# REVERSE MOVEMENTS
# OF RED KNOTS *CALIDRIS CANUTUS*
# DURING NORTHWARD MIGRATION IN ARGENTINA

## VUELOS REVERSOS
## DE CORRELIMOS GORDOS *CALIDRIS CANUTUS*
## DURANTE LA MIGRACIÓN AL NORTE EN ARGENTINA

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SUMMARY.—Migratory birds are sometimes known to make reverse movements to seek better fuelling sites before undertaking long-distance migratory flights across ecological barriers. Red knots *Calidris canutus rufa* regularly make prodigious migratory flights of ~ 8,000 km from southern South America to North America; these flights depend critically on the birds being able to store adequate fuel at southern staging sites. Knots staging at San Antonio Oeste (SAO) in northern Patagonia in Argentina could potentially backtrack ~200 km southwards to complete refuelling at Península Valdés (PV). We therefore analysed resightings of birds individually marked in SAO or the flyway at these two staging sites in 2006, 2007, 2009 and 2010 to investigate whether reverse movements occurred between them. In the four-year period, 63 detected individuals backtracked south from SAO to PV in one or more years. These movements occurred in all years of the study thus demonstrating the annual occurrence of flights of ~200 km in the opposite direction to the normal northward migration. There was no significant difference in body condition (mass), sex or day of first sighting in SAO between birds that made or did not make reverse movements to PV. However, individuals (N = 11) that backtracked to PV from SAO had significantly lower hematocrit levels at the time of capture than SAO resident birds (N = 205). Because migrating shorebirds have been shown to restore low hematocrit levels before undertaking rapid fuel storage to power long flights, we hypothesise that red knots backtracking to PV were probably behind schedule on migration, and thus may have traded-off the small cost of a ~200 km flight for

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the increased foraging time and high quality soft-shell prey available late in the season at PV. This hypothesis helps to explain the later staging phenology of red knots using PV, and its role as an alternative staging area in the northward migration.

*Key words*: Patagonia, Península Valdés, reverse movements, San Antonio Oeste, shorebirds.

RESUMEN.—Las aves limícolas migratorias suelen realizar migraciones reversas con el fin de buscar mejores lugares de abastecimiento antes de realizar vuelos de larga distancia. Los correlimos gordos *Calidris canutus rufa* migran ~ 8.000 km desde el sur de América del Sur hasta América del Norte. Estos vuelos dependen fundamentalmente de que las aves puedan almacenar la energía necesaria en los sitios de escala trófica. Por ello, las aves que realizan una escala en San Antonio Oeste (SAO), norte de la Patagonia, Argentina, podrían potencialmente realizar un vuelo reverso, es decir, en dirección opuesta a la normal dirección de migración hacia el norte, de ~ 200 km hacia el sur para poder completar su alimentación en Península Valdés (PV). En este trabajo se presentan los registros de aves anilladas individualmente en ambos sitios durante las temporadas 2006, 2007, 2009 y 2010 con el fin de investigar si hubo aves que realizaron vuelos desde SAO hasta PV. En el periodo de estudio, 63 individuos realizaron un vuelo reverso desde SAO a PV en uno o varios años. No hubo diferencias significativas en la masa corporal, sexo y primer avistamiento en SAO, entre las aves que realizaron el vuelo reverso a PV y las que no. Algunos de ellos (N = 11) tenían niveles de hematocritos significativamente más bajos en el momento de ser capturados en SAO que las aves que no realizaron el vuelo reverso (N = 205). Las aves limícolas necesitan restaurar sus niveles de hematocrito antes de emprender un vuelo de larga distancia. Por ello, es probable que los correlimos gordos realicen un corto vuelo hasta PV para aprovechar las presas disponibles en este sitio hacia el final de la temporada de alimentación. Esta hipótesis podría explicar la fenología tardía de los correlimos gordos en PV, y su papel como área de escala alternativa en la migración hacia el norte.

*Palabras clave*: aves limícolas, migración reversa, Patagonia, Península Valdés, San Antonio Oeste.

