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Mark S. Martell
mmartell@audubon.org

Richard O. Bierregaard Jr.
University of North Carolina

Brian E. Washburn
U.S.D.A. Wildlife Services, brian.e.washburn@aphis.usda.gov

John E. Elliott

Charles J. Henry
U.S. Geological Survey

See next page for additional authors

Authors
Mark S. Martell, Richard O. Bierregaard Jr., Brian E. Washburn, John E. Elliott, Charles J. Henry, Robert S. Kennedy, and Iain MacLeod

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THE SPRING MIGRATION OF ADULT NORTH AMERICAN OSPREYS

MARK S. MARTELL[1]
Audubon Minnesota, 1 Water Street West, Suite 200, St. Paul, MN 55107 U.S.A.

RICHARD O. BIERREGAARD, JR.[2]
Biology Department, University of North Carolina at Charlotte, 9201 University City Boulevard, Charlotte, NC 28223 U.S.A.

BRIAN E. WASHBURN
U.S.D.A. Wildlife Services, National Wildlife Research Center, 6100 Columbus Avenue, Sandusky, OH 44870 U.S.A.

JOHN E. ELLIOTT
Environment Canada, Science and Technology Branch, Pacific Wildlife Research Centre, 5421 Robertson Road RR #1, Delta, British Columbia, V4K3N2 Canada

CHARLES J. HENNY
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331 U.S.A.

ROBERT S. KENNEDY
Maria Mitchel Association, 4 Vestal Street, Nantucket, MA 02554 U.S.A.

IAIN MACLEOD
Squam Lakes Natural Science Center, 23 Science Center Road, Holderness, NH 03245 U.S.A.

ABSTRACT.—Most North American Ospreys (*Pandion haliaetus*) are migratory, breeding in northern latitudes and migrating long distances to and from their wintering grounds in the tropics. Although fall migration patterns of North American Ospreys have been described and studied, very little has been published about the spring migration of these birds. We used satellite telemetry to: (1) determine the characteristics (timing, duration, migratory routes) of spring migrations of Ospreys; (2) determine if differences in spring migration patterns existed between sexes and among three breeding populations (east coast, midwestern, and western); and (3) compare consecutive fall and spring migrations of individual Ospreys. The median dates for departure from the wintering grounds and arrival on the breeding grounds did not differ significantly between adult male and female Ospreys. Compared to their fall migrations, all male and all east coast Ospreys spent fewer days on migration, fewer days in stopover periods along the migration route, traveled shorter distances overall, and traveled farther (on average) each day during spring. In contrast, fall and spring migration characteristics of all female and western Ospreys were similar. Our findings suggest that, although sex and breeding location might influence the spring migration strategy used by individual Ospreys, both males and females minimize the time spent on migration to ensure a timely arrival on the breeding grounds to establish or defend a nesting territory.

KEY WORDS: *Osprey*; Pandion haliaetus; *loop migration*; *North America*; *satellite telemetry*; *spring migration.*

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[1] Email address: mmartell@audubon.org
[2] Present address: 421 Cotswold Lane, Wynnewood, PA 19096 U.S.A.

MIGRACIÓN PRIMAVERAL DE INDIVIDUOS ADULTOS DE *PANDION HALIAETUS*

RESUMEN.—La mayoría de los individuos de *Pandion haliaetus* son migratorios, reproduciéndose en latitudes hacia el norte y migrando largas distancias hacia y desde los sitios de invernada en los trópicos. Aunque los patrones de migración otoñal de *P. haliaetus* han sido descriptos y estudiados, se ha publicado muy poco sobre la migración primaveral de esta especie. Utilizamos telemetría satelital para: (1) determinar las características (tiempos, duración, rutas migratorias) de la migración primaveral de *P. haliaetus*; (2) determinar si las diferencias en los patrones de migración primaveral existieron entre sexos y entre tres poblaciones reproductivas (costa este, medio oeste y oeste); y (3) comparar migraciones consecutivas de otoño y primavera de individuos de *P. haliaetus*. Las fechas medianas de partida desde los sitios de invernada y de arribo a los sitios de reproducción no difirió significativamente entre individuos macho y hembra de *P. haliaetus*. En comparación con las migraciones otoñales, todos los individuos de *P. haliaetus* macho y todos los individuos de la costa este emplearon menos días migrando, menos días en periodos de descanso a lo largo de la ruta de migración, viajaron distancias más cortas en general y viajaron más lejos (en promedio) cada día durante la primavera. En contraste, las características migratorias de otoño y primavera de todos los individuos hembra y macho de *P. haliaetus* fueron similares. Estos hallazgos sugieren que aunque el sexo y la ubicación del sitio de reproducción pueden influir en la estrategia de migración primaveral utilizada por los individuos de *P. haliaetus*, tanto hembras como machos minimizan el tiempo empleado en la migración para asegurarse un arribo a tiempo a los sitios de reproducción para establecer o defender un territorio de nidada.

[Traducción del equipo editorial]

Most Ospreys breeding in North America and Europe are migratory (Poole et al. 2002), and data from watch sites, banding, and satellite telemetry have revealed general patterns of fall migration. Band recovery analyses (Henny and Van Velzen 1972, Poole and Agler 1987, Mestre and Bierregaard 2009) and satellite-tracking studies of adults in North America (Martell et al. 2001, Elliott et al. 2007, Farmer et al. 2010) revealed the broad spatial and temporal distributions of Ospreys during fall migration.

The breeding area used by North American Ospreys influences their fall migration patterns. Adult Ospreys that breed in eastern North America, with very rare exceptions, are funneled to Florida and from there pass over Cuba and Hispaniola before crossing the Caribbean to South America. Ospreys from the U.S. Midwest follow one of three paths to South America: some join the east coast birds on the Florida-Cuba-Hispaniola route, some fly south to Texas and Mexico, arriving in South America via the isthmus of Panama, and some follow the Mississippi River south, cross the Gulf of Mexico to the Yucatan peninsula, and then proceed through Central America to wintering sites across much of South America. In marked contrast, most Ospreys from the Pacific Northwest winter in Mexico and Central America, and only a few make their way into South America (Melquist and Johnson 1984, Johnson and Melquist 1991, Martell et al. 2001, Elliott et al. 2007).

During migration, individuals are typically seen alone over northern watch sites (Kerlinger 1989). Although Ospreys do cross wide expanses of open water, when possible they tend to stay over land; this results in a funneling effect through Florida and the Caribbean, with relatively large groups reported over Cuba (Rodríguez-Santana et al. 2003, 2014) and Haiti (Crouse and Keith 1999).

