Número especial

Nuevas miradas sobre las aves migratorias americanas: técnicas, patrones, procesos y mecanismos

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NUEVAS MIRADAS SOBRE LAS AVES MIGRATORIAS AMERICANAS: TÉCNICAS, PATRONES, PROCESOS Y MECANISMOS

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La migración es generalmente considerada como un mecanismo que permite explotar incrementos estacionales en la abundancia de los recursos y evadir los momentos del año cuando éstos escasean. Entre las aves la migración está muy extendida, siendo quizá el grupo de vertebrados en el cual se producen los mayores desplazamientos de especies e individuos (por ejemplo, se estima que aproximadamente 50 000 millones de aves realizan movimientos migratorios en algún momento del ciclo anual[1]). En América, las aves migratorias de los dos hemisferios comparten un origen evolutivo común, la avifauna Neotropical, y muestran un número similar de especies[2]. Sin embargo, nuestro conocimiento sobre ambos sistemas migratorios difiere notablemente. A pesar de que ya a principios del siglo XIX Azara[3] había descripto los patrones migratorios de varias especies rioplatenses, muy poco se adelantó en la comprensión de la biología de las aves migratorias en América del Sur comparado con América del Norte[4–6].

La migración en las aves es un proceso complejo que requiere la adecuación de un conjunto de factores biológicos para que el viaje sea exitoso. Estos factores incluyen instrucciones genéticas sobre el calendario y la duración de los desplazamientos migratorios, cambios fisiológicos para el almacenamiento de nutrientes (lípidos y proteínas) que utilizan como combustible durante el vuelo y adaptaciones del comportamiento para la navegación y orientación[1]. Además, la supervivencia de las poblaciones de las especies migratorias depende de las condiciones que enfrentan en sus áreas de reproducción, en las de reposo y en las que utilizan durante el viaje entre ambas zonas. Esta característica del ciclo de vida de las aves migratorias les confiere un grado importante de vulnerabilidad a las variaciones ambientales y a los cambios producidos por las actividades del hombre. Por ejemplo, en varias especies de paseriformes migratorias que se reproducen en Europa e invernan en África, y en otras que se reproducen en América del Norte y pasan el invierno en América Central y América del Sur, se han registrado importantes declinaciones poblacionales en los últimos 30–40 años[7]. Sin embargo, las causas de estas declinaciones no fueron similares. En el Viejo Mundo los motivos parecen estar relacionados con los efectos de las sequías y con el incremento de la desertificación en África (i.e., en el área no reproductiva). En cambio, en el Nuevo Mundo las causas serían principalmente los cambios provocados por el hombre en amplias zonas de América del Norte (i.e., en el área de reproducción), en especial la fragmentación de los bosques, con el consecuente incremento de predadores de nidadas y del parasitismo por *Molothrus ater*[7]. En el caso de las aves que migran en América del Sur no hay actualmente posibilidad de evaluar el estado de sus poblaciones y, menos aún, especular sobre sus tendencias poblacionales. Sin embargo, considerando las profundas alteraciones de hábitat que el hombre ha producido, es de esperar que las especies migratorias estén enfrentando un escenario complejo para su conservación. Por ejemplo, registros históricos indican que las poblaciones de *Alectrurus risora* llegaban hasta Buenos Aires durante la época reproductiva y se desplazaban hasta Paraguay y Brasil durante la época de reposo reproductivo [8], pero actualmente estas poblaciones están restringidas al noreste de Argentina y son consideradas residentes [9].

Conocer los aspectos biológicos básicos que caracterizan a las aves migratorias tiene un valor fundamental para mejorar nuestras posibilidades de organizar planes que ayuden a conservar a este grupo de aves. Pero, además, ese conocimiento puede jugar un papel importante frente a problemas epidemiológicos. En sus desplazamientos, las aves pueden actuar como transporte de virus y bacterias perjudiciales para la salud y la economía del hombre [1]. En estos últimos tiempos se han registrado dos situaciones de expansión de enfermedades en las que han participado aves migratorias y que tuvieron gran repercusión internacional: el virus del Oeste del Nilo [10] y el virus de la influenza aviar [11]. Por lo tanto, conocer los patrones migratorios y las causas que los determinan puede ser de gran ayuda para planificar escenarios epidemiológicos.

Buscando desafiar la escasez de conocimientos sobre las aves migratorias en América del Sur, se desarrolló el simposio "Aves migratorias americanas: algunos apuntes para conocerlas" durante la XI Reunión Argentina de Ornitología, llevada a cabo en Buenos Aires en septiembre de 2005. Los objetivos del simposio eran aportar información sobre diversos aspectos de la migración en el continente americano y presentar nuevas técnicas para su estudio. Como las migraciones están presentes en casi todos los órdenes taxonómicos de las aves, el simposio se caracterizó por el aporte de trabajos sobre grupos muy diferentes, incluyendo Falconiformes, Charadriiformes y Passeriformes. Un conjunto de investigadores de Argentina y EEUU que trabajan principalmente en América del Sur fueron invitados a participar, y cinco de los expositores que formaron parte del simposio aceptaron volcar en el papel sus presentaciones. El resultado es este número especial de *El Hornero* sobre aves migratorias americanas titulado "Nuevas miradas sobre las aves migratorias americanas: técnicas, patrones, procesos y mecanismos".

En el primero de los artículos presentados, Bechard y colaboradores (pp. 65–72) examinan, utilizando telemetría satelital, las características del patrón migratorio de *Buteo swainsoni* entre América del Norte y América del Sur, analizando la velocidad y la duración de la migración y los cambios en la masa corporal de machos, hembras y juveniles en diferentes momentos del ciclo migratorio. Sus resultados refutan la hipótesis del ayuno durante la migración y sugieren, en cambio, que las aves utilizan las áreas de parada para recuperar reservas antes de continuar sus desplazamientos migratorios. Considerando que *Buteo swainsoni* ha sufrido importantes eventos de mortalidad debido al uso de insecticidas (particularmente en su área no reproductiva en Argentina), este descubrimiento es de suma importancia para los planes de conservación, ya que plantea la necesidad de considerar no solo las áreas de reproducción y reposo, sino también las zonas de parada para un efectivo manejo de las poblaciones de esta rapaz.

Torres Dowdall y colaboradores (pp. 73–84) describen una nueva técnica para determinar la conectividad de las poblaciones de especies migratorias que utiliza la composición de isótopos estables de los tejidos de las aves (principalmente en las plumas remeras), un campo de intensa investigación en los últimos años [12]. Si bien la técnica ha sido aplicada exitosamente en varias especies de aves, los autores precisan sus alcances y limitaciones, y proveen recomendaciones para mejorar los diseños de los estudios de manera de minimizar la variabilidad de las mediciones e incrementar la determinación del origen geográfico de los individuos.

La biología de las golondrinas durante la migración y en las áreas de reposo reproductivo ha recibido muy poca atención en comparación con los estudios en las áreas de cría. En el tercer trabajo de este número especial, Winkler (pp. 85–97) ofrece una revisión de esta temática. Su análisis remarca la importancia de los sitios con dormideros en el patrón de desplazamientos de estas aves, lo que las hace extremadamente flexibles con respecto a otras paseriformes. Además, destaca la utilidad del incremento en la disponibilidad de radares climáticos en EEUU como herramienta para mejorar el estudio de los patrones de distribución de *Tachycineta bicolor* y *Progne subis* durante la época de reposo reproductivo.

Por su parte, Jahn y colaboradores (pp. 99–108) examinan la importancia de estudiar los mecanismos involucrados en los patrones migratorios de las aves en América del Sur, y particularmente el patrón de superposición entre áreas de reproducción y de reposo que muestran muchas especies migratorias. Como el desarrollo teórico y empírico de lo que se sabe actualmente sobre el fenómeno de la migración en aves se ha generado principalmente en sistemas migratorios del Hemisferio Norte, la dilucidación de las causas de los patrones migratorios en América del Sur permitirá poner a prueba las hipótesis derivadas de los otros sistemas, mejorando nuestro conocimiento general del fenómeno de la migración e incrementando las bases científicas para la conservación de las aves migratorias.

En el último de los artículos de este número, González y colaboradores (pp. 109–117) enfocan sobre un problema poco representado en la literatura sobre aves migratorias: la ecología de los sitios de parada. En particular, analizan el papel de las escalas migratorias en la dinámica poblacional de *Calidris canutus rufa*, un chorlo que sufrió una drástica declinación poblacional debido a la disminución de su principal alimento por sobrepesca en su última escala en la migración hacia las áreas de reproducción en el Ártico. Los autores encontraron un efecto dominó sobre la supervivencia y reproducción de esta ave, debido a que el efecto de la disminución de alimento en su última parada antes de arribar a las áreas de reproducción se amplifica en los individuos que tardan más en abandonar los sitios de parada australes.

En conjunto, estos aportes brindan nuevos enfoques, información novedosa y explicaciones alternativas para aumentar nuestro entendimiento de la biología de las aves migratorias americanas. Esperamos que esta diversidad de temas y puntos de vista sirva para estimular el estudio de este fascinante grupo de aves, especialmente en América del Sur.

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A RE-EVALUATION OF EVIDENCE RAISES QUESTIONS ABOUT THE FASTING MIGRATION HYPOTHESIS FOR SWAINSON'S HAWK (*BUTEO SWAINSONI*)

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Abstract.— We examined the fasting migration hypothesis for Swainson's Hawks (*Buteo swainsoni*) by estimating the length, duration, and speed of the migration between North and South America and measuring changes in their body masses at various times throughout the year. We instrumented 34 adult Swainson's Hawks with satellite radios on their breeding grounds in western North America to determine the duration, length, and speed of the migration. Migrating south at 188 km/day, it took Swainson's Hawks 51 days to complete their 13504 km migration to their austral summer grounds. Averaging only 150 km/day on their return migration, it took them 60 days to complete the shorter 11952 km migration back to North America. Adult male and female Swainson's Hawks had average body masses of 872 g and 1131 g, respectively, when they departed from North America in September and their body masses upon arrival in Argentina averaged 759 g for adult males and 933 g for adult females, indicating they lost only an average of 18% of their body masses during migration. Adult male and female Swainson's Hawks had body masses of 792 g and 1013 g, respectively, in February prior to their departure from Argentina and they returned to the breeding grounds in North America weighing 802 g and 1087 g in April. Our results indicate that the fasting migration model does not predict the actual body masses of Swainson's Hawks during the migration season and it should be modified to account for either lower energy expenditures during migration or the possibility that the birds use a stopover strategy during migration, feeding and regaining, or maintaining, fat stores along the migration route.

Key words: *body mass,* Buteo swainsoni*, fasting, migration, Swainson's Hawk.*

Resumen. Nuevas evidencias cuestionan la hipótesis del ayuno durante la migración para el Aguilucho Langostero (*Buteo swainsoni*).— Se examinó la hipótesis del ayuno durante la migración para el Aguilucho Langostero (*Buteo swainsoni*) mediante la estimación de la longitud, la duración y la velocidad de migración entre América del Norte y del Sur, y la medición de los cambios en el peso corporal en varios momentos a lo largo del año. Se colocaron transmisores satelitales a 34 aguiluchos adultos en sus áreas de cría en el oeste de América del Norte para determinar la duración, la longitud y la velocidad de la migración. En su migración al sur, a 188 km/día, el Aguilucho Langostero tarda 51 días para completar los 13504 km hasta las áreas donde permanece durante el verano austral. A un promedio de solo 150 km/día en su migración de retorno, le toma 60 días completar los 11952 km de regreso a América del Norte. Los machos y hembras adultos de Aguilucho Langostero tuvieron un peso corporal promedio de 872 g y 1131 g, respectivamente, cuando partían de América del Norte en septiembre, y su peso corporal al arribar a Argentina promedió 759 g en los machos adultos y 933 g en las hembras adultas, indicando que pierden, en promedio, solo el 18% de su peso corporal durante la migración. En febrero, antes de su partida de Argentina, los machos y hembras adultos de Aguilucho Langostero tuvieron un peso corporal de 792 g y 1013 g, respectivamente, y llegaron a sus áreas de cría en América del Norte pesando 802 g y 1087 g, en abril. Los resultados indican que el modelo de ayuno durante la migración no predice los pesos corporales reales del Aguilucho Langostero durante la estación migratoria y que debería ser modificado para dar cuenta de menores gastos energéticos durante la migración o la posibilidad de que las aves usen una estrategia de paradas durante la migración, alimentándose e incorporando (o manteniendo) grasa a lo largo de la ruta migratoria.

Palabras clave: *Aguilucho Langostero, ayuno,* Buteo swainsoni*, migración, peso corporal.*

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Migration poses numerous behavioural and physiological challenges for birds. For most species, fat is the fuel used on migration. Prior to and during migration, birds deposit fat and then use it to meet their energy demands (Weis-Fogh 1952, Blem 1980, Ramenofsky 1990, McWilliams et al. 2004). Most warblers and shorebirds undergo rapid premigratory fattening depositing more than 50% of their body weight in fat to make long, non-stop flights over oceans, deserts, or other inhospitable areas where refuelling is difficult if not impossible (Blem 1980, Moore and Kerlinger 1987, Ramenofsky 1990, Jenni and Jenni-Eiermann 1998). However, for most species including raptors, migration is a slower, more extended process, involving a "stop and go" migration pattern with birds typically feeding en route as they encounter opportunities to eat. Using this strategy, migrants may maintain somewhat elevated levels of stored body fat, perhaps using this depot to carry them through periods of food scarcity. Nevertheless, they do not store enough premigratory fat to fuel their entire migration. This necessitates a refuelling strategy which spares their reserve energy supply and may augment their fat stores when food supplies are plentiful along the migration route (Berthold 1975).

There is very little quantitative information on how birds use stored fat during migration. Most studies that have dealt with this issue have focused on birds that use powered (flapping) flight during migration (Berger and Hart 1974, Blem 1980, Ramenofsky 1990). There is little information about fat deposition and use by falconiforms either before or during migration. However, several authors have maintained that migrating raptors take on fat deposits during migration. For example, American Kestrels (*Falco sparverius*) deposit 2–4% body fat during early autumn (Gessaman 1979) and it is well-known that Amur Falcons (*F. amurensis*) are extremely fat prior to their long migration over the Indian Ocean from India to East Africa (Ali and Ripley 1978). Western Honey-buzzards (*Pernis apivoris*) also undergo large variations in weight that are attributed to massive fat deposition prior to migration (Glutz von Blotzheim et al. 1971). Despite this, there is little information on the energy expenditure involved when birds use soaring flight in long-distance migrations.

The Swainson's Hawk (*Buteo swainsoni*) is one such long-distance, "stop and go" soaring migrant. Each year, it migrates back and forth between the plains, shrublands, steppes, and pampas of North and South America. Prior to its southward migration, it changes from a carnivore to an insectivore diet and hawks are frequently observed in flocks of hundreds of birds gorging themselves on insects such as grasshoppers (Johnson et al. 1987). As they migrate through the Mesoamerican land corridor at about 30°N latitude these small flocks coalesce into fewer, very large flocks consisting of tens of thousands of individuals. As they continue to migrate southward, the hawks are funnelled into extremely dense concentrations with an estimated 800000 hawks passing over the Isthmus of Panama during a nine-day period in late October (Bildstein, unpublished data). Some individuals drop out of the migration in Central America (Smith et al. 1986). Nevertheless, most continue their southward migration with some settling in Brazil, Uruguay, and Bolivia, but most not stopping until they reach their austral grounds in the pampas region of Argentina (England et al. 1997).

Based on the assertion that Swainson's Hawks observed roosting overnight in Panama seemed not to have cast pellets or defecated in roost trees (on the basis of a lack of "whitewash" on the forest floor below roosts), and because the species migrates in such large numbers over most of its migratory route, it has been suggested that Swainson's Hawks may complete most or all of their migration without feeding by fasting and metabolizing fat stores laid down before they depart on migration (Brown and Amadon 1968, Smith et al. 1986). Smith et al. (1986) presented a model based on estimates of the energetic cost and duration of this migration. Their model predicted that hawks would need to accumulate body fat deposits equalling about 55% of their lean body mass before migration to successfully complete the journey in either direction. Using the model's assumptions, a male Swainson's Hawk with a lean body mass of 600 g would have to store 330 g of body fat prior to migration. This model has received criticism (Kirkley 1991) and it is plagued with weaknesses because there have never been any records of premigratory weights for the Swainson's Hawk.

Table 1. Southward and northward migration tracks of satellite-tagged Swainson's Hawks.

	Southward	Northward
Number of individuals tracked	27	19
Departure dates	28 Sep–10 Oct	25 Feb–12 Mar
Arrival dates	15 Nov–30 Nov	13 Apr–10 May
Mean total migration distance (km)	13503.70	11951.63
Mean rate of migration (km/day)	188.00	149.59
Mean duration of migration (days)	51	60
Range in duration of migration (days)	46–58	43–75

Due to the lack of information on migrant Swainson's Hawks, we undertook a study to document the timing and geographic length of the Swainson's Hawk migration and the changes in its body mass prior to its departure on migration and after its arrival on their breeding and austral summer grounds. We used these body mass estimates to test the fasting migration model proposed by Smith et al. (1986) in an effort to determine if Swainson's Hawks store sufficient amounts of fat to fuel their migration without stopping to eat along the way.

METHODS

We carried out our main sampling work in two study areas. One was in the Snake River Plain of southern Idaho in North America and the other was located in the pampas region of South America in Buenos Aires Province and La Pampa Province, central Argentina. Both study areas have undergone extensive agricultural alteration and currently most of the landscape is dominated by croplands planted in row crops and plantations of exotic tree species including black locust (*Robinia pseudoacacia*) trees in Idaho and eucalyptus (*Eucalyptus* spp.) trees in Argentina.

To track the migration of hawks between the two study areas, we captured breeding female Swainson's Hawks at their nest sites throughout their North American breeding grounds and instrumented them with Microwave Electronics, Inc. satellite transmitters (PTTs). Details on trapping methods, attachment techniques, and duty cycles of PTTs can be found in Fuller et al. (1998). We used the locations obtained from PTTs to determine the length of the migration route, the duration of migration period, and the speed of migration between North and South America.

To estimate fat stores before and after migration, we captured and weighed male and female Swainson's Hawks between 1998–2001 to obtain body mass estimates for Swainson's Hawks throughout the time they were on their breeding grounds in North America and on their austral summer grounds in Argentina. We captured hawks using either bal-chatri traps with mouse lures or dho-gaza nets with Great Horned Owl (*Bubo virginianus*) lures. Captured hawks were weighed using 1000 and 2000 g Pesola scales. We also took measurements of wing chord, tail length, culmen length, tarsus length and width, and hallux length using steel rulers or calipers. Breeding adults were sexed on the basis of their behaviour at their nest sites. Juveniles and adults captured on their austral summer grounds were sexed using blood samples and PCR amplification of chromohelicase-DNA genes located on the two sex chromosomes (Griffiths et al. 1998). Blood samples were obtained from the brachial vein of captured birds using 1 ml syringes, and blood was stored in either EDTA buffer solution or 80% alcohol (Burgoyne et al. 1994).

RESULTS

We captured and attached satellite radios to 34 breeding Swainson's Hawks throughout the species' North American breeding range in nine states and provinces. From these instrumented hawks, we obtained 27 complete southward and 19 complete northward migration tracks (Table 1). All of the tracks extended between western North America and central Argentina and both the southward

Table 2. Numbers of adult and juvenile Swainson's Hawks captured in southern Idaho and Argentina.

	North America		Argentina			
	Adult Male	Adult Female	Adult Male	Juvenile Male	Adult Female	Juvenile Female
April-May	16	5				
July	10	8				
September	15	12				
December			40	29	19	10
January-February			34	46	18	29

and northward tracks followed a similar route, almost entirely inland except through southern Mexico and Central America where some of the segments of the tracks were along the coast. There were no crossings of large bodies of water. Departure dates on the southward migration varied between late September and early October, and on the northward migration departure dates varied between late February and mid-March. The mean total distance hawks migrated southward was slightly over 13500 km, compared to a mean of slightly less than 12000 km on the northward migration. Hawks migrating southward migrated at an average rate of 188 km/day, and those migrating northward averaged 150 km/day. The duration of the southward and northward migrations averaged 51 and 60 days, respectively. Arrival dates in Argentina varied between mid- to late November. Arrival dates on the North American breeding grounds varied between mid-April and early May.

We captured and obtained body mass measurements for a total of 41 adult males and 25 adult females on their North American breeding grounds in 1998 between the time of their arrival in April and May until their departure on migration in September and October (Table 2). Of these 66 individuals captured in their breeding area, 21 adults were captured shortly after their arrival at nesting areas in April and May. An additional 18 breeding adults were captured in July prior to the fledging of their young. In September, 27 adults were captured in the vicinity of their nesting areas prior to their departure on migration. In Argentina, we captured a total of 74 adult males and 37 adult females and 75 juvenile males and 39 juvenile females between the time of their arrival on and departure from their austral summer grounds. Of these 225 captured hawks in Argentina, a total of 59 adults and 39 juveniles were captured in December, whereas 52 adults and 75 juveniles were captured in January and February prior to their departure on the northward migration (Table 2). From the literature, we also obtained estimates of the body mass data for 9 adult male and 12 adult female Swainson's Hawks and 14 juvenile male and 6 juvenile female Swainson's Hawks that were captured in October from 1972–1983 in Panama, approximately midway through their southward migration (Smith et al. 1986).

