Boise State University
ScholarWorks

Biology Faculty Publications and Presentations | Department of Biological Sciences

2-1-2011

Migration Patterns, Use of Stopover Areas, and Austral Summer Movements of Swainson's Hawks

Michael N. Kochert
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center

Mark R. Fuller
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center

Linda S. Schueck
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center

Laura Bond
Boise State University

Marc J. Bechard
Boise State University

See next page for additional authors

Authors

Michael N. Kochert, Mark R. Fuller, Linda S. Schueck, Laura Bond, Marc J. Bechard, Brian Woodbridge, Geoff L. Holroyd, Mark S. Martell, and Ursula Banasch

MIGRATION PATTERNS, USE OF STOPOVER AREAS, AND AUSTRAL SUMMER MOVEMENTS OF SWAINSON'S HAWKS

Michael N. Kochert[1,7], Mark R. Fuller[1], Linda S. Schueck[1], Laura Bond[2], Marc J. Bechard[3], Brian Woodbridge[3], Geoff L. Holroyd[5], Mark S. Martell[6,8], and Ursula Banasch[5]

[1]*U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, Boise, ID 83706*
[2]*Boise State University, Department of Biology, Boise, ID 83725*
[3]*Boise State University, Raptor Research Center, Boise, ID 83725*
[4]*U.S. Fish and Wildlife Service, Yreka Fish and Wildlife Office, Yreka, CA 96097*
[5]*Environment Canada, Edmonton, AB T6B 2X3, Canada*
[6]*University of Minnesota, Raptor Center, St. Paul, MN 55125*

Abstract. From 1995 to 1998, we tracked movements of adult Swainson's Hawks (*Buteo swainsoni*), using satellite telemetry to characterize migration, important stopover areas, and movements in the austral summer. We tagged 46 hawks from July to September on their nesting grounds in seven U.S. states and two Canadian provinces. Swainson's Hawks followed three basic routes south on a broad front, converged along the east coast of central Mexico, and followed a concentrated corridor to a communal area in central Argentina for the austral summer. North of 20° N, southward and northward tracks differed little for individuals from east of the continental divide but differed greatly (up to 1700 km) for individuals from west of the continental divide. Hawks left the breeding grounds mid-August to mid-October; departure dates did not differ by location, year, or sex. Southbound migration lasted 42 to 98 days, northbound migration 51 to 82 days. Southbound, 36% of the Swainson's Hawks departed the nesting grounds nearly 3 weeks earlier than the other radio-marked hawks and made stopovers 9.0–26.0 days long in seven separate areas, mainly in the southern Great Plains, southern Arizona and New Mexico, and north-central Mexico. The birds stayed in their nonbreeding range for 76 to 128 days. All used a core area in central Argentina within 23% of the 738 800-km² austral summer range, where they frequently moved long distances (up to 1600 km). Conservation of Swainson's Hawks must be an international effort that considers habitats used during nesting and non-nesting seasons, including migration stopovers.

Key words: Buteo swainsoni, *migration, migratory behavior, movements, stopovers, Argentina, austral summer, connectivity, Swainson's Hawk.*

Patrones de Migración, Uso de Áreas de Parada y Movimientos durante el Verano Austral en *Buteo swainsoni*

Resumen. Desde 1995 a 1998, seguimos los movimientos de adultos del halcón *Buteo swainsoni* usando telemetría satelital para caracterizar la migración, las áreas importantes de parada y los movimientos durante el verano austral. Marcamos 46 halcones desde julio a septiembre en sus áreas de anidación en siete estados de EEUU y dos provincias de Canadá. Los individuos siguieron tres rutas básicas hacia el Sur en un frente amplio, convergieron a lo largo de la costa este del centro de México y siguieron un corredor concentrado hacia un área común en el centro de Argentina para el verano austral. Al norte de los 20° N, las trayectorias hacia el Sur y hacia el Norte difirieron poco para los individuos de la mitad este del continente pero difirieron mucho (hasta 1700 km) para individuos de la mitad oeste del continente. Los halcones dejaron las áreas de anidación desde mediados de agosto hasta mediados de octubre; las fechas de partida no difirieron por localidad, año o sexo. Las migraciones en dirección al Sur duraron entre 42 y 98 días, y las migraciones en dirección al Norte entre 51 y 82 días. En dirección al Sur, el 36% de los halcones dejaron las áreas de anidación cerca de tres semanas antes que los otros halcones marcados e hicieron paradas de 9.0–26.0 días en siete áreas separadas, principalmente en el sur de las Grandes Planicies, en el sur de Arizona y Nuevo México, y en el norte-centro de México. Las aves permanecieron en sus áreas no reproductivas entre 76 y 128 días. Todas usaron un área núcleo en el centro de Argentina del 23% o menos del rango austral de verano de 738 800 km², donde frecuentemente se movieron largas distancias (hasta 1600 km). La conservación de *B. swainsoni* debe ser un esfuerzo internacional que considere los ambientes usados durante las estaciones de anidación y no anidación, incluyendo las paradas migratorias.

INTRODUCTION

The Swainson's Hawk (*Buteo swainsoni*) is one of many birds whose long-distance migration has implications for management and conservation of the species (e.g., Webster et al. 2002, Greenberg and Marra 2005, Bildstein 2006). Migration is a critical period for many birds, and data from breeding and nonbreeding periods are needed for migratory bird populations to be managed (Sillett and Holmes 2002). Documenting the timing and location of the year-round movements of wide-ranging birds is essential for identifying factors that influence their survival and for developing conservation strategies (Steenhof et al. 2005, McIntyre et al. 2008).

Most Swainson's Hawks migrate between the breeding grounds in North America and the the pampas of South America, where they spend the austral summer (England et al. 1997). Mass mortality of Swainson's Hawks from poisoning by organophosphate pesticides in Argentina during the austral summer of 1994–1995 (Woodbridge et al. 1995, Goldstein et al. 1999a) prompted an international conservation effort to assess threats to these hawks during migration and the austral summer. This effort included toxicological assessments (Goldstein et al. 1999b), a study of habitat relationships of Swainson's Hawks in Argentina (Canavelli et al. 2003), and investigations of the species' migration and movements with satellite telemetry. In reporting the last, Schmutz et al. (1996) and

Martell et al. (1998) described migration routes and timing of one Swainson's Hawk from Saskatchewan and five from Minnesota. Fuller et al. (1998) and Bechard et al. (2006) described the timing, routes, distances, and rates of migration of 34 adult Swainson's Hawks from seven U.S. states and two Canadian provinces in 1995 and 1996. Our paper builds on this work and includes unpublished data on hawks radio marked in 1997.

Although information has been gathered from band recoveries (Houston and Schmutz 1995) and tracking by satellite telemetry (Woodbridge et al. 1995, Schmutz et al. 1996, Fuller et al. 1998, Martell et al. 1998, Bechard et al. 2006), little is known about Swainson's Hawk's ecology during migration, use of stopover areas, and movements on the austral summer grounds (England et al. 1997). In this paper, we characterize annual patterns of long-range movement and more thoroughly delineate the migration routes of adult Swainson's Hawks from separate nesting localities throughout their breeding range. In addition, we identify important stopover areas and describe movements and identify areas used by Swainson's Hawks during the austral summer.

METHODS

FIELD PROCEDURES

Adult Swainson's Hawks were radio marked on the nesting grounds in seven U.S. states and two Canadian provinces from July to September 1995–1997 (Table 1). We solicited colleagues,

TABLE 1.   Number of Swainson's Hawks marked with satellite-received transmitters by year and location, 1995–1997.

| Year | Location | Number | | | | Dates deployed |
		Males	Females	Unknown	All	
1995	Southeastern Alberta	1	1		2	24 Aug
	Northern California		1		1	4 Sept
	Central Colorado			2	2	13 and 18 Sep
	Southwestern Idaho		4		4	18–25 Aug
	Northeastern Utah			1	1	29 Jul
	Subtotal	1	6	3	10	
1996	Southeastern Alberta	1	4		5	10–31 Aug
	Southeastern Arizona		1	1	2	21 and 23 Sep
	Northern California	1			1	6 Sep
	Central Colorado			3	3	29 and 30 Aug
	Southwestern Idaho	1	5		6	29 Aug–4 Sep
	Southwestern Minnesota		2		2	24 Jul
	Northeastern Oregon		6		6	6–27 Aug
	Southwestern Saskatchewan			2	2	27 and 28 Jul
	North-central Utah		3		3	6 to 8 Sep
	Subtotal	3	21	6	30	
1997	Southwestern Minnesota		2		2	22 and 23 Jul
	Southwestern Idaho	1	3		4	6–21 Sep
	Subtotal	1	5		6	
All years	Grand total	5	32	9	46[a]	22 Jul–23 Sep

[a]No data received from one hawk from Idaho in 1995 and one hawk from Saskatchewan in 1996.

many who provided funding, throughout the breeding range to capture and radio-mark hawks. Specific trapping sites were selected by local cooperators. The birds were trapped near nests (<50 m) with dho gaza nets with a Great Horned Owl (*Bubo virginianus*) as a lure or away from nests with bal chatri traps baited with live gerbils (*Gerbillus* spp.; Bloom et al. 2007). We followed established guidelines (e.g., Hull and Bloom 2001) when capturing and handling hawks. All unbanded birds received an aluminum U.S. Geological Survey (USGS) leg band. Those banded in California, Idaho, Oregon, and Utah also received an anodized colored leg band with alphanumeric symbols (Acraft Sign & NamePlate Company, Edmonton, AB). All hawks captured in Alberta were wearing USGS and anodized alphanumeric leg bands when trapped. We weighed and measured 32 of the captured hawks and sexed them by weight, wing chord, and/or footpad length (Kochert and McKinley 2008). Four Swainson's Hawks not weighed or measured were sexed by their size relative to their mates (the larger hawk was considered the female) or behavior (the bird attending the young at the nest was considered the female).

We attached platform transmitter terminals (PTTs; PTT 100, Microwave Telemetry, Inc., Columbia, MD) to Swainson's Hawks with a backpack harness (Dunstan 1972) constructed from 6-mm Teflon ribbon (Bally Ribbon, Bally, PA). The PTT and harness weighed between 32 and 36 g, and we radio-marked hawks only if they weighed ≥900 g.

DATA COLLECTION AND PROCESSING

We used the Argos–Tiros satellite system (Strikwerda et al. 1986, Argos 2007) to estimate locations of PTTs. Argos assigned each location estimate to a nominal location class (LC) on the basis of its accuracy estimates. Standard location classes (LC = 3, 2, and 1) have an estimated 1-sigma error radius of 250, 500, and 1500 m, respectively, while the accuracy of auxiliary location classes (LC = 0, A, B, C, and Z) was undocumented at the time of our study (Argos 2007).