Although most published studies of bird migration have focused on fall, some studies have presented spring migration data and compared the details of spring vs. fall migration (e.g., Klaassen et al. 2010). Martell et al. (2004) reported on spring and fall migration of seven ospreys that migrated from Florida to South America and Alerstam et al. (2006) found differences in spring and fall migration strategies among seven Ospreys tagged in Sweden. Studies of other avian species have shown differences between the duration of fall and spring migration, with both faster spring than autumn migration (Peregrine Falcons [*Falco peregrinus*]; Fuller et al. 1998) and faster autumn than spring migration (Swainson's Hawk [*Buteo swainsoni*; Fuller et al. 1998] and White Stork [*Ciconia ciconia*; Shamoun-Baranes et al. 2003]), along with differences in routes taken.

Osprey band returns indicate spring migrations are quicker than fall migrations (Poole and Agler 1987). Thorup et al. (2006) found that European Ospreys spent proportionally more traveling than stopover days in spring compared to autumn. Stopover days were more frequent in spring than fall for White Storks due to a period of foraging in the Middle East (Shamoun-Baranes et al. 2003).

Table 1. Capture and satellite-tagging location of North American Ospreys from three breeding populations (regions), 1996–2013. Only birds from which we obtained migration data are included.

		NUMBER OF BIRDS		
SITE	CENTRAL COORDINATES	MALES	FEMALES	TRAP DATES
EAST COAST				
Sutton Island, ME	44°16.38′N, 68°15.06′W	2	2	1999–2000
Bridgewater, NH	43°42.84′N, 71°39.36′W	2	0	2012–2013
Montezuma NWR, NY	42°58.56′N, 76°44.46′W	0	3	1999
Westport, MA	41°36.78′N, 71°04.08′W	6	0	2012
Conanicut Island, RI	41°35.10′N, 71°28.68′W	1	0	2010
Martha's Vineyard, MA	41°22.80′N, 70°38.70′W	7	4	2001–2013
Fishers Island, NY	41°15.84′N, 71°59.70′W	1	0	2013
Shelter Island, NY	41°04.08′N, 72°20.34′W	7	7	1997–2010
Peconic Bay, NY	40°59.76′N, 72°30.18′W	2	0	2010–2012
Jamaica Bay, NY	40°35.82′N, 73°49.68′W	1	0	2012
Cape May, Cumberland, and Salem counties, NJ	39°10.26′N, 74°41.28′W	3	8	1997–2001
Annapolis, MD	38°59.88′N, 76°25.32′W	1	0	2013
Washington, DC	38°52.08′N, 77°00.30′W	2	0	2013
Tangier Island, VA	37°49.26′N, 75°59.46′W	2	0	2013
Hampton, VA	37°04.74′N, 76°21.66′W	2	2	2006–2007
Mt. Holly, NC	35°17.22′N, 81°00.36′W	0	1	2001
Brunswick Co., SC	33°56.16′N, 78°38.10′W	1	3	1999–2000
Total (east coast)		**40**	**30**	**1997–2013**
MIDWEST				
Minneapolis-St. Paul metropolitan area and central MN	45°24.42′N, 93°46.98′W	14	6	1996–1999
Total (midwest)		**14**	**6**	**1996–1999**
WEST				
Columbia River/Willamette Valley, OR/WA	45°39.66′N, 121°18.78′W	2	14	1996–1999
British Columbia, Canada	51°30.00′N, 126°36.00′W	1	11	1996–2003
Total (western)		**3**	**25**	**1996–2003**
Total (all regions)		**57**	**61**	**1996–2013**

In this report, we: (1) describe the nature of Osprey spring migration (e.g., timing, distance, duration, and routes) in the western hemisphere; (2) compare spring migration patterns between sexes and among birds from three North American breeding regions; and (3) examine how spring migration differs from fall migration across groups and by individual birds.

METHODS

From 1996 to 2013, we captured adult Ospreys at their nests on study areas in the eastern, midwestern, and northwestern United States and southwestern Canada (''western'') using dho-ghaza traps with Great Horned Owls (*Bubo virginianus*) as lures, or noose carpet traps placed over nests (Bloom 1987, Martell et al. 2001; Table 1). Birds were sexed based on behaviors observed at the nest, as well as body size and plumage color pattern (Poole 1989, Poole et al. 2002). We used a backpack harness (Kenward 2001, Martell et al. 2001, Bierregaard 2014) to attach to each bird a 30- to 35-g Platform Transmitter Terminal (PTT) produced by Microwave Telemetry Inc. (Columbia, Maryland, U.S.A.).

Over the course of this study, PTT technology improved so the birds we studied were fitted with a range of PTTs, from early models with limited battery time to solar-powered units capable of multiyear performance. Early in the study, birds were tracked using NOAA satellites with on-board Doppler-based tracking equipment operated by CLS America (formerly ARGOS Inc., Largo, Maryland, U.S.A.). We began using PTTs with GPS-accurate location capability in 2006.

All the Doppler-based satellite telemetry units (ARGOS PTTs) were programmed to transmit data for an 8- or 10-hr period followed by a 20–72-hr off period. Accuracy of ARGOS provided location estimate depends on a variety of factors which have been commented on by other researchers (see Keating et al. 1991, Britten et al. 1999, Vincent et al. 2002, Soutullo et al. 2007).

GPS-equipped PTTs (with location errors estimated to be <30 m) were programmed to provide 12 to 13 hourly locations per d or 10 locations at 2-hr intervals each d (depending on the study location). During migratory periods, Osprey locations were collected from 0800 to 2000 H (one location per hr) or 0500 to 2300 H (with one location every 2 hr). In 2012 and 2013, we deployed eight GSM (Global System for Mobile Communication) PTTs. These GSM PTTs provided GPS locations 24 hr per d, with locations as frequent as one location per min with a fully charged battery.

For this study we used a ''best of day'' approach, selecting the most accurate location for each day for ARGOS-calculated PTTs and the last location of the day for the GPS and GSM PTTs. We determined the most accurate location based on reported location classes, and removed locations that appeared to be in error (based on visual inspection). We made an effort to use only those location estimates with LCs of 3, 2, or 1, but when there were no location estimates of that quality, we used less accurate locations as logic dictated (i.e., when they were on the path between two more reliable locations, or when there were clusters of these lower accuracy locations). When there were more than one ''best of day'' LC on a given day, we used the last one for that day.