Adult male and female Swainson's Hawks arrived on their breeding grounds in April and May averaging (± SD) 802 ± 54 g and 1087 ± 87 g, respectively (Fig. 1). During the breeding season, adults lost body mass and averaged only 707 ± 29 g for males and

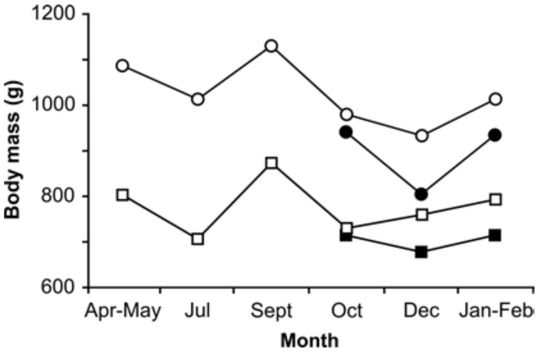

Figure 1. Annual variations in the body masses (in g) of adult (open circles) and juvenile (filled circles) female and adult (open squares) and juvenile (filled squares) male Swainson's Hawks in North, Central, and South America.

1013 ± 38 g for females in July. By September, they had regained body masses averaging 872 ± 61 g for males and 1131 ± 72 g for females. Body mass measurements reported for Swainson's Hawks in Panama (Smith et al. 1986), approximately midway through their southward migration, showed that adult male and female Swainson's Hawks had lower body masses and averaged only 730 ± 42 g, and 980 ± 134 g, respectively. Likewise, juvenile male and female Swainson's Hawks in Panama had body masses of only 715 ± 38 g and 941 ± 51 g, respectively (Smith et al. 1986). Adult hawks arriving in Argentina had slightly higher body masses for adult males which averaged 759 ± 86 g, but about 47 g lower for adult females which averaged 933 ± 61 g. Juvenile hawks arrived in Argentina with lower body masses averaging 678 ± 29 g for juvenile males and 802 ± 68 g for juvenile females. After they settled onto their austral summer grounds in Argentina both sexes gained body mass. By January and February, adult males averaged 792 ± 50 g, adult females averaged 1013 ± 70 g, juvenile males averaged 714 ± 54 g, and juvenile females averaged 932 ± 99 g (Fig. 1).

DISCUSSION

The fasting model proposed by Smith et al. (1986) is based on an assumption of a fat-free body mass of 600 g for a male Swainson's Hawk, and it assumes that males must gain 330 g of fat to fuel their 9000 km southward migration. Then, they must regain that same amount of body fat before their northward migration in March (Fig. 2). This model does not address females; therefore, we assumed a lean body mass of 800 g for a female Swainson's Hawk and assumed that they also would need to deposit at least 330 g of body fat prior to their southward and northward migrations (Fig. 3). Comparison of our body mass measurements with those of the model showed that, while both sexes and age classes underwent large losses of body mass during their migration, they did not fluctuate as much as the fasting model predicted. Both adult male and female Swainson's Hawks arrived on their breeding grounds with masses greater than those predicted. Nevertheless, prior to their departure on their southward migration, their body masses were nearly identical to those predicted by the model. Body mass measurements for adult and juvenile hawks of both sexes were also similar to those predicted by the model when the hawks were midway through their southward migration in Panama. Our measurements for adult and juvenile male Swainson's Hawks showed opposite trends for the remainder of the migration. Juvenile males lost a small amount of body mass (average of 37 g), whereas adult males gained body mass (average of 29 g) between Panama and Argentina. Both adult and juvenile females continued to lose body mass between Panama and Argentina. Nevertheless, upon their arrival in Argentina, both sexes and age classes had body masses in excess of those predicted by the model.

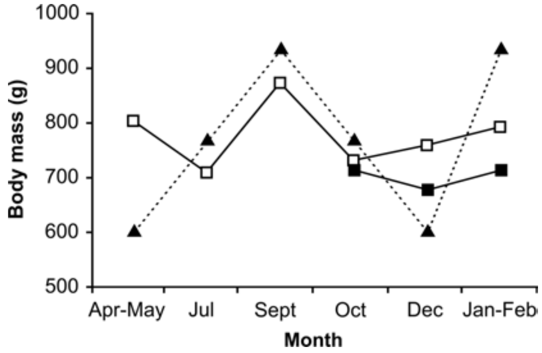

Figure 2. Comparison of annual variations in the body masses (in g) of adult (open squares) and juvenile (filled squares) male Swainson's Hawks to those predicted by the fasting migration hypothesis model (filled triangles, broken line).

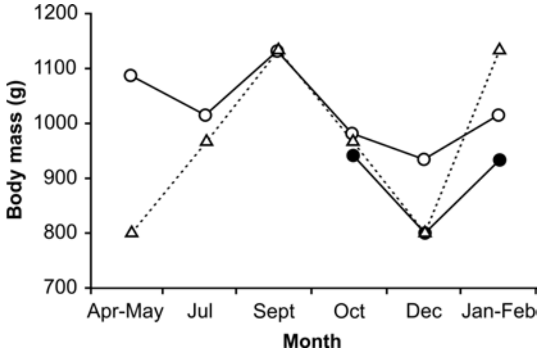

Figure 3. Comparison of annual variations in the body masses (in g) of adult (open circles) and juvenile (filled circles) female Swainson's Hawks to those predicted by the fasting migration hypothesis model (open triangles, broken line).

Our satellite telemetry data showed that Swainson's Hawks undergo a migration pattern that Berthold (1993) has described as a concentration migration. It begins on a broad front at its onset in North America and then funnels down to a narrow flight path as the southward migration moves through Mexico to the southern Gulf of Mexico. The flight path remains narrow throughout Central and South America. All of the hawks we tracked spent the austral summer in central Argentina and none went to Florida or central California where small numbers of wintering Swainson's Hawks are regularly reported. The northward migration again fans out with birds becoming more widely dispersed as they traverse Mexico and enter the southern United States. Hawks making the southward migration departed from their North American breeding grounds by early October and completed their 13 500 km journey in 51 days. For the migration north, hawks departed from their austral grounds by mid-March, migrating more slowly and completing their 11 950 km migration in 60 days. The northward migration is shorter because, unlike southward migrants which cross to the Pacific Ocean side of Central America following the coastline, northward migrants remain on the Caribbean side of Central America shortening their migration. Nevertheless, the hawks took longer to complete the migration primarily due to their slower rate of travel. In their model for fasting migration, Smith et al. (1986) assumed that between Las Cruces (New Mexico) and Argentina the length of the migration route was 9000 km and the migration took 37.5 days for completion. Because we tracked migrants the entire length of the migration route from breeding areas to austral grounds in Argentina, our estimated length for the total migration route was over 4500 km longer than the length used by Smith et al. (1986) in their model. Consequently, our estimated time for the duration of the migration was 13 days longer in autumn and 22 days longer in spring, or 35 and 59% longer, respectively, than assumed in the model.

Our body mass measurements showed that, like other migrants, Swainson's Hawks undergo large-scale annual changes in their body masses. While little is known about the size of fat deposits of diurnal raptors, it is generally assumed that sizeable changes in body masses at different times of the year represent changes mainly in the amount of stored fat (Gessaman 1979, Newton 1979, Blem 1980). Our results showed that adult male and female Swainson's Hawks gained in excess of 150 g of fat following the breeding season in preparation for their southward migration. Males departed weighing an average of 872 g and females departed weighing an average of 1131 g. Upon their arrival in Argentina in late November and early December, both sexes had lost nearly all of this fat reserve losing an average of 127 and 143 g, respectively. Adults gained body mass on the austral grounds gaining an average of only approximately 50 g of fat by January and February. Goldstein et al. (1999) found that body masses of Swainson's Hawks increased from approximately 800 g to 900 g over this same time period. Surprisingly, male and female Swainson's Hawks arrived on their breeding grounds in North America weighing 802 and 1087 g, or more than they did when they were in Argentina. Fat levels shown by juveniles of both sexes were consistently lower than those we recorded in adults. Juveniles of both sexes had sustained greater losses in body mass than adults when they arrived in Argentina. Juveniles also departed from Argentina with less body fat than adults had.

Our test of the fasting migration model indicated that the body mass fluctuations that Swainson's Hawks experienced prior to and after migration were not great enough for them to have made their migration using only stored fat. Neither adult nor juvenile male Swainson's Hawks had body masses as low as the lean body mass of 600 g that the model is based upon. Similarly, neither adult nor juvenile females had body masses as low as the 800 g lean body mass that we used as an estimate in our comparison. Both sexes arrived in North America and South America weighing more that they should have, if they conformed to the fasting model, and they all departed from Argentina weighing far less than they should have to successfully complete the northward migration using only stored fat. Clearly, the fasting model does not predict the actual body masses of this species throughout the year. The hawks do not arrive lean enough nor do they depart fat enough to accomplish their migration solely using pre-departure fat stores of sufficient magnitude as predicted by the fasting migration hypothesis.

There are several possible explanations for the failure of the fasting model to account for our body mass data. It is possible that the model is based on incorrect assumptions. The assumption that lean male Swainson's Hawks weigh 600 g seems to be too low. The leanest males we measured were captured in July in the middle of the breeding season when energy demands would have been extremely high for males. None of the males we captured had a body mass of 600 g and only one male, the lightest, weighed 655 g. Most males had body masses greater than 700 g, indicating that the estimated lean body mass of male Swainson's Hawks should be increased to about 700 g. A second questionable assumption of the fasting model is the metabolic cost of migration. The model assumes that the cost of soaring flight is twice that of basal metabolic rate (BMR). Smith et al. (1986) suggest that the value for the costs of migratory flight used in their model may vary between 1–3 times BMR. In order for the model to fit the body mass fluctuations we observed, a flight metabolism rate of 1 BMR would need to be assumed as the estimated cost of soaring flight. When we did so, the model conformed to our body mass data much more closely. This implies that migrating Swainson's Hawks would need to use far less energy for flight during their migration than has been previously considered. There are few estimates of the cost of soaring flight in large migratory raptors. The question our data raises is whether it is possible for soaring raptors to expend no more energy than they do at rest. Preliminary data on the heart rates of migrating Turkey Vultures (*Cathartes aura*) indicate that the heart rate of vultures actually falls below their resting rate (Mandel and Bildstein, unpublished data). Like Turkey Vultures, Swainson's Hawks may also experience very little added energy costs while soaring. A confounding issue is that there are no data available concerning the amount of time that Swainson's Hawks spend using flapping flight during migration. Swainson's Hawks have been observed in Chiapas (Mexico) using flapping flight in the early morning and near roosts in the evening, and during windy days, particularly when there is a head wind (Kirkley, unpublished data). While there are no good estimates of the metabolic costs of flapping flight, if it is used to any extent during the migration period, this would increase the metabolic costs of migration necessitating an adjustment in the model's estimated cost of migration. Clearly, the fasting model needs to be revised extensively in order for it to accurately reflect the trends in body mass we observed.

One puzzling aspect of our findings for the annual body mass fluctuations of Swainson's Hawks is the fact that these hawks depart from the austral summer grounds with far less fat than they should have stored and they arrive on their breeding grounds with far more fat than they should have left. One obvious possibility is that Swainson's Hawks feed during their migratory journeys. Our satellite data indicate that Swainson's Hawks remain in specific locations along the migration route for as long as one week (unpublished data). For example, some hawks remain in Texas for 10 days and some linger in Colombia for nearly one week. Flocks of Swainson's Hawks have been observed feeding on crickets and grasshoppers in Texas (Littlefield 1973) and Costa Rica (Slud 1964). Our telemetry data suggest that, during migration, flocks of hawks may settle into strategic stopover places along the route where they feed and regain fat stores. Their stopover in Texas appears to be important because it allows them to gain fat fuel to power their migration through the Mesoamerican land corridor. It may be speculated that they settle again in Central America or northern South America where they regain fat stores to fuel the remainder of the migration to Argentina. Or, perhaps, they simply feed continually while on migration. Swainson's Hawks become insectivorous during the migration season. They can potentially feed in flight on airborne insects such as dragonflies, grasshoppers, and crickets that collect in columns of rising air called thermals. We have observed flying Swainson's Hawks catching and eating what appear to be insects while migrating through Colombia (unpublished data). The implication is that Swainson's Hawks feed while soaring by eating insects that are in the same thermals they use while migrating.

While our findings argue convincingly that the fasting migration hypothesis for Swainson's Hawks is not correct, there is a need for more data to fully explain how this species successfully completes its long-distance migration each year between North and South America. Further studies are needed which document the body masses of migrating Swainson's Hawks midway through their migration. Capture of migrants in Costa Rica, Panama, and Colombia would better document our estimates of the body masses and fat stores of these birds when they are halfway through their migration. Observations of flocks at roost sites in Central America are also needed. Further documentation of opportunistic feeding and the occurrence of pellets and faeces at roost sites will enable us to ascertain if these birds do, in fact, utilize a stopover strategy to feed and maintain fat stores along the migratory route.

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USO DE ISÓTOPOS ESTABLES PARA DETERMINAR CONECTIVIDAD MIGRATORIA EN AVES: ALCANCES Y LIMITACIONES

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RESUMEN.— La necesidad de determinar la conectividad migratoria en diversas especies de aves ha generado el surgimiento de numerosas técnicas de marcado para determinar el origen geográfico de individuos. El uso de la composición de isótopos estables en tejidos animales es una de las técnicas que más se desarrollaron en los últimos tiempos. Su uso se basa, primero, en que los valores isotópicos de diferentes elementos químicos varían espacialmente debido a procesos naturales y de origen humano. Segundo, en que un individuo, al alimentarse, asimila y eventualmente refleja en sus tejidos la composición isotópica del sitio donde se está alimentando. El tejido más utilizado en este tipo de análisis es el de las plumas remeras, ya que, al crecer, asimilan la composición isotópica del alimento, y luego permanecen metabolicamente inactivas hasta el próximo evento de muda. Aunque esta técnica ha sido exitosamente aplicada en distintas especies de aves, la variabilidad observada entre individuos limita de cierta forma su precisión. Esta variabilidad puede ser producto de diferentes procesos que afectan el cambio isotópico entre la dieta y los tejidos de la especie de interés, de desplazamientos durante el periodo de muda o de variaciones en la línea de base isotópica (cambios en los valores isotópicos de hidrógeno en las precipitaciones). Conocer y entender las fuentes de error puede ayudar a diseñar mejores estudios que minimicen la variabilidad y a desarrollar mejores modelos predictivos para determinar el origen geográfico de un individuo.

PALABRAS CLAVE: *aves migratorias, deuterio, marcadores naturales, variabilidad isotópica.*

ABSTRACT. USING STABLE ISOTOPES TO DETERMINE MIGRATORY CONNECTIVITY IN BIRDS: EXTENT AND LIMITATIONS.— The need to unravel migratory connectivity in different bird species has generated the development of several techniques to determine the geographical origin of individuals. Using the stable isotopes composition of animal tissues is one of the emerging techniques that had the greatest development. The principles of the technique are, first, that there is a geographical pattern in stable isotopes values, as a result of natural and anthropogenic processes, and, second, that stable isotopes are assimilated when an organism eats, and eventually they become fixed in animal tissues, in proportions related to the natural abundance in the environment. The most commonly used tissue is from flight feathers, since they incorporate the stable isotope composition of the food and, once moult is finished, they stay metabolically inactive until they are replaced. Although this technique has been applied with success in several species, variability found within birds from the same origin limits its potential accuracy. This variability could be the result of different processes affecting the isotopic change between food and tissues of the target species, winter movements, or baseline changes through time (temporal changes in the hydrogen isotopic values in precipitation). A better understanding of the sources of error would help to design better studies in order to minimize variability and to develop better models to determine the geographic origin of individual birds.

KEY WORDS: *deuterium, isotopic variability, migratory birds, natural markers.*

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La complejidad del ciclo de vida de las aves migratorias hace evidente la necesidad de determinar la conectividad migratoria de estas especies (Webster et al. 2001). Los parámetros poblacionales de distintas especies migratorias están relacionados con la conexión entre los sitios reproductivos y no reproductivos (Myers et al. 1987, Marra et al. 1998, Sillett et al. 2000, Webster et al. 2001, Webster y Marra 2005). Sin embargo, determinar esta conexión no ha resultado fácil y la principal causa es nuestra limitada habilidad para seguir a los individuos a través de su ciclo migratorio anual (Webster y Marra 2005). Gran parte de la información obtenida hasta el momento se debe al uso de marcadores externos, como anillos numerados o de colores (Webster et al. 2001). Estos, en general, han sido exitosos para el estudio de especies cuyos individuos son fáciles de volver a observar o capturar (e.g., especies de interés cinegético, especies de distribución limitada). Sin embargo, no resultan útiles cuando la observación de individuos anillados es característicamente baja, aún cuando se realice un gran esfuerzo de marcado (Bairlein 2001, Webster et al. 2001). Este problema se observa comúnmente en especies de tamaño corporal pequeño o mediano, con distribución amplia o comportamiento esquivo, por lo que volver a observarlas es difícil. El uso de isótopos estables surge como una técnica alternativa para el estudio de la conectividad migratoria en aves (Hobson 1999, 2005a, Webster et al. 2001), intentando salvar el problema de recapturar o volver a observar individuos. Esta técnica utiliza la información química de los tejidos de individuos capturados para determinar su origen geográfico. La técnica presenta un gran potencial ya que no requiere el marcado de individuos, sino la determinación de parámetros poblacionales (e.g., los valores isotópicos promedio de la población), permitiendo pasar del uso de marcadores artificiales (i.e., anillos) al de marcadores naturales (i.e., isótopos estables).

Se pueden señalar tres motivos por los cuales los isótopos estables son buenos para determinar conectividad migratoria. En primer lugar, se encuentran naturalmente en el ambiente y su abundancia varía geográficamente debido a distintos procesos, tanto naturales como de origen humano (Rubenstein y Hobson 2004). El segundo motivo es que cuando un animal consume alimentos o agua asimila isótopos estables en las proporciones en las que estos están presentes en el ambiente, y esto se refleja en los tejidos (Fig. 1). De esta forma, todos los individuos de una especie que comparten un ambiente con características isotópicas comunes presentarán en sus tejidos una composición isotópica similar, llamada "firma isotópica del ambiente". En tercer lugar, debido a que todas las aves de un sitio comparten la misma firma isotópica, no es necesario recapturar al mismo individuo para poder inferir sobre su lugar de origen, sino que todos los individuos están naturalmente marcados. Es necesario aclarar que, en ciertos casos específicos, la firma isotópica puede variar entre individuos de una misma especie que utilizan un área común, dependiendo de la edad o el sexo (Lott et al. 2003).

Esta técnica, sin embargo, presenta algunos problemas y limitaciones. Para usar isótopos estables se debe conocer la firma isotópica de los distintos sitios de origen de la especie en estudio. Existe información a partir de la cual inferir el patrón de variación espacial para algunos isótopos a escala mundial (IAEA 2001, Bowen y Wilkinson 2002, Still et al. 2003), y estos datos son relativamente precisos en América del Norte (Hobson y Wassenaar 1997) y Europa (Hobson 2002). Pero esta información es limitada para América del Sur (Bowen et al. 2005). Además, algunos autores han encontrado una gran variabilidad en la composición isotópica de los tejidos de individuos del mismo origen (Farmer et al. 2004, Wunder et al. 2005). Estos factores, y en particular el último, reducen la posibilidad de aplicar con éxito esta técnica o la precisión al asignar muestras a los sitios de origen, dependiendo de la pregunta y la especie de interés. Por lo tanto, afirmar que esta técnica sirve o no es incorrecto (Hobson 2005a).

En este trabajo intentamos introducir al lector en el uso de isótopos estables, sus beneficios y complicaciones. Dado que este campo de la biología crece diariamente y constantemente se presentan revisiones de la técnica y nuevos trabajos, no pretendemos realizar una nueva revisión detallada, sino más bien una introducción a la técnica. Este trabajo está organizado en seis secciones. En primer lugar, presentamos las notaciones y terminologías usadas en estudios de isótopos estables. Luego resumimos brevemente el uso de isótopos estables en estudios ecológicos y, principalmente, en estudios de conectividad migratoria. A continuación resumimos los principales patrones de variación espacial de isótopos estables. En cuarto lugar presentamos información sobre las tasas de recambio de isótopos estables en distintos tejidos y las consecuencias de la elección de un tejido en particular. En la siguiente sección discutimos los supuestos del uso de isótopos estables y, finalmente, el problema de la variación en la composición isotópica entre individuos de un mismo origen.