Each PTT transmitted for 8 hr (hereafter a "transmission period") every 1 to 6 days (hereafter a "duty cycle"). During a transmission period, a PTT transmitted approximately every 60 sec. We assigned data received from PTTs into three categories of duty cycle on the basis of average time elapsed between each transmission period start date and time: category 1, <1.5 days; category 2, 1.5–3.5 days; category 3, >3.5 days. We focused intensive study on southward migration and, to conserve batteries, programmed most PTTs for transmission (duty-cycle categories 1 and 2) more frequent during southward migration and less frequent (category 3) during the rest of the year. We programmed all PTTs on a category 1 duty cycle and half on a category 2 duty cycle to change to category 3 during the austral summer. To maintain consistency among seasons, we also programmed a few PTTs on duty-cycle categories 2 and 3 to not change in any season.

We filtered all location estimates except for LC 3, with the Douglas (2006) Argos filter, which evaluated Argos locations by two independent methods. The first filtering method required that locations have at least one other location consecutive in time and redundant in space, which we defined as <15 km. The second filtering method evaluated movement rates and turning angles among consecutive location estimates. We defined 90 km hr^{-1} to be a maximum rate of movement. We retained all locations that passed the first filter, considering them "anchor points." If the distance between two consecutive anchor points was >15 km, we evaluated locations that passed the second filter during the intervening period individually with an additional directionality test. If passing through the candidate location did not increase the total distance traveled by >50%, the location was accepted. The Argos filter selected one location per duty cycle on the basis of the best LC, or, in case of ties based on the sequence, the highest IQX value, the most messages received during the satellite's overpass, the highest IQY value, and the earliest date–time (see Argos 2007 for descriptions of IQX and IQY). After filtering, we computed the lengths of each vector formed by two consecutive locations as orthodromes (great circle routes) and the azimuth of each vector as the true departure bearing. Each individual's path consisted of a series of vectors connecting all location estimates, and a route was a collection of paths of several birds that delineated a common course of travel. The migration corridor consisted of all paths used by all birds.

We defined four periods of the Swainson's Hawk's annual movements: southward migration, austral summer, northward migration, and breeding season. Southward migration began with a bird's first location that was >150 km and south (<270° and >90°) of its capture location and from which the bird continued south. The departure azimuth for southward migration was the azimuth from the location where the transmitter was attached to the first location estimate during southward migration. Southward migration ended when the hawk stopped consistent southward movement of >150 km and started omnidirectional movements on the austral summer grounds. Northward migration began with the first location of consistent northward movements (>150 km per duty cycle) away from the austral summer range and ended with the first location <150 km from the bird's capture location. The departure azimuth for northward migration was the azimuth from the last location in the austral summer range to the first location during northward migration. Austral summer movements extended from the end of the southward migration to the start of the northward migration. We considered locations <150 km from the capture site to be on the breeding grounds. We defined stopovers as movements of ≤150 km for ≥24 hr during migration preceded and followed by movements of >150 km per duty cycle. A prolonged stopover lasted >9 days. We defined a "data gap" as a period with no location estimates that spanned ≥1 duty cycle for category-3 duty cycles or 12 days for the other categories.

A gap at the beginning or end of migration precluded use of the bird in calculations of migration duration, departure dates, arrival dates, and departure azimuths.

STATISTICAL ANALYSES

We analyzed spatial data with ArcGIS 9 (Earth Systems Research Institute, Inc., Redlands, CA). We report distance moved as the sum of the length of all vectors during each season. To assess short-term tracking velocities (e.g., ground speeds; Pennycuick 2008), we examined lengths and velocities of within-duty-cycle vectors that spanned >1 hr, extended ≥50 km, and had successive location estimates of LC A or better. We report long-distance travel rates based on elapsed time and cumulative tracking distance between the start of migration and the first location in the austral range.

To quantify the progression of migration we interpolated between successive location estimates the date (day of year) and time that vectors for each bird crossed lines of 10° of latitude between 30° N and 30° S. We calculated the duration (in days) between the dates and times that vectors of the first and last Swainson's Hawk crossed each 10° line and calculated travel rates between the lines from the elapsed time and distance between crossings. We restricted our analyses to 25 Swainson's Hawks that completed southward migration in 1996 and 20 that completed northward migration in 1997.

We modeled cumulative tracking distance as a function of variables that we believed could influence the progress of migrating Swainson's Hawks. Because preliminary observations suggested that duty cycle may influence tracking distance we also included duty cycle in the model. We modeled cumulative tracking distance for southward and northward migration separately. We first evaluated differences in distance due to duty cycle with analysis of variance. We addressed year marked as a random effect, but the contribution of variance by year was inconsequential, so we evaluated it as a fixed effect with the other variables. We used Akaike's information criterion (AIC_c; corrected for sample size, Burnham and Anderson 2002) and residual analyses to identify the simplest model that was satisfactory on the basis of duty cycle, longitude and latitude, and any necessary interactions. Once we identified this simplest model, we considered additional predictors (year marked, departure date [day of year], departure azimuth, and number of stops on migration) one at a time to verify whether they should be included. None of the resulting AIC_c scores differed materially from that for the simplest model, justifying these variables' exclusion. Thus we considered only the simplest model for analysis of migration distance. We constructed the models with PROC MIXED (SAS Institute 2006), using maximum likelihood for comparable values of AIC_c.

We employed the software Ranges 6 v1.106 (Kenward et al. 2002) to define the hawks' austral summer range and core use areas within that range. We used the best location estimate for each transmission period for all hawks in all years to develop a 100% minimum convex polygon to delineate the austral summer range. We delineated core areas by hierarchical incremental cluster analysis with a "nearest neighbor" joining rule (Kenward 1987) and used clusters that included 90% of locations to define core use area. We used clusters formed by 80% of locations to assess Swainson's Hawk movements in the austral range because they retained the maximum number of locations yet provided a number of clusters adequate to demonstrate movement within the core area. To assess the hawks' seasonal movements on a landscape scale, we categorized the 80% clusters into those located in the north and northeast portions and those in the southeast portion of the austral range. We restricted our assessments to 22 Swainson's Hawks that carried functioning PTTs during the entire 1996–1997 austral season. Because of the inconsistency of duty cycles among PTTs, we tallied the number of hawk occurrences in each cluster by 2-week intervals starting in mid-November when most instrumented hawks had arrived in the austral range. We defined a hawk occurrence as the presence of an individual hawk in a cluster during the 2-week interval, regardless of the number of locations. We totaled the number of hawk occurrences in each northern and southern cluster and calculated a proportion based on the total number of occurrences for the 2-week period. Because some hawks used more than one cluster in a 2-week interval the total number of occurrences sometimes exceeded the number of hawks.

We used SAS version 9.1.3 (SAS Institute 2006) for modeling and SYSTAT 12 (SYSTAT 2007) for two-sample *t*-tests, analysis of variance, Pearson correlations, and nonparametric tests for assessing factors related to departure dates, travel rates, distances moved, velocity rates, distance between north and south vectors, and use of clusters. We used Oriana software for circular statistics (http://www.kovcomp.co.uk/index.html) to calculate the circular mean departure azimuth for both southward and northward migration. Except where noted, values reported under Results are means ± SD, and we used an α level of 0.05 for all tests.

RESULTS

THE MARKED SAMPLE

We radio-marked 46 adult Swainson's Hawks on the breeding grounds in seven U.S. states and two Canadian provinces (Table 1). Idaho, the only site studied in all three years, had the most radio-marked hawks of any locality and the only radio-marked mated pair (Table 1).

We received 6813 location records from 44 PTTs between July 1995 and September 1998 and obtained no data from two PTTs. Filtering retained 4619 location estimates (68% of the total); 7% were classed in the highest categories (LC 2 or 3), 16% were LC 1, 40% were LC 0, 17% were LC A, and 20% were LC B or Z. The time each hawk was tracked ranged from 1.05 to 13.05 months. We obtained data for part of a second southward migration from one bird from Colorado.
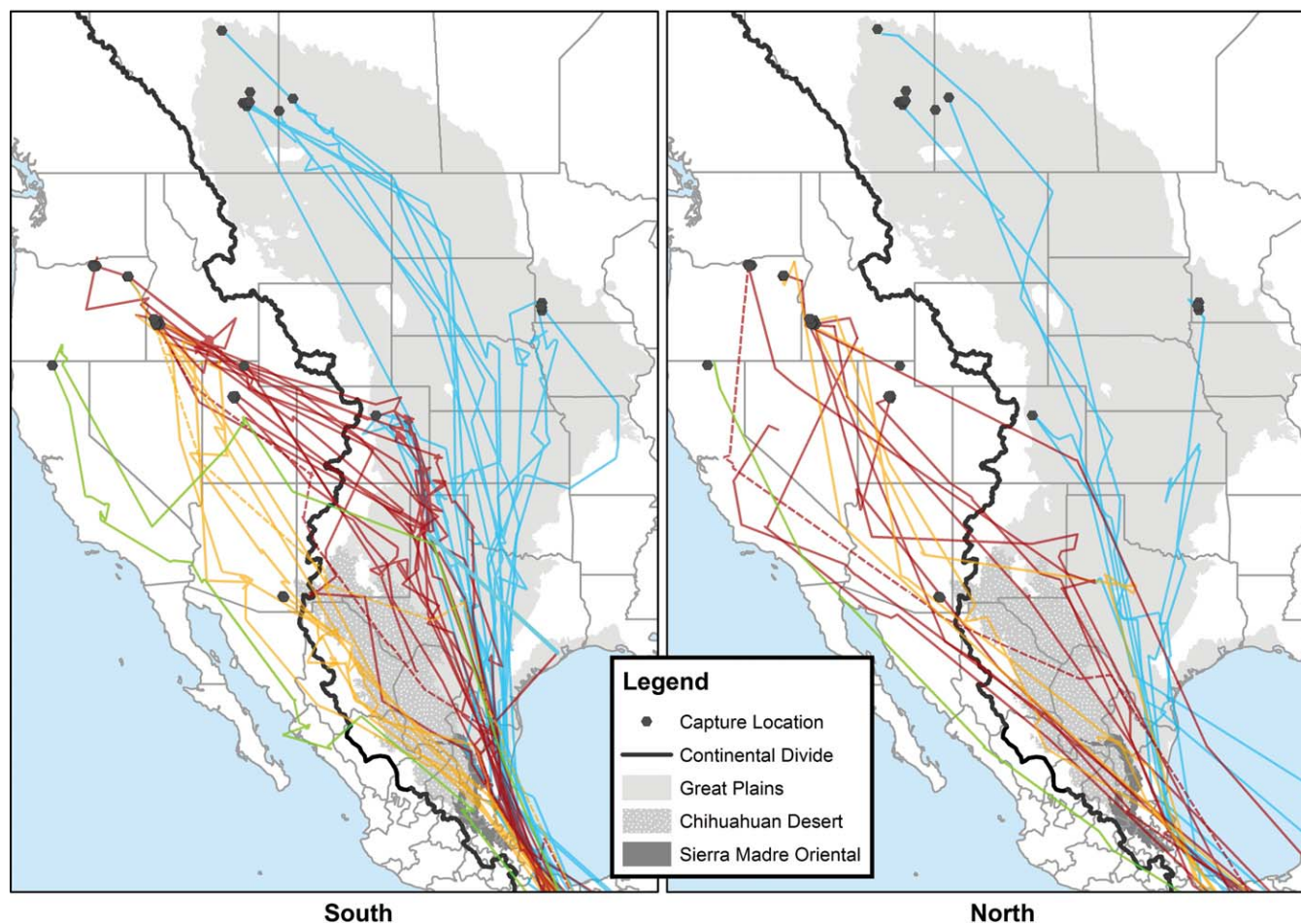
FIGURE 1.   Migration paths north of 20° N used by 17 and 25 adult Swainson's Hawks from east and west of the continental divide, respectively, on southward migration and by 8 and 15 hawks from east and west of the continental divide, respectively, on northward migration, 1995–1998. Blue lines depict paths of hawks from east of the continental divide. Red and orange lines depict paths of hawks that cross the continental divide on southward migration at >35° N and <35° N, respectively. Green lines depict paths of two California hawks. Dotted lines show paths that deviated from the routes of the group.