When exact dates were unavailable for departure or arrival, we used the median date between the last signal from the wintering area and the first signal on spring migration (departure) and for arrival, the median date between the last signal on spring migration and the first signal from the breeding area. If there was more than a 10-d gap between locations, we did not calculate a departure or arrival date. Loxodromic distances travelled were calculated between daily locations for each segment over the entire route and the total migration distance was the sum of these segments. Distances were determined using measuring tools available in Google Earth Pro™ (Google Inc., Mountain View, California, U.S.A.) or ArcGIS (ESRI, Redlands, California, U.S.A.).

The number of days on migration was calculated using the best estimate of departure and arrival dates. Mean distance traveled per day was calculated using total migration distance divided by the number of days from the start to end of migration. A stopover day was defined as a day when a bird travelled ≤25 km, and we determined, when possible, the number of stopover days during each migration. To compare stopover data between birds with different migration periods, we calculated the percentage of the total migration days that were spent as stopovers.

Some individual Ospreys were tracked for more than one year. Because each individual migration by a given bird is not independent from other migration events by that bird, for Ospreys that were tracked for at least part of two or more spring migrations ($n = 15$), we randomly selected one migration event for each individual bird for the statistical analyses (see below).

Migration Routes. For each population we measured the breadth of the spring and fall migration fronts as the distance between the easternmost and westernmost individual tracks at ''checkpoints'' at selected latitudes to determine the median longitude where the birds crossed those latitudes (Fig. 2–4). The number of checkpoints chosen for each population varied based on the amount of data available and the nature of the migration movement. For east coast Ospreys, our ''checkpoints'' were at six latitudes: 39°N (approximately the northern end of Chesapeake Bay); 33.5°N (South Carolina, midway between North Carolina's Outer Banks and northern Florida); 30°N (just south of the Florida–Georgia border); 24°N (the Florida Straits between Cuba and the Florida Keys), 17°N (roughly 60 km south of Hispaniola—the beginning of the approximately 570–730 km crossing of the Caribbean Sea for southbound birds); and 13°N (roughly 60 km into the Caribbean crossing for northbound birds).

For midwestern birds, we measured the migration front at 30°N, which is the northern coast of the Gulf of Mexico. Three latitudinal checkpoints were used for western birds: 44°N (roughly 50–100 km south of our Oregon tagging locations); 37°N; and 30°N (roughly the U.S.–Mexico border).

Statistical Analyses. Departure dates from wintering grounds and arrival dates onto breeding areas were compared among Osprey breeding regions and between sexes using Kruskal-Wallis tests (test statistic H; Zar 1996). We used two-way analysis of variance (ANOVA) to test for differences in the number of days spent on spring migration, total

Figure 1. Migration routes of adult female Osprey #03-06234 following similar paths in two consecutive migration cycles.

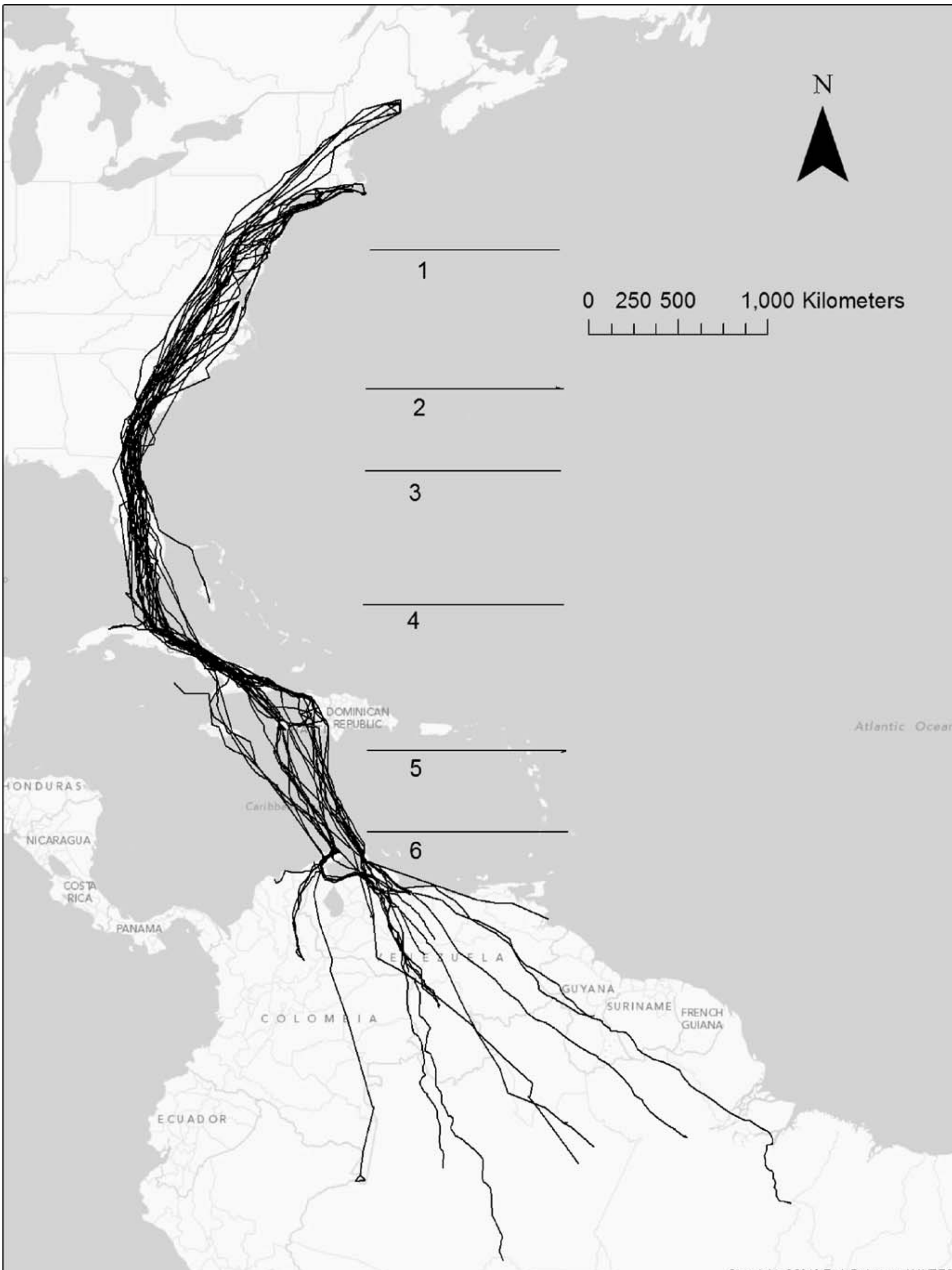

Figure 2. Routes of eastern adult Ospreys on their spring migration ($n = 5$). Numbered line marks latitudinal ''checkpoint'' used to measure the breadth of the migration front (see text for further explanation). Tracks connect either GPS or ARGOS Doppler locations and do not necessarily reflect the exact path traveled.