ISÓTOPOS ESTABLES: NOTACIÓN Y FRACCIONAMIENTO

Los isótopos estables son medidos en una relación entre la abundancia del isótopo estable raro, más pesado, y la del isótopo estable común, más liviano. Los isótopos estables que generalmente se utilizan en estudios de conectividad migratoria y otros estudios ecológicos son los de hidrógeno o deuterio ($^2H/^1H$ o $D/^1H$), carbono ($^{13}C/^{12}C$), nitrógeno ($^{15}N/^{13}N$), oxígeno ($^{18}O/^{16}O$) y azufre ($^{34}S/^{32}S$). Estos cocientes son a su vez comparados con la relación de estos isótopos en un estándar internacional, presentándose finalmente un valor en notación delta (δ),

$$\delta X = [(R_{muestra} / R_{estandar}) - 1] * 1000,$$

donde X es el isótopo de interés y R es la proporción de átomos del isótopo pesado en relación al isótopo liviano. De esta forma, valores de δX positivos implican que la muestra está enriquecida en el isótopo más pesado en relación con el estándar y valores negativos implican que está empobrecida. Esta notación permite comparar resultados de análisis realizados en distintos momentos y laboratorios. No obstante, esto no es posible para el deuterio, ya que los tejidos presentan un porcentaje de hidrogeno que puede ser intercambiado con la humedad ambiental (Wassenaar y Hobson 2003). Variaciones en la humedad ambiental entre estaciones del año y entre distintos laboratorios impiden realizar comparaciones (Hobson 2005a).

Cuando un organismo consume recursos del ambiente, los isótopos estables son asimilados en sus tejidos de acuerdo a la proporción en que se hallan en estos recursos, aunque con cierta diferencia debida a distintos procesos metabólicos. Esta diferencia se conoce como fraccionamiento isotópico y se expresa en la siguiente ecuación:

$$\delta X_t = \delta X_d + \delta \Delta_{dt},$$

donde t es el tejido de interés, d la dieta y Δ_{dt} el fraccionamiento entre la dieta y el tejido (Hobson 2005a). Este valor de fraccionamiento puede variar entre especies, tejidos (Hobson y Clark 1992) y en distintas condiciones ambientales (Hobson et al. 1993). Sin embargo, debido a que el valor final de un isótopo estable es la suma de numerosos eventos de consumo de alimento (Hobson 1999), puede determinarse un valor promedio de fraccionamiento. Por ejemplo, hay un patrón constante

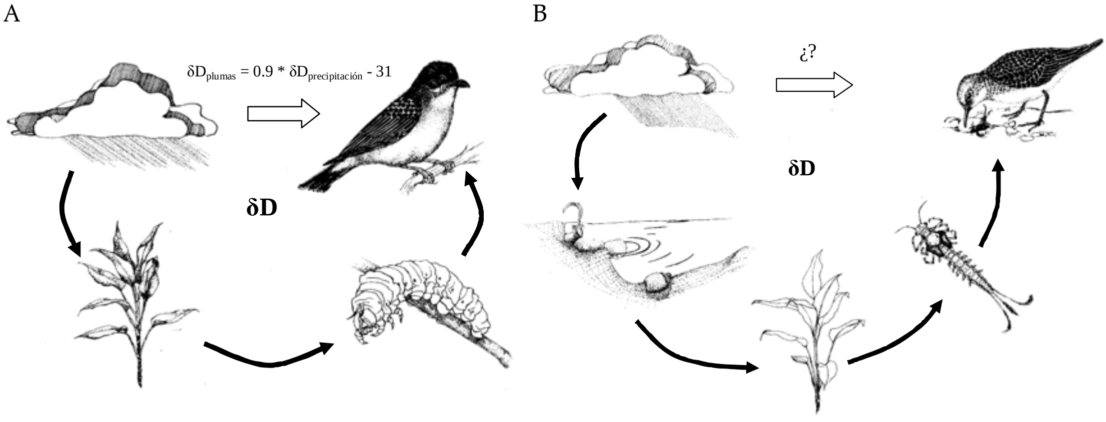

Figura 1. Esquema del camino de los isótopos estables desde procesos productores de variación espacial hasta las plumas de las aves, ejemplificado con el deuterio. En especies terrestres la cadena más simple incluye cuatro eslabones (A), mientras que para especies acuáticas comprende cinco eslabones (B). Cada uno de los pasos produce un fraccionamiento entre el valor inicial y el valor final (flechas sólidas). En la figura se utiliza como ejemplo del valor del fraccionamiento entre precipitaciones y plumas (flechas vacías) a la función para passeriformes de América del Norte (Hobson y Wassenaar 1997, Wassenaar y Hobson 2000). No es claro si puede desarrollarse una función para las aves acuáticas.

entre el valor de deuterio en las precipitaciones de una determinada localidad y el existente en las plumas de pájaros capturados en esa localidad (Hobson y Wassenaar 1997); para América del Norte este valor promedio ha sido estimado entre -5‰ y -25‰ (Wassenaar y Hobson 2000, Lott y Smith 2006). Igualmente, se ha determinado que el valor de fraccionamiento de $\delta^{15}N$ es de aproximadamente 2‰, lo que resulta de gran utilidad en estudios de dieta y de cadenas tróficas (DeNiro y Epstein 1981, Hobson 1999).

PATRONES NATURALES DE VARIACIÓN ESPACIAL

Los isótopos estables son buenos marcadores naturales ya que presentan patrones naturales de variación espacial (Webster et al. 2001, Rubenstein y Hobson 2004). Debido a esta variación podemos distinguir entre muestras de diferentes orígenes geográficos. Por ejemplo, Farmer et al. (2004) encontraron que chorlos provenientes de localidades relativamente cercanas, como Río Grande en Tierra del Fuego, Laguna Nimez en Santa Cruz y Bahía Lomas en Chile, presentan en sus plumas valores isotópicos de C, N y S claramente diferentes. Basados en estas diferencias, Atkinson et al. (2005) calcularon que de los individuos de Playero Rojizo (*Calidris canutus*) que paran en la Bahía Delaware en su migración a los sitios reproductivos, el 58% presenta valores isotópicos similares a los de Bahía Lomas, mientras que solo el 6% presenta valores isotópicos similares a los de Río Grande.

El deuterio y el oxígeno presentan el patrón de variación que ha resultado más útil para estudios de conectividad migratoria (Hobson 2005b). Este patrón fue determinado a partir de los valores isotópicos en las precipitaciones, basándose en información de la Asociación Internacional de Energía Atómica, de su programa Cadena Global de Isótopos en Precipitación (IAEA 2001). Existe un claro empobrecimiento en deuterio y ^{18}O desde los trópicos a los polos y con la altitud (Daansgard 1964, Poage y Chamberlain 2001, Bowen y Wilkinson 2002). Mapas de la variación espacial de los valores de δD y $\delta^{18}O$ en las precipitaciones han sido desarrollados para prácticamente todos los continentes, incluyendo América del Sur (Bowen et al. 2005). Meehan et al. (2004) han desarrollado un mapa alternativo para los valores de δD en las precipitaciones considerando los efectos de la altitud. Estos mapas son de clara utilidad para el estudio de migración, principalmente en América del Norte y Europa donde se ha demostrado que los valores de δD en las precipitaciones y en las plumas están relacionados (Hobson y Wassenaar 1997, Meehan et al. 2004, Hobson 2005b).

El carbono muestra diferencias geográficas importantes a escala mundial producto de la distribución de plantas C3 y C4. De acuerdo a su proceso fotosintético, las plantas fijan distintas cantidades de ^{13}C, produciendo valores fácilmente distinguibles: las plantas C3 producen tejidos empobrecidos en ^{13}C con relación a plantas C4 o CAM (Guy et al. 1993, Lajtha y Marshall 1994). Adicionalmente, existen variaciones en los valores de ^{13}C debido a características ambientales asociadas a la cantidad de agua disponible (Lajtha y Marshall 1994). Así, en ambientes más secos las plantas producen tejidos enriquecidos en ^{13}C comparado con los valores isotópicos en ambientes más húmedos (Rubenstein y Hobson 2004). Por ahora no existen mapas de variación espacial de los valores de $\delta^{13}C$; sin embargo, hay mapas disponibles que presentan las proporciones entre plantas C3 y C4 (Still et al. 2003), permitiendo determinar regiones potencialmente diferentes con relación a los valores de $\delta^{13}C$ (Hobson 2005a). Estos patrones geográficos presentan relativamente poca estabilidad debido a la producción agrícola, que reemplaza la vegetación natural (Wassenaar y Hobson 2000).

El ^{15}N presenta un patrón de variación menos claro, determinado principalmente por la humedad de los ambientes. Los ambientes más secos presentan valores más altos de $\delta^{15}N$ que los más húmedos (Handly et al. 1999, Rubenstein y Hobson 2004). Los valores de $\delta^{15}N$ en el ambiente están notablemente modificados por el uso de fertilizantes nitrogenados en la agricultura y por su transporte en los cursos de agua. Por ejemplo, patos residentes en humedales afectados por procesos agrícolas presentan valores de $\delta^{15}N$ en sus plumas más altos que los patos de ambientes naturales (Hebert y Wassenaar 2001).

Los valores de $\delta^{34}S$ presentan principalmente diferencias entre ambientes marinos y terrestres (Rubenstein y Hobson 2004). En general, los ambientes terrestres con influencia marina están enriquecidos en ^{34}S comparado a los ambientes sin influencia marina. Lott et al. (2003), analizando plumas, utilizaron las diferencias en los valores de $\delta^{34}S$ entre ambientes marinos y terrestres para diferenciar rapaces que se alimentan sobre la base de una cadena trófica con origen marino, de aquellos que se alimentan principalmente de una cadena trófica terrestre.

Otro elemento cuyos isótopos estables pueden ser de utilidad para estudios de conectividad migratoria es el estroncio. Este varía espacialmente correlacionado con características geológicas. Suelos más nuevos están empobrecidos en ^{87}Sr comparados con suelos viejos (Rubenstein y Hobson 2004). El ^{87}Sr es usado comúnmente en estudios de migración en peces (Thorrold et al. 2001, Elsdon y Gillanders 2003).

TEJIDOS Y TASAS METABÓLICAS

Uno de los factores más importantes para el éxito de un estudio de conectividad migratoria en el que se usan isótopos estables es la elección del tejido a utilizar. Distintos tejidos presentan diferentes tasas metabólicas, por lo que reflejan los valores isotópicos del alimento ingerido en distintos lapsos temporales (Hobson 2005a). El hígado y el plasma sanguíneo tienen una tasa de recambio muy alta, reflejando la composición isotópica del alimento ingerido en los últimos días, mientras que las células sanguíneas o los músculos presentan una tasa de recambio más lenta y reflejan los valores isotópicos de los alimentos ingeridos en los últimos meses.

El tejido más usado para determinar la conectividad migratoria en aves son las plumas. La ventaja de éstas es que son metabólicamente inactivas una vez que terminó su crecimiento, conservando la firma isotópica de la localidad donde crecieron hasta el siguiente evento de muda. Esto supone que las aves no utilizan reservas endógenas para la formación de las plumas (Murphy 1996), lo cual está respaldado por estudios de laboratorio en los que se observó que cambios en la dieta producen cambios consecuentes en los valores isotópicos de las plumas (Bearhop et al. 2002). Una desventaja es el desconocimiento de los ciclos de muda de muchas especies migratorias (Hobson 2005a). Conocer el área donde la especie en estudio muda es fundamental, ya que áreas distantes como América del Sur y del Norte presentan valores similares en algunos isótopos. Sin embargo, el uso de plumas presenta la ventaja de ser un método no destructivo de muestreo y, al permanecer metabólicamente inactivo, permitiría usar ejemplares de museo para determinar valores isotópicos en distintas localidades (Lott et al. 2003).

Otro tejido comúnmente utilizado para determinar movimientos migratorios es el sanguíneo. Los tejidos metabólicamente activos brindan información sobre un periodo de tiempo anterior al evento de muestreo que depende de la tasa de recambio isotópico del tejido. La tasa de recambio de la sangre ha sido determinada para distintas especies en condiciones de laboratorio (Hobson y Clark 1992, Bearhop et al. 2002, Hobson y Bairlein 2003, Evans-Oegen et al. 2004). Pero las condiciones de laboratorio raramente simulan las que enfrentan los individuos durante las migraciones (Bearhop et al. 2002, Hobson 2005b). No obstante, ciertos estudios de laboratorio sugieren que la tasa de recambio isotópico de la sangre podría no estar afectada por la actividad física (Hobson 2005a). Individuos de Gorrión (*Passer domesticus*) mantenidos a 5 °C presentan diferencias en la tasa metabólica con aquellos mantenidos a 22 °C, pero esto no se refleja en la tasa de recambio isotópico de ^{13}C y ^{15}N (Carleton y Martinez del Rio 2005). Esto sugiere que los estudios de laboratorio que determinaron la tasa de recambio isotópico en sangre podrían ser utilizados para animales silvestres.

EL USO DE ISÓTOPOS ESTABLES EN ECOLOGÍA Y CONECTIVIDAD MIGRATORIA

Los isótopos estables han sido usados ampliamente como marcadores naturales en diversos estudios ecológicos y su uso se incrementó a partir de la década de 1970. Su utilidad radica en que el agua o los nutrientes de distintos orígenes presentan diferentes valores isotópicos y, al ser asimilados por plantas o animales, mantienen estas diferencias. Por ejemplo, el agua subterránea y la de las precipitaciones en general difieren en los valores de deuterio, por lo que es posible determinar, analizando la composición isotópica de la savia de una planta, si está consumiendo agua de lluvia o subterránea (White 1989). Así, es potencialmente posible analizar los isótopos estables en los tejidos de un individuo y rastrear su origen a través de la cadena trófica. El lector interesado en otras aplicaciones de isótopos estables en estudios ecológicos puede consultar los trabajos de Rundel et al. (1989) y Lajtha y Michener (1994).

La utilización de los isótopos en estudios de migración tiene su origen en los trabajos de Hobson y Wassenaar (1997), Marra et al. (1998) y Chamberlain et al. (1997), a fines de la década de 1990, y recientemente el número de publicaciones sobre el tema se ha incrementado exponencialmente (Hobson 2005a). Sin embargo, la idea de utilizar marcadores químicos para el estudio de movimientos estacionales en aves se remonta a los trabajos de Kelsall, quien utilizó la composición química de las plumas como marcadores (Kelsall 1970, Kelsall y Calapric 1972, Kelsall y Burton 1977).

El principio del uso de isótopos estables para determinar conectividad migratoria es simple. Al ingerir alimentos, un individuo está asimilando las características isotópicas del ambiente donde se está alimentando, las cuales se verán reflejada en sus tejidos. Como la composición isotópica del ambiente varía espacialmente, cuando un individuo se desplaza de una localidad A a una nueva localidad B, la cual difiere isotópicamente de la primera, sus tejidos reflejarán la composición isotópica de A (i.e., su localidad de origen) por un periodo de tiempo que depende de la tasa metabólica del tejido analizado. Así, al capturar a este individuo en B podemos inferir si es residente en B o proviene de otra localidad, en este caso A, en base a los valores isotópicos en sus tejidos.

Numerosos trabajos han tenido éxito al relacionar hábitats o localidades reproductivas y de invernada en distintas especies. Por ejemplo, Marra et al. (1998), analizando los valores isotópicos del carbono en sangre y músculo pectoral, relacionaron la fecha de arribo a los sitios reproductivos con la calidad del hábitat de los sitios invernales de *Setophaga ruticilla*. Los primeros individuos en arribar presentaron valores isotópicos de carbono relacionados a bosques húmedos, considerados de mejor calidad para la especie, mientras que los últimos en arribar mostraron valores asociados a arbustales secundarios, que representan un hábitat pobre. Rubenstein et al. (2002) determinaron la conectividad migratoria de *Dendroica caerulescens*, la cual se reproduce en el este de América del Norte y migra en invierno a las islas del Caribe. Utilizando isótopos de hidrógeno y carbono en plumas, estos autores demostraron que las poblaciones que nidifican en el norte de su área de distribución pasan el invierno en las islas del oeste, mientras las que se reproducen en el sur migran a las islas del este del Caribe.

SUPUESTOS EN EL USO DE ISÓTOPOS ESTABLES PARA DETERMINAR CONECTIVIDAD MIGRATORIA

La técnica requiere primero determinar la firma isotópica de las localidades donde el tejido de interés permanece metabólicamente activo (i.e., crece y asimila isótopos estables), para luego poder relacionar con esta localidad a un individuo capturado en otra sobre la base de su composición isotópica. Existen dos aproximaciones a este problema. Una es determinando la firma isotópica de la localidad de interés de forma directa, midiendo en cada sitio los valores isotópicos en plumas de la especie de interés. La segunda, propuesta por Hobson y Wassenaar (1997), es inferir la firma isotópica a partir de mapas de variación espacial de los isótopos estables, como por ejemplo los mapas de variación del deuterio y ^{18}O en las precipitaciones (Bowen et al. 2005). Ambos métodos presentan problemas y ventajas en su aplicación, y la elección de uno u otro depende de la especie en estudio y de su área de distribución.

Indudablemente, medir la firma isotópica en plumas en los sitios donde el tejido está metabólicamente activo es el método más preciso para determinar el origen de especies migratorias. Sin embargo, como raramente es posible hacer un muestreo de toda el área de distribución de una especie, se infieren por intrapolación los valores isotópicos esperados en los sitios no muestreados usando una regresión inversa (Kelly et al. 2002, Rubenstein et al. 2002, Torres Dowdall 2005, Wunder et al. 2005). En general, este método ha producido resultados poco precisos (Wunder et al. 2005). Por eso, hasta el momento, considerar el espacio como discreto parece ser la mejor aproximación a la técnica (Royle y Rubenstein 2004). Mas aún, Royle y Rubestein (2004) y Wunder et al. (2005) mostraron que el uso de métodos estadísticos bayesianos y de probabilidades condicionadas, basados en información previa de las abundancias relativas de los individuos en cada sitio y el conocimiento de los valores isotópicos esperados, mejora la calidad predictiva de la técnica.

La segunda posibilidad consiste en inferir los valores isotópicos de los sitios de interés a partir del uso de mapas de variabilidad isotópicas (ver *Patrones naturales de variación espacial*). Esta aproximación es propuesta por Hobson y Wassenaar (1997) a partir de la determinación de una relación constante entre los valores de δD en las precipitaciones y en las plumas de distintas especies de paseriformes (Hobson y Wassenaar 1997, Wassenaar y Hobson 2000). Básicamente, consiste en determinar el valor de δD en las plumas de un individuo de origen no conocido, utilizar una función para relacionar el valor de deuterio en las plumas con el valor en las precipitaciones (e.g., $\delta D_{\text{plumas}} = 0.9 * \delta D_{\text{precipitaciones}} - 31$; Hobson y Wassenaar 1997) y asignar al individuo muestreado a la región donde la especie muda que presente este valor de δD en las precipitaciones. Esto podría describirse como el uso de un "atajo", ya que no se conocen los valores de deuterio en las plumas en los sitios de muda, sino que se los infiere a partir de los valores promedios de deuterio en las precipitaciones (Fig. 1).

Para el deuterio, la relación entre los valores de $\delta D_{\text{precipitaciones}}$ y δD_{plumas} fue demostrada en algunas especies de paseriformes en América del Norte (Hobson y Wassenaar 1997, Wassenaar y Hobson 2000) y Europa (Hobson et al. 2004b, Bowen et al. 2005), y en aves rapaces (Lott y Smith 2006). Sin embargo, este es un valor promedio; por lo tanto, el fraccionamiento en individuos puede alejarse más o menos de lo esperado. Además, las diferencias en las funciones entre los paseriformes en América del Norte y en Europa (Bowen et al. 2005) y entre éstas y la función para rapaces (Lott y Smith 2006) sugieren que quizás no sea recomendable aplicarlas a otros grupos de aves o en otros continentes. Sin embargo, hasta desarrollar funciones que relacionen los valores de deuterio en plumas y precipitaciones, las funciones ya desarrolladas pueden ser usadas si se consideran ciertas limitaciones. Por ejemplo, este valor no es constante para rapaces en distintas localidades de América del Norte (Lott y Smith 2006). Además, es posible que este valor no sea aplicable a especies cuya dieta tiene una base de organismos acuáticos (Hobson 2005a), ya que el deuterio sigue un camino diferente dependiendo si la especie de interés es terrestre o acuática (Fig. 1). En aves acuáticas, el camino del deuterio hasta el individuo es más largo, ya que cuenta con la acumulación de agua en los humedales. Esta es una diferencia importante, ya que la entrada (e.g., precipitaciones, aportes fluviales) y salida (e.g., evaporación) van a regular el valor isotópico del humedal (Fig. 1b). A pesar de que se ha encontrado cierta relación entre los valores isotópicos en precipitaciones y en humedales, en general no existe tal relación para grandes sistemas hídricos (Kendall y Coplen 2001). En concordancia con esto, análisis de deuterio en plumas de chorlos no mostraron relación alguna ni con el valor de deuterio en las precipitaciones ni con el valor en los cuerpos de agua (Torres Dowdall 2005). Mapas de variación de los valores de deuterio en plumas de chorlos en Argentina muestran un patrón diferente al esperado a partir de mapas de precipitaciones, con un enriquecimiento en deuterio en el centro del país y valores más bajos al norte y al sur (datos no publicados).