At the start of southward migration, 16 (36%), 21 (48%), and 7 (16%) PTTs transmitted on duty cycles of category 1, 2, and 3, respectively (see Methods for definitions), and 34 functioning PTTs completed the trip. During the austral season, eight (33%) and 16 (67%) PTTs transmitted on category 2 and 3 duty cycles, respectively. Of 20 PTTs on hawks that completed northward migration, 1 and 19 transmitted on category 2 and 3 duty cycles, respectively.

MIGRATION ROUTES AND PATTERNS

Southward migration. All Swainson's Hawks nesting east of the continental divide (*n* = 17) migrated on a route east of the divide and along the east side of the Sierra Madre Oriental in eastern Mexico (Fig. 1). Most Swainson's Hawks nesting west of the continental divide (*n* = 25) followed one of two routes to eastern Mexico (Fig. 1). Fifteen (60%) crossed the continental divide between northwestern Colorado and west-central

New Mexico and went to the southern Great Plains or northern Chihuahuan Desert before flying south along the east side of the Sierra Madre Oriental. Eight hawks (32%) crossed the continental divide between west-central New Mexico and central Mexico, traversed the southern Chihuahuan Desert, and crossed the Sierra Madre Oriental to the coastal plains of eastern Mexico. Only two hawks deviated from these two general routes (Fig. 1).

Swainson's Hawk locations converged in east-central Mexico, with locations concentrating on the east side of the Sierra Madre Oriental around 20° N (Fig. 2). The width of the corridor of southward migration (the distance between the outermost east and west orthodrome tracking vectors of <500 km) measured 3220 km at 40° N, 1310 km at 30° N, 180 km at 20° N, and <100 km at Veracruz, Mexico (19° N). We excluded vectors of ≥500 km because they artificially widened the corridor. The corridor remained relatively narrow as it crossed the

FIGURE 2.   Southward and northward migration between nine localities throughout the breeding grounds and the austral summer range, based on all filtered location estimates of 43 radio-marked adult Swainson's Hawks, 1995–1998.

TABLE 2.   Northward paths in relation to departure from southward paths north of 20 N° for eight Swainson's Hawks from west of the continental divide where north and south vectors were separated by >600 km.

Nesting grounds	Year	Number of hawks	Location of departure from southward path	Azimuth of path after departure	Path to nesting grounds
Idaho, Oregon, Utah	1997	4	Mexico 18° to 22° N	310° to 320°	Central and northern Mexico to nesting grounds via central and southern California and central Arizona
Oregon	1997	1	Texas–Mexico border 27° N	296°	Northern Mexico to Oregon via central California
Oregon	1997	1	Texas panhandle 34° N	310°	Continental divide 450 km south of the southward path and to Oregon via northern Nevada
Idaho	1997, 1998	2	Texas panhandle 33° to 34° N	275° and 282°	West 775 to 1000 km to western and central Arizona and to Idaho

Andes near Medellín, Colombia, rounded the "elbow" of the Andes near Santa Cruz, Bolivia, and reached the austral summer grounds in Argentina (Fig. 2), measuring about 380 km at 0° and 20° S and remaining <400 km wide to the austral range.

Northward migration. Although the corridors of northward and southward migration were similar (Fig. 2), the paths of many individuals varied. Of 23 Swainson's Hawks tracked completely on both migrations, only 4 (17%) had northward and southward vectors <200 km apart at all 10° lines of latitude. The maximum separation of northward and southward migration vectors at these lines for an individual hawk ranged from 189 to 485 km between 30° S and 10° N and from 198 km to 1036 km north of 10° N. For all individuals, northward vectors were predominantly east of southward vectors south of 10° N and west of southward vectors north of 10° N.

All Swainson's Hawks from east of the continental divide (eastern hawks; $n = 8$) followed the same route on northward and southward migration north of 20° N (Fig. 1), and <200 km separated individuals' north and south migration vectors at 30° N and 40° N. In contrast, north of 20° N northbound and southbound paths of most hawks from west of the continental divide (western hawks; $n = 15$) varied greatly. Northward migration paths of most western hawks were south and west of the paths they took in the autumn (Fig. 1). Northward and southward tracking vectors for 11 (73%) western Swainson's Hawks were separated by >200 km, with >600 km separating northward and southward vectors for eight of these hawks (Table 2). Nine (60%) of the western hawks crossed the Sierra Madre Oriental, migrated through central and northwestern Mexico, and crossed the continental divide between southwestern New Mexico and southern Mexico (Fig. 1). The remaining six flew north along the east side of the Sierra Madre Oriental, after which five went to the southern Great Plains or northern Chihuahuan Desert and crossed the continental divide north of west-central New Mexico. The remaining hawk traversed the central Chihuahuan Desert and crossed the continental divide near the Mexico–Arizona border at 31° N. Of the hawks with northward and southward vectors separated by >600 km, four diverged from their southbound paths in east-central Mexico and four continued along the east side of the Sierra Madre Oriental and departed west from their southward paths between 27° and 34° N (Table 2).

PROGRESSION OF MIGRATION

Effect of duty cycle on distance. The cumulative tracking distances of Swainson's Hawks carrying PTTs with category 1 duty cycles on southward migration were significantly larger ($F_{2,28} = 4.18$, $P = 0.03$) than those of hawks carrying PTTs with category 2 and 3 duty cycles. The simplest model indicated that cumulative tracking distance for the southward migration was significantly related to duty cycle ($F_{2,24} = 6.11$; $P = 0.007$), latitude of attachment of the PTT ($F_{1,24} = 21.66$; $P = 0.001$), duty cycle by latitude ($F_{2,24} = 7.79$; $P = 0.003$), and longitude of attachment of the PTT ($F_{1,24} = 6.25$; $P = 0.02$). The interaction between latitude and duty cycle was the key element of the model, and coefficients of the best-fitting model represented changes in cumulative distance per unit change in latitude for each duty-cycle category (Table 3). Cumulative tracking distance increased 287 km per degree increase in latitude of origin for PTTs with a category 1 duty cycle, which was higher than the change per degree of latitude for the other two duty-cycle categories. Also, for each degree increase in longitude (westward offset), the distance of southward migration increased by 53 km (Table 3).

TABLE 3.   Coefficients for terms in the best fitting model for south migration of 31 adult Swainson's Hawks, 1995–1997.

Effect	Coefficient	SE	95% CI
Latitude, duty cycle 1[a]	286.9	54.7	(147.1; 399.7)
Latitude, duty cycle 2[b]	35.1	35.8	(−38.8; 109.0)
Latitude, duty cycle 3[b]	67.3	50.5	(−36.9; 171.5)
Longitude[c]	−52.7	21.1	(−96.2; −9.2)

[a]Per unit change for category 1 duty cycle was significantly higher than for category 2 ($P = 0.005$) and 3 ($P = 0.01$) duty cycles.
[b]Duty-cycle categories 2 and 3 are not statistically different from 0.

TABLE 4.   Start and end dates of southward migration of radio marked Swainson's Hawks from nine localities arranged by decreasing latitude, 1995–1997.

Year/state/province	Number of hawks	Mean start date	SD	Range	Number of hawks	Mean end date	SD	Range
1995								
Southeast Alberta	2	23 Sep	0.7	22–23 Sept	1	7 Nov		
Southwest Idaho	3	12 Sep	13.6	27 Aug–20 Sep	3	29 Nov	5.1	23 Nov–3 Dec
Northern California	1	20 Sep			1	23 Nov		
Central Colorado	2	26 Sep	16.3	14 Sep–7 Oct	2	25 Nov	9.9	18 Nov–2 Dec
Northeast Utah	1	6 Oct						
Subtotal	9	21 Sep	12.1	27 Aug–7 Oct	7	24 Nov	9.2	7 Nov–3 Dec
1996								
Southeast Alberta	5	28 Sep	3.5	24 Sep–5 Oct	4	27 Nov	17.7	15 Nov–23 Dec
Southwest Saskatchewan	1	21 Sep			1	30 Nov		
Northeast Oregon	4	8 Sep	21.9	12 Aug–30 Sep	5	30 Nov	11.8	13 Nov–10 Dec
Southwest Minnesota	2	27 Sep	3.5	24–29 Sep	1	18 Nov		
Southwest Idaho	6	19 Sep	7.8	6–30 Sep	6	26 Nov	6.5	15 Nov–4 Dec
Northern California	1	8 Sep			1	4 Dec		
Central Colorado	3	23 Sep	12.0	11 Sep–5 Oct	3	1 Dec	25.2	14 Nov–30 Dec
North-central Utah	3	25 Sep	0.6	25–26 Sep	3	17 Nov	7.6	12–26 Nov
Southeast Arizona	2	9 Oct		9 Oct	1	25 Nov		
Subtotal	27	22 Sep	12.3	12 Aug–9 Oct	25	27 Nov	12.5	13 Nov–30 Dec
1997								
Southwest Minnesota	2	28 Sep	2.8	26–30 Sep				
Southwest Idaho	3	7 Sep	15.5	21 Aug–19 Sep	1	7 Dec		
Central Colorado[a]	1	28 Sep						
Subtotal	6	16 Sep	15.7	21 Aug–30 Sep	1			
Grand total	42[b]			12 Aug–9 Oct	33			7 Nov–30 Dec

[a]Second southbound departure for a bird instrumented in 1996.
[b]Five of the 46 radio-marked hawks were excluded because of PTT failure and data gaps at onset of migration.

Southward migration. In all years and breeding localities combined, Swainson's Hawks left their breeding areas between 12 August and 9 October (Table 4). Departure dates did not differ by locality ($F_{7,15} = 1.72$, $P = 0.18$) or sex (Mann–Whitney $U = 28.5$, $P = 0.75$, $n = 20$), when just hawks with PTTs on category 1 and 2 duty cycles in 1996 were considered and when all localities were represented. Both members of a pair in Idaho began migration on 12 September 1996. Mean departure day did not differ by year (18, 20, and 21 September for 1995, 1996, and 1997, respectively; $F_{2,32} = 0.64$, $P = 0.55$) for all localities combined, nor did it differ by year in Idaho alone for all other variables held constant ($F_{2,8} = 1.88$, $P = 0.21$). Departure differed by 8 days in two consecutive years for a hawk from Colorado. Departure azimuth tended to be southeast ($\bar{x} = 133 \pm 21°$ SD; range 102–203; $n = 42$). Only two hawks (both from Minnesota) departed west of south. The male and female of the Idaho pair departed at 165° and 121°, respectively. The departure azimuth of a hawk from Colorado differed little (155° vs. 159°) in two consecutive years.

