argos, Landover, Maryland, U.S.A.
- Berthold, P. 1993. Bird Migration: A General Survey. – Oxford University Press, Oxford.
- Bloom, P. H. 1987. Capturing and handling raptors. – In: Pendleton, B. G., Millsap, B. A., Cline, K. W. and Bird, D.M. (eds), Raptor Management Techniques Manual. National Wildlife Federation Scientific and Technical Series No. 10, pp. 99–123.

- Brodeur, S., Décarie, R., Bird, D. M. and Fuller, M. 1996. Complete migration cycle of golden eagles breeding in northern Quebec. – *Condor* 98: 293–299.
- Cochran, W. W. and Applegate, R. D. 1986. Speed of flapping flight of merlins and peregrine falcons. – *Condor* 88: 397–398.
- England, A. S., Bechard, M. J. and Houston, C. S. 1997. Swainson's Hawk (*Buteo swainsoni*). – In: Poole, A. and Gill, F. (eds). *The Birds of North America*, No 265. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, D.C.
- Fancy, S. G., Pank, L. F., Douglas, D. C., Curby, C. H., Garner, G. W., Amstrup, S. C. and Regelin, W. L. 1988. Satellite telemetry: a new tool for wildlife research and management. – U.S. Fish Wildl. Serv., Resour. Publ. 172.
- Fuller, M. R., Levanon, N., Strikwerda, T. E., Seegar, W. S., Wall, J., Black, H. D., Howey, P. W. and Partelow, J. 1984. Feasibility of bird-borne transmitter for tracking via satellite. – In: Kimmich, H. P. and Klewe H. J. (eds). *Biotelemetry VIII*. Kimmich/Klewe, Nijmegen, pp. 375–378.
- Fuller, M. R., Seegar, W. S. and Howey, P. W. 1995. The use of satellite systems for the study of bird migration. – *Israel J. Zool.* 41: 243–252.
- Hedenström, A. 1993. Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. – *Phil. Trans. R. Soc. Lond. B* 342: 353–361.
- Hedenström, A. and Alerstam, T. 1998. How fast can birds migrate? – *J. Avian Biol.* 29: 000–000.
- Kerlinger, P. 1989. *Flight Strategies of Migrating Hawks*. – University of Chicago Press, Chicago.
- Kjellén, N., Hake, M. and Alerstam, T. 1997. Strategies of two Ospreys *Pandion haliaetus* migrating between Sweden and tropical Africa as revealed by satellite tracking. – *J. Avian Biol.* 28: 15–23.
- Meyburg, B.-U., Mendelsohn, J. M., Ellis, D. H., Smith, D. G., Meyburg, C. and Kemp, A. C. 1995a. Year-round movements of a Wahlberg's eagle *Aquila wahlbergi* tracked by satellite. – *Ostrich* 66: 135–140.
- Meyburg, B.-U., Scheller, W. and Meyburg, C. 1995b. Zug und Überwinterung des Schreiadlers *Aquila pomarina*: Satellitentelemetrische Untersuchungen. – *J. Ornithol.* 136: 401–422.
- Mita, N. and Kanmuri, N. 1994. Development of super-compact platform transmitter terminals for satellite tracking. – In: Higuchi, H. and Minton, J. (eds). *The Future of Cranes and Wetlands*. Wild Bird Soc. Japan, Tokyo, pp. 51–54.
- Nowak, E., Berthold, P. and Querner, U. 1990. Satellite tracking of migrating Bewick's swans. – *Naturwissenschaften* 77: 549–550.
- Palmer, R. S. 1988. *Handbook of North American Birds*. Vol. 5. – Yale University Press, New Haven.
- Pennycuik, C. J. 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. – *Ibis* 114: 178–218.
- Pennycuik, C. J., Einarsson, Ó, Bradbury, T. A. M. and Owen, M. 1996. Migrating Whooper Swans *Cygnus cygnus*: satellite tracks and flight performance calculations. – *J. Avian Biol.* 27: 118–134.
- Priede, I. G. and Swift, S. S. 1992. *Wildlife Telemetry, Remote Monitoring and Tracking of Animals*. – Ellis Horwood, New York.
- Smith, N. G. 1985. Dynamics of trans-isthmusian migration of raptors between Central and South America. – In: Newton, I. and Chancellor, R. D. (eds). *Conservation Studies of Birds of Prey*. ICBP Tech. Publ. 5. International Council for Bird Preservation, Thessaloniki, pp. 271–290.
- Snyder, N. F. R., Beissinger, S. R. and Fuller, M. R. 1989. Solar radio-transmitters on snail kites in Florida. – *J. Field Ornithol.* 60: 171–177.
- Strikwerda, T. E., Fuller, M. R., Seegar, W. S., Howey, P. W. and Black, H. D. 1986. Bird-borne satellite transmitter and location program. – *Johns Hopkins Appl. Phys. Lab. Technol. Digest* 7: 203–208.
- SYSTAT 1992. *Statistics*. Version 5. – SYSTAT, Evanston, IL.
- Taillade, M. 1992. Animal tracking by satellite. – In: Priede, I. G. and Swift, S. S. (eds). *Wildlife Telemetry, Remote Monitoring and Tracking of Animals*. Ellis Horwood, New York, pp. 149–160.
- Yates, M. A., Riddle, K. E. and Ward, F. P. 1988. Recoveries of peregrine falcons migrating through the eastern and central United States, 1955–1985. – In: Cade, T. J., Enderson, J. H., Thelander, C. G., and White, C. M. (eds). *Peregrine Falcon Populations: Their Management and Recovery*. The Peregrine Fund, Inc., Boise, pp. 471–483.