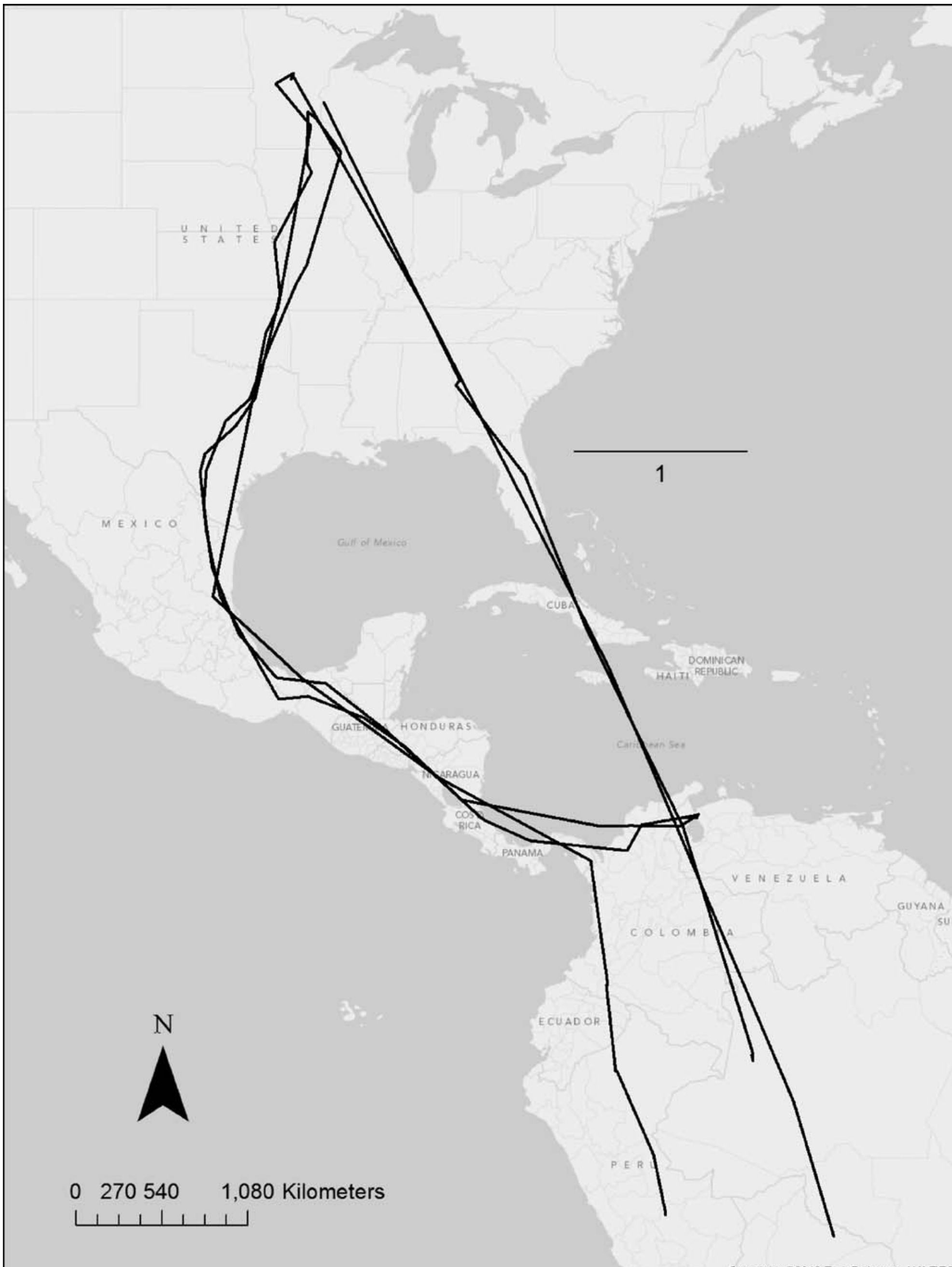

Figure 3. Routes of midwest adult Ospreys on their spring migration (n = 5). Numbered line marks latitudinal ''checkpoint'' used to measure the breadth of the migration front (see text for further explanation). Tracks connect either GPS or ARGOS Doppler locations and do not necessarily reflect the exact path traveled.