The interval between departure of the first and last radio-marked Swainson's Hawk from the breeding grounds in 1996 spanned 58 days. Duration between the crossing of the first and last radio-marked hawk at each 10° of latitude varied from 21 to 25 days between 30° N and 10° N, increased sharply to 40 days at 0°, and changed little thereafter (Fig. 3A). The increase in the duration between the first and last birds crossing 0° over that at 10° N resulted from four hawks that traveled significantly slower than the rest of the group between 10° N and 0° ($t_{26} = 3.44$, $P = 0.002$) and lagged behind for the remainder of their migration. Travel rates differed by 10° latitudinal zone ($F_{5,115} = 4.53$, $P = 0.001$), with rates highest between 30° and 20° N and lowest between 20° and 10° N (Fig. 3B). Rates increased significantly between 10° N and 30° S (Fig. 3B). Travel rates for the entire southward migration averaged 176.7 ± 36.0 km day^{-1} (range 136–263) for 16 hawks with category 1 PTTs. Velocities for within-duty-cycle vectors ranged from 8.9 to 86.4 km hr^{-1} ($\bar{x} = 38.6 \pm 17.4$) for intervals lasting 1.0 to 7.2 hr and vectors 50 to 274 km long ($n = 133$). We pooled tracking velocities for all migration periods because velocities did not differ at any season ($F_{3,129} = 1.12$, $P = 0.34$). The higher velocity range (e.g., ≥70 km hr^{-1}, $n = 8$ vectors) represents our best estimate of the speed of the hawks' short-term sustained flight.

Swainson's Hawks ended their southward migration in November and December (Table 4), 42 to 98 days after start of migration (Table 5). We observed no correlation between latitude at the end of southward migration and latitude of origin
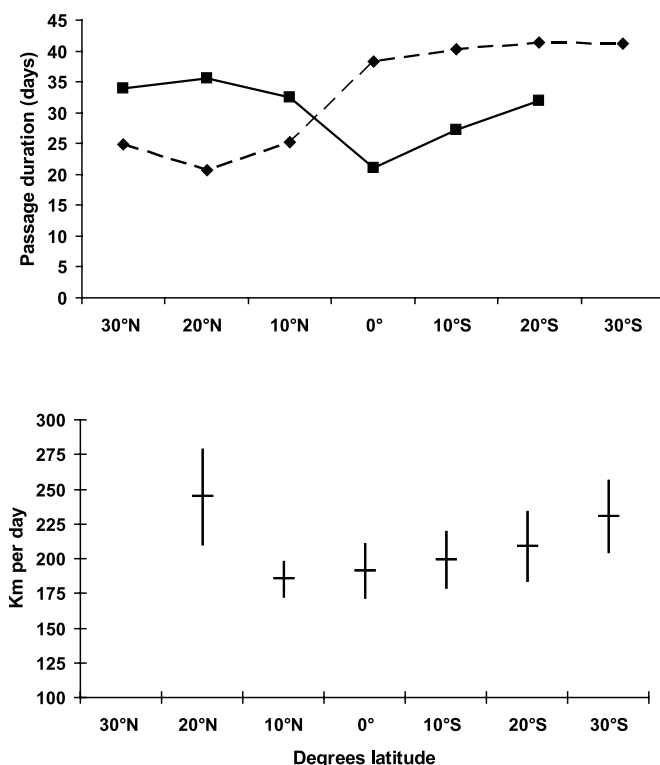
The interval between the dates of departure from the austral range of the first and last radio-marked Swainson's Hawk spanned 41 days in 1997. We began assessing the time it took all the hawks to cross each line of 10° latitude at 20° S because northward migration began north of 30° S for 70% of the instrumented hawks. This duration decreased steadily from 32 days at 20° S to 21 days at 0°, after which it tended to increase (Fig. 3A). The decrease resulted from two hawks that departed 6 and 16 days later than the others but caught up with the group at the equator. Travel rates for these two hawks averaged 272 km day^{-1} between 10° S and 0° but 123 km day^{-1} for the remainder.

STOPOVERS

We recorded at least one stopover by 33 of 41 Swainson's Hawks migrating south. We detected stops by all 16 hawks carrying PTTs on category 1 duty cycles, 16 (84%) of 19 in category 2, and only 1 (16%) of 6 in category 3. Those in category 1 stopped 2 to 7 times, and 14 of the 16 stopped 3 to 6 times. The first stopover ($\bar{x} = 12.1 \pm 8.1$ days) was longer than all the others combined (2.3 ± 1.7 days; $t_{68} = 8.38$; $P > 0.001$). The mean duration of stopovers tended to decrease with the number of stopovers made ($r = 0.72$, $P = 0.07$, $n = 7$). Stopovers occurred throughout the southward migration and were longer at more northern latitudes (Fig. 4). Most hawks with PTTs on category 1 or 2 duty cycles made at least one stopover north of 25° N. These comprised 11 (85%) of 13 hawks from east of the continental divide, 13 (87%) of 15 hawks that crossed the continental divide to the southern Great Plains, and 9 (100%) of 9 hawks that crossed the continental divide and the Sierra Madre Oriental. The duration of southward migration was correlated with total number of days birds stopped on southward migration ($r = 0.58$, $P = 0.004$, $n = 23$).

Of 41 Swainson's Hawks migrating south, 15 (36%) made prolonged stopovers (range 9.3–26.0 days) in seven widely separated areas north of 25° N (Fig. 5). Only 2 (12%) of 17 hawks from east of the continental divide made prolonged stopovers, but 6 (46%) of 13 that crossed the continental divide to the southern Great Plains and 6 (67%) of 9 that crossed the continental divide and the Sierra Madre Oriental did so. All but one of the prolonged stopovers occurred on the first stop and north of the U.S.–Mexico border. The exception was a prolonged stop in northern Mexico on the second of the hawk's six stops. Of the 15 prolonged stopovers, 12 (80%) occurred in the southern Great Plains and in the deserts of north-central Mexico and southern Arizona and New Mexico (Fig. 5). Swainson's Hawks that made prolonged stopovers departed the nesting grounds earlier than those that made no prolonged stops ($\bar{x} = 9$ September ± 12.4 days vs. 27 September ± 8.1 days; $t_{33} = -4.911$, $P > 0.001$; category 1 and 2 PTTs only). Swainson's Hawks from 4 of 9 breeding localities made prolonged stopovers (Fig. 5), and most (67%) came from Idaho. Ten of 12 (83%) Swainson's Hawks from Idaho used 5 of the 7 areas of prolonged stopovers (Fig. 5). The Idaho hawks began

FIGURE 3.   (Upper graph) Duration of passage (number of days between the dates and times that vectors of the first and last radio-marked Swainson's Hawk crossed each line of 10° latitude) for southward (dashed line) and northward (solid line) migration. (Lower graph) Rates of travel (km day^{-1}) between lines of 10° of latitude from 30° N to 30° S for Swainson's Hawks on southward migration. Means are depicted by horizontal lines, 95% confidence intervals by vertical lines. Based on 24 and 20 radio-marked Swainson's Hawks completing migration south in 1996 and north in 1997, respectively.

($r = 0.30$, $P = 0.80$, $n = 36$). For all years, the cumulative tracking distance for southward migration ranged from 8449 to 13 209 km ($\bar{x} = 11052 \pm 1123$; Table 6).

Northward migration. Swainson's Hawks ($n = 23$) began migrating north from mid-February through March (Table 7), 76 to 128 days after start of the austral period ($\bar{x} = 92.7 \pm 12.1$). The azimuth of departure from the last location in the austral range to the first location >150 km away averaged $1.5 \pm 20.3°$ (range 299°–48°). Swainson's Hawks ended their northward migration from mid-April through May (Table 7), 51 to 82 days after start of migration. For all years combined, the duration of northward and southward migration did not differ ($t_{50} = 0.70$, $P > 0.49$), nor did they in 1996, the year of our best sample ($t_{41} = 1.03$, $P = 0.30$, Table 5). We observed no correlation between breeding locality (latitude [$r = -0.17$] or longitude [$r = 0.04$]) and duration of northward migration. For northward migration, cumulative tracking distance ranged from 9740 to 11 585 km ($\bar{x} = 10394 \pm 649$; Table 6). Cumulative tracking distance for 20 hawks was positively related with latitude ($F_{1,16} = 11.11$; $P = 0.004$) and longitude ($F_{1,16} = 19.39$; $P > 0.001$).

TABLE 5.   Duration (days) of southward and northward migrations of adult Swainson's Hawks from nine nesting localities arranged by latitude, 1995–1997, as determined by satellite telemetry.

Year/locality	Southward migration				Northward migration			
	Number of hawks	Mean	SD	Range	Number of hawks	Mean	SD	Range
1995								
Southeast Alberta	1	45.3						
Southwest Idaho	3	78.5	9.0	71.6–88.7				
Northern California	1	64.1						
Central Colorado	2	60.4	26.0	42.0–78.8				
Subtotal	7	66.5	17.3	42.0–88.7				
1996								
Southeast Alberta	4	59.6	14.0	47.8–79.6	2	58.0	9.9	51.0–65.0
Southwest Saskatchewan	1	62.6			1	56.3		
Northeast Oregon	4	83.8	22.1	65.5–97.8	4	68.7	10.7	54.8–80.2
Southwest Minnesota	1	49.3			1	70.4		
Southwest Idaho	6	68.2	8.0	46.3–77.8	5	64.1	9.4	51.6–74.8
Northern California	1	87.1			1	53.7		
Central Colorado	3	69.5	14.7	58.1–86.1	2	60.0	4.0	57.2–62.7
North-central Utah	3	53.1	6.9	48.2–61.0	2	65.8	2.4	64.1–67.5
Southeast Arizona	1	46.9						
Subtotal	24	66.5	15.5	46.3–97.8	18	63.5	8.5	51.6–80.2
1997								
Southwest Idaho	1	79.0			2	71.8	2.4	60.2–81.9
Grand total	32[a]	66.9	15.5	42.0–97.8	20[a]	61.6	9.1	51.0–81.9

[a]Excludes 14 of 44 hawks that started southward and 13 of 33 that started northward migration because of PTT failure, bird mortality, and data gaps.

TABLE 6.   Cumulative distance (km) adult Swainson's Hawks tracked by satellite telemetry from nine nesting localities arranged by latitude during southward and northward migration, 1995–1997.