INTRODUCTION

Migrating birds sometimes fly from a few to thousands of kilometres in different or opposite directions to normal (Richardson, 1982; Åkesson *et al*., 1996; Thorup, 1998), a phenomenon known as reverse migration (Åkesson, 1999; Komenda-Zehnder *et al*., 2002). Migrating birds with low fuel stores may make reverse flights to obtain more resources before crossing ecological barriers such as the open ocean (Alerstam, 1978). Orientation errors, effects of wind drift, responses to unsuitable weather, competition, low food availability and physiological state have also been suggested as possible explanations for deviations from normal migratory flight paths, including reverse movements (Richardson, 1978; Sandberg,

1994; Åkesson *et al*., 1996; Åkesson, 1999; Komenda-Zehnder *et al*., 2002). Red knots (*Calidris canutus rufa*) fitted with geolocators (N = 50 with migration tracks downloaded after recapture) were found to make long-distance flights of up to 8,000 km during northward migration, but the only deviations detected were to avoid weather conditions during migration to or from wintering sites in Tierra del Fuego (R. R. Porter, pers. comm.).

During migration from Tierra del Fuego to breeding sites in the Canadian Arctic, the first major stopover sites for red knots are San Antonio Bay at San Antonio Oeste (SAO) and Península Valdés (PV) (fig. 1) on the coast of Patagonia, Argentina (González *et al*., 1996; Bala *et al*., 2001). Evidence from resightings and geolocators show that from

these sites, red knots either make short flights to southern Brazil or long flights to northern South America or the United States, depending on their fuel stores (Harrington *et al.*, 1986; Vooren and Chiaradia, 1990; Morrison and Harrington, 1992; Niles *et al.*, 2010a). Although the SAO and PV staging sites are relatively close (~200 km apart) and regular back and forth movements between them might be consistent with a large home range of the birds, reverse movements during the northern migration to another staging site can be discerned if they are predominantly unidirectional to the south from SAO. At the population and individual level, these movements may indicate that both sites function to ensure adequate refuelling and survival during long migratory flights. Although passerines are known to sometimes make reverse movements to complete refuelling before long flights (Alerstam, 1978), additional studies are needed to determine if this occurs in non-passerines, and whether differences in migration timing of individuals are due to sex and condition-dependent variables during fuelling, such as body mass
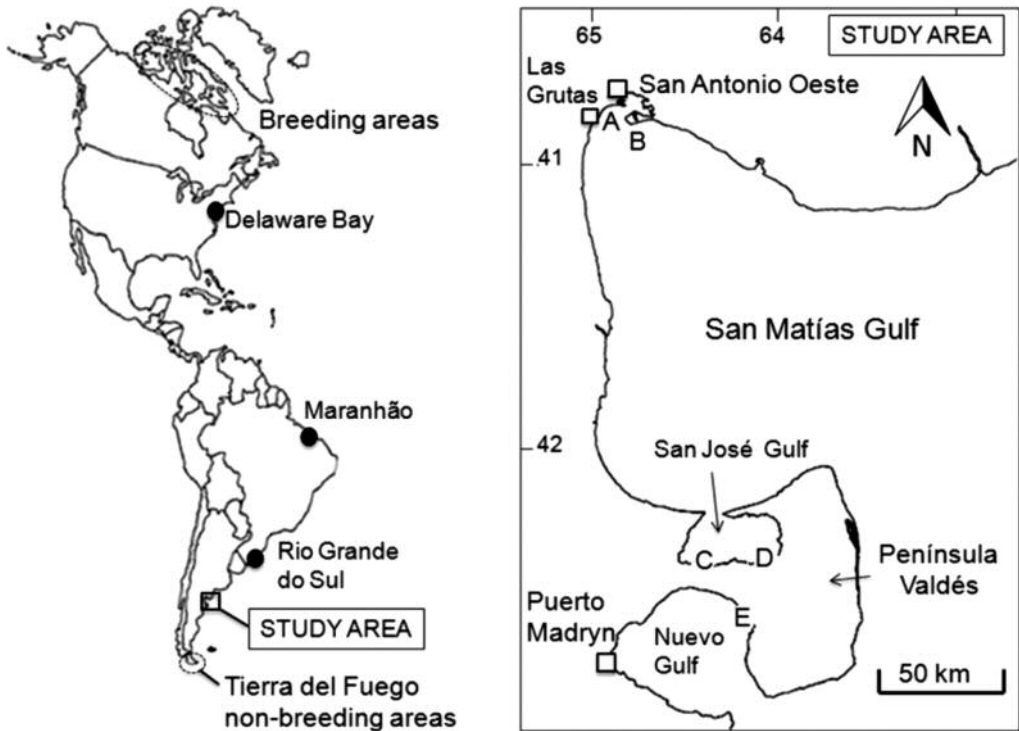