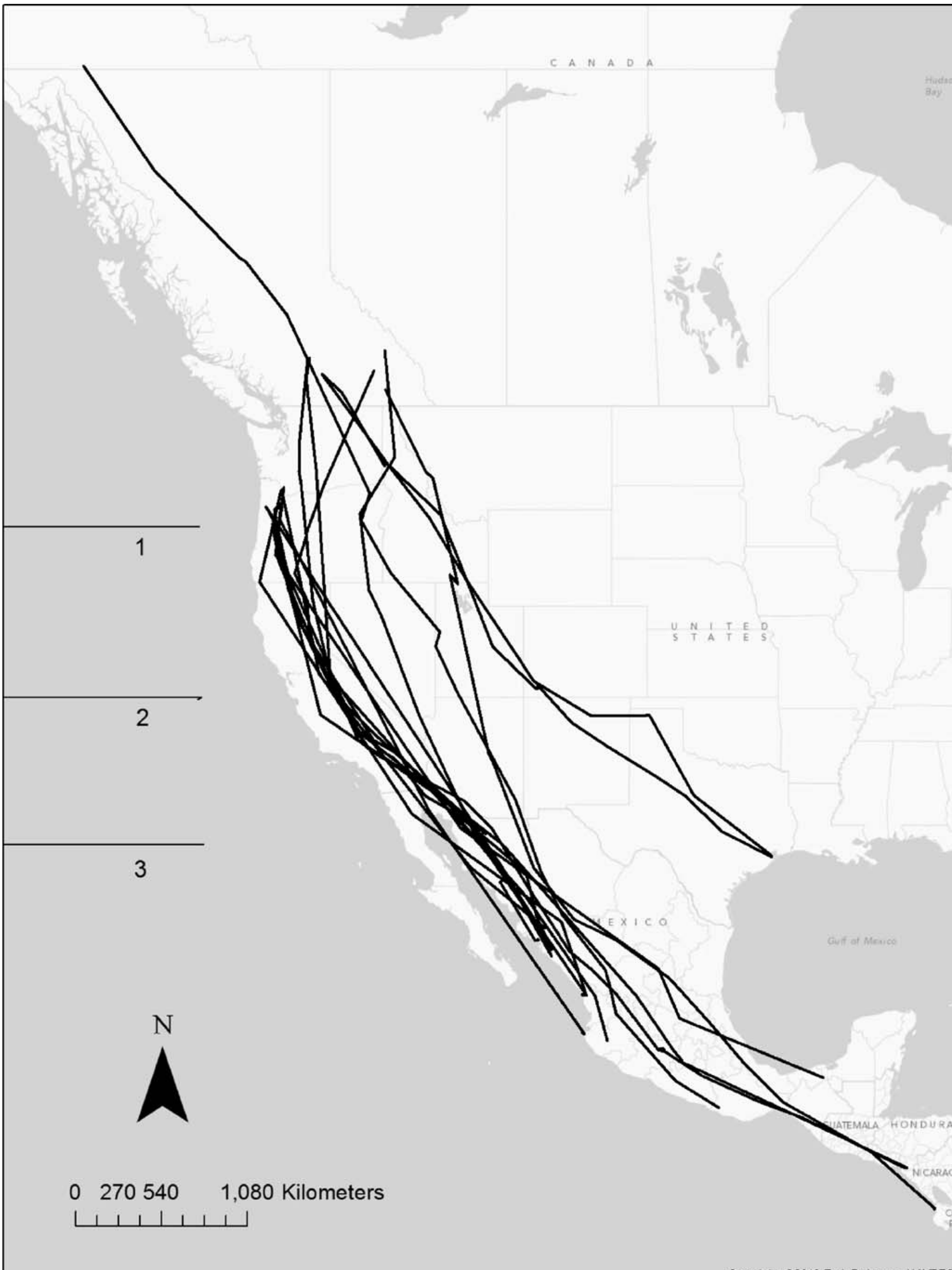

Figure 4. Routes of western adult Ospreys on their spring migration (n = 18). Numbered lines mark latitudinal ''checkpoints'' used to measure the breadth of the migration front (see text for further explanation). Tracks connect either GPS or ARGOS Doppler locations and do not necessarily reflect the exact path traveled.

Table 2. Breadth of migration front (km) and median longitude at six latitudes for south- and northbound Ospreys nesting in the eastern U.S.A.

	FALL			SPRING			RATIO
LATITUDE	n	FRONT (km)	MEDIAN LONG. (W)	n	FRONT (km)	MEDIAN LONG. (W)	SPRING/FALL
39°N	32	460	75°49.0′	13	231	76°25.7′	0.502
33.5°N	41	691	79°28.3′	19	148	80°19.6′	0.214
30°N	42	718	81°38.8′	19	107	81°42.0′	0.149
24°N	42	765	80°35.5′	18	155	80°44.1′	0.203
17°N	38	850	71°26.5′	18	456	73°31.1′	0.537
13°N	37	960	71°49.7′	18	269	71°32.1′	0.280

distance traveled on spring migration, and average daily distance traveled during spring migration among breeding regions and between sexes. Fisher's protected LSD tests were used to compare among means when main effects or interactions were significant (Zar 1996).

Wilcoxon signed rank tests (test statistic T; Zar 1996) were used to determine if the number of days spent on migration, total distance traveled on migration, and average daily distance traveled varied for paired fall and spring migrations for individual Ospreys.

We considered differences to be significant at $P \leq 0.05$ and conducted all analyses using SAS statistical software version 9.3 (SAS Institute, Cary, North Carolina, U.S.A.). Data are presented as median; first quartile, third quartile, or as mean ± 1 standard error.

RESULTS

From 1995 to 2013, we deployed PTTs on 135 nesting adult Ospreys (77 from the east coast, 25 from the midwest, and 33 from the west). All midwestern and western Ospreys were tagged with ARGOS PTTs. Fifty birds from the east coast received ARGOS PTTs, 19 were tagged with GPS PTTs, and 8 were tagged with GSM PTTs. Overall, we tagged more female Ospreys (n = 77) than males (n = 58).

Seven east coast, five midwestern, and five western birds provided no migratory information, due to PTT failure, so our analyses are based on 118 satellite-tagged Ospreys (Table 1). We tracked these 118 Ospreys through at least some part of their fall migrations from their nesting grounds to their wintering areas. Of these we received some information regarding spring migration from 53 individual birds during a total of 74 spring migration attempts.

Migration Routes. In all three breeding populations, individual Ospreys followed roughly similar routes in spring and fall with notable exceptions in each region. Individuals tracked more than one year followed the same routes each spring (Fig. 1).

East coast Ospreys. Most of our east coast Ospreys wintered in South America. Two wintered in Florida and four wintered on Caribbean islands. On their fall migrations, Ospreys were typically funneled by geography to Florida, on to Cuba and then Hispaniola, where they began their crossing of the Caribbean (Martell et al. 2001). The fall migration front broadened from 460 km at 39°N to almost 800 km as the birds moved toward Florida. The front narrowed remarkably to approximately 20 km near the eastern tip of Cuba, and then expanded again to 960 km at 13°N as the birds approached South America (Table 2).

As in autumn, geography focuses the spring migration front for birds on this flyway. As spring migrants approached the northern coast of South America, they were funneled to the two peninsulas on either side of the Gulf of Venezuela (Guajira in Colombia and the Paraguaná in Venezuela (Fig. 2). Leaving South America, the birds headed northwest and typically made landfall in Haiti, Jamaica, or Cuba, after an overwater crossing of between 680 and 1200 km, a flight typically of 27 to 40 hr, which inevitably involved nocturnal migration (DeCandido et al. 2006). The median longitude for birds crossing the 17°N latitude in the spring was 230 km west of that for southbound birds. Once across the Caribbean Sea, almost all birds followed the spine of Cuba, crossed to the Florida Keys and then proceeded northward to their breeding grounds.

The spring migration front for this population was much narrower than in the fall. At 17°N and 39°N, the spring front was about half as wide as in the fall. From 24°N to 33.5°N, the front was <200 km wide, between 47.3% and 14.9% of the fall front at those points, and median longitudes at each checkpoint were no more than 75 km apart (Table 2).