Year/locality	Southward migration					Northward migration				
	Number of hawks	Mean	SD	Range	Duty cycle[a]	Number of hawks	Mean	SD	Range	Duty cycle[a]
1995										
Alberta	1	10016								
Idaho	3	11127	547	10518–11577	2					
California	1	11659			2					
Colorado	2	10436	41	10407–10465	2, 3					
Subtotal	7	10847	648	10016–11659	2					
1996										
Alberta	4	11437	249	11227–11778	2, 3	2	11095	343	10852–11337	2, 3
Saskatchewan	1	10327			3	1	10049			3
Oregon	5	11294	1310	10051–12831	1, 2	4	10833	616	10090–11585	3
Minnesota	1	11368			1	1	9047			3
Idaho	6	12094	539	11455–12809	1	5	10594	511	10081–11231	3
California	1	13209			1	1	10214			3
Colorado	3	9946	413	9653–10465	1, 2, 3	2	9575	487	9230–9919	3
Utah	3	10160	1182	9263–11499	2, 3	2	10185	294	9977–10393	3
Arizona	1	8449			1					
Subtotal	25	11156	1224	8449–13209		18	10417	667		
1997										
Idaho						2	10279			3
Grand total	32[b]	11058	1126	8449–13209		20[b]	10394			

[a]Duty-cycle category. See text for definition.
[b]Excludes 14 of 44 hawks that started south and 13 of 33 that started north because of PTT failure, bird mortality, and data gaps.

TABLE 7.   Start and end dates of northward migration of radio-marked Swainson's Hawks from nine breeding localities arranged by decreasing latitude, 1995–1997.

| Year/locality	Number of hawks	Mean start date	SD	Range	Number of hawks	Mean end date	SD	Range
1995								
Central Colorado	1	11 Mar						
1996								
Southeast Alberta	4	15 Mar	11.8	2–26 Mar	2	11 May	7.1	6–16 May
Southwest Saskatchewan	1	3 Mar			1	21 Apr		
Northeast Oregon	3	5 Mar	4.8	1–10 Mar	3	5 May	15.1	25 Apr–16 May
Southwest Minnesota	1	25 Feb			1	6 May		
Southwest Idaho	5	24 Feb	7.8	14 Feb–5 Mar	5	29 Apr	11.4	21 Apr–19 May
Northern California	1	26 Feb			1	20 Apr		
Central Colorado	2	8 Mar	11.6	21 Feb–16 Mar	2	6 May	15.6	25 Apr–17 May
North-central Utah	2	28 Feb	9.0	22 Feb–6 Mar	2	4 May	11.4	27 Apr–13 May
Southeast Arizona	1	13 Feb						
Subtotal	20	3 Mar		13 Feb–26 Mar	17			20 Apr–19 May
1997								
Southwest Minnesota	1	16 Mar						
Southwest Idaho	2	6 Mar	7.6	1–11 Mar	2	16 May		30 Apr–1 Jun
Subtotal	3	9 Mar			2	16 May		
Grand total	24			13 Feb–26 Mar	19			20 Apr–1 Jun
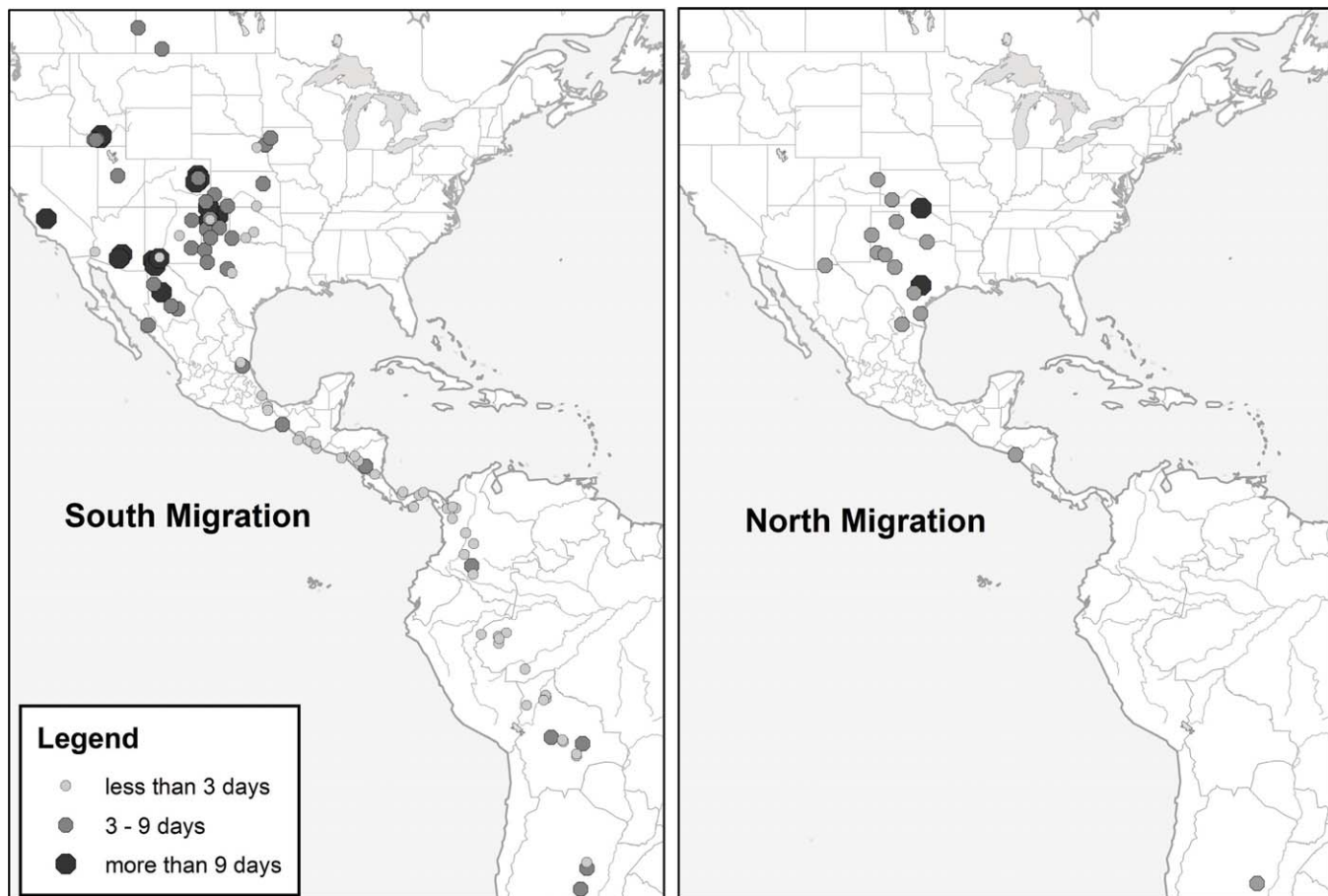
FIGURE 4.   Distribution of stopover locations by duration class for northward and southward migrations of adult Swainson's Hawks, 1995–1998. Based on 33 hawks stopping 98 times on southward migration and 10 hawks stopping 16 times on northward migration.
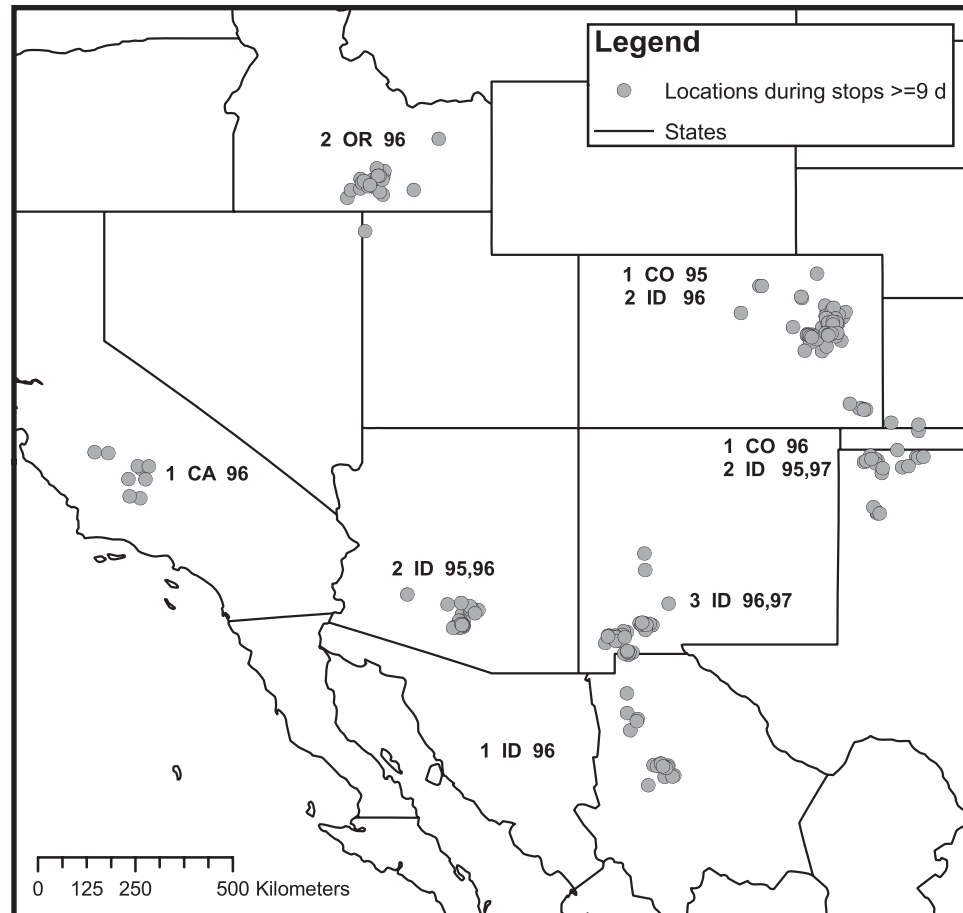
FIGURE 5.   Location of prolonged stopovers of 15 adult Swainson's Hawks on southward migration, 1995–1997. The first digit depicts the number of hawks in the stopover area, and the U.S. Postal Service abbreviation identifies the state from where they originated. The last two digits depict the year of the stop.

prolonged stopovers between 2 and 27 September each year 1995–1997 with no difference by year in starting date ($F_{2,7}$ = 7.57, P = 0.50). Four of the areas of prolonged stopover were used in multiple years, and two areas were used by birds from more than one breeding locality (Fig. 5).

Ten (43%) of 23 Swainson's Hawks that migrated north made one or two stopovers ($\bar{x}$ = 6.1 ± 1.1 days, range 4.0–8.4). One hawk made two additional stopovers, stopping 12.8 and 13.0 days before the PTT quit moving, and evidence suggests it did not return to its nesting area. Because all but one of these hawks wore category 3 PTTs, we considered only stops of ≥3.5 days. Although the proportion of hawks stopping ≥3.5 days in northward and southward migration did not differ (χ^2 = 1.82, df = 1, P > 0.10), fewer hawks made prolonged stopovers on northward migration (χ^2 = 8.17, df = 1, P = 0.003). All but two stopovers occurred north of 25° N (Fig. 4). Of 14 stopovers north of 25° N, 13 occurred in the southern Great Plains, one in the Chihuahuan Desert. Eight of 13 hawks migrating north through the southern Great Plains stopped at least once, including six of eight hawks and two of six from east and west

of the continental divide, respectively. Hawks that migrated up the eastern Sierra Madre Oriental and through the Great Plains or Chihuahuan Desert stopped over more than those that crossed the Sierra Madre Oriental and migrated through central Mexico (χ^2 = 4.87, df = 1, P = 0.03).