Un problema importante es que el uso de mapas de deuterio en las precipitaciones ignora la varianza temporal y espacial en el fraccionamiento del deuterio desde las precipitaciones hasta el individuo (Wunder et al. 2005). Aunque existen diferencias en el camino del deuterio desde las precipitaciones hasta las plumas entre aves acuáticas y terrestres (Fig. 1), en esta discusión se va a considerar la cadena terrestre, ya que es más simple. En una cadena terrestre sencilla, con tres eslabones (i.e., productor, herbívoro, carnívoro; Fig. 1a), se observa que hay cuatro pasos que pueden afectar el valor final de deuterio en las plumas de un individuo. Por lo tanto, el uso de un "atajo" desde el valor de deuterio en las precipitaciones y el valor de deuterio en las plumas presenta, al menos, los siguientes supuestos implícitos: (1) no hay variación temporal de los valores de δD en las precipitaciones, (2) los productores primarios asimilan exclusivamente agua de lluvia, (3) tanto los consumidores primarios como los secundarios presentan una dieta estable, y (4) no existen factores que afecten los valores de fraccionamiento isotópico ni en los consumidores primarios ni en los secundarios.

Los mapas de variación isotópica presentan un valor promedio de δD en las precipitaciones para una determinada región en la época de crecimiento (i.e., primavera-verano) (Hobson 2005a). Sin embargo, el valor de deuterio en las precipitaciones puede ser altamente variable entre años (Farmer et al. 2003), afectando la precisión en las predicciones del lugar de origen de un individuo. Por ejemplo, en Buenos Aires, los valores de δD en las precipitaciones puede variar notablemente entre años, abarcando gran parte del rango de variación de deuterio en Argentina (Farmer et al. 2003). Hobson (2005a) aclara al respecto que no podemos esperar que los valores de deuterio en plumas en una localidad dada sean iguales a los valores inferidos a partir del deuterio en las precipitaciones, ya que los valores en los mapas isotópicos de deuterio son un promedio obtenido a partir de cuarenta años de registro de la Asociación Internacional de Energía Atómica (IAEA 2001). Por lo tanto, es probable que, en un año particular, los valores de δD se alejen más o menos de este promedio. Por esto, debe considerarse este valor como una guía, pero de ser posible es recomendable calibrar los datos con plumas colectadas en los sitios de interés.

La técnica también supone que los productores primarios asimilan principalmente agua de lluvia. No obstante, el grado con que las plantas asimilan agua de lluvia depende del grado en que el agua es disponible de otras fuentes (White 1989). En sitios áridos, donde el agua es limitante, el agua asimilada por las plantas proviene en general de las precipitaciones, y esto es reflejado en los valores isotópicos en la savia de las plantas (White 1989). A medida que otras fuentes de agua están disponibles, los valores de δD en plantas se relacionan pobremente con los valores en las precipitaciones (White 1989). Esto puede afectar notablemente el patrón de variación espacial del deuterio en plantas, produciendo valores diferentes a aquellos inferidos a partir de las precipitaciones.

Otro supuesto clave es que los herbívoros presentan un valor característico del sitio. Esto es, que se alientan en proporciones que reflejan la proporción de plantas C3 y C4 en el ambiente. Esto es importante, ya que los valores de los isótopos estables en plantas, principalmente los valores de δD y $\delta^{13}C$, dependen del proceso fotosintético (Ehleringer y Rundel 1989, Ziegel 1989). De esta forma, el valor final de la proporción en los tejidos de un organismo de interés depende de la proporción de plantas C3 y C4 de las que se alimenta (Gannes et al. 1997). Esto es igualmente válido para carnívoros, ya que las especies especialistas reflejarán el valor isotópico de sus presas, pero las generalistas mostrarán valores promedio y una gran variabilidad entre individuos (Bearhop et al. 2004, Matthews y Mazumder 2004). Hobson (2005a) señala que la cantidad de deuterio en un determinado tejido representa numerosos eventos de alimentación; por esto, a pesar de la variación espacial o temporal, el valor isotópico final representa un valor promedio.

Al usar un "atajo" entre las precipitaciones y las plumas para determinar el origen geográfico de un individuo usando isótopos estables, el supuesto de que no hay factores que afecten el fraccionamiento (ver más arriba) entre el alimento y los tejidos de un organismo dado es el más débil. Numerosos trabajos realizados en laboratorio con diferentes especies sugieren que hay diversos factores que afectan el valor isotópico final en tejidos animales. Experimentos en cuervos demostraron que una especie puede presentar valores de fraccionamiento diferentes dependiendo del tipo de alimento (Hobson y Clark 1992). Trabajos en perdices sugieren que el fraccionamiento también es afectado por la cantidad de alimento. Individuos con acceso limitado al alimento presentan valores más altos de $\delta^{15}N$ que aquellos con acceso ilimitado al alimento (Hobson et al. 1993). Resultados similares se encontraron en peces, donde la calidad y la cantidad de alimento suministrado afectaron los valores de $\delta^{13}C$ y $\delta^{15}N$ (Gaye-Siessegger et al. 2003). Por el contrario, la temperatura ambiental no afectó los valores de $\delta^{13}C$ y $\delta^{15}N$ en un estudio realizado en gorriones (*Passer domesticus*) (Carleton y Martinez del Rio 2005).

VARIABILIDAD ISOTÓPICA

Al ser violados los supuestos discutidos en la sección anterior disminuye la precisión con la cual es posible determinar el origen geográfico de una muestra usando isótopos estables, ya que se incrementa la variabilidad de la firma isotópica en los sitios de origen. Esta variabilidad se ve reflejada en distintos trabajos en diferentes especies. Sin embargo, este tema ha sido explícitamente tratado en pocos trabajos, principalmente en aves playeras (Farmer et al. 2004, Wunder et al. 2005) y rapaces (Lott et al. 2003). Sin embargo, la variabilidad máxima encontrada en estos trabajos no es mayor a la encontrada en otros trabajos que no consideran el problema explícitamente (Farmer et al. 2003, 2004, Torres Dowdall 2005). Bowen et al. (2005) tratan explícitamente el problema de la variabilidad incorporando en los intervalos de confianza de las predicciones de origen distintos factores productores de variabilidad. Como resultado, la precisión de la determinación del origen de paseriformes, tanto en América del Norte como Europa, es limitada (e.g., Fig. 9 en Bowen et al. 2005).

Comparando los valores isotópicos de H, C, N, O y S en plumas de chorlos en tres sitios en el noroeste argentino, Torres Dowdall (2005) encontró diferencias significativas entre dos años consecutivos en al menos un isótopo estable en los tres sitios. Wunder et al. (2005), analizando isótopos de H, C y N en plumas de *Charadrius montanus* encontró gran variabilidad entre individuos en un mismo sitio, afectando significativamente la calidad predictiva de los modelos que desarrollaron. Los valores de deuterio en plumas de individuos adultos de *Catharus bicknelli* en un sitio del este de Canadá presentaban un rango de -114.8‰ a -51.6‰ (Hobson et al. 2004a), mientras que el rango esperado de δD en precipitación para este sitio en particular es mucho menor (-79‰ a -60‰; Meehan et al. 2004). Estos ejemplos sugieren que la variabilidad, a pesar de que no sea considerada explícitamente en muchos estudios, es un factor determinante en el uso de isótopos estables para determinar conectividad migratoria. Por esto el estudio de las causas de la variabilidad y el análisis de los supuestos de la técnica requieren mayor atención.

En primer lugar, es necesario determinar si hay especies que presentan naturalmente mayor variabilidad que otras. Es esperable que especies con dietas especializadas presenten menor variabilidad en la firma isotópica que aquellas oportunistas o generalistas. Esto que parece obvio es, sin embargo, de relevancia en la aplicación de la técnica. Si existen especies naturalmente más variables que otras, esto significa que el uso de isótopos estables será más útil en algunas especies que en otras. Por lo tanto, no se puede afirmar que la técnica sirve o no sirve para estudiar migraciones, sino más bien que la técnica es útil o no para una especie determinada (Hobson 2005a). En este sentido, también es necesario entender la historia natural de la especie de interés y resulta imprescindible conocer los ciclos de muda. Muchas especies mudan las plumas de vuelo en los sitios reproductivos antes de migrar, otras lo hacen una vez que han llegado a los sitios de invernada, mientras que otras presentan patrones intermedios con mudas suspendidas o mudas en sitios de parada durante las migraciones. De esta forma, la información isotópica en las plumas refleja sitios diferentes de acuerdo al patrón de muda.

En segundo lugar, un punto importante en especies que mudan en sitios no reproductivos es determinar si realizan movimientos invernales, es decir, si permanecen toda la temporada no reproductiva en un sitio especifico o realizan desplazamientos entre diferentes sitios (Farmer et al. 2004, Torres Dowdall 2005). Si un individuo permanece en un mismo sitio toda la temporada se espera que todas sus plumas de vuelo presenten valores isotópicos similares (i.e., baja variabilidad entre plumas) y que estos valores reflejen la firma isotópica del sitio de muda. Por el contrario, si un individuo se desplaza durante el periodo de muda, la variabilidad entre plumas será alta y cada pluma reflejará la firma isotópica de distintos lugares. Entonces no existe un único sino múltiples sitios de origen, y la determinación dependerá de la pluma que se analice. Análisis de alas completas de chorlos neárticos sugieren que al menos algunos individuos se desplazan durante el periodo de muda (Farmer et al. 2003). Esta variabilidad dificulta la caracterización de sitios no reproductivos basada en la firma isotópica y, por los tanto, reduce la precisión de la técnica, aunque brinda información sobre los posibles desplazamientos invernales.

Es necesario continuar los experimentos de laboratorio para poner a prueba los supuestos de la técnica (Gannes et al. 1997). Este es un campo de investigación que está creciendo rápidamente y las publicaciones sobre experimentos con isótopos estables son frecuentes. Por esto, es de esperar que nuevos estudios ayuden a entender la variabilidad observada en algunas especies (Farmer et al. 2004, Torres Dowdall 2005, Wunder et al. 2005).

Entender cuáles factores afectan la firma isotópica de cada especie, produciendo variabilidad entre individuos en un mismo sitio, ayudará a mejorar los modelos predictivos.

Conclusiones

El uso de isótopos estables presenta un gran potencial para responder preguntas de conectividad migratoria que no eran abordables usando técnicas más tradicionales. Indudablemente, su aplicación en el estudio de especies migratorias aportará valiosa información para mejorar los criterios de conservación y manejo, y mejorará nuestro conocimiento sobre la biología y ecología de estas especies. Sin embargo, el uso de isótopos estables es una técnica relativamente nueva y, a medida que se realicen nuevos estudios, se podrá determinar más claramente sus límites y alcances. Por esto, se presentaron aquí algunos de los problemas con el uso de isótopos estables para determinar conectividad migratoria, en la creencia que entender los límites y problemas de una técnica ayuda a diseñar mejores estudios y a interpretar mejor los datos. Al mismo tiempo, conocer previamente estas limitaciones puede ayudar a predecir en qué especies o ecosistemas el uso de isótopos estable puede ser más útil y en cuáles puede ser más limitado. Las especies especialistas presentan más potencial que las generalistas para el uso de isótopos estables. Igualmente, especies que utilizan diferentes ambientes van a presentar mayor diferenciación en los valores isotópicos y por ende mayor posibilidad de éxito en el estudio de migraciones. Finalmente, la elección del tejido a ser analizado va a depender principalmente de la pregunta del investigador. Para estudiar conectividad migratoria en aves, las plumas parecen ser la mejor aproximación. Para desplazamientos de corta distancia, la sangre puede ser más conveniente.

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ROOSTS AND MIGRATIONS OF SWALLOWS

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ABSTRACT.— Swallows of the north temperate zone display a wide variety of territorial behaviour during the breeding season, but as soon as breeding is over, they all appear to adopt a pattern of independent diurnal foraging interleaved with aggregation every night in dense roosts. Swallows generally migrate during the day, feeding on the wing. On many stretches of their annual journeys, their migrations can thus be seen as the simple spatial translation of nocturnal roost sites with foraging routes straightening out to connect them. However, swallows that must make long journeys over ecological barriers clearly fly at night as well as in the day, and many suggestions indicate that there is considerable complexity in the altitude and bearing of flights even during the day. There are especially intriguing indications that much swallow migration may take place high out of sight of ground observers with movements near the ground often associated with foraging in passage. Provided that roost sites can be reliably found, swallow migration can be extremely flexible, and there are interesting contrasts in the biogeography and phenological flexibility of swallows compared to other passerine birds. Even within the swallows, there is considerable interspecific and intraspecifc variability in the distances of their annual migrations, and we are only just beginning to understand the biological causes and consequences of this variation. The profusion of Doppler weather radar stations in the eastern United States has allowed the characterization in considerable detail of the North American distributions of Tree Swallows (*Tachycineta bicolor*) and Purple Martins (*Progne subis*) throughout the non-breeding season. Evaluating the relative roles of movements and mortality in creating these patterns remains an important challenge for further research.

KEY WORDS: *diurnal, Hirundinidae, martins, migration, nocturnal, roost, swallows.*

RESUMEN. DORMIDEROS Y MIGRACIONES DE GOLONDRINAS.— Las golondrinas de la zona templada de América del Norte poseen una amplia variedad de comportamientos territoriales durante la estación de cría, pero ni bien culmina la reproducción todas parecen adoptar un patrón común, alternando la alimentación diurna independiente con el agrupamiento en populosos dormideros durante la noche. Las golondrinas generalmente migran durante el día, alimentándose en vuelo; sus migraciones, entonces, pueden ser vistas como si fuesen un simple traslado entre distintos sitios que poseen dormideros nocturnos, con las rutas de alimentación conectándolos directamente. Sin embargo, las golondrinas que deben realizar largos viajes cruzando barreras ecológicas vuelan tanto de noche como de día, y hay evidencias que indican que hay una considerable complejidad en la altitud y en las características de los vuelos aún durante el día. Hay evidencias especialmente interesantes de que la mayor parte de la migración de las golondrinas puede tener lugar a una altura tal que no es advertida por los observadores en tierra, pero con movimientos cercanos al suelo a menudo asociados con la alimentación. Si los sitios con dormideros pueden ser encontrados con certeza, la migración de las golondrinas sería extremadamente flexible, y existen interesantes contrastes en la biogeografía y la flexibilidad de la fenología de las golondrinas en comparación con otros paseriformes. Entre las golondrinas mismas hay una considerable variabilidad inter e intraespecífica en la distancia de migración anual, y estamos aún empezando a entender las causas y las consecuencias biológicas de esta variación. La creciente disponibilidad de estaciones con radares climatológicos Doppler en el este de Estados Unidos ha permitido la caracterización, con un considerable detalle, de las distribuciones norteamericanas de la Golondrina Bicolor (*Tachycineta bicolor*) y la Golondrina Purpúrea (*Progne subis*) durante la estación no reproductiva. La evaluación del papel relativo que juegan los movimientos y la mortalidad en la conformación de esos patrones es un importante desafío para futuras investigaciones.

PALABRAS CLAVE: *diurno, dormidero, golondrinas, Hirundinidae, migración, nocturno.*

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The spatial biology of swallows and martins (Hirundinidae) in the breeding season is extremely diverse, ranging from dense and large colonial aggregations to dispersed territorial breeding (Turner and Rose 1989). Most species are central-place foragers spending most of their foraging time well away from the immediate vicinity of the nest (Bryant and Turner 1982, Turner 1982, McCarty and Winkler 1999). The diversity of summer sociality has engendered a rich literature in the comparative behavioural ecology of breeding social systems (e.g., Hoogland and Sherman 1976, Møller 1987, Brown and Brown 1996, Safran 2004). The plethora of data on breeding biology and ecology (e.g., Winkler and Allen 1996, Burness et al. 2001, Hasselquist et al. 2001, Ardia et al. 2003, Czarnowski et al. 2004, Lombardo et al. 2004, Safran and McGraw 2004, Safran et al. 2005) contrasts sharply with the relatively few studies that have been published about the biology of swallows during migration and in the non-breeding season (e.g., Lyuleeva 1973, Mead and Harrison 1979, Szep 1995). My goal here is to review what we know about swallow migration and wintering biology and present hypotheses to explain some of the patterns that are beginning to appear. I must emphasize that we know far too little, and this review is thus intended to serve as an invitation to further research rather than a compendium of established facts.

SWALLOWS AS NOCTURNAL ROOSTERS

At least in the Northern Hemisphere, hirundinids outside the breeding season tend to spend every evening in large dense roosts. These roosts can sometimes be very large (well in excess of a million birds; van den Brink et al. 2000, Burney 2002, Bijlsma and van den Brink 2005), and there are interesting differences in roosting behaviour among species. Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Tachycineta bicolor*) prefer to roost in reed or cane beds usually over water (van den Brink et al. 2000, Burney 2002), occasionally using trees or wires (e.g., Moreau 1972). In contrast, the larger martins in the genus *Progne* prefer to roost in shrubbery or trees or on ledges under bridges and in large industrial buildings (Oren 1980, Russell and Gauthreaux 1999, Purple Martin Conservation Association 2005). All species appear to prefer to roost over water, although all will roost in their favoured substrate over dry land on occasion (e.g., Skutch 1960). Species in the genus *Progne* are variable in their approach to roosts, in some locations flying into the roost in small parties as sunset approaches (Russell and Gauthreaux 1999) and, in others, funnelling-in in one huge concentration (Oren 1980). By contrast, Barn, Tree and rough-winged swallows of the genus *Stelgidopteryx* generally enter their roosts in very large, tight and short-duration streams.

One factor determining why *Progne* species prefer to roost in woody vegetation and on firm structures may be that their larger mass serves as a deterrent to perching in the tips of herbaceous marsh vegetation. This may explain why *Progne* species are less tied to roosting over water than are the smaller species. The fact that these species enter the roost in a less organized fashion than do the smaller swallow species may also indicate that the smaller species may have had their roosting habits most strongly molded by the threat of predation. The smaller swallow species tend to come to roost some time in the hour after sundown. Our observations of Tree Swallow roosts (Burney 2002, pers. obs.) appear to be fairly typical of these smaller species (see Skutch 1960 on *Stelgidopteryx* species): the swallows display their normal reluctance to settle into vegetation, and the birds congregate a few hundred meters above the roost site, milling around the site in an increasingly large and dense cloud of birds. Finally, as the last daylight fades, a few courageous birds make the plunge downward into the reeds of the roost site, followed immediately by a swirling stream of birds pouring into the vegetation, with hundreds of thousands of birds settling in only a few minutes' time. Few who have witnessed these spectacles can avoid describing the descending cloud as a tornado. Both the late hour of gathering and what seems to be the birds' extreme reluctance to venture solo into the vegetation suggest that the principal selective force molding this behaviour has been the risk of predation. Observations on Barn Swallows being preyed upon by aerial raptors as they come to roost in Africa (Bijlsma and van den Brink 2005) support this interpretation. This concern about predation may also explain why the birds appear to gather higher over the roost on clearer evenings (Skutch 1960).

The truly large roosts of hirundinids occur in migratory species, with the largest roosts generally being reported in wintering areas that support birds that bred over much larger areas in the north. It remains to be seen to what extent the non-migratory or short-distance species visit roosts in the non-breeding season. Resident Southern Rough-winged Swallows (*Stelgidopteryx ruficollis*) appeared to join roosts of migrant Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) in cane when they were in the vicinity, but they also roosted in smaller aggregations in the same site when the migrants were gone (Skutch 1960). Skutch (1960) also describes a small group of seven Black-capped Swallows (*Notiochelidon pileata*) roosting together every night after the breeding season in cold cloud forest habitat, in a burrow that was not used for nesting. He also reports that the Blue-and-white Swallow (*Notiochelidon cyanoleuca*) can roost year-round in and near its nest; thus, these species apparently do not join large post-breeding roosts. I have seen a White-winged Swallow (*Tachycineta albiventer*) pair settle down for the night with a fully volant juvenile on small branches over a running stream near Eldorado, Misiones Province, Argentina, on a date (9 March 2001) that appeared to be outside the local breeding season (Belton 1985). Roosts of 2000–10000 swallows (mostly the migrants *Hirundo rustica* and *Riparia riparia* in southern summer and *Tachycineta leucorrhoa* and *Tachycineta meyeni* in southern winter) occur regularly in the state of Rio Grande do Sul in Brazil (R Dias and C Fontana, pers. com.). And all the South American *Progne* species appear to occur in large roosts at some time in their annual cycles (Oren 1980, Hill 1995). Further reports on the sizes and locations of the roosts of tropical swallows and data on whether they live their more sedentary lives without visiting large nocturnal roosts, would be very interesting. Such data would help us understand to what extent nocturnal roosting aggregations are tied with migratory behaviour.