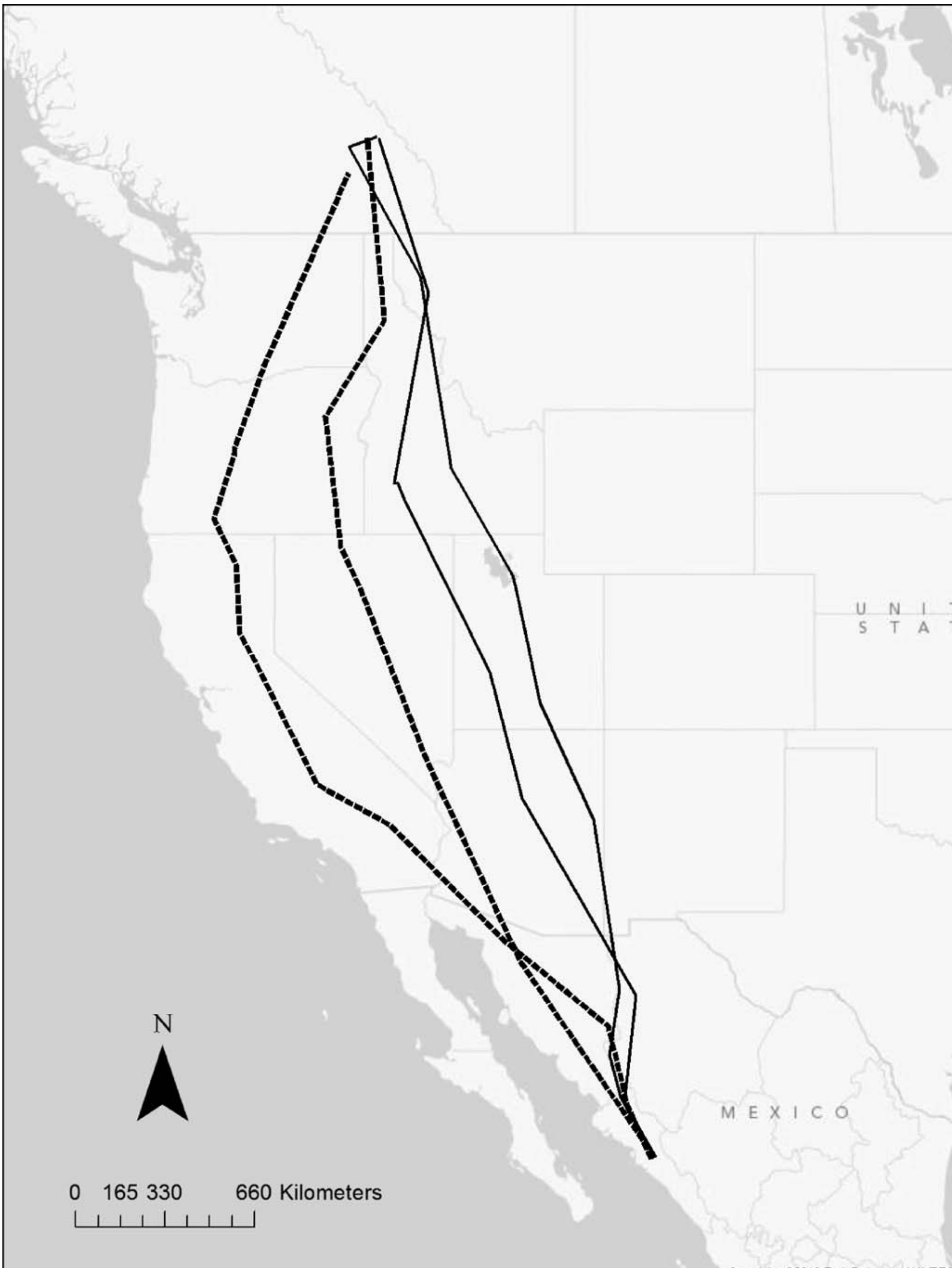

Figure 5. Unusual ''loop migration'' by adult female Osprey #00-24486 over two migration cycles (spring = dashed lines, fall = solid lines) between her breeding area in British Columbia and wintering area in Sinaloa, Mexico. Tracks connect ''best of day'' ARGOS Doppler locations and do not necessarily reflect the exact route traveled. The easternmost track was fall 2000 and the westernmost was the return in spring 2001.

Table 3. Dates of departure from wintering areas and arrival on breeding grounds by North American breeding Ospreys grouped by breeding region and sex, 1997–2013.

Measurement		East Coast		Midwest		Western	
		Males	Females	Males	Females	Males	Females
n	Departure	24	15	5	5	4	15
n	Arrival	24	15	6	6	4	14
Earliest	Departure	25 February	9 February	16 March	10 March	13 February	10 March
Earliest	Arrival	11 March	22 March	2 April	7 April	4 April	28 March
Latest	Departure	7 April	6 April	1 April	22 March	19 April	11 April
Latest	Arrival	15 May	23 April	23 April	27 April	13 May	23 April
Mean	Departure	16 March	9 March	24 March	16 March	14 March	30 March
Mean	Arrival	4 April	6 April	14 April	17 April	15 April	13 April
Median	Departure	18 March	8 March	24 March	15 March	10 March	1 April
Median	Arrival	5 April	6 April	15 April	19 April	6 April	16 April

Midwest Ospreys. Because data for the midwest birds were collected early in the study, using ARGOS PTTs with limited battery capacity, large segments of migration tracks were missing, and many locations were of poor accuracy. As a result our sample size is small, especially for spring migrations when PTT battery strength was often failing; thus, our measurements of the migration fronts were not particularly reliable.

Southbound Ospreys from the midwest passed 30°N latitude in an apparently broad front approximately 1600 km wide. This is deceptive, however, because the population splits into two fronts. Birds heading to the Caribbean passed 30°N in a front approximately 220 km wide. Ospreys using the Central American route to South America cross 30°N in a front roughly 950 km wide. Most of these birds stayed overland, traveling west of the Gulf of Mexico, but a few crossed the Gulf of Mexico to the Yucatan Peninsula.

For all but one bird, the available spring migration data showed that individuals returned via the same flyway they took heading south. The one exception arrived in Colombia in the fall of 1995 via Florida and the Caribbean. His return trip in the spring of 1996 and the subsequent fall migration that year passed through Central America. There were no data to determine if he crossed the Gulf of Mexico or stayed over land west of the Gulf. In either case, this is an example of a ''loop migration.''