FIG. 1.—Location of the study area and main staging sites during northward migration of red knots (left map). Sites used by red knots at San Antonio Oeste and Península Valdés: A) Los Alamos and Banco Reparo, B) Banco Lobos, C) Blancas Beach, D) Fracasso Beach and E) Colombo Beach (right map). *[Situación del área de estudio y sitios principales de parada durante la migración hacia el norte de los correlimos gordos (mapa de la izquierda). Sitios utilizados por los correlimos gordos en San Antonio Oeste y Península Valdés: A) Los Alamos y Banco Reparo, B) Banco Lobos, C) Playa Blancas, D) Playa Fracasso y E) Playa Colombo (mapa de la derecha).]*

and hematocrit at initial capture. We predict that long-distance migrant shorebirds like red knots in southern Argentina also might make reverse movements to sites if they are in poor body condition and need to complete refuelling within a short period. Here we describe the association between these variables and reverse movements to normal northward migration in red knots at staging sites prior to long flights across ecological barriers such as the Amazonian rainforest and the Caribbean Sea.

MATERIAL AND METHODS

*Study sites*

Our study was conducted during the northward migration of red knots in 2006-2010 at two sites ~200 km apart on the coast of Patagonia, Argentina: the provincial Protected Natural Area of San Antonio Bay at San Antonio Oeste (64° 55' 0, 40° 45' S in Río Negro Province), and the provincial Protected Natural Area of Península Valdés (63° 61' 0, 42° 31' S in Chubut Province; fig. 1). About 25-50% of the Tierra del Fuego austral oversummering population (González *et al*., 2004) (~17,000 birds during the study period; Niles *et al*., 2010b) refuels at the SAO staging site from February to early May, and at least 7.5% stopover at PV from March to early May (D'Amico *et al*., 2006; Musmeci *et al*., 2012). At SAO, birds use feeding and roosting sites in an area around the beaches of Los Alamos, Banco Reparo and Banco Lobos, flying up to 25 km between sites (Sitters *et al*., 2001). At PV, birds use beaches on the northern (San José Gulf: Blancas and Fracasso beaches) and southern (Nuevo Gulf, Colombo Beach) sides of the peninsula that are ~30 km apart (fig. 1). Both sites have semidiurnal tides of large average amplitudes (8.04 m at SAO and 6.14 m at PV) that differ in timing by 6 h, exposing ex-

tensive intertidal areas where red knots feed on marine invertebrates, mainly bivalves (González *et al*., 1996; Hernández *et al*., 2007; Musmeci *et al*. 2012).

*Resighting individuals*

From 2006-2010, birds that were individually marked by us in SAO or in Tierra del Fuego (Río Grande), or by international teams in Chile (Bahía Lomas), USA (New Jersey and Delaware) and Mingan in Quebec, were resighted in SAO and PV by the authors (95% of observations) and up to six other experienced observers (5% of observations) using 20-60 X spotting scopes. The individual marks consisted of colour band combinations or flags engraved with a unique alphanumeric code. Flocks were scanned repeatedly at a distance of 50-100 m when the birds were coming or leaving the high-water roosts, and when feeding on exposed intertidal flats where both legs were in view. Scanning sessions typically lasted 2-6 hr or ended when the flock moved to another site. At SAO, birds were resighted almost every day from February to early May at three feeding and roosting sites at Los Alamos, Banco Reparo, and Banco Lobos (fig. 1), whereas they were observed at Fracasso, Blancas and Colombo beaches at PV (fig. 1) on two or three days per week during the same period since this was sufficient to scan the smaller number of birds at this site. The number of resightings per day was recorded, excluding duplicate observations of the same bird within each day.