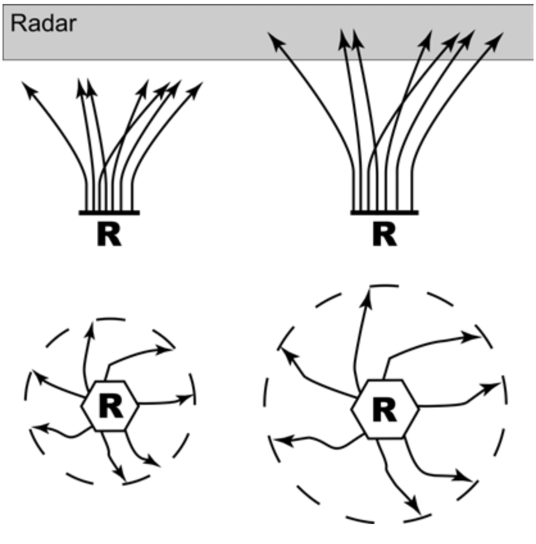

Figure 1. How a flock of swallows emerging in early morning from their roost (R) climbs into the altitudes being scanned by weather radar (above), and spreading out from there in foraging flights (below) leaves a distinctive ring echo in the radar image before it spreads out enough that the density of flying swallows becomes so low as to be undetectable by the radar.

ROOSTS AND RADAR

Roosts generally empty out a few minutes before sunrise the next morning, and the birds tend to leave the roost once again en masse, retracing their flight upward to even higher altitudes before flaring out on foraging flights in all directions (Skutch 1960). This upward flight, followed by the near-symmetric exodus of foraging birds in all direction, makes these large roosts of swallows apparent in the Doppler weather radar now deployed throughout the United States (Russell and Gauthreaux 1999, Burney 2002; Fig. 1). The resulting roost "ring-echoes" provide the prospect of a synthetic view of the size and seasonal distribution of swallow roosts throughout North America (Russell and Gauthreaux 1998, Russell et al. 1998, Burney 2002). These remote methods are being supplemented by organized citizen science projects in both North America (Purple Martin Conservation Association 2005) and the United Kingdom (British Trust for Ornithology 2006) from which a great deal is being learned about comparative roosting biology.

One of the interesting aspects of roosting biology is that roost sites vary considerably in how consistently they are used from year to year. For instance, only a few coastal sites, such as the one at Icklesham, Sussex, are reliable Barn Swallow migratory stopover sites from year to year in the United Kingdom, while all others being monitored so far in this country seem to move around from year to year (Griffin et al. 2005). Similarly, a large swallow roost seems to occur every fall in the marshes of Montezuma National Wildlife Refuge near Ithaca, New York, but its precise location can vary by 5 km or so from year to year (Burney 2002, Winkler and Haber, unpublished data). As we learn more about hirundinid roosting biology, it will be interesting and of considerable conservation importance to try to understand just what makes a site attractive from year to year: it may actually be the case that unpredictability per se is an advantage in reducing the familiarity of roost sites to local predators.

ROOSTS AND MIGRATION

Over much of their migratory and wintering ranges, hirundinid roost sites appear to have fairly consistent roost spacing. Roost sites in North America tend to be about 100 to 150 km apart, though there are certainly consecutive roost sites in prospective northbound or southbound directions that are farther apart (Fig. 2). Spacing at distances approximating 100 km is very similar to the scale of movements reported for roosts of migrant species of the genus *Hirundo* in South Africa (Oatley 2000). By contrast, roost sites in Britain are often much closer together, averaging as little as 25–30 km apart (Ormerod 1991), and the wave of Barn Swallows returning to Britain moves about 50 km/day (Huin and Sparks 1998). This suggests that migrating hirundinids in Britain may actually have the luxury of hopping over some roost sites in their journeys. However, even in North America, the distances between many of the roost sites are well within the range of a day's fairly leisurely flight. Flight speeds of migrating hirundinids are in the range of 40–80 km/h (Lyuleeva 1973), and even if the speeds of leisurely foraging birds are half those, most roost spacings would appear to accommodate an unhurried itinerary from site to site.

These observations suggest an interesting model for swallow migration, with birds migrating through the day linking every night to the next site in their successive chain of nocturnal roost sites. Wintering swallows are reasonably seen as classical central place foragers, with birds radiating out from the roost site in early morning and most often returning to the same roost the following evening. Thus, migration for swallows may often be a simple extension of the loops of daily central place foraging into line segments of approximately the same length linking up to the next roost site (Fig. 3). It would be interesting to explore how these connections to the next roosts are made. Individual birds may set out from a roost in the morning with a memory

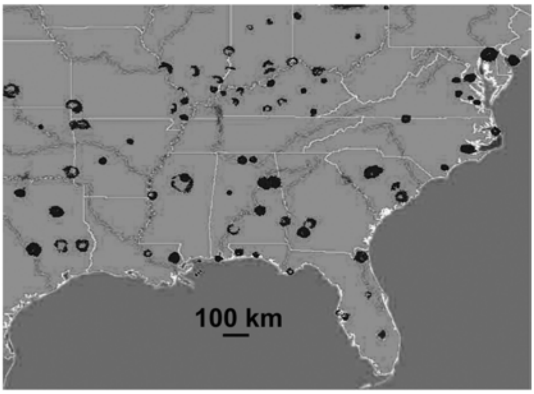

Figure 2. A compilation of weather radar data throughout the southeastern United States for an early morning in late summer. The image shows the clear signatures of roost "ring-echoes" spaced fairly regularly at about 100 km throughout the region.

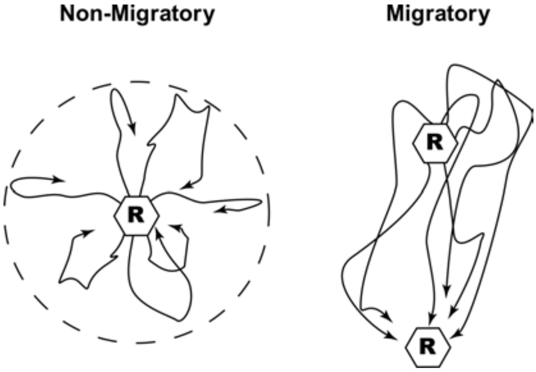

Figure 3. A simple graphical interpretation of how movements by foraging swallows between roost sites may involve very little if any increase in the distance flown per day (right) relative to birds returning to the same roost site in succeeding nights (left).

of the next site on their migratory chain, or they may simply forage more in the preferred migratory direction and then be recruited to the next roost site by aggregating near the end of the day with birds that used the next site for their own roost the night before. These behavioural mechanisms of roost joining would also presumably illuminate the mystery of which sites are used from year to year and serve as a clue to the causes of the inter-annual ebb and flow of roost size.

HIRUNDINIDAE MIGRATORY BEHAVIOUR

This view of swallow migrations as journeys stitched together by roost sites suggests that the exertion of migration on many parts of their journeys may not differ substantially from that expended during the daily and routine foraging movements out from and back to a nocturnal central place. Thus, most movements of swallows appear to take place during the day with these fairly routine movements from one roost site to the next. Yet, no matter what the details of how roosts and migration are integrated, it is clear that not all parts of all hirundinid migrations are a simple redirection of routine foraging patterns. There are records of marked Barn Swallows covering 12000 km in 34 days (320 km/day) and 3028 km in 7 days (433 km/day; Turner 2004). These rates of movement are much greater than those likely to be achieved by birds making more leisurely movements from roost to roost. In addition, many of the longest and fastest passages made by swallows are those made by the three long-distance European swallow migrants as they cross the Mediterranean and Sahara. Like most passerines that make this trip twice annually, or die trying, it seems likely that the vast majority head south from staging areas in Spain or Italy (Rubolini et al. 2002b), then cross directly to Africa, some probably stopping to "coast" along the Saharan verge of the sea and others probably continuing directly to areas south of the Sahara (reviewed by Moreau 1961). *Hirundo rustica* is the most commonly seen bird crossing the Sahara, and, especially in spring, it is often seen flying against, and not uncommonly succumbing to, the northerly winds that prevail at that season (Moreau 1961). As elsewhere in their annual cycle, *Hirundo* species tend to fly lower than other hirundinids, probably making them more visible than *Delichon* and *Riparia* species during passage (Lyuleeva 1973). Moreau (1961) estimated that all the passerines making the non-stop trans-Saharan trip in spring must fly 50–60 h non-stop against head-winds. Recent radar evidence (Schmaljohann et al. 2007) suggests, however, that the 2100–2400 km trip between Europe and tropical Africa is not made non-stop by most European passerines that cross the Sahara and Mediterranean. Much more detail is needed on the biology of these migrants. Nevertheless, the sudden and sporadic appearance of large numbers of all three European swallow genera at low elevations during migration, together with correlations between the intensity of observed migrations and local weather, suggest the hypothesis that hirundinids under very favourable winds fly out of sight high above the ground and that they fly nearer the ground when they are faced with head winds or the need to refuel on insects en route. Flying insects are generally more abundant near the ground (e.g., Glick 1939, Taylor 1974), and it appears likely that, when insects are relatively abundant over the terrain being over-flown, hirundinids descend to lower levels (i.e., nearer the ground) to refuel, returning, once fed, to higher elevations to cover much larger distances when and where the winds are favourable. This possible alternation between higher altitude cruising and lower altitude foraging flight could also explain: (1) why migrating swallows often do not appear at migration observation stations until hours after sunrise (Lyuleeva 1973) when they presumably leave the roosts many hours earlier, and (2) why adults and juveniles appear to fly for different amounts of the day (e.g., Gatter and Behrndt 1985). Nearly exclusive high altitude foraging may also explain the extreme sparseness of observations of some common species (e.g., *Delichon urbicum*; Moreau 1972) on the wintering grounds.

J. Cobb (in Griffin et al. 2005) reported that *Hirundo* species lured down to nets near a roost site in the United Kingdom by playback of swallow song in the afternoon, well before swallows would be coming to roost, were never captured in the roost later in the day and averaged about 2 g heavier than those captured later in the evening at the same site. This seemed to happen after warm days, sug-

Table 1. Counts of migratory swallows made on the coastal plain of the Gulf of Mexico at La Mancha (19°36'N, 96°22'W), Veracruz, Mexico, in the autumn of 1999 by Robert Straub, assisted by Tom Valega and Leticia Cruz. Counts were conducted approximately every other day from 24 August to 30 November, 1999. The count was made from sunrise to sunset whenever possible; however, efforts tended to be concentrated on the higher activity of the morning and afternoon flights. Data compiled by, and courtesy of, Ernesto Ruelas Inzunza of the Centro de Investigaciones Costeras de La Mancha (CICOLMA).

Species	Total	Day of "peak" flight
Barn Swallow (*Hirundo rustica*)	2 819 674	11–16 September
Sand Martin (*Riparia riparia*)	1 785 996	5–16 September
Cliff Swallow (*Petrochelidon pyrrhonota*)	1 301 181	12–13 September
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	1 121 414	8–30 October
Purple Martin (*Progne subis*) and Grey-breasted Martin (*Progne chalybea*)	179 466	27 August–5 September
All swallows combined	7 077 906	11–16 September

gesting interesting environmental effects on this behaviour; however, it also suggests not only that high-flying birds may have greater energy stores but also that, even in the United Kingdom, there may be a diversity of migratory strategies in the *Hirundo* population and that some birds might even be migrating at night and making much more direct over-land progress over the United Kingdom as a result. The generality and interpretation of this result would be strengthened enormously by playback experiments well in advance of the roosting hour near hirundinid roost sites in other places.

Any journey of two days or more requires both nocturnal and diurnal migrants to abandon their preferred hours of flight, and it is clear that hirundinids fly both day and night during these long migratory passages (reviewed in Moreau 1961). It remains an open question whether and how much hirundinids fly at night outside the most extreme legs of their journeys, but it seems safe to continue to designate them as diurnal migrants.

In the Western Hemisphere, observations of enormous numbers of migrant swallows passing through Central America (Table 1; Brown and Brown 1999, Ruelas Inzunza et al. 2005), suggest that the bulk of North American swallows access wintering ranges south of the Gulf of Mexico by an overland route; but the presence of some individuals from all North American species in Caribbean islands and migrating over water in the Gulf confirm that at least some individuals attempt the over-water route to the Southern Hemisphere (Hailman 1962, Yunick 1977, Russell 2005). Given what closely related birds are able to do in the Eastern Hemisphere, it would be interesting and important to try to determine the actual proportions of birds using the overland vs. direct aquatic route over the Gulf of Mexico, especially given that north-bound birds appear to take more varied routes over land during spring migration than fall (Ruelas Inzunza et al. 2005, E Ruelas Inzunza, pers. com.).

BIOLOGY OF THE MIGRANTS

Southbound *Hirundo* species in Europe can accumulate up to about 40% of their mass as fat (Rubolini et al. 2002a) preparing for the Mediterranean–Saharan journey, and they have different fat dynamics if heading over Gibraltar vs. Italy (Rubolini et al. 2002b). By contrast, *Hirundo* species in fall appear to gain only 1–2 g (<25% of body mass) on average in the United Kingdom before heading south to mainland Europe. Other hirundinids in Europe also appear to store less fat than does *Hirundo rustica* before heading to Africa (Cramp 1988). The dynamics of fat stores in different age and geographic classes of *Hirundo rustica* appears to make sense relative to the ecologies of those groups (Pilastro and Magnani 1997). However, given the potentially biased qualities of birds caught during migrations (see *Hirundinidae migratory behaviour* above), interpretation of the masses reported must be made cautiously. If indeed the migratory behaviours of hirundinids are

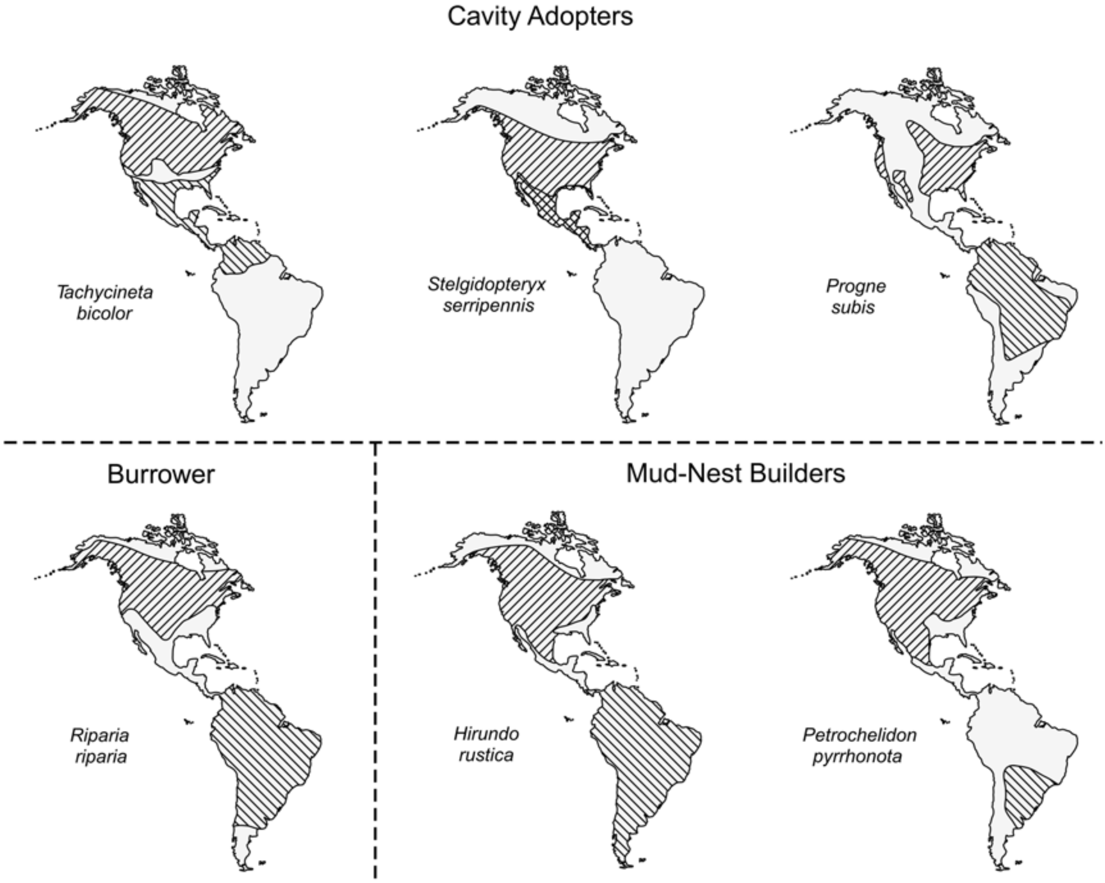

Figure 4. The breeding (right diagonal hatching) and wintering (left diagonal hatching) ranges of six eastern North American swallow species relative to the type of nest they build at their northern nesting sites.

actually quite heterogeneous, a careful study of how changes in body mass and individual body components relate to the migratory behaviour of individual birds could be both extremely difficult and enlightening.

The biology of moult and how it relates to hirundinid breeding and migration appears to be equally diverse. Among species, there is a gradient from species (such as *Tachycineta bicolor*; Stutchbury and Rohwer 1990) that complete a full moult of body feathers, rectrices and remiges before and during migration; through populations that moult body feathers as they initiate migration, stopping to complete moult of rectrices and remiges before making a long-distance migration (e.g., eastern *Stelgidopteryx serripennis*; Yuri and Rohwer 1997); through species moulting body feathers before and during migration and not initiating or interrupting early flight feather moult until reaching the wintering ground (apparently all trans-Saharan species: *Riparia* and *Delichon* species, Cramp 1988; *Hirundo rustica*, Cramp 1988, van den Brink et al. 2000, Rubolini et al. 2002b, Griffin et al. 2005). Once again, there is ample evidence of flexibility in moult schedules within species, with Western *Stelgidopteryx serripennis* adopting a strategy more like *Tachycineta bicolor*, moulting while it migrates without interruption, in contrast to the "moult migration" of the Eastern population (Yuri and Rohwer 1997).

Why do some migrate so much farther than others?

Winkler (2000) suggested that there were multiple selective reasons that have made changes in swallow nest-type less evolutionarily flexible than other aspects of the life-history, and much of the spring life history of these birds can be seen as adjustments to the mode of nesting. The swallow fauna of eastern North America is distinctive in the presence of six obligate migrant species with diverse nesting mode among them (Fig. 4). Of these, three are cavity adopters, reliant on other species or processes to create a nest-cavity in which they build a grass-nest cup. It seems more than coincidence that these three cavity-adopting species migrate the shortest distances of the lot, a feature that likely allows them to return to the breeding grounds earlier in spring to compete for and secure a nest-cavity, which, unlike the burrowing and mud-nesting species, they cannot make for themselves (see also Rubolini et al. 2005).

HOW PHYLOGENETICALLY FLEXIBLE IS MOVEMENT IN SWALLOWS?

An alternative hypothesis to explain the more northerly wintering of the cavity-adopters is that patterns of movement may be nearly as difficult to evolve as are patterns of nest construction, and that all the longest-distance migrants in the New World hirundinid fauna (*Riparia riparia, Hirundo rustica* and *Petrochelidon pyrrhonota*; Fig. 4) are derived from Old World forms (Sheldon et al. 2005) that presumably colonized the Western Hemisphere relatively recently. However, available evidence in support of this phylogenetic inertia hypothesis is less than compelling. First, there are two tropical species in the New World fauna, *Petrochelidon fulva* and *Petrochelidon rufocollaris*, that appear to have derived from *Petrochelidon pyrrhonota* in the New World, and both are short-distance- or non-migrants. Second, *Riparia riparia*, together with its short-distance congener *Riparia paludicola* from the Old World, appears to be sister group to the genus *Tachycineta* and much more closely related to the endemic New World swallows than they are to other Old World forms. Thus, the short-distance or non-migratory habits of *Tachycineta* species and *Riparia paludicola* appear not to have been constrained by the habits of their long-distance close relative *Riparia riparia.* Finally, *Hirundo rustica* has begun breeding in South America, on what were solely its wintering grounds, within the past 30 years (Martínez 1983). Though the movement patterns of this small breeding population are not known, it appears extremely unlikely that these birds have retained the long-distance migratory habit of their immediate ancestors and perform a long migration all the way to North America in the austral winter (GH Huber, pers. com.). *Hirundo rustica* is known for the complexity of movement patterns within its large populations in both the Eastern and Western hemispheres (Moreau 1972, Phillips 1986, Cramp 1988), with some resident forms interacting during parts of the year with both long- and short-distance forms passing through. Furthermore, *Hirundo rustica* is closely related to a large number of other species of the genus *Hirundo* in sub-Saharan Africa, many of which are residents or short-distance migrants (for all phylogenetic statements in this paragraph see Sheldon et al. 2005). Finally, patterns of movement within the New World endemic hirundinids are very flexible. Though there are no long-distance migrants that go as far as *Petrochelidon, Hirundo* or *Riparia* species do in the New World, there is a great deal of diversity in distances travelled in the genera *Tachycineta, Progne* and *Stelgidopteryx.* In short, the distance of movement seems to be quite flexible in swallows (see also Turner and Rose 1989), and the patterns observed above for the summer and winter ranges of North American breeding species seem more readily explained by nest-site competition on the breeding grounds than by phylogenetic conservatism of the traits.