Western Ospreys. Both the fall and spring migration routes taken by western Ospreys demonstrated that the species is indeed a ''broad-front'' migrant in the west. At 44°N in the fall, the front was 800 km wide and spread to 1640 km by 30°N. The width of the spring migration at these points was nearly identical. All but two individuals stayed in the valleys west of the Rocky Mountains' front range (Fig. 4).

Although most individual western birds followed roughly similar routes on their fall and spring migrations, one female exhibited a remarkable loop migration over two migration cycles (Fig. 5). In the fall of 2000, she left her nest in the Canadian Rocky Mountains and flew through Montana and Idaho to the Great Salt Lake. From there, she flew south to her wintering range in Sinaloa, Mexico. On her return the next spring, she migrated up the eastern edge of the San Joaquin Valley in central California. At 37°N, she was 760 km west of where she had been on the previous fall migration. Her fall 2001 route was roughly 100 km west of the 2000 track, and the spring 2002 route was 250–370 km east of the spring 2001 trip, but the spring route was still 180 km west of the fall track at 44°N and 300 km east of it at 37°N.

Spring Migration Departure Dates. The median departure date for spring migration of female Ospreys (22 March – Median; 9 March – 1st quartile, 1 April – 3rd quartile) was not significantly different from the median departure date of male Ospreys (20 March; 7 March, 25 March; $H = 0.25$, df = 1, $P = 0.62$). In contrast, the median departure date from the wintering grounds for east coast Ospreys (13 March; 5 March, 23 March) was earlier than for western Ospreys (31 March; 21 March, 5 April; $H = 11.16$, df = 2, $P = 0.004$); the median departure date of Midwest Ospreys (21 March; 14 March, 26 March) was intermediate.

We obtained 68 dates of departure from the wintering area for 49 different birds. Overall, Ospreys departed from their wintering areas as early as 9 Feb-

Table 4. Days spent in migration, total distance traveled, and distance traveled per d during spring migration by North American breeding Ospreys grouped by breeding region and sex, 1997–2013.

	EAST COAST		MIDWEST		WESTERN	
MEASUREMENT	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES
Days in migration						
n	23	12	5	5	4	14
Mean	17.8	31.1	24.6	31.4	33.0	15.0
± standard error	±1.3	±4.9	±2.6	±3.6	±9.5	±2.5
Total distance traveled (km)						
n	23	11	1	4	4	12
Mean	4514.0	5437.3	5952.0	7000.3	4739.3	3341.3
± standard error	±263.9	±448.6	5952.0	±438.3	±679.8	±105.5
Distance traveled per d (km)						
n	23	11	4	4	4	12
Mean	261.8	193.9	225.3	223.8	181.8	251.8
± standard error	±12.30	±19.19	±29.78	±18.20	±43.74	±29.68

ruary and as late as 19 April, with a median departure date of 20 March (Table 3). We obtained departure dates in more than one year for 13 individual Ospreys during 33 spring migrations, with three birds providing three years, and one bird providing four years of data. The departure dates for individual Ospreys that were tracked for more than one spring migration varied from 1 to 24 d (5 d; 3, 6).

Days Spent on Spring Migration. We found a significant interaction between sex and breeding region for the number of days Ospreys spent on spring migration ($F_{2,45}$ = 3.57, P = 0.04). For east coast Ospreys, females spent more days on spring migration than males. Female and male Ospreys breeding in the midwest spent a similar number of days on spring migration. Male western Ospreys spent almost twice as many days on spring migration than did female western Ospreys.

Overall, the number of days Ospreys spent on spring migration ranged from 5 to 68, with a mean migration period of 22 d (n = 63; Table 4). We obtained the number of days spent in spring migration during more than one year for 14 individual Ospreys during 32 spring migrations, with three birds each providing three years of data. The length of spring migration for individual Ospreys that were tracked for more than one spring migration varied from 0 to 17 d (4.4 ± 0.98 d).

Distance Traveled on Spring Migration. Overall, the total distance Ospreys traveled on spring migration ranged from 1918 to 8071 km, with an average distance of 4666 km traveled (n = 55; Table 4). We obtained the total distance traveled in more than one year for 14 individual Ospreys during 31 spring migrations, with three birds each providing three years of data. The total distance traveled by individual Ospreys that were tracked for more than one spring migration varied between years by 5 to 550 km (131.6 ± 29.7 km). We found no differences in the average daily distance traveled by Ospreys during spring migration between sexes ($F_{1,37}$ = 0.82, P = 0.37) or among breeding regions ($F_{2,37}$ = 0.23, P = 0.80).

Overall, the average daily distance traveled by individual Ospreys ranged from 74 to 458 km per d, with a mean of 237 km per d (n = 55; Table 4). We obtained the average daily distance traveled during spring migration in more than one year for 14 individual Ospreys during 31 spring migrations, with three birds each providing three years of data. The average daily distance traveled by individual Ospreys that were tracked for more than one spring migration varied between years by 3 to 287 km per d (60.4 ± 14.99 km per d).

Breeding Area Arrival Dates. The median arrival of female Ospreys (15 April; 2 April, 21 April) was the same as the median arrival date of male Ospreys (7 April; 1 April, 15 April; H = 2.21, df = 1, P = 0.14). Comparing regions, the median arrival date onto the breeding grounds for east coast Ospreys (6

Table 5. Median number of days spent in migration, and distance traveled per d during a total of 51 consecutive fall and spring migrations by 34 individual North American breeding Ospreys grouped by sex and breeding region, 1997–2013.

Measurement	*n*	Median		T Statistic; *P*
		Fall	Spring	
Number of days in migration				
Females (all)	25	17	20	0.08; 0.94
Males (all)	26	29	18	2.86; 0.004
East coast (all)	34	31	19	3.09; 0.002
Midwest (all)	2	24	27	— [a]
Western (all)	15	14	18	0.48; 0.63
Distance traveled per d (km)				
Females (all)	25	226	214	0.05; 0.96
Males (all)	26	195	254	2.16; 0.03
East coast (all)	34	185	244	2.51; 0.01
Midwest (all)	2	193	240	— [a]
Western (all)	15	259	234	0.94; 0.35

[a] There was insufficient data to conduct a statistical test.

April; 26 March, 13 April) was earlier than for midwest Ospreys (17 April; 9 April, 23 April) and western Ospreys (15 April; 6 April, 21 April; $H = 11.75$, df = 2, $P = 0.003$).