Most individuals were marked with orange flags, colour bands or both at SAO in March 1998, 2003 and from March 2006-2010 (N = 1057) or at Río Grande from November-December 2000-2009 (N = 2350). Although 16,151 red knots were marked with flags at Delaware Bay from May 2003-2008 (McGowan *et al*., 2011), they constituted

only 27.5% of the resighted birds seen at our study sites. Small numbers of birds with inscribed red flags were also banded in Bahía Lomas in Tierra del Fuego (Chile) from January-February 2004 onwards (N = 540), and with inscribed white flags in Quebec in July-August 2008-2009 (*N* = 189).

*Body condition and hematocrit*

To investigate whether body condition may influence reverse movements, we determined the body mass of adult birds (> 2 years old) captured at SAO. Using cannon-nets, we captured a total of 798 red knots in March 2006-2010 (table 1). Body mass (± 1 g) and bill length (± 1 mm) were recorded for all birds by AJB. A body condition index was derived from data on body masses that were standardised to a mean of zero independently for yearly catches by subtracting the year mean from each datum and dividing by the standard deviation, thus allowing the pooling of body masses from different years. To control for differences in body size in the condition index, the respective bill lengths of each bird were included as a covariate in an analysis of covariance (ANCOVA, Garcia-Berthou, 2001). Bill length was selected to represent the size of individuals as it can be measured accurately, and has a significant correlation with standardised body mass (r = 0.347, p < 0.0001). Blood samples (0.1 ml) were taken from the brachial vein and stored in 95% ethanol, for molecular sexing of 583 of 798 adults that were captured. Sex was determined using methods outlined by Fridolfsson and Ellegren (1999), but using red knot-specific primers that avoid misleading amplicon patterns that can occur in shorebirds (Casey *et al.*, 2009). Birds were sexed in each year of the study (table 2). In addition, hematocrits (percentage volume of red blood cells in blood) were determined for some birds captured from 2006-2008 and

in 2010 (table 1). Blood was spun in a microcapillary tube in a hematocrit centrifuge for 12 minutes at 12,000 *g* to compact the red blood cells, and hematocrit was determined by measuring red cells and total samples with a microhematocrit ruler (J. P. Selecta, Abrera, Spain) calibrated in %. All hematocrit measurements were made by one person (VLD). Hematocrit in birds can also be considered an index of condition when evaluated with other hematological parameters and body mass (Fair *et al.*, 2007), due to potential variation associated with season, sex, energy needs or disease that might confound interpretation. In our study, we simply wanted to test whether there were differences in hematocrit in birds that might make reverse movements, where these same factors might affect the timing of migration. Hematocrit data in 2006 (N = 52) and 2007 (N = 23) were reported by D'Amico *et al.* (2009), and we also determined hematocrits for another 79 and 62 birds in 2008 and 2010, respectively, using the same methods.

*Statistical analyses*

Staging phenology at SAO and PV

To investigate whether there was differential timing of the birds between SAO and PV, we used a Mann-Whitney U test with day of first resighting as the dependent variable and location (SAO or PV) as a group. To address independence between samples we assigned the birds seen both at SAO and PV (N = 73) to the smaller PV sample.

Effects on movements from SAO to PV

We conducted three different analyses for sex, standardised body mass and hematocrit because of the unbalanced sampling design, and the need to use resighting data or catch

data to maximise sample size. To test whether there was a sex effect (as factor) and day effect (as continuous predictor) in birds moving from SAO to PV in the same year we used the Generalised Linear Model/Nonlinear Model module (GLZ) in Statistica with logit link function for appropriately modelling the binomial response variable (observed in PV or not) on the resighting data in SAO. To satisfy independence assumptions we used a single resighting per bird at the day of its first resighting in SAO.

Possible effects on the body condition index (as dependent variable), using bill length as a continuous covariate to control for body size, day of sampling in SAO and the reverse movements to PV by birds captured at SAO in the same year (as binary factor: observed in PV or not), were tested with ANCOVA in GLZ with log link. Model building was carried out using the forward stepwise method.