FLEXIBILITY WITHIN SPECIES IN WHETHER TO MIGRATE

There are at least two observations that suggest considerable flexibility in migratory scheduling within populations of hirundinids. First, many first-year male *Progne subis* return to the breeding grounds even though they do not generally breed their first year. This suggests that the observation of first-year males in the wintering grounds during the northern breeding season (Hill 1995) may actually be the result of a strategy by these younger birds to forego the return to breeding areas until their chances of breeding are higher (see also comment by Oren 1980). It would be interesting to investigate the properties of those birds that stay in the south their first year and compare them to those that complete the annual migratory circuit without attempting breeding on the northern end.

The other exceptional indicator of flexibility in breeding and migration is provided by those northern migrants that have begun breeding in the southern wintering grounds. *Delichon urbicum* has bred and produced fledglings intermittently in South Africa, with individual colonies sometimes lasting "for some years", but no sustained population has been established (McLachlan and Liversidge 1957, Maclean 1988:465). By contrast, and as mentioned above, a breeding population of *Hirundo rustica* in Buenos Aires Province, Argentina, colonized in the early 1980's (Martínez 1983) and is still slowly growing (P Petracci and GH Huber, pers. com.). It is not yet clear whether this population is being sustained by local production of offspring or continued recruitment from the migrant pool. In any event, these cases of re-distribution of major life events in the annual cycle suggest a flexibility in swallows that is equalled only by nomadic passerines of boreal forest or tropical deserts, and swallows appear to be the only long-distance migrant passerines with such flexibility. Just how, physiologically, this readjustment of the life history is performed is a fascinating area for on-going research.

IMPLICATIONS OF DIURNAL MIGRATION

Unlike the bulk of other migrant bird species, the Hirundinidae are cosmopolitan. Few other bird groups have achieved this breadth of distribution, and the migrations of swallows seem analogous with other broadly distributed migrants, such as Apodidae, Accipitridae and Anatidae, with thriving Northern Hemisphere populations linked by migration to habitats further south in the northern winter. All of these groups also share the property of being diurnal migrants, and other aerial insectivore long-distance migrants (e.g., Tyrannidae in the Western Hemisphere and Muscicapidae in the East) are nocturnal and are limited to one hemisphere or the other in their distributions. Of course, there are numerous insectivorous diurnal migrants that migrate smaller distances and do not currently occur in both hemispheres (e.g., Meropidae, Artamidae). To test the possibility that diurnality of migration per se is associated with the broad-scale distributions of birds at the family level, I categorized each avian family into residents and migrants. I further divided the migrants into diurnal, nocturnal, or both, and recorded whether these types are distributed solely in the Eastern or Western Hemispheres or both (a much more detailed species-level treatment of migration modes world-wide is forthcoming; Farnsworth et al., unpublished data). In characterizing distributions, I ignored single species in one hemisphere that otherwise were endemic to the other in four families (Alaudidae, Troglodytidae, Timaliidae and Sylviidae). The resulting analysis (Table 2) shows, not surprisingly, that residents are much more likely to be endemic to one hemisphere or the other (i.e., there are far fewer distributed in both than expected by chance). By contrast, diurnal migrants are significantly more likely to occur in both hemispheres. Exactly how this pattern arises is unclear, but the broad array of visual cues available to diurnal migrants may lend them increased flexibility and the ability to explore routes for migratory possibilities that change with changing Earth climate and that may not be available to a more pre-programmed navigation–orientation system in nocturnal migrants. Hirundinids are clearly one of the most flexible groups both in their migratory biology and breeding schedules, and it is perhaps a bit surprising that there are so many tropical forms in this group with such limited distributions (e.g., *Hirundo megaensis*, *Tachycineta stolzmanni*, *Tachycineta cyaneoviridis*, *Tachycineta euchrysea*, *Notiochelidon pileata*).

THE WAY FORWARD:
MIGRATION AND MORTALITY

The exceptional flexibility of hirundinid lifecycles raises many interesting possibilities for research, many of which will become available as soon as digital telemetry tags and dataloggers become small enough to deploy on swallows. These technological developments raise the prospect of following individuals through their annual cycles and relating their personal histories and physiological states to the movements that they undergo. Such tags may also eventually lead to a refinement of our estimates of where in the life cycle most swallows die and why.

Improved information on mortality could dramatically increase our understanding of the lives of these resourceful birds and give

Table 2. Summary of the distributions of families of birds of the world as they relate to the migratory modes of their members. For each cell, the number of families is followed (in parentheses) by the deviation of the observed cell frequency from that expected from the marginal totals. Global analysis: $\chi^2_6 = 66.091$, $P < 0.001$. The two cells that contribute the most to the observed χ^2 are indicated by an asterisk. Four families with unknown major migratory mode (Acanthizidae, Eopsaltridae/Petroicidae, Chionididae and Thinocoridae) were left out of this analysis.

	Hemisphere of distribution			
Migratory mode	Eastern	Both	Western	Total
Diurnal	8 (-2.175) [a]	28 (4.099 *) [e]	3 (-1.978) [i]	39
Nocturnal	11(-1.268) [b]	17 (1.284) [f]	9 (0.191) [j]	37
Both	4 (-1.247) [c]	11 (2.203) [g]	2 (-0.955) [k]	17
Resident	57 (2.772) [d]	6 (-4.454 *) [h]	28 (1.586) [l]	91
Total	80	62	42	184

[a] Alaudidae (one species Holarctic), Anseranatidae, Artamidae, Coliidae, Meliphagidae, Meropidae, Ploceidae, Sturnidae.

[b] Campephagidae, Cisticolidae, Monarchidae, Muscicapidae, Oriolidae, Pittidae, Prunellidae, Pycnonotidae, Remizidae, Sylviidae, Upupidae.

[c] Coraciidae, Dicruridae, Glareolidae, Zosteropidae.

[d] Acanthisittidae, Aegithinidae, Apterygidae, Atrichornithidae, Balaenicipitidae, Batrachostomidae, Brachypteraciidae, Bucerotidae, Callaeatidae, Casuariidae, Cinclosomatidae, Climacteridae, Corcoracidae, Cracticidae, Drepanididae, Dromadidae, Estrildidae, Eurylaimidae, Grallinidae, Hemiprocnidae, Hypocoliidae, Ibidorhynchidae, Indicatoridae, Irenidae, Leptosomatidae, Lybiidae, Maluridae, Megalaimidae, Megapodiidae, Melanocharitidae, Menuridae, Mesoenatidae, Musophagidae, Nectariniidae , Numididae, Orthonychidae, Otididae, Pachycephalidae, Paradisaeidae, Paramythiidae, Pardalotidae, Passeridae, Pedionomidae, Philepittidae, Phoeniculidae, Picathartidae, Podargidae, Pomatostomidae, Pteroclididae, Ptilonorhynchidae, Rhynochetidae, Sagittariidae, Scopidae, Struthionidae, Timaliidae, Turnicidae, Vangidae.

[e] Accipitridae, Alcidae, Anhingidae, Apodidae, Bombycillidae, Ciconiidae, Corvidae, Dendrocygnidae, Diomedeidae, Falconidae, Fringillidae, Gaviidae, Hirundinidae, Hydrobatidae, Laridae, Motacillidae, Pandionidae, Pelecanidae, Pelecanoididae, Phaethontidae, Phalacrocoracidae, Phoenicopteridae, Procellariidae, Psittacidae, Spheniscidae, Stercorariidae, Sternidae, Sulidae.

[f] Burhinidae, Caprimulgidae, Certhiidae, Charadriidae, Cinclidae, Cuculidae, Haematopodidae, Jacanidae, Picidae, Podicipedidae, Rallidae, Recurvirostridae, Regulidae, Rostratulidae, Sittidae, Strigidae, Tytonidae.

[g] Alcedinidae, Anatidae, Ardeidae, Columbidae, Emberizidae, Gruidae, Laniidae, Paridae, Scolopacidae, Threskiornithidae, Turdidae.

[h] Aegithalidae, Aegothelidae, Fregatidae, Heliornithidae, Phasianidae, Trogonidae.

[i] Cathartidae, Cotingidae, Trochilidae.

[j] Cardinalidae, Mimidae, Parulidae, Pluvianellidae, Polioptilidae, Thraupidae, Troglodytidae, Tyrannidae, Vireonidae.

[k] Icteridae, Rynchopidae.

[l] Anhimidae, Aramidae, Bucconidae, Capitonidae, Cariamidae, Conopophagidae, Cracidae, Dendrocolaptidae, Dulidae, Eurypygidae, Formicariidae, Furnariidae, Galbulidae, Momotidae, Nyctibiidae, Odontophoridae, Opisthocomidae, Oxyruncidae, Phytotomidae, Pipridae, Psophiidae, Ramphastidae, Rheidae, Rhinocryptidae, Steatornithidae, Thamnophilidae, Tinamidae, Todidae.

us powerful new knowledge to help sustain their populations on Earth. It appears that most adults die in non-breeding quarters and juvenile survival is most affected by conditions on or near the breeding grounds (Szep 1995, Stokke et al. 2005). The huge preponderance of juveniles in roosts in northern latitudes (Griffin et al. 2005), their variable proportions in African roosts from year to year (van den Brink et al. 2000), and the frequent observation of dead and dying *Hirundo rustica* during trans-Saharan migration (Moreau 1961, 1972) all indicate that mortality can be swift and severe at times.

Understanding the causes of mortality in these long-distance migrants is a fascinating and important challenge, but it may also be extremely interesting to apply this increased knowledge to interpretation of patterns of seasonal movement. If gathering the traces of roost ring-echoes from weather radar from across North America can be automated, there is the prospect of understanding the changing distributions of a very large fraction of the world's population of at least *Tachycineta bicolor* through the annual cycle. When viewing the changing distributions and sizes of these roosts, it is tempting to interpret the changes in distributions as representing the movements of birds up and down the north Atlantic coast. But the survival rates of *Tachycineta bicolor* at our Ithaca study site are, if anything, lower than those of *Hirundo rustica* (unpublished data). Thus, if we attribute shifts in distribution to movement, we may forget that a large number of the birds detected in the radars will not be returning to the breeding grounds. Just as dispersal from the natal grounds confounds estimates of survival, movement and mortality may well be confounded in the non-breeding season as well. When large roosts on the north Atlantic coast disappear from the radar in autumn, some of the animals have no doubt migrated to the south, but a large proportion of them may have died instead. Short-distance facultative migrants retain the possibility of getting back to the breeding grounds earlier, but the mortality cost of doing so may be larger than the extreme costs incurred by their cousins migrating longer distances.

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TOWARDS A MECHANISTIC INTERPRETATION OF BIRD MIGRATION IN SOUTH AMERICA

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Abstract.— Research to date has demonstrated that bird migration is comprised of highly diverse and plastic behavioural patterns. Our objective is to highlight the importance of studying mechanisms underlying these patterns in austral migrants. We focus on the high incidence of overlap in breeding and non-breeding ranges as a particularly thought-provoking pattern. We then explore the opportunities afforded by partial migration theory to elucidate the mechanisms underlying seasonal range overlap. We propose that a mechanistic understanding of migration in South America will both provide a deeper appreciation of the ecology, physiology and evolution of migratory species in the New World, and improve the scientific foundation for their conservation.

Key words: *mechanism, partial migration, population, range overlap,* Tyrannus.

Resumen. Hacia una interpretación mecanística de la migración de aves en América del Sur.— La investigación reciente sobre aves migratorias ha demostrado que constituyen un grupo que presenta comportamientos altamente diversos, plásticos y complejos. Nuestro objetivo general es resaltar la importancia de estudiar los mecanismos que generan los patrones que caracterizan la migración de aves en América del Sur. Para ello nos enfocamos en un patrón interesante (la alta incidencia de superposición en la distribución reproductiva y de invernada), analizando las oportunidades ofrecidas por la teoría de migración parcial para dilucidar los mecanismos que producen tal superposición. Proponemos que una comprensión mecanística de la migración de aves en América del Sur no solo proveería una apreciación más profunda sobre la ecología, la fisiología y la evolución de las especies migratorias del Nuevo Mundo, sino que también mejoraría los fundamentos científicos para su conservación.

Palabras clave: *mecanismos, migración parcial, población, superposición de distribuciones,* Tyrannus.

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Research on various aspects of bird migration — from biogeography to ecology and physiology — has demonstrated that migratory behaviour is an extraordinarily diverse and complex phenomenon. For example, it can evolve relatively rapidly (Able and Belthoff 1998, Berthold 1999, Piersma et al. 2005), is phylogenetically flexible (Böhning-Gaese and Oberrath 1999), and can appear and disappear through time within a lineage (Zink 2002, Joseph et al. 2003, Outlaw et al. 2003) or even within an individual's lifetime (e.g., Schwabl and Silverin 1990). In the New World, a continuum of migratory strategies exists, from long-distance migrations undertaken by all populations of a species to short-distance migrations undertaken by only some populations (Levey and Stiles 1992) or individuals (e.g., Ketterson and Nolan 1976). Migration can even play a central role in speciation (Winker 2000, Winker and Pruett 2006).

To solve persistent riddles about the evolution and regulation of migration requires teasing apart factors confounded in space and time. This is difficult to accomplish without a broad geographic scope. In the New World, almost all work on migration has been restricted to the north-temperate latitudes (Levey 1994, Jahn et al. 2004), with relatively little attention paid to migration within South America (austral migration, sensu Chesser 1994). Some species of Neotropical austral migrants move annually between the temperate zone and tropical latitudes and some species migrate within either tropical or temperate latitudes of the continent (Joseph 1997). There are more than 220 species of Neotropical austral migrants, comprising the largest migratory system in the Southern Hemisphere (Chesser 1994). Recent literature on migration in South America principally explores biogeographic patterns (e.g., Chesser 1994, da Silva 1999, Capllonch and Lobo 2005), evolution (Joseph et al. 2003), habitat associations (e.g., Chesser 1995, Stotz et al. 1996, Jahn et al. 2002) and the timing of migratory movements (e.g., Hayes et al. 1994).

The geographical patterns of migration in the Neotropics are complex (Morton 1977, Winker et al. 1997, Bildstein 2004). In some species all populations migrate, but in others different populations migrate in the same or in different directions. Furthermore, all of these strategies can occur within one genus (e.g., genus *Tyrannus*, Fig. 1; Ridgely and Tudor 1994, Chesser 1995). This stands in sharp contrast to the situation in North America, where all the populations of migratory species generally move in the same direction during each season.

Given the diversity of migration strategies evident within South America, it is clear that the phrase "bird migration in South America" encompasses a multitude of inter- and intraspecific patterns at smaller scales than the overall pattern at the continental level would suggest. Thus, to better understand how migratory birds respond to competing ecological and physiological demands, it will be essential to form links between patterns observed at different spatial and temporal scales and among taxonomic (e.g., families and species) and biological levels of organization (e.g., genotypes, individuals, ecosystems) (Levin 1992).

Our objective is to demonstrate that research on the mechanisms generating specific patterns of bird migration in South America is a prerequisite to gaining a better theoretical foothold, as well as for the ability to formulate sound, proactive conservation and management strategies. We use as an example the high incidence of seasonal range overlap in the distributions of South American migratory bird populations to highlight the power of existing theory on intrapopulation variation in migratory behaviour to explain such patterns.

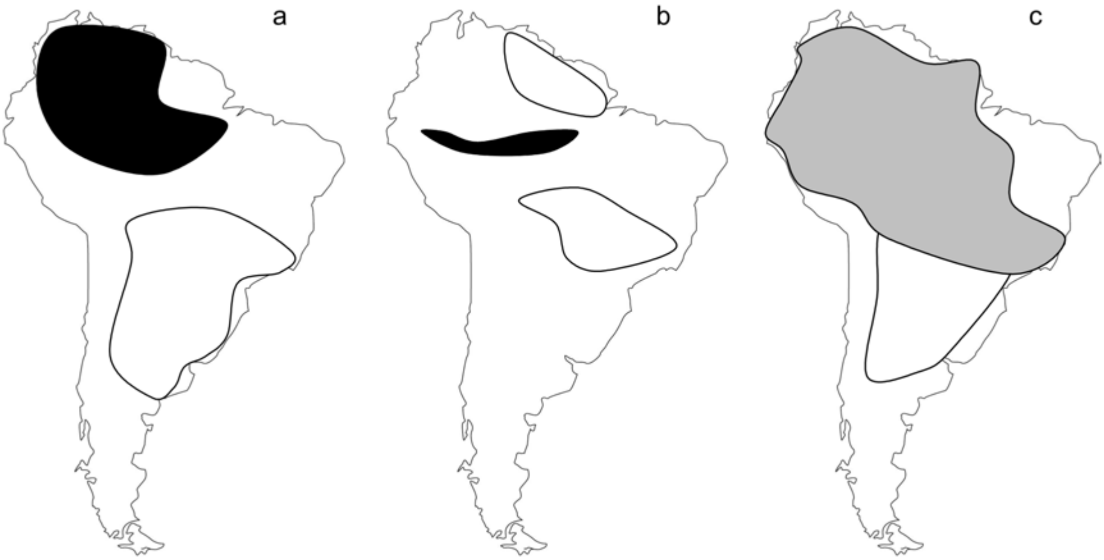

Figure 1. Generalized seasonal distributions of *Tyrannus savana savana* (a), *Tyrannus albogularis* (b), and *Tyrannus melancholicus melancholicus* (c) in South America. Black polygons represent seasonal non-breeding ranges, white polygons represent seasonal breeding ranges and the gray polygon represents area of overlap in which permanent residents as well as non-breeding (i.e., overwintering) migratory individuals from the south occur together. Adapted from Chesser (1995).

A FOCUS ON MECHANISMS

Studying mechanisms — the proximate relationships between what an individual experiences and how it responds — is the key to being able to explain the causes for observed patterns, advancing both basic science (i.e., explanations, predictions, the formulation of original questions) as well as practical applications (i.e., conservation and environmental planning and management). Such rewards will only result from studies that are focused on specific questions and employ testable hypotheses (Vuilleumier 2004).

Tests of mechanistic hypotheses (i.e., how component parts of the phenomenon interrelate) — rather than phenomenological explanations (i.e., models that extrapolate future trends based on past trends) — are useful for interpreting the reasons for changes observed in a pattern (e.g., migratory timing or direction) (Koehl 1989), especially in light of the magnitude and speed of contemporary anthropogenic changes in global biogeochemical cycles (Lubchenco 1998). From an applied perspective, knowing where species are located during the entire annual cycle is necessary to formulate a basic conservation plan. However, an understanding of the factors influencing survival and reproduction at smaller spatial scales enables a more effective conservation strategy. For example, Marra et al. (1998) demonstrated that the quality of habitats occupied by *Setophaga ruticilla* individuals during the non-breeding season can affect their physical condition and thus their arrival date on North American breeding ranges, which has consequences for their reproductive success. In this case, knowledge of the life-history consequences of habitat use opens the door to the formulation of more detailed conservation priorities.

Studying the mechanisms that regulate the components of a system also allows patterns to be placed within an evolutionary context. As pointed out by Moore and Aborn (2000), research about habitat selection during migration has historically focused on describing habitat use rather than examining the mechanisms through which selection acts. Thus, to elucidate the processes responsible for observed patterns, it is important to consider the evolutionary history of a species as well as contemporary constraints. Taking just such an approach, Böhning-Gaese and Oberrath (2003) concluded that contemporary habitat preferences of migrants have been strongly influenced by the historical occupation of relatively open habitats in Africa (by ancestors of Holarctic migrants) and of Neotropical forests (by ancestors of Nearctic migrants), as well as by contemporary processes.

Nevertheless, an ability to understand the causes of patterns evident at the population level demands research on processes occurring at the individual level (Koehl 1989). This is because the evolutionary mechanisms that generate population-level migratory patterns originate from variation among individuals. Thus, a focus on the individual is essential for formulating and testing hypotheses about the evolution of migration (Bell 2000). Research focused at the level of the individual requires consideration of the ecological constraints encountered by individuals on different scales throughout their annual cycle. For example, a bird that forages on a scale of hundreds of meters may migrate hundreds of kilometers to search for similar resources at another site. Thus, migratory species are affected by processes occurring on vastly different temporal and spatial scales (e.g., Alerstam and Åkesson 2003). Forming links between these disparate scales is one of the central challenges not only of migrant bird ecology, but of science in general (Levin 1992).

Finally, since migratory behaviour is an attribute regulated by a suite of characters (e.g., physiological, social; Piersma et al. 2005), it is important to formulate hypotheses about these characters within an explicitly phylogenetic context (Zink 2002). In South America, the diversity of movement patterns, even within a single species (e.g., *Myiarchus swainsoni*; Joseph et al. 2003), may be a complex and long-term response to changing environmental conditions on the continent. However, diverse migratory behaviours can also appear on much shorter time scales. One notable example is the appearance of populations of *Hirundo rustica* that are beginning to reproduce within their historical non-breeding range, particularly in the coastal zone of the province of Buenos Aires, Argentina (Martínez 1983).