MOVEMENTS IN THE AUSTRAL SUMMER

The austral summer range of 36 Swainson's Hawks from 1995 to 1998 encompassed 738 800 km^2 in northern Argentina and western Uruguay (Fig. 6). The core area, the cluster of 90% of the locations, encompassed 172 700 km^2 (23% of the 100% minimum convex polygon) in northeastern La Pampa, northwestern Buenos Aires, southern and eastern Córdoba, and southwestern Santa Fe provinces of Argentina (Fig. 6).

Swainson's Hawks frequently moved among 26 clusters formed by 80% of the locations from all instrumented hawks (Fig. 6). We recorded more clusters used (Mann–Whitney U = 99.5, P = 0.03), more moves among clusters (Mann–Whitney U = 104.5, P = 0.01), and larger cumulative tracking distances (Mann–Whitney U = 98.0, P = 0.04) by eight birds carrying
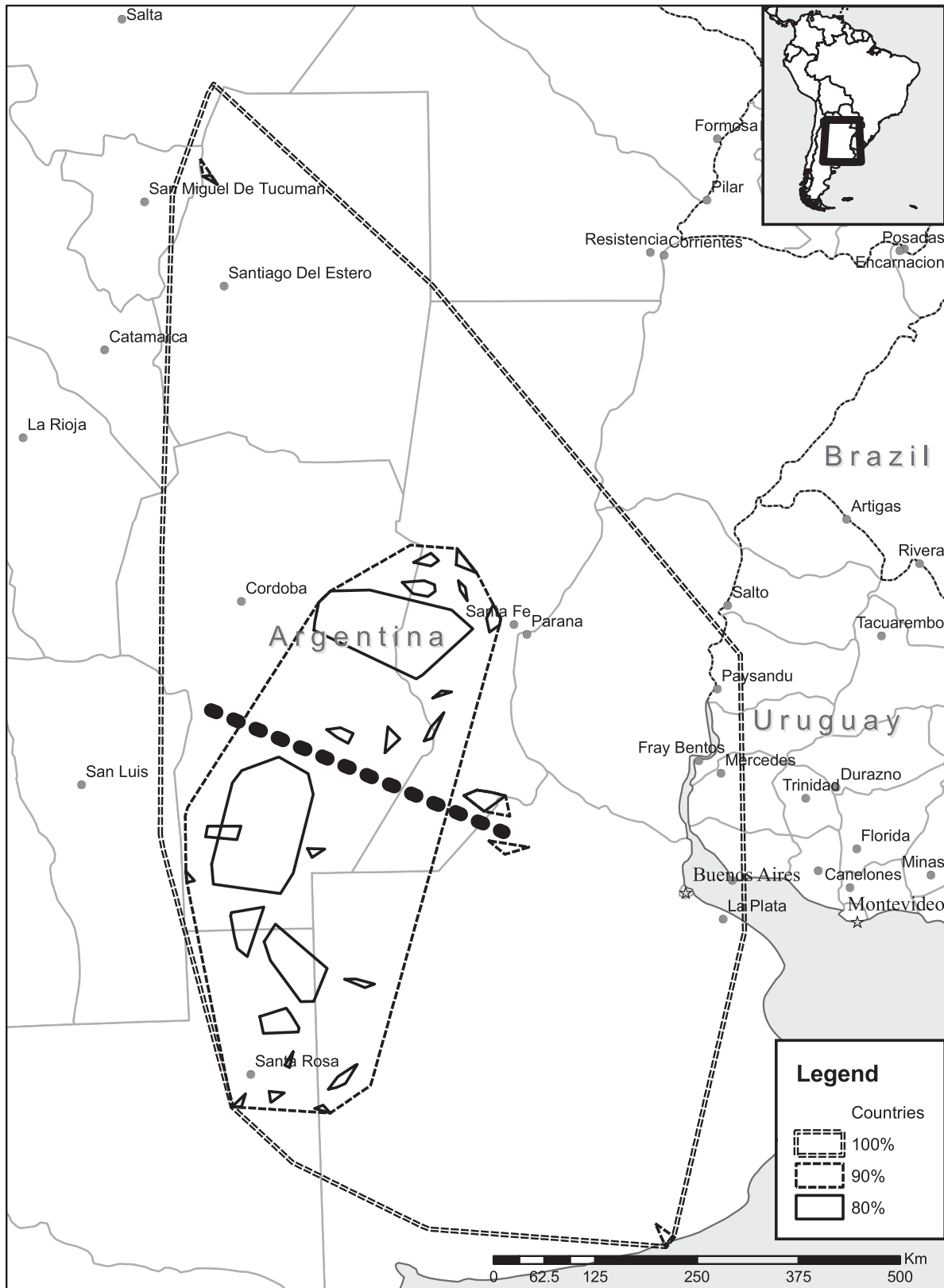
FIGURE 6.   Austral summer range (100% convex polygon) and core areas (90% and 80% use areas, cluster analysis) of 36 radio-marked adult Swainson's Hawks, based on all filtered location estimates, 1995–1998. Dotted line separates the northern and southern 80% clusters.

TABLE 8.   Use of 80% clusters and movements of 24 radio-marked adult Swainson's Hawks during the austral summer season, 1995–1998.

	Number of clusters used	Number of moves among clusters	Number of clusters reused	Cumulative distance tracked (km)	Maximum vector distance (km)
Mean	5.3	6.0	1.5	1795	307
SD	2.4	4.0	1.3	785	169
Range	1–10	0–16	0–6	791–3553	100–893

PTTs on category 2 duty cycles than by 16 carrying PTTs on category 3. Maximum vector length for the two groups did not differ (Mann–Whitney $U = 57.0$, $P = 0.67$). Therefore, we examined number of clusters used and moves among clusters by Swainson's Hawks carrying PTTs on category 2 as well as by all birds combined. Of 24 hawks that carried functioning PTTs for the entire austral season, 23 (96%) used ≥3 clusters, and 15 (62%) used 5 to 10 clusters. All clusters used by male Swainson's Hawks were also used by females. Of 23 hawks that used >1 cluster, 17 (74%) reused 1 to 6 clusters ($\bar{x} = 1.5 \pm 1.3$) and revisited the same cluster up to three times. Birds moved among clusters from 0 to 16 times ($\bar{x} = 6.0 \pm 4.0$) during the season (Table 8). Of the eight Swainson's Hawks with PTTs on a category 2 duty cycle, 7 (88%) used 5 to 10 clusters and moved an average of 9.1 ± 5.1 times between clusters. During the austral summer cumulative tracking distances ranged from 791 to 3553 km for all 24 Swainson's Hawks (from 1370 to 3184 for eight with category 2 PPTs). For each bird, the maximum distance of a single vector ranged from 100 to 893 km (Table 8).

In the 1996–1997 season, we observed seasonal shifts in the hawks' use of the northern and southern 80% clusters. During the first 2 weeks of the austral season (last 2 weeks of November), 60% of the Swainson's Hawks' occurrences were in the northern clusters (Fig. 7). By the first week of December this fraction decreased to 24%. It remained low to mid-January and
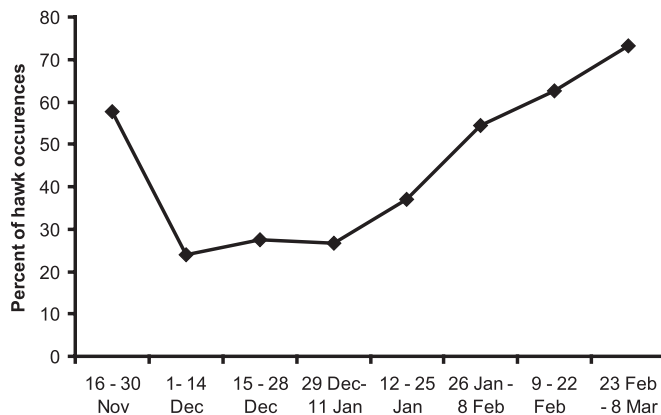

FIGURE 7.   Percent of occurrences of radio-marked adult Swainson's Hawks in the 13 northern 80% clusters of 26 total clusters (see Fig. 6) in the austral range in Argentina by 2-week intervals during the austral summer of 1996–1997.

then steadily increased to 73% by 8 March (Fig. 7). With exception of the one cluster in the extreme north of the austral range, the distance between the northeasternmost and southwesternmost cluster was 700 km (Fig. 7).

We did not see evidence of hawks from specific breeding localities using exclusive areas. Of 26 clusters, 22 contained hawks from 2 to 4 breeding localities, and 4 clusters contained hawks from 5 to 8 localities. The two largest clusters (one in the south and one in the north; Fig. 6) each contained birds from eight of the nine breeding localities. Collectively these two clusters contained hawks from all the nine breeding localities.

DISCUSSION

MIGRATION

Our findings support the assertion that most of the Swainson's Hawk population migrates between the breeding grounds in North America and the austral summer grounds in the pampas of South America (England et al. 1997, Sarasola et al. 2008a). None of the hawks we radio marked went to Florida or central California, where Swainson's Hawks winter regularly in small numbers (Clark 1990), and none wintered in Mexico, as have Swainson's Hawks radio-marked in the Central Valley of California (M. Bradberry, unpubl. data; Wheeler 2003).

Swainson's Hawks from across the breeding range followed various routes south on a broad front in a funnel pattern (Berthold 2001) to converge along the east coast of central Mexico into a common corridor to a communal austral summer range in central Argentina. The pattern constricted between the Sierra Madre Oriental and the Gulf of Mexico at about 20° N and remained concentrated to the austral range. Patterns of northward and southward migration were similar.

Swainson's Hawks differed from other migratory raptors studied thus far in that the timing of their migration did not differ by sex and was relatively synchronous across geographic locations. In contrast, dates of departure of Ospreys (*Pandion haliaetus*) from their breeding grounds in North America and Sweden differed significantly by sex (females depart significantly earlier) and geographic region (Hake et al. 2001, Martell et al. 2001). Female Honey Buzzards (*Pernis apivorus*) leave the breeding grounds in Sweden somewhat earlier than do males (Hake et al. 2003). Although our failure to find a difference between sexes of Swainson's Hawks

may have been due to the small size of our sample of males, we have no evidence to suspect a difference. Values for males were well within the range of females, and the departure date of both members of a pair was the same. The northward migration is faster than the southward migration for adult Ospreys and Peregrine Falcons (*Falco peregrinus*; Alerstam et al. 2006, McGrady et al. 2002) but not for Swainson's Hawks.