Because the sample of birds with hematocrits was much smaller (N = 216) than for body mass (table 1), we used a separate GLZ with log link function to test whether hematocrit differed between birds making reverse

movements from SAO to PV or not, and the possible effect of day of sampling in SAO. Statistical analyses were conducted using Statistica 8 software (StatSoft Inc., 2007).

RESULTS

*Resightings of birds marked in the hemispheric flyway and in SAO*

At SAO, the number of resightings of birds marked in the hemispheric flyway was highest in March and April, contrasting with a later peak of resightings in April at PV (fig. 2A). Comparison of the overall resighting distribution of individuals in SAO and PV, based on the day when birds were first resighted, showed migration phenology was significantly later at PV than at SAO (Mann-Whitney U test, U = 59719, Z = –14.28, P < 0.0001, SAO N = 2240, PV N = 162). We detected 83 marked birds at both SAO and PV in either the same year or different years, representing 50.9% of all 162 flagged birds observed at PV (table 3) or 3.6% of the 2,314 flagged birds observed at SAO. Thus

TABLE 1

Sample details for catches, body mass, bill length and hematocrit at San Antonio Oeste. Sample sizes at Península Valdés are shown in parenthesis.
*[Detalles del muestreo de las capturas, masa corporal, longitud del pico y hematocrito en San Antonio Oeste. Los tamaños muestrales en Península Valdés se muestran entre paréntesis.]*

| Date | N Caught | N Body Mass and Bill length | N Hematocrit |
|---|---|---|---|
| March 28, 2006 | 224 | 219 (13) | 52 (4) |
| March 22, 2007 | 148 | 148 (8) | 23 (5) |
| March 26, 2008 | 86 | 84 (0) | 79 (0) |
| March 30, 2009 | 138 | 138 (1) | 0 (0) |
| March 30, 2010 | 202 | 201 (3) | 62 (2) |

only a small proportion of the birds in SAO actually changed their staging sites in different years, but they represent about half of the birds resighted in PV. Sixty-three of the 83 detected birds (75.9%) moved from SAO to PV in one or more years (fig. 2B) and were seen at PV in the same year from 0 to 60 days after the last resighting in SAO (median = 18 days, 25% quartile = 9, 75% quartile = 28 days); these southward movements occurred during each year of our study (table 3). Two of the 83 birds (2.4%) moved from PV to SAO, eight (9.6%) moved between SAO and PV more than once in the same year, and ten (12%) were seen only in SAO or PV in different years.

Southward movements by adult red knots captured and banded at SAO included 13 of 224 (5.8%) caught in 2006, eight of 148 (5.4%) in 2007, one of 138 (0.7%) in 2009, and three of 202 (1.5%) in 2010. These birds were resighted at PV in the same year from 6 to 41 days after capture at SAO (median = 24, 25% quartile = 13, 75% quartile = 31, N = 25), including two birds observed back at SAO seven days after being observed at PV in 2006 and 2009, respectively.

Birds that moved from SAO to PV in the same year were seen largely in March at SAO, with a mode on April 18 at PV (fig. 2B, white bars). However, in other years when birds observed previously at SAO were seen only
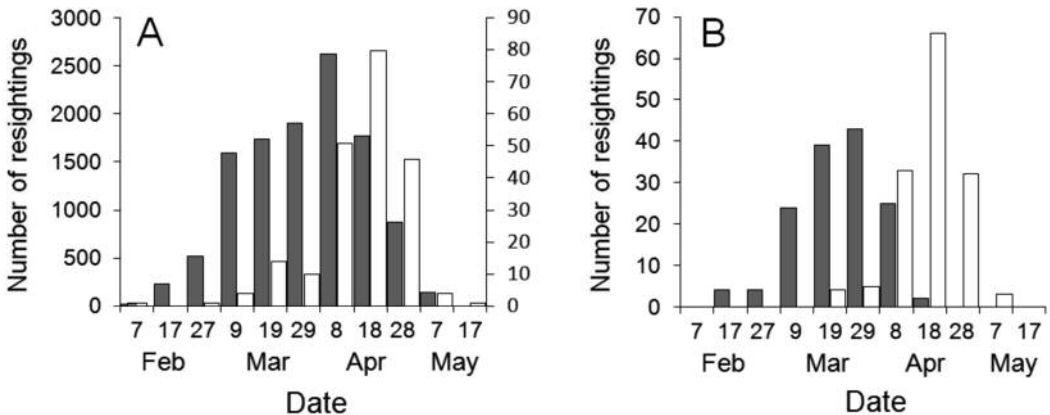