We now have the opportunity to design studies within South America to test theories formulated in other migration systems. With such an approach, we can both enrich our understanding of migration within South America and test the explanatory power of extant theories across migratory systems. We can begin to answer such questions as: do similar ecological, physiological, and genetic mechanisms underlie all migratory systems?; does migration within South America operate under different "rules" than in other systems? For example, the capacity for nocturnal compass orientation is highly conserved phylogenetically in migratory birds around the world (Piersma et al. 2005). In mid- and high-latitudes, migratory birds can use a magnetic inclination compass for orientation, but this system cannot function at equatorial latitudes (Wiltschko and Wiltschko 1995). Thus, what alternative cues can migrants use to orient and navigate in equatorial South America? Clearly, research in this area will allow us to test extant mechanistic theories as well as formulate new hypotheses about the migrations of birds.

In the next section, we use the seasonal overlap of ranges to launch a discussion of how to distinguish between populations of migratory species, as well as how to study the mechanisms operating within these populations.

RANGE OVERLAP

What patterns characterize bird migration within South America? Stotz et al. (1996) and Chesser (1994) identified several key features: (1) taxonomic composition (in South America, the family Tyrannidae makes up nearly a third of all migratory species on the continent); (2) distance of migration (within South America, most migrants move over shorter distances than do Nearctic-Neotropical migrants); (3) proportion of migratory species along a latitudinal gradient (in South America, the gradient of increasing number of migratory species with latitude is less dramatic than in North-temperate latitudes); and (4) range overlap (approximately two-thirds of Neotropical austral migrants — 159 species — exhibit overlap in population ranges across seasons; i.e., migrants of one population migrate to areas already occupied by conspecifics that do not migrate). Although these four patterns are coarse-grained and described at a continental scale, they offer a point of departure from which to look for more specific patterns (Stotz et al. 1996). We focus on the pattern of range overlap among populations as an interesting pattern to explore the mechanisms that may underlie it.

Several biogeographical explanations have been offered to explain the causes of range overlap. Chesser (1994) offered two hypotheses. First, given that the South American continent is wider towards the equator, birds moving northwards towards the equator after the breeding season could experience a reduction in interspecific competition as a consequence of lower population densities due to the increasing land area, reducing their need to continue migrating northward. Second, there are no evident geophysical barriers to the east of the Andean Cordillera to segregate breeding and non-breeding ranges. In a similar vein, Hayes et al. (1994) proposed that the diminished land area at high latitudes corresponded to a reduced capacity to sustain breeding populations of migratory species, thus producing relatively short migrations between tropical and temperate latitudes.

To test mechanistic hypotheses on the pattern of range overlap, however, we must know something about the variation in migratory distance among individuals, since different strategies among individuals may be present across the species' range. In essence, seasonally overlapping ranges obscure any pattern of exactly where migratory individuals pass the non-breeding season (Stotz et al. 1996). Some populations may even be migrating within the area of overlapping ranges. For example, within any one species, there may be populations that are completely resident, as well as some that are partially migratory (ie., some individuals of a population migrate; Fig. 2). Thus, the area of overlap may "mask" substantial variation in migratory movements among populations. Furthermore, migrant and resident individuals may be partitioning the area of overlap in different ways. For example, Tellería and Pérez-Tris (2004) studied habitat associations in *Erithacus rubecula*, a European migrant species comprised of migratory populations whose non-breeding distribution overlaps with the distribution of resident populations in the south of the continent. They found that residents and migrants were physiologically different and occupied distinct habitats during the period of overlap. Consequently, in order to study the mechanisms underlying range overlap, it will be important to differentiate between populations and to define their "connectivity": the origin and destination of migratory populations (for a review, see Webster et al. 2002). Once the migratory patterns of populations have been characterized as migratory, resident, or partially migratory, research can turn to the question of which processes underlie their migratory pattern.

Information on connectivity of populations and, at a local scale, on habitat use by different individuals (i.e., migrants vs. residents) has obvious relevance for conservation policy. For example, if one population is in decline in the breeding area, knowledge of where it spends the non-breeding season within the area of overlap can greatly help to pinpoint the part of the life cycle in which the greatest threats to the survival of that population occur.

We now focus on some ideas about how to study mechanisms that operate on an intra-population level and produce population-level patterns. We use partial migration as an example (Fig. 2). For a recent review of other population-level migration patterns, see Boulet and Norris (2006).

PARTIAL MIGRATION

Partial migration is perhaps the most common type of bird migration in the world (Berthold 2001). From an evolutionary standpoint, partial migration is thought to be an intermediate step in the evolution of complete migratory behaviour in birds (Berthold 1999). Consequently, studying the processes that produce partial migration could be a key to understanding more about the proximate and ultimate processes that govern migratory movements in species with overlapping ranges.

Before discussing the processes producing partial migration, it is important to distinguish between population-level partial migration and intra-population partial migration. In population-level partial migration, some populations of a species migrate and other populations do not. For example, in *Tyrannus savana*, the nominate subspecies is a Neotropical austral migrant, while another subspecies (*Tyrannus savana sanctaemartae*) remains as permanent resident in the northern part of the continent (Chesser 1995, Stiles 2004). This population-level variation in migration

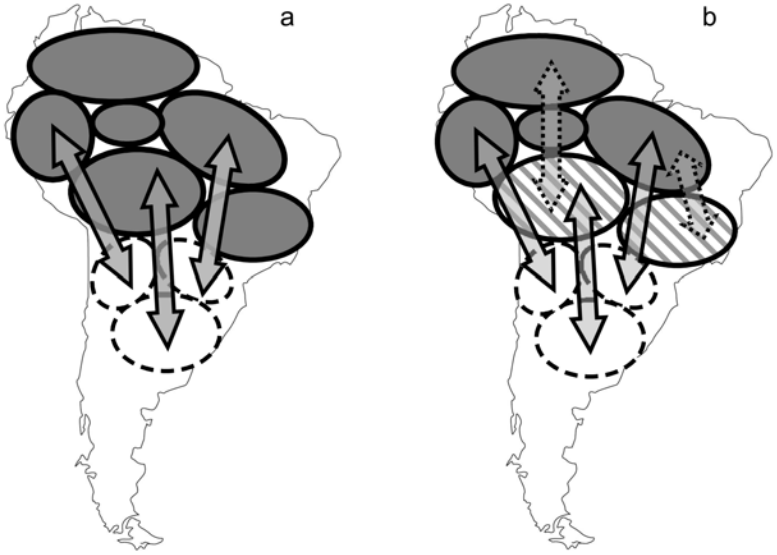

Figure 2. Two hypothetical patterns of population-level migration of *Tyrannus melancholicus melancholicus*: (a) migration exclusively of populations between a seasonal breeding area and an area of range overlap, and (b) migration of populations between a seasonal breeding area and an area of overlap, as well as partial migration of some populations within the area of overlap. Gray areas: populations of permanent residents, hatched areas: partially migratory populations, white areas: completely migratory populations, dashed arrows: partial migration, closed arrows: complete migration.

characterizes at least 70% of the migratory species in South America (Parker et al. 1996). In the case of intra-population partial migration, some individuals of the same population migrate after the breeding season and others do not (sensu Lack 1943; for a review, see Berthold 2001, Jahn et al. 2004). Differences in migratory behaviour between individuals in the same population have been widely documented in other migratory systems but have not yet been documented in South America. Hereafter, when we refer to "partial migration", we consider specifically intra-population partial migration.

The first studies on partial migration tended to be descriptive or to focus on evolutionary, population-level processes (e.g., Lack 1943, 1954, Kalela 1954, Cohen 1967, von Haartman 1968, Biebach 1983). More recently, emphasis has moved towards identifying and weighing the differences between individuals. Within this context, "migrant" and "resident" are considered to be alternative strategies with different benefits for different individuals in a population (e.g., Swingland 1983). Individual asymmetries (e.g., age, size) are postulated to determine migratory status because of differences in competitive advantage between individuals. Lundberg (1987) contributed to this framework by adding the parameter of frequency-dependent choice, in which individuals of different social rank (e.g., juveniles low in the social hierarchy) decide whether to migrate, depending upon the relative frequencies of the dominant and subdominant individuals in the population with which they have to compete. Indeed, factors such as age, sex and social status in a population have been shown to determine migratory behaviour (e.g., Gauthreaux 1982, Schwabl 1983, Adriaensen and Dhondt 1990). For example, Able and Beltoff (1998) demonstrated that among *Carpodacus mexicanus* migrating within North America, younger individuals were characterized by a higher tendency to migrate. These demographic and social conditions are often tightly linked to such parameters as competitive ability, physiological tolerance and habitat associations, which in turn are postulated to affect migratory status (Ketterson and Nolan 1983, Cristol et al. 1999, Tellería and Pérez-Tris 2004). Thus, a test of the relationship between these parameters (e.g., physiological tolerance, social dominance) and migratory strategy (e.g., migratory timing, migratory distance) produces mechanistic models on the causes of such patterns as range overlap. It follows that identifying demographic (e.g., age, sex), social (e.g., dominance), and morphological (e.g., body size) differences between individuals is a prerequisite to studying the processes responsible for variation in the migratory behaviour among individuals of a partially migratory population (i.e., whether or not an individual migrates).

What, then, are some specific, testable mechanistic hypotheses that can begin to tease apart potential causes for range overlap? Partial migration is one class of the broader category of differential migration, in which individuals within a population undertake migrations of varying distances (e.g., Ketterson and Nolan 1976). In partial migrants, the distance travelled by some members of the population falls at an extreme of a gradient: zero migration (i.e., residence). Thus, since partial migration is a class of differential migration (Alerstam and Hedenström 1998), much of the theory about differential migration is applicable to partial migration and vice versa. A great variety of theories attempt to explain partial and differential migration, but the majority are variations on three general hypotheses (Bell 2005). The first one is the Dominance Hypothesis. Subdominants are poor competitors for available food; when there are not sufficient resources for all the individuals in a population, subdominants are therefore more likely to migrate in order to avoid competition with dominant individuals. Supporting data are principally indirect, based upon the observation that in different species younger individuals or females are subdominant and migrate longer distances (e.g., *Junco hyemalis*; Ketterson and Nolan 1976). The second hypothesis is the Arrival Time Hypothesis. Individuals that establish territories at the beginning of the breeding season are less likely to migrate as far because a short migration distance ensures a rapid return to the breeding range and access to the best territories. For example, in a study of *Anser caerulescens*, Bêty et al. (2004) found a significant relationship between the arrival date on the breeding grounds and the probability of reproducing (although excessively early arrivals suffered from negative climatic effects). Finally, the third hypothesis is the Body Size Hypothesis. In accordance with the relationship between body surface area and volume, larger individuals can better withstand lower temperatures and endure food limitations, giving them a lower probability of migrating away for the winter. For example, in *Carpodacus mexicanus*, females are socially dominant, but also smaller in size and tend to migrate further than males (Belthoff and Gauthreaux 1991). Studies evaluating these hypotheses have generally failed to produce data that predict migratory distance (e.g., *Junco hyemalis*; Ketterson and Nolan 1985). Future research in South America could test the explanatory power of these hypotheses in a context independent of the North-temperate system within which the hypotheses were originally formulated.

FUTURE DIRECTIONS

Given the challenge of understanding the mechanisms underlying such a complex system, it is timely to note several themes that may put this type of research in perspective.

Comparisons among common taxa in the New World

Current theory postulates a Neotropical origin for migratory species in the New World, both Nearctic-Neotropical and Neotropical austral migrants (Levey and Stiles 1992, Rappole 1995, Joseph 1997, Chesser and Levey 1998, Joseph et al. 1999, Böhning-Gaese and Oberrath 2003). A review of the data from Parker et al. (1996) reveals that at least 34 families, 56 genera and 23 species have populations of both Nearctic-Neotropical and Neotropical austral migrants. For example, *Pyrocephalus rubinus* have populations that are Nearctic-Neotropical migrants and other populations that are Neotropical austral migrants (Parker et al. 1996). Intraspecific comparisons of populations employing different strategies (Neotropical austral vs. Nearctic-Neotropical migration) are therefore possible and have the advantage of avoiding the confounding effects of phylogeny that commonly haunt interspecific comparative studies. Specifically, intraspecific research among populations of one species rather than comparisons between species decreases the effects of a shared phylogenetic history, which is problematic because it leads to a lack of independence in the parameters being compared (e.g., Gittleman and Luh 1992, Garland and Adolph 1994).

Conducting comparative studies among migratory systems offers the additional benefit of avoiding the circular logic of attempting to test a hypothesis explaining the causes of a pattern in the same system within which the hypothesis was originally developed. For example, within South America, at least two distinct migratory sub-systems have evolved (Joseph 1997). Extant hypotheses can be evaluated in each sub-system independently.

Available techniques and technologies

The complexity of migration within South America demands an interdisciplinary research approach, incorporating a variety of techniques and technologies (Alerstam and Åkesson 2003, Barlein 2003). What tools can be applied to migration research in South America? New technologies exist that can supply data on diverse temporal scales (between years, months, or days), spatial scales (meters or kilometers), and between levels of biological organization (cellular, organismal, population-level). One particularly exciting new tool is stable isotope analysis, which can be used to determine the origins of migratory individuals (see Hobson 2005 for a review, and Torres Dowdall et al. 2006, in this volume). Base isotope maps do not currently exist for most isotopes throughout the whole of South America, but may be available in the near future.

International collaboration

Because migratory species confront varying constraints throughout the annual cycle (Sillett and Holmes 2002), and since events in one season can exert substantial influence over processes in subsequent seasons (e.g., Marra et al. 1998, Norris et al. 2004), research should be conducted throughout all phases of the annual cycle. This may most easily be accomplished by establishing collaborative international networks of researchers and conservation practitioners (e.g., Barlein 2003). Such associations could standardize methods and share data about the same species and populations. These activities will be essential for advancing the study of patterns and mechanisms (see Stiles 2004 for suggestions and interesting questions), as well as advancing the conservation of populations of migratory species that cross political boundaries.

Research at the individual level

We emphasize the value of collecting individual-specific data (e.g., through colour-banding and genetics). Mechanisms apparent at the population level originate at the individual level; therefore, descriptive studies conducted at the individual level, such as McNeil's (1982) work documenting winter site fidelity in *Elaenia parvirostris*, are particularly useful to guide the development and testing of mechanistic hypotheses.

CONCLUSION

Numerous questions are wide-open lines of research — both descriptive and hypothesis-based — in South America. Much progress has been made on other continents about problems that remain unsolved in South America, such that existing bodies of theory, technologies and methods could be readily applied to research on South American migration. Interesting questions concerning the evolution of migration for which we know little in South America include: (1) biogeography (what is the relationship between speciation rates and migratory behaviour across clades?, how does this relationship compare in South America to other migratory systems?); (2) ecology (what is the winter ecology of Neotropical austral migrants?, what is the relationship between migratory timing and biotic vs. abiotic factors?); (3) physiology (do Neotropical austral migrants employ a similar navigation system as migrants in other systems?, what are the energetic constraints to migration in South America relative to other systems?); (4) life-history (which part of the life cycle is most limiting in terms of reproductive success and survival?, are there carry-over effects for reproductive success between seasons?). The answers to such questions will provide a basis upon which to ask more questions and further develop more detailed, mechanistic hypotheses. Given the complexity that characterizes austral migration, our understanding of New World bird migration will be greatly enriched when we undertake a multidisciplinary approach that incorporates both descriptive and theoretical research to elucidate the origins and maintenance of migratory patterns in South America.

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ANNUAL SURVIVAL OF RED KNOTS (*CALIDRIS CANUTUS RUFA*) USING THE SAN ANTONIO OESTE STOPOVER SITE IS REDUCED BY DOMINO EFFECTS INVOLVING LATE ARRIVAL AND FOOD DEPLETION IN DELAWARE BAY

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ABSTRACT.— Ecological conditions in breeding and non-breeding areas of migrant birds have been linked to their annual survival and production of young, but the role of stopover sites is under-appreciated. Through banding studies and censuses along the flyway from Tierra del Fuego to the Canadian Arctic, the drastic decline in 2000–2001 of Red Knots (*Calidris canutus rufa*) population summering in southern South America in the northern winter was shown to be related to the overharvesting of horseshoe crabs (*Limulus polyphemus*) in Delaware Bay, USA, their last stopover site before reaching their breeding grounds, and to the late arrival of the birds at this site. In San Antonio Oeste, Argentina, where 25–50% of the Tierra del Fuego Red Knots population congregates every northward migration season, annual survival of the cohort of experienced birds banded in March 1998 was impacted a year later than the general decline. Knots marked at San Antonio Oeste earlier in March arrived in Delaware Bay on average before those marked 15 days later. Additionally, early migrating knots with active body moult in San Antonio Oeste exhibited a higher return rate in the following years than late and non-moulting birds. Since the decline, birds arriving late in Delaware Bay have been at increased risk of not being able to refuel properly or on time because food is no longer superabundant at that stopover site. These domino effects indicate that there are fitness consequences to individual migration strategies adopted by birds at austral summering and stopover sites, which can be amplified by compressed timing in Delaware Bay when food is depleted at this final stopover site.

KEY WORDS: Calidris canutus, *domino effects, migration, population decline, Red Knot, stopover ecology.*

RESUMEN. REDUCCIÓN DE LA SUPERVIVENCIA ANUAL DEL PLAYERO ROJIZO (*CALIDRIS CANUTUS RUFA*) EN SU ESCALA MIGRATORIA DE SAN ANTONIO OESTE, ARGENTINA, POR EFECTOS DOMINÓ DE LLEGADA TARDÍA Y DEPRESIÓN DEL RECURSO TRÓFICO EN BAHÍA DELAWARE.— Si bien se ha relacionado la condición de las áreas de estadía no reproductiva y reproductiva de las aves migratorias con su supervivencia y producción de crías, el papel de los sitios de escala como limitante del tamaño poblacional es escasamente conocido. Mediante estudios de anillado y censos a lo largo de la ruta de vuelo desde Tierra del Fuego hasta el Ártico de Canadá, hemos relacionado la drástica declinación de la población de Playero Rojizo (*Calidris canutus rufa*) ocurrida durante 2000–2001 con la sobrepesca del cangrejo herradura (*Limulus polyphemus*) en su última escala en la migración hacia el norte (Bahía Delaware, EEUU) y la llegada tardía de las aves. En San Antonio Oeste, Argentina, donde se congrega el 25–50% de la población de Tierra del Fuego durante la migración al norte, el seguimiento de aves experimentadas de la cohorte anillada en marzo de 1998 permitió estimar que su supervivencia fue afectada un año más tarde que la declinación general. Las aves marcadas más temprano en marzo llegaron antes a Bahía Delaware, en promedio, que las marcadas 15 días después. Además, las aves tempranas con presencia de muda activa de plumaje corporal mostraron una tasa de retorno significativamente mayor en años posteriores que las aves sin muda activa. Desde la declinación, las aves tardías incrementaron el riesgo de no acumular reservas apropiadamente o a tiempo, debido a que el recurso trófico dejó de ser superabundante en Bahía Delaware. Estos efectos dominó indican que las estrategias de migración individuales originadas en las áreas de estadía austral y en los sitios de escala migratoria tienen consecuencias sobre la adecuación biológica y que éstas pueden ser amplificadas por la reducción en el tiempo de estadía en Bahía Delaware cuando el recurso trófico es escaso en este sitio.

PALABRAS CLAVE: Calidris canutus, *declinación poblacional, ecología de escala migratoria, efecto dominó, migración, Playero Rojizo.*

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The role of the condition of birds in non-breeding staging areas, breeding sites, or both in limiting long-term or year-to-year population sizes in migrants has been the subject of many studies in different bird taxa, especially in shorebirds (e.g., Evans and Pienkowski 1984, Evans et al. 1984, Pienkowski and Evans 1985, Newton 2004). In some species, habitats occupied in wintering areas (also known as "austral summering areas" in the Southern Hemisphere) and migration flyways, and their associated food supplies, can influence the body condition, migration dates and subsequent breeding success of migrants (Marra et al. 1998, Drent et al. 2003). Similarly, the numbers of young produced in one region could, through density-dependent processes, affect subsequent overall mortality in another region (e.g., Goss-Custard et al. 1995). Thus, events in breeding, migration and "wintering areas" are interdependent in their effects on bird numbers (reviewed in Newton 2004). Although less is known about long distance migrants, we hypothesize that population size might be limited by intra- or interspecific competition at key stopover sites if they face low food availability, higher predation risk, and increased disturbance or poor quality roosting places.

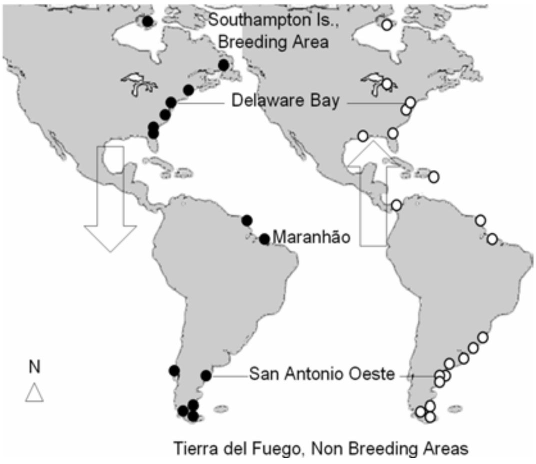

Figure 1. Red Knot flyway depicted on the basis of resightings of individuals colour-banded in Argentina from 1995 onwards. Black dots indicate resighting places during southern migration and white dots during northward migration. Key stopover study sites are indicated (González et al., unpublished data).