In both southward and northward migration the distribution of migrating Swainson's Hawks varied in space and time. Although hawks departed from the nesting grounds over a 2-month period, their migration south across 20° N became concentrated into 3 weeks. This latitude is just north of Veracruz, Mexico, where the migration corridor was most constricted and appeared to be a temporal goal. Migrating hawks slowed and duration of their passage lengthened through southern Mexico and Central America, which is an area where migrating hawks may feed (Kirkley 1991). The equator may have been an intermediate temporal goal for Swainson's Hawks migrating north, as most hawks slowed but trailing birds accelerated as they approached the equator. In contrast to southward migration, travel rates in northward migration increased between 0° and 20° N, suggesting that 20° N may have been a temporal goal as it was in southward migration

Many factors affected our estimate of total migration distance. Swainson's Hawks from farther north and west traveled farther. Hawks from the west of the breeding range moved longitudinally more than did birds from the east to reach the east coast of Mexico, where all Swainson's Hawks converged. A critical factor in estimating migration distance is the role of the PTTs' transmission frequency (duty cycle). Shorter duty cycles produce more transmission periods and more location estimates, yielding more vectors, which result in greater cumulative distance. Any studies that depend on transmissions in multiple duty cycles must account for this to prevent faulty comparisons, either qualitatively or quantitatively. Any statistical analysis must incorporate correction for multiple duty cycles if more than one is used in the study.

USE OF STOPOVER AREAS

Birds use stopovers on migration to refuel and replenish fat reserves (Berthold 2001, Skagen 2006) and/or to complete molt (Leu and Thompson 2002, Newton 2008). Although data suggest that we missed brief stopovers of hawks carrying PTTs operating on categories 2 and 3 duty cycles, results from hawks carrying category 1 PTTs suggest that all Swainson's Hawks tended to stop on southward migration. About half of the hawks departed the breeding grounds early and stopped at intermediate destinations for prolonged periods, possibly to refuel (Bechard et al. 2006). The other half stayed on the breeding grounds nearly 3 weeks longer where they could add fuel and complete molt before migrating south. Ospreys that depart early (mainly females) make prolonged stopovers, presumably to amass fuel, whereas late-departing Ospreys that

accumulate energy for migration and complete their molt on the breeding grounds spend fewer days stopping over (Alerstam et al. 2006, Hake et al. 2001, Kjellén et al. 2001). Most of the areas of prolonged stopovers by our tagged Swainson's Hawks were used by different birds from the same breeding locality (Idaho) in the same and different years, and some of the areas were used by birds from different localities in the same year. This fidelity suggests that these stopover areas are important destinations (Newton 2008). Most Idaho hawks made prolonged stops in widely separated areas 1200 to 1500 km (straight-line distance) from their nesting area at about the same time in all 3 years. These birds may have departed the breeding grounds early to exploit seasonal food such as insects (Littlefield 1973) during these prolonged stopovers before continuing their migration.

Smith et al. (1986) proposed that Swainson's Hawks must acquire all the fat they need at some region in the Northern Hemisphere to complete the migration south while fasting. Alternatively, Kirkley (1991) suggested that Swainson's Hawks feed on migration, and measurements of the mass of hawks before and after migration support this idea (Goldstein et al. 1999c, Bechard et al. 2006). Swainson's Hawks that made prolonged stops in the southern Great Plains and northern Chihuahuan Desert probably were accumulating fuel for the rest of migration, as proposed by Smith et al. (1986). However, most of these hawks made subsequent stops along the route south. Stopovers by Swainson's Hawks elsewhere along the route present an opportunity to accumulate fuel before the next segment of the migration (Kirkley 1991, Bechard et al. 2006). Swainson's Hawks migrating north tended not to stop for prolonged periods. These hawks may have obtained food resources in the austral range sufficient to reduce the need to refuel at intermediate destinations, as discussed by Alerstam et al. (2006)

Stopover behavior can influence birds' migration patterns (Berthold 2001) and might have influenced differences in migration patterns north of 20° N between Swainson's Hawks from east and those from west of the continental divide. Hawks from east of the divide tended to stopover in the southern Great Plains on both southward and northward migration, and individuals followed similar paths on both migrations. In contrast, hawks from west of the continental divide tended not to stop while migrating north and to use different routes in southward and northward migration. In southward migration many hawks from west of the continental divide deviated from a direct trajectory to east-central Mexico to stopover in the southern Great Plains. In northward migration most of these hawks crossed the Sierra Madre Oriental, a logical strategy for a direct path to the western nesting grounds. Although some of these hawks took fairly direct paths to their nesting areas, we tracked others to the west, resulting in a wide separation between southward and northward paths for these individuals. Alerstam et al. (2006) attributed the wide separation of outbound and return tracks of migrating Ospreys to

wind drift. Wind drift allows birds to complete their journey in less time and at a lower cost than does correcting for crosswinds en route (Bildstein 2006). Swainson's Hawks whose northbound paths diverged northwest from their southbound paths between 20° and 30° N migrated at northwesterly azimuths perpendicular to the prevailing winds, which are from the northeast (http://www.ace.mmu.ac.uk/eae/climate/older/Prevailing Winds.html) in this area. These Swainson's Hawks tended not to stop over and may not have had a need to do so. Wind drift, however, does not explain the wide separation of tracks for the three hawks whose northbound and southbound tracks north of 30° N diverged widely.

AUSTRAL SUMMER MOVEMENTS

All radio-marked Swainson's Hawks from nine widely separated localities across the breeding range used common austral summer grounds. Stable-isotope analyses have shown that flocks of Swainson's Hawks in the austral range consist of a mixture of individuals from across the breeding range (Sarasola et al. 2008a). Although the austral summer range of radio-marked Swainson's Hawks encompassed a large expanse in north-central Argentina and western Uruguay, these hawks concentrated in a core area in central Argentina constituting about 20% of the austral range. The large total range resulted from 80% of the hawks making infrequent forays outside the core area. In contrast, Ospreys from different parts of the breeding range, as well as individuals from the same areas on the breeding grounds, winter in widely separated regions (Kjellén et al. 1997, Martell et al. 2001). Unlike Ospreys from North America and Europe, where males and females from the same breeding area wintered in separate areas (Kjellén et al. 2001, Martell et al. 2001), male and female adult Swainson's Hawks used the same regions of the austral range, in agreement with Sarasola et al. (2008a). In their austral range, Swainson's Hawks forage in large flocks on swarms of insects, a behavior that favors communal behavior (Canavelli et al. 2003, Sarasola and Negro 2005). In contrast, factors including competition for food favor separation of the Osprey (Martell et al. 2001).

Adult Swainson's Hawks frequently moved long distances (up to 1600 km) in their austral summer range. In late January 1997 Goldstein et al. (2000) located four radio-marked adult Swainson's Hawks 500 km north of where they were trapped 6 weeks earlier. These hawks moved from a southern to a northern cluster, supporting our observations. In contrast, adult Peregrine Falcons and Ospreys and juvenile Golden Eagles (*Aquila chrysaetos*) remain in relatively small areas in their winter ranges, moving short distances (<75 km) (Kjellén et al. 1997, Hake et al. 2001, McGrady et al. 2002, Ganusevich et al. 2004, McIntyre et al. 2008). The smaller home ranges of wintering Peregrine Falcons have been attributed to concentrations of relatively stable prey in localized areas (McGrady et al. 2002, Ganusevich et al. 2004). The frequent and long-distance

movements of Swainson's Hawks on their austral summer grounds reflected behavior of a bird preying on temporarily abundant, easily captured, and often spatially unpredictable insect prey (Alerstam 1990, Sherry and Holmes 1995). In their austral summer range Swainson's Hawks associated with agricultural habitats and fed mainly on grasshoppers (order Orthoptera) and other insects, which can be sporadic, locally abundant, and often unpredictable (Goldstein et al. 2000, Canavelli et al. 2003, Sarasola and Negro 2005). Swainson's Hawks track migrating swarms of insects, and migrant raptors that depend on swarming insects on the wintering grounds travel long distances to find food (Jaramillo 1993, Newton 1998). Swainson's Hawk movements among clusters and the shift of use from the southern to the northern regions of the core area as the austral summer progressed might have reflected responses to agriculture (tilling, mowing, harvesting, burning, etc.) and the availability of abundant but transient food sources, such as insect outbreaks (Canavelli et al. 2003, Sarasola and Negro 2005).

CONSERVATION IMPLICATIONS

Strategies for conservation of migratory birds often rely on information that identifies areas used during migration, molt, staging, and resting as well as information on potential limitations or threats in these areas (Senner and Fuller 1989, Berthold 2001, Bildstein 2006). Migratory species face particular risks, and long-distance migrations are some of the most difficult and dangerous activities birds undertake (Bildstein 2006). Results of our radio-tracking study in Argentina were used to define the area in which the pesticide monocrotophos was banned to provide immediate protection to the species on its austral summer grounds (Goldstein et al. 1999b). Our study also provided insights into connectivity among the areas used by Swainson's Hawks. The hawks' survival and condition in any of these areas can have carry-over effects for the birds' performance at other locations, such as the breeding grounds (Norris and Marra 2007, Newton 2008). Within the Swainson's Hawk's migration corridor, paths of many individuals are overlaid in a pattern that suggests there are commonly used routes and thus resources (e.g., perches and roosts) and conditions (e.g., thermals that allow soaring flight) the hawks require. The concentrated migration of Swainson's Hawks from across the breeding range, particularly from east-central Mexico through the Isthmus of Panama, has broad implications. Conservation or catastrophes in these corridors could affect most of the population. Conservation efforts also should consider potential risks to migrants, such as construction of wind-energy farms across the Isthmus of Tehuantepec, where Swainson's Hawk migration is particularity concentrated. Stopover areas are likely used for feeding and resting and are candidates for conservation efforts such as those implemented for waterfowl and waterbirds (Berthold 2001) and needed for other groups of avian migrants (Moore 2000). The intermingling

of the sexes and individuals from numerous breeding localities on the austral range has implications for localized mass mortality (e.g., pesticide poisoning, hailstorms; Goldstein et al. 1999a, Sarasola et al. 2005) because effects would be diluted across the Swainson's Hawk's breeding range, not focused on a local nesting population (Sarasola et al. 2008a).

Our study also provided new information on the movements of adult Swainson's Hawks from across their breeding range, but much remains to be learned. How Swainson's Hawks respond to environmental and land-use changes in their austral range is largely unknown. Record high precipitation during the summers of 1997 and 2000 through 2002 resulted in a distinct change in the species' distribution in its austral summer range (Canavelli 2000, Sarasola et al. 2008b; J. Sarasola, pers. comm., M. Bechard, pers. obs.). The areas occupied with large numbers of Swainson's Hawks in northern La Pampa province during our study were virtually devoid of Swainson's Hawks after these rains. Also, much of the pasturelands that Swainson's Hawks used during our study (Canavelli et al. 2003) have been converted to row crops (Sarasola et al. 2008b). Transformation of Argentinean agriculture from primarily range-based livestock production to intensive cultivation could affect Swainson's Hawks negatively (Woodbridge et al. 1995). Our research identified important stopover areas for migrating adult Swainson's Hawks; however, why certain birds make prolonged stopovers and others do not and what these birds do during their stopovers remain to be answered.

ACKNOWLEDGMENTS

LITERATURE CITED

ALERSTAM, T. 1990. Bird migration. Cambridge University Press, Cambridge, UK.

ALERSTAM, T., M. HAKE, AND N. KJELLÉN. 2006. Temporal and spatial patterns of repeated migratory journeys by Ospreys. Animal Behaviour 71:555–566.

ARGOS [ONLINE]. 2007. Argos user's manual. Collecte Localisation Satellites, Ramonville Saint-Agne, France. <https://www.argos-system.org/manual/> (14 October 2008).