We obtained 69 arrival dates from 50 different birds returning to their breeding grounds. Overall, arrival dates of Ospreys onto their breeding grounds ranged from 11 March to 15 May, with a median arrival date of 8 April (Table 3). We obtained arrival dates in more than one year for 15 individual Ospreys during 34 spring migrations, with three birds each providing three years of data. Arrival dates onto the breeding areas for Ospreys that were tracked for more than one year varied from 0 to 16 d (3 d; 2, 9).

Comparison of Fall and Spring Migration of Individuals. We compared fall to spring travel for 34 birds over a total of 51 migration cycles and found that male Ospreys spent twice as many days migrating in the fall than in spring. In contrast, female Ospreys spent a similar amount of time during fall and spring migrations. The distance that female Ospreys traveled each day (including stopover days) during fall and spring migration was similar, whereas males traveled farther each day during fall migration compared to spring migration (Table 5).

The geographic location of the breeding areas of Ospreys influenced their migration characteristics. East coast Ospreys spent fewer days on spring migration and traveled a shorter distance along their migration pathways during spring migration compared to fall migration. In contrast, the migration characteristics of western Ospreys were similar during their fall and spring migrations. The sample size for midwestern Ospreys was too small to allow for statistical comparisons between spring and fall migrations (Table 5).

Stopovers During Migration. We examined migration data for 27 birds that completed a consecutive fall and spring migration, for which we were able to determine the proportion of days spent in stopovers. We compared the percentage of time spent in stopovers during fall vs. spring migrations by individual birds and found that male Ospreys spent four times as many of their travel days on stopovers during fall migration compared to spring migration. In contrast, female Ospreys spent a similar amount of time during stopovers during fall and spring migrations (Table 6).

The geographic location of the breeding areas of Ospreys influenced the stopover patterns during migration. East coast Ospreys spent approximately four times as much of their fall migration in stopovers compared to spring migrations. In contrast, for western Ospreys, the proportion of days spent in stopovers during their fall and spring migrations were similar (Table 6).

Discussion

The degree to which birds use different spatial and temporal migration strategies in spring versus fall has important implications for understanding the nature of migration (Alerstam et al. 2006) and

Table 6. Proportion of Osprey fall and spring days spent in stopovers (i.e., nonmigratory travel days) by 27 individual North American breeding Ospreys grouped by sex and breeding region, 1997–2013[a].

		MEAN ± SE		
	n	FALL	SPRING	*T* STATISTIC; DF; *P*
Females (all)	9	11.8 ± 4.4%	11.7 ± 3.4%	0.02; 8; 0.99
Males (all)	18	18.2 ± 3.7%	4.3 ± 1.3%	3.71; 17; 0.002
East coast (all)	19	16.7 ± 3.7%	4.4 ± 1.2%	3.23; 18; 0.005
Western (all)	8	14.5 ± 4.3%	12.3 ± 3.9%	0.32; 7; 0.76

[a] No midwestern Ospreys were included in these analyses because we were not able to obtain this information from the satellite telemetry units.

for the conservation of migratory birds. Alerstam et al. (2006) defined a migration strategy as ''the set of rules that determine the total process of migration, incorporating periods of both flight and energy accumulation/stopover.'' In our study, the strategy of spring migration, and the difference between spring and fall migrations, varied by sex and region.

Overall, dates of departure from the wintering area and arrival on the breeding area were the same for males and females. There was, however, a difference in both departure and arrival dates based on region, with east coast Ospreys leaving their wintering grounds and arriving on their breeding areas before their counterparts in the midwest and western North America. We speculate that this may be related to the availability of open water and thus food. Our east coast nesting sites were primarily coastal, with waters that rarely freeze, allowing early returning Ospreys more opportunity to forage than their counterparts in the midwest, which have to wait for frozen inland lakes and rivers to thaw.

The number of days spent on migration also varied by region and sex: in the east, females spent more days on migration than males; however, in the midwest males and females spent the same number of days on migration and in the west males spent more days on migration. In all three regions the numbers of days spent on migration was offset by the average distance travelled per day. This difference in strategies among the sexes and regions has no obvious reason and may be the result of small sample sizes.

Our data showed no trend for sex-specific arrival behavior. We believe this is because early breeding is strongly correlated with fledging success (Poole 1989), so the selective pressure is equal on both sexes to arrive on the breeding grounds as soon as possible. Additionally, both male and female Ospreys show great fidelity to their nesting sites and may face similar pressures to arrive at those sites and defend them from conspecifics. In saturated populations, competition for nest sites can be so intense that the average age at first breeding can approach 6 yr (P. Spitzer unpubl. data). Late arrival for either sex can lead to intense battles to reclaim the nest from an early-arriving, same-sex individual. One of our satellite-tagged males was unable to supplant an early-arriving rival and died as a result of wounds incurred while trying to regain his nest.

However, there was a difference in fall vs. spring migration strategies, with males spending more time on fall migration while females spent a similar amount of time during fall and spring migration. The shorter distances covered by spring migrants compared to fall on the east coast appear to be the result of a much more directed movement during the spring migration, both crossing the Caribbean and heading up the east coast. Because early arrival on the breeding grounds is advantageous, selection should favor birds that expend the extra energy needed to compensate for wind drift (Alerstam 1979), enabling them to take the shortest route to their breeding areas. That weather so strongly affects counts at fall hawk watches (e.g., Seeland et al. 2012, Vansteelant et al. 2014), and the broad front of the tagged birds as they head south, suggests that fall migrants minimize energy expenditure by not fighting wind-induced drift. We suspect there is no biological benefit to arriving on the wintering grounds early; thus, it is logical that selection would favor birds that employ a fall migration strategy that minimizes energy expenditure.

Fall migration by east coast migrants is longer because the southbound birds continue over land from Cuba to Hispaniola, and from there proceed across the Caribbean. This is a longer overall route than flying directly from eastern Cuba to South America, but minimizes the distance covered over the open water of the Caribbean Sea. This is important because the fall migration coincides with the hurricane season in the Caribbean and Ospreys are vulnerable to bad weather over open water. In contrast, Ospreys on spring migration do not have to contend with this challenge and therefore can use a more direct migration route. On the spring trip, birds leaving South America are funneled to the peninsulas on either side of the Gulf of Venezuela. From there, as they head north the prevailing trade winds push them west, resulting in a longer overwater crossing than in the fall, but a shorter overall trip across the Caribbean region.

In summary, North American Ospreys use a spring migration strategy that ensures timely arrival onto their breeding areas for territory and nest establishment or defense. Sex and breeding area location influence the specific characteristics of spring migration events, as well as differences in the fall and spring migration routes of Ospreys.

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