One of the best known shorebird species is the Red Knot *Calidris canutus* (Scolopacidae) which has a circumpolar breeding distribution in the Northern Hemisphere comprised of six discrete populations that are recognized as subspecies on the basis of differences in morphometrics and plumage (Piersma et al. 2005). Of these subspecies, *Calidris canutus rufa* travels the longest migration of about 16000 km twice a year between their breeding grounds in the Arctic and their summering (= northern wintering areas) sites in Tierra del Fuego and Patagonian Argentina (Morrison and Harrington 1992, Piersma and Davidson 1992, Harrington 2001, Tomkovich 2001). During their journeys, they congregate at the scarce wetlands extensive enough to support large flocks of birds. Such wetlands occur thousands of kilometres apart in the Atlantic flyway, like San Antonio Oeste at Río Negro Province in Argentina, Rio Grande do Sul and Maranhão in Brazil, and Delaware Bay in USA (Fig. 1).

The majority of adults in the Tierra del Fuego population make a stopover in Delaware Bay every May, and mix with separate populations that spend the non-breeding season in Maranhão in northern Brazil and Florida, respectively (Atkinson et al. 2005, Baker et al. 2005). Until 2000 Red Knots and other migrant shorebirds fed almost exclusively on a superabundant supply of eggs of spawning horseshoe crabs (*Limulus polyphemus*) (Castro and Myers 1993, Tsipoura and Burger 1999), enabling them to store nutrients quickly and almost double their body mass for the final leg of migration to the Arctic breeding grounds. Extra stores are carried not only so that the birds can survive poor weather or lack of food after arrival, which can cause high levels of mortality (Morrison 1975, 2006, Boyd 1992), but also to enable the birds to undergo a series of physiological transformations from a state suitable for migration to one for breeding (Morrison et al. 2005). Beginning in 1990 and peaking in 1995-1996, there was a dramatic increase in commercial fishing to provide bait for eel and conch fisheries (Walls et al. 2002), which resulted in a six-fold decline in the numbers of horseshoe crabs caught in survey trawls in Delaware Bay (S. Michels, unpublished data; cited in Andres 2003). Since 2000, crab eggs are no longer superabundant in Delaware Bay.

Several lines of evidence suggest linkages between events at stopover sites in San Antonio Oeste and Delaware Bay and the breeding grounds. First, studies that captured and colour-banded northbound Red Knots (9851 individuals) in Delaware Bay during each May from 1997 to 2002 showed that fewer Red Knots reached threshold departure masses of 180–200 g (Baker et al. 2004). As the abundance of crab eggs declined from 1997-1998 to 2001-2002, the predicted proportion of well-conditioned knots (200 g or greater) in Delaware Bay near departure time on 28 May decreased significantly by 70% (Baker et al. 2004). In the 2–3 days before the peak departure for the Arctic, mean body masses declined significantly from 183 g in 1997 to 162 g in 2002. Return rates of northbound adults caught in Delaware Bay also showed that Red Knots known to survive to a later year by being recaptured or resighted throughout the flyway were significantly heavier at initial capture than birds never seen again (Baker et al. 2004). Second, emerging evidence suggests that northbound birds from Tierra del Fuego may be arriving in Delaware Bay later in the spring than in earlier years, and that late birds are increasingly delaying departure for the breeding grounds (Baker et al. 2004). Late arrival on the breeding grounds often confers a strong reproductive disadvantage; late arrivals are predicted to have a lower probability of surviving and producing offspring if they attempt to breed. Resights of colour-banded birds showed that arrival time of the Tierra del Fuego birds in Delaware Bay relative to the more northerly summering birds in Florida and Maranhão have differed over time, although in most years the former on average arrive later in Delaware Bay than birds from northern Brazil or Florida. In 2000 and 2001 the highest proportion of Tierra del Fuego birds occurred at or after the peak aerial count, meaning that Florida and Maranhão birds may have departed earlier, or there were more late arrivals from Tierra del Fuego, or both (Baker et al. 2004).

Fitness consequences of reduced adult survival and recruitment are consistent with the alarming decline in population size of Red Knots in Tierra del Fuego from 51 000 to 27 000 in 2000–2002 (González et al. 2004, Morrison et al. 2004); such a rapid decline may seriously threaten the viability of this subspecies. Annual survival of adult birds at Delaware Bay arriving from Tierra del Fuego and northern South America decreased by 37% between May 2000 and May 2001. In addition, annual survival estimated from captured and marked birds (3644 individuals) from 1995 to 2003 in San Antonio Oeste and in Tierra del Fuego declined significantly from an average of 85% in the three migration years from 1994-1995 to 1997-1998 to 56% in the ensuing three-year period to 2000-2001. Recruitment, as measured by the proportion of second-year birds, comprised 19% of annual catches of 500–600 Knots in Tierra del Fuego in 1995, 16% in 2000 and 10% in 2001 (Baker et al. 2004).

In this paper we examine the role of two key stopover sites in the flyway of *Calidris canutus rufa* and assess the possible flow-on or domino effects (Piersma 1987) that can accrue after the birds leave the austral summering sites in Tierra del Fuego and migrate northwards en route to the breeding grounds. These sites are (1) San Antonio Oeste in Argentina, the main stopover site on the coast of Patagonia for Red Knots, where most adults undergo body moult into breeding plumage before undertaking long flights northwards, and (2) Delaware Bay in USA, the critical final spring refuelling site where they must accumulate large stores of nutrients before departing for the breeding grounds in the Arctic. San Antonio Oeste is located at 40°45'S, 64°55'W in Río Negro Province of Argentina, and hosts 25–50% of the total population from Tierra del Fuego during northward migration from late January to April (González et al. 2004). Here the primary food for Red Knots during the day (Sitters et al. 2001) is the mussel *Brachidontes rodriguezi* that they find on a rocky intertidal habitat locally known as "restinga" (González et al. 1996). Specifically, our objectives were to investigate whether habitat conditions and the timing of migration at a stopover site in the southern end of the flyway might be exacerbated by the declining food supplies in Delaware Bay, and the flow-on fitness consequences of decreased refuelling rates on late arriving Red Knots at this penultimate staging site.

METHODS

We analyzed arrival time of Red Knots in Delaware Bay in relation to their banding time

Table 1. Details of Red Knots catches (number of individuals) made at San Antonio Oeste, Río Negro, Argentina, in March, 1998. Retraps indicates knots banded previously in this or other expeditions. Analyses were based only on the 906 colour-banded birds.

Date	Juveniles	Retraps	With standard combination	With individual combination	Total colour marked	Total catch
5 March	5	12	270	33	303	321
13 March	6	5	79	39	118	124
16 March	5	24	241	7	248	280
20 March	5	23	137	17	154	178
28 March	7	10	53	30	83	97
Total	28	74	780	126	906	1000

in San Antonio Oeste. As part of an international research project on Red Knot populations throughout the flyway, a banding expedition to San Antonio Oeste was organized in 1998 (Baker et al. 1999, 2001, Piersma et al. 2005), during which knots were caught with cannon nets in five catches on 5, 13, 16, 20 and 28 March during the peak of migration (n = 1000, Table 1). Age class (juvenile or adult), body mass, body moult activity on the breast, and percentage of breeding plumage were recorded on captured birds. In addition to a metal numbered band most knots (n = 780) were banded with standard combinations of two colour bands and a coloured flag to identify "time cohorts" (distinctive combinations for 5 and 13 March, 16 and 20 March, and 28 March), while 126 birds were marked with individual schemes of orange flag and four colour bands.

In May 1998 we compared the return rates in Delaware Bay of birds previously colour-banded at San Antonio Oeste during the first half ("early cohort": knots colour-banded during 5 and 13 March) and the second half ("late cohort": knots colour-banded during 16 and 20 March) of March 1998. To keep resighting probabilities approximately equal for the two time cohorts the sample from 28 March was not included in the analysis. Three observers regularly carried out scans of the flocks of Red Knots at different sites on the shores of Delaware Bay in New Jersey and Delaware and recorded the numbers of banded individuals relative to the numbers of unbanded birds. To avoid any biases introduced by the visual attraction of colour-banded birds, we made sure that all observed birds received scores as we examined as many different parts of feeding flocks as possible. We analyzed the data for each time cohort using Binary Logistic Regression with dependent variable (1: banded; 0: non-banded) on independent categorical variables (shore, observer) and day as a continuous variable.

In subsequent years from 1999 to 2003, resighting efforts of individually colour-banded adults at San Antonio Oeste were used to estimate annual apparent survival of the "1998 year cohort". The data conformed to Cormack-Jolly-Seber assumptions according to Choquet et al. (2001). Survival analyses were run in Mark 3.2 (White and Burnham 1999) using Cormack-Jolly-Seber models by cohort. Model selection was based on the Akaike Information Criterion. Binary Logistic Regression with logit link and sigma-restricted parameterization was used to analyze the return rate in the six following years (1: seen again, 0: not seen again) from recapture and resighting of banded birds (n = 228) related to the presence of active body moult, percentage of breeding plumage (categorical independent variables), body mass and day of initial capture (continuous independent variables).

RESULTS

Arrival times in Delaware Bay

Return rates in Delaware Bay estimated from resightings or recaptures of both early and late cohorts of Red Knots banded in San Antonio Oeste in 1998 (n = 19884) increased through the season (Day $b = 0.064$, SE = 0.02, $P < 0.001$; Fig. 2), either because birds from the unbanded Maranhão or Florida summering populations were leaving or more banded knots from San Antonio Oeste were present at the end of the season, or both. Despite the similar numbers of birds banded at San Antonio Oeste in both time cohorts, the late cohort had a lower return rate than the earlier banded cohort (Fig. 2), indicating that the late cohort was on average arriving later in Delaware Bay, that at least some birds had not reached the bay by the end of May, or that a higher proportion of the late cohort used sites other than Delaware Bay, or a combination of these factors. Red Knots from San Antonio Oeste were more represented on the shores of Delaware than New Jersey (Shore $b = 0.36$, SE = 0.10, $P < 0.0001$), but the same trend in true detection rates was apparent in both states.

Apparent survival

Because we have shown previously (Baker et al. 2004) that a two time period model (1998-1999 to 2000-2001) was the best-fitting model for the Tierra del Fuego population, we compared this model for the 1998 San Antonio Oeste cohort with another that allowed a one year lag in survival effects between the periods 1998-2001 and 2001-2002. We also computed standard time dependent and constant survival and resighting probability models to check for goodness of fit. The model with the one year lag in the decline of annual survival and with a constant resighting probability was the best model (Table 2A). Annual survival of the San Antonio Oeste 1998 cohort was estimated to drop from 80.3% between 1998 and 2001 to 65.9% between 2001 and 2002, one year after the general population passing through Delaware Bay had suffered a similar drop in annual survival (Table 2B). Although the 95% confidence intervals of the estimates of annual survival in the San Antonio Oeste 1998 cohort model before and after 2001 partly overlap because of the relatively small size of the colour-banded 1998 cohort ($n = 126$), there is no indication of a decline in annual survival before 2001.

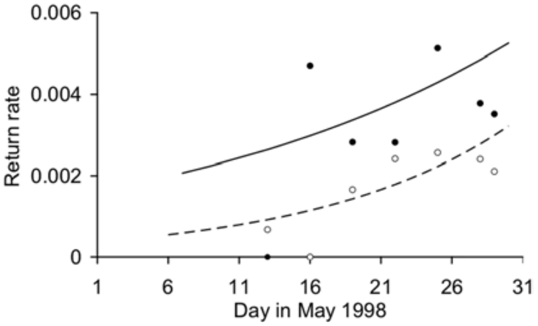

Figure 2. Return rates in Delaware Bay of "early" (filled circles) and "late" (open circles) cohorts of Red Knots banded at San Antonio Oeste, Río Negro, Argentina. The time dependent model of the return rate of colour-banded knots during the first half of March 1998 (early cohort, solid line; $n = 421$, $b = 0.049$, SE = 0.024, $P < 0.043$) is compared with the model for those banded in the second half of March 1998 (late cohort, dashed line; $n = 402$, $b = 0.092$, SE = 0.034, $P < 0.007$). Number of checked birds was 19884.

Variables explaining return rates

The best logistic regression model for return rates of San Antonio Oeste 1998 knots according to the Akaike Information Criterion included the effect of both day of initial capture and presence of body moult they were undergoing ($P < 0.0001$). The probability for a 1998 cohort bird to be seen in the following years was negatively correlated ($b = -0.090$, SE = 0.025) with day of initial capture ($P < 0.0001$), indicating that birds captured late in March were less likely to be seen again than those captured in the early half of the month. Red Knots in body moult had a higher probability of being seen in future years than birds that were not moulting ($b = 4.43$, SE = 0.277, $P < 0.0001$), thereby relating the condition of the bird to an indirect measure of survival. Although percentage of breeding plumage and body mass are indices of body condition and thus we would expect that redder-plumaged and heavier birds exhibit a higher probability of survival, these variables are collinear (positively correlated) with day of initial capture through the season. Thus, a model with percentage of breeding plumage and presence of body moult showed that redder knots had a lower likelihood of being seen in following years ($b = -0.412$, SE = 0.16, $P < 0.01$; number of birds seen again = 57, number of birds not seen again = 171). A model including only body mass and presence

Table 2. Apparent survival of the San Antonio Oeste 1998 cohort from Cormack-Jolly-Seber capture-recapture analysis: (A) model selection, (B) real function parameters of the best-fitting model for individually colour-banded Red Knots. AIC: Akaike Information Criterion, φ: apparent survival, *p*: probability of recapture or resighting, (.): constant model, (*t*): time dependent model, t_1: 1998–2001, t_2: 2001-2002, t_3: 1998–2000, t_4: 2000–2002. Model selection based on correction for over-dispersion with *c*-hat = 1.509.

(A)

Model	AIC *c*	δ AIC *c*	AIC *c* weights	Model likelihood	Number of parameters	Deviance
$\varphi\ (t_1, t_2)\ p\ (.)$	442.3	0	0.2943	1	3	24.14
$\varphi\ (t_3, t_4)\ p\ (.)$	443.4	1.04	0.1747	0.59	3	25.18
$\varphi\ (.)\ p\ (t)$	443.6	1.30	0.1535	0.52	6	19.21
$\varphi\ (.)\ p\ (.)$	444.4	2.06	0.1049	0.36	2	28.25
$\varphi\ (t)\ p\ (.)$	444.4	2.11	0.1026	0.35	5	22.18
$\varphi\ (t_1, t_2)\ p\ (t)$	444.6	2.28	0.0943	0.32	7	18.08
$\varphi\ (t_3, t_4)\ p\ (t)$	445.4	3.09	0.0629	0.21	7	18.89
$\varphi\ (t)\ p\ (t)$	448.6	6.27	0.0128	0.04	9	17.81

(B)

Model	Parameter	Period	Estimate	SE	95% confidence interval
$\varphi\ (t_1, t_2)\ p\ (.)$	φ 1	1998–2001	0.803	0.037	0.721–0.866
	φ 2	2001-2002	0.659	0.112	0.420–0.838
	p	1998–2002	0.508	0.045	0.421–0.595

of body moult as independent variables was not significant for body mass because late cohort knots were heavier than early cohort birds (128.0 ± 0.9 g, $n = 122$, and 123.7 ± 1.0 g, $n = 106$, respectively, mean ± SE; ANOVA: $F_{1,226} = 13.66, P < 0.0003$). However, moulting birds were heavier on average than non-moulting birds (127.2 ± 0.8 g, $n = 191$, and 122.5 ± 1.7 g, $n = 37$, respectively; ANOVA: $F_{1,226} = 6.26, P < 0.0130$). These results suggest that later captured Red Knots stayed later at the San Antonio Oeste stopover site to gain mass and complete the acquisition of redder breeding plumage than did earlier captured Red Knots.

DISCUSSION

Domino effects at stopover sites

Baker et al. (2004) argued that food supplies at Delaware Bay, the last stopover site before the flight to the High Arctic breeding grounds, limited the Patagonian wintering population of Red Knots. The new analyses presented here further suggest that different segments of the population may be differently affected by staging site problems; in particular, the late migration strategy adopted by some individuals is now associated with greater risks of mortality than in the past. Long-distance migrants from the Red Knot population in southern South America are more restricted in their timing of migration into Delaware Bay than are northern populations. On average they arrive later in Delaware Bay than do northerly wintering knots as shown here for the migration season of 1998, when conditions in Delaware Bay were good (see also Baker et al. 2004). In the years of severe food limitation that occurred in Delaware Bay after 2000, we predicted that Red Knots would suffer potentially drastic consequences on survival and recruitment. Prior to 2000, knots refuelling in Delaware Bay departed en masse for the Arctic in the period May 28–30, but as the supply of horseshoe crab eggs was depleted in subsequent years more birds have been delaying their departure by 7–14 days (Baker et al. 2004, pers. obs.). A domino effect between the two stopover sites in San Antonio Oeste and Delaware Bay has thus appeared and been exacerbated mainly by poor refuelling conditions in the final stopover site. Drent et al. (2003:274) emphasized the "critical role of the final take-off site" of Pink-footed Geese (*Anser brachyrhynchus*) as suggested by a positive relationship between en route body condition and subsequent breeding success.

Fitness consequences of individual migration strategies

The migration schedules of the austral summering population in Tierra del Fuego potentially could have fitness consequences, as northbound knots arriving later at their first southern stopover site in San Antonio Oeste on average also arrive later in Delaware Bay and thus have compressed refuelling time and later departure for the breeding grounds. However, arrival timing in San Antonio Oeste could be related to habitat condition in Tierra del Fuego or differences in individual strategies of Red Knots or both, rather than to a limitation from poor quality stopover. This is because day of initial capture at San Antonio Oeste does not necessarily reflect departure date, as some earlier arrivals left in a few days while others remained until the end of the season in April, and thus late arrivals might depart together with some early birds (González et al., unpublished data). The rate of storage of nutrients at the San Antonio Oeste stopover site is around 0.5 g/day (Piersma et al. 2005), which is very low compared with the average 4.6 g/day that knots achieve at Delaware Bay, the highest recorded among the world's subspecies and staging sites (Piersma et al. 2005). Thus, birds departing from San Antonio Oeste in early March are likely to have lower body mass than those that remain until the middle of April. Birds that are minimizing the cost of energy transport are expected to stop at all useful sites along the route to carry the smallest possible fuel loads (Gudmundsson et al. 1991, Alerstam and Hedenström 1998); while our results suggest that early cohort knots in San Antonio Oeste are following this general strategy, late cohort knots in contrast seems to adjust to time-selected migration, where birds should accrue substantial fuel loads to minimize migration time to Delaware Bay.

These differences in individual migratory strategies indicate why body mass could not explain the likelihood of return rates at San Antonio Oeste, whereas at Delaware Bay it is a significant explanatory variable. While Red Knots at Delaware Bay appear more synchronized in migration timing for refuelling and departures because the Arctic breeding grounds are only available during a short period in the year, at San Antonio Oeste Red Knots have a broader window of time where individual strategies can be employed.

Apparent survival estimates for the San Antonio Oeste 1998 cohort indicate that birds in this cohort did not suffer the decline that the average adult passage population in Delaware Bay did between 2000-2001, but instead had a lag until one year later when they had a significant drop in survival. We interpret this to mean that early migrating and experienced birds in the San Antonio Oeste 1998 cohort (whose survivors would have been older than the general population in 2000-2001) were able to avoid mortality better than the general population in Tierra del Fuego which includes younger adult birds, and only were affected late in the population decline.

Role of stopover sites in population limitation

The importance of the last stopover as a refuelling site before departing for the breeding grounds and of late arrival has been shown to have fitness consequences in birds (Alerstam and Hedenström 1998, Madsen 2001, Drent et al. 2003, Morrison 2006). Morrison (2006) found that *Calidris canutus islandica* departing from their last stopover site in Iceland in better than average condition had a higher probability of being seen again following a series of years with difficult weather conditions in the Arctic. This shows that being in superior condition was linked with higher survival; in this case conditions were normal at the final stopover area but the birds encountered unusually difficult conditions on the breeding grounds. The situation in Delaware Bay again demonstrates the link between condition and survival; birds were unable to reach suitable departure condition because of a reduction in the available food supplies resulting in reduced survival. In the Wadden Sea, reduction in food stocks for shorebirds due to overharvesting in the cockle fishery has resulted in a concomitant reduction in bird numbers, providing another example of how human activities can severely impact population sizes in migratory shorebirds (Stroud et al. 2006). Under conditions of food depletion in Delaware Bay there can be a domino effect from the timing of refuelling in southern stopover sites in South America like San Antonio Oeste, as birds arriving late in the USA will then be delayed further in their departure or be underfuelled, resulting in overall lower breeding success and increased mortality in the population. This emphasizes the migratory connectivity of populations of knots at these and other sites as well as the role of individual migration strategies. An integrated flyway-wide approach to management and recovery is required for effective conservation of this rapidly declining population. In the absence of effective management at sites throughout the flyway we can expect the worldwide decline in shorebird numbers to continue, and face the grim prospect of extinction of populations or species at an accelerating rate.

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