BECHARD, M. J., J. H. SARASOLA, AND B. WOODBRIDGE. 2006. A re-evaluation of evidence raises questions about the fasting migration hypothesis for Swainson's Hawk (*Buteo swainsoni*). Hornero 21:65–72.

BERTHOLD, P. 2001. Bird migration: a general survey. 2nd ed. Oxford University Press, New York.

BILDSTEIN, K. L. 2006. Migrating raptors of the world: their ecology and conservation. Cornell University Press, Ithaca, NY.

BLOOM, P. H., W. S. CLARK, AND J. F. KIDD. 2007. Capture techniques, p. 193–219. *In* D. M. Bird and K. L Bildstein [EDS.], Raptor research and management techniques. Hancock House, Blaine, WA.

BURNHAM, K. P., AND ANDERSON, D. R. 2002. Model selection and multimodel inference: a practical information-theoretical approach. 2nd ed. Springer, New York.

CANAVELLI, S. B. 2000. Abundance, movement and habitat use of Swainson's Hawks in their wintering grounds, Argentina. M.Sc. thesis, University of Florida, Gainesville, FL.

CANAVELLI, S. B., M. J. BECHARD, B. WOODBRIDGE, M. N. KOCHERT, J. J. MACEDA, AND M. E. ZACCAGNINI. 2003. Habitat use by Swainson's Hawks on their austral wintering grounds in Argentina. Journal of Raptor Research 37:125–134.

CLARK, W. S. 1990. Migration and movements, p. 152–167. *In* I. Newton [ED.], Birds of prey. Facts on File, New York.

DOUGLAS, D. C. [ONLINE]. 2006. The Douglas Argos-filter algorithm. Version 7.02. <http://alaska.usgs.gov/ science/ biology/spatial/ douglas.html> (1 August 2006).

DUNSTAN, T. C. 1972. A harness for radio-tagging raptorial birds. Inland Bird Banding Association News 44:4–8.

ENGLAND, A. S., M. J. BECHARD, AND C. S. HOUSTON. 1997. Swainson's Hawk (*Buteo swainsoni*), no. 265. *In* A. Poole and F. Gill [EDS.], The birds of North America. Academy of Natural Sciences, Philadelphia.

FULLER, M. R., W. S. SEEGAR, AND L. S. SCHUECK. 1998. Routes and travel rates of migrating Peregrine Falcons (*Falco peregrinus*) and Swainson's Hawks (*Buteo swainsoni*) in the Western Hemisphere. Journal of Avian Biology 29:433–440.

GANUSEVICH, S. A., T. L. MAECHTLE, W. S. SEEGAR, M. A. YATES, M. J. MCGRADY, M. FULLER, L. SCHUECK, J. DAYTON, AND C. J. HENNY. 2004. Autumn migration and wintering areas of Peregrine Falcons *Falco peregrinus* nesting on the Kola Peninsula, northern Russia. Ibis 146: 291–297.

GOLDSTEIN, M. I., T. E. LACHER JR., B. WOODBRIDGE, M. J. BECHARD, S. B. CANAVELLI, M. E. ZACCAGNINI, G. P. COBB, E. J. SCOLLON, R. TRIBOLET, AND M. J. HOOPER. 1999a. Monocrotophos-induced mass mortality of Swainson's Kawks in Argentina, 1995–96. Ecotoxicology 8:201–214.

GOLDSTEIN, M. I., T. E. LACHER JR., M. E. ZACCAGNINI, M. L. PARKER, AND M. J. HOOPER. 1999b. Monitoring and assessment of Swainson's Hawks in Argentina following restrictions on monocrotophos use, 1996–97. Ecotoxicology 8:215–224.

GOLDSTEIN, M. I., P. H. BLOOM, J. H. SARASOLA, AND T. E. LACHER. 1999c. Post-migration weight gain of Swainson's Hawks in Argentina. Wilson Bulletin 111:428–432.

GOLDSTEIN, M. I., M. J. BECHARD, M. L. PARKER, M. N. KOCHERT, AND A. E. LANUSSE. 2000. Abundance, behavior, and mortality of *Buteo swainsoni* near San Francisco, Cordoba, Argentina in 1997. Hornero 15:117–121.

GREENBERG, R., AND P. P. MARRA. 2005. Birds of two worlds: the ecology and evolution of migratory birds. Johns Hopkins University Press, Baltimore.

HAKE, M., N. KJELLÉN, AND T. ALERSTAM. 2001. Satellite tracking of Swedish Ospreys *Pandion haliaetus*; autumn migration routes and orientation. Journal of Avian Biology 32:47–56.

HAKE, M., N. KJELLÉN, AND T. ALERSTAM. 2003. Age-dependent migration strategy in Honey Buzzards *Pernis apivorus* tracked by satellite. Oikos 103:385–396.

HOUSTON, C. S., AND J. K. SCHMUTZ. 1995. Swainson's Hawk banding in North America to 1992. North American Bird Bander 20:120–127.

HULL, B., AND P. BLOOM. 2001. The North American banders' manual for raptor banding techniques. North American Banding Council, Point Reyes Station, CA.

JARAMILLO, A. P. 1993. Wintering Swainson's Hawks in Argentina: food and age segregation. Condor 95:475–479.

KENWARD, R. E. 1987. Wildlife radio tagging. Academic Press, London.

KENWARD, R. E, A. B SOUTH, AND S. S WALLS. 2002. Ranges 6: for the analysis of tracking and location data. Anatrack Ltd., Wareham, Dorset, UK.

KIRKLEY, J. S. 1991. Do migrant Swainson's Hawks fast en route to Argentina? Journal of Raptor Research 25:82–86.

KJELLÉN, N., M. HAKE, AND T. ALERSTAM. 1997. Strategies of two Ospreys *Pandion haliaetus* migrating between Sweden and tropical Africa as revealed by satellite tracking. Journal of Avian Biology 28:15–23.

KJELLÉN, N., M. HAKE, AND T. ALERSTAM. 2001. Timing and speed of migration in male, female and juvenile Ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. Journal of Avian Biology 32:57–67.

KOCHERT, M. N., AND J. O. MCKINLEY. 2008. Use of body mass, footpad length, and wing chord to determine sex in Swainson's Hawks. Journal of Raptor Research 42:138–141.

LEU, M., AND C. W. THOMPSON. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. Biological Conservation 106:45–56.

LITTLEFIELD, C. D. 1973. Swainson's Hawks preying on fall armyworms. Southwestern Naturalist 17:443–448.

MARTELL, M. S., C. J. HENNY, P. E. NYE AND M. J. SOLENSKY. 2001. Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. Condor 103:715–724.

MARTELL, M., S. WILLEY, AND J. SCHLADWEILER. 1998. Nesting and migration of Swainson's Hawks in Minnesota. Loon 70:72–81.

MCGRADY, M. J., T. L. MAECHTLE, J. J. VARGAS, W. S. SEEGAR, AND M. C. PORRAS PEÑA. 2002. Migration and ranging of Peregrine Falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. Condor 104:39–48.

MCINTYRE, C. L, M. D. C. DOUGLAS, AND M. W. COLLOPY. 2008. Movements of Golden Eagles (*Aquila chrysaetos*) from interior Alaska during their first year of independence. Auk 125:214–224.

MOORE, F. R. [ED]. 2000. Stopover ecology of nearctic–neotropical landbird migrants: habitat relations and conservation implications. Studies in Avian Biology 20.

NEWTON, I. 1998. Migration patterns in the west palaearctic raptors, p. 603–612. *In* R. D. Chancellor, B.-U. Meyberg, and J. J. Ferrero [EDS.], Holarctic birds of prey. World Working Group on Birds of Prey, Berlin.

NEWTON, I. 2008. The migration ecology of birds. Academic Press, London.

NORRIS, D. R., AND P. P. MARRA. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. Condor 109:535–547.

PENNYCUICK, C. J. 2008. Modeling the flying bird. Academic Press, Boston.

SARASOLA, J. H., AND J. J. NEGRO. 2005. Hunting success of wintering Swainson's Hawks: environmental effects on timing and choice of foraging method. Canadian Journal of Zoology 83:1353–1359.

SARASOLA, J. H., J. J. NEGRO, V. SALVADOR, AND J. J. MACEDA. 2005. Hailstorms as a cause of mass mortality of Swainson's Hawks in their wintering grounds. Journal of Wildlife Diseases 41:643–646.

SARASOLA, J. H., J. J. NEGRO, K. A. HOBSON, G. R. BORTOLOTTI, AND K. L. BILDSTEIN. 2008a. Can a "wintering area effect" explain population status of Swainson's Hawks? A stable isotope approach. Diversity and Distributions 14:686–691.

SARASOLA, J. H., J. BUSTAMANTE, J. J. NEGRO, AND A. TRAVAINI. 2008b. Where do Swainson's Hawks winter? Satellite images used to identify potential habitat. Diversity and Distributions 14:742–753.

SAS INSTITUTE, INC. 2006. SAS/STAT user's guide. Version 9.1.3. SAS Institute, Cary, NC.

SCHMUTZ, J. K., C. S. HOUSTON AND G. L. HOLROYD. 1996. Southward migration of Swainson's Hawks: over 10,000 km in 54 days. Blue Jay 54:70–76.

SENNER, E. S., AND M. R. FULLER. 1989. Status and conservation of North American raptors migrating to the neotropics, p. 3–57. *In* B.-U. Meyburg and R. D. Chancellor [EDS.], Raptors in the modern world. World Working Group on Birds of Prey and Owls, Berlin.

SHERRY, T. W., AND R. T. HOLMES 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence?, p. 85–120. *In* T. E. Martin and D. M. Finch [EDS.], Ecology and management of migratory birds. Oxford University Press, London.

SILLETT, T. S., AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

SKAGEN, S. K. 2006. Migration stopovers and the conservation of arctic-breeding *Calidris* sandpipers. Auk 123:313–322.

SMITH, N. G., D. L. GOLDSTEIN, AND G. A. BARTHOLOMEW. 1986. Is long-distance migration possible for soaring hawks using only stored fat? Auk 103:607–611.

STEENHOF, K., M. R. FULLER, M. N. KOCHERT, AND K. K. BATES. 2005. Long-range movements and breeding dispersal of Prairie Falcons from southwest Idaho. Condor 107:481–496.

STRIKWERDA, T. E., M. R. FULLER, W. S. SEEGAR, P.W. HOWEY, AND D. BLACK. 1986. Bird-borne satellite transmitter and location program. Johns Hopkins APL Technical Digest 7:203–208.

SYSTAT. 2007. SYSTAT user's guide. Version 12. SYSTAT Software, San Jose, CA.

WEBSTER, M. S., P. P. MARRA, S. M. HAIG, S. BENSCH, AND R. T. HOLMES. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

WHEELER, B. K. 2003. Raptors of eastern North America. Princeton University Press, Princeton, NJ.

WOODBRIDGE, B., K. K. FINLEY, AND S. T. SEAGER. 1995. An investigation of the Swainson's Hawk in Argentina. Journal of Raptor Research 29:202–204.