FIG. 2.—Total number of resightings by 10-day intervals of individually marked red knots seen at San Antonio Oeste (SAO, grey bars) and Península Valdés (PV, white bars) during 2006, 2007, 2009 and 2010 northward migrations. Same-day resightings of the same individual were removed. A) Number of resightings (11,803 from 2,314 different individuals) at SAO (left axis) and at PV (448 from 162 different individuals) (right axis) during the study period. B) Number of resightings of birds that moved from SAO to PV in the same year, comprised by 63 individual birds seen earlier at SAO (141 resightings) and later at PV (143 resightings).

*[Número total de reavistamientos en intervalos de 10 días en San Antonio Oeste (SAO, barras grises) y Península Valdés (PV, barras blancas) durante las migraciones hacia el norte en 2006, 2007, 2009 y 2010 de correlimos gordos marcados individualmente. Se descartaron los duplicados diarios de un mismo individuo. A) Número de reavistamientos (11.803 de 2.314 individuos diferentes) en SAO (eje de la izquierda) y en PV (448 de 162 individuos diferentes) (eje de la derecha) durante el periodo de estudio. B) Número de reavistamientos de aves que se movieron en el mismo año de SAO a PV, lo que incluye a 63 individuos que se observaron primero en SAO (141 reavistamientos) y después en PV (143 reavistamientos).]*

TABLE 2

Sample details of individually marked red knots that were sexed from San Antonio Oeste (SAO) and Río Grande in Tierra del Fuego (TDF), and the number of sexed birds that were resighted in SAO (N = 920) and Península Valdés (PV, N = 83) in the study period.
*[Detalles del muestreo de correlimos gordos individualmente marcados que fueron sexados en San Antonio Oeste (SAO) y Río Grande en Tierra del Fuego (TDF), y número de aves sexadas que fueron reavistadas en SAO (N = 920) y Península Valdés (PV, N = 83) durante el periodo de estudio.]*

| Year | During the study period in SAO (March) | | Before the study period in SAO (March) | | At Río Grande in TDF (Nov-Dec) | |
|---|---|---|---|---|---|---|
| | N sexed | N seen | N sexed | N seen | N sexed | N seen |
| 1998 | | | 67 | 18 | | |
| 2000 | | | | | 16 | 3 |
| 2001 | | | | | 3 | 2 |
| 2002 | | | | | 99 | 16 |
| 2003 | | | 107 | 30 | 162 | 28 |
| 2004 | | | | | 270 | 48 |
| 2005 | | | | | 109 | 46 |
| 2006 | 104 | 98 | | | 224 | 77 |
| 2007 | 157 | 144 | | | 272 | 67 |
| 2008 | 76 | 61 | | | 136 | 38 |
| 2009 | 134 | 105 | | | 176 | 50 |
| 2010 | 195 | 172 | | | | |
| **Total** | 666 | 580 | 174 | 48 | 1467 | 375 |

at PV, they were resighted earlier with a mode on 8 April coinciding with the mode at SAO (fig. 2A, grey bars).

*Reverse movements and individual condition*

The GLZ testing for effects of sex and day of first sighting showed that neither sex or day were significant between birds that stayed in SAO (N = 920) or moved to PV (N = 52) in the same year (table 2; for sex Wald statistic = 0.372, P = 0.542, for day Wald statistic = 0.078, P = 0.078). Standardised body mass at capture was positively correlated to bill length (Wald statistic = 46.67, slope: 0.60 ± 0.09, P < 0.000001), but no differences in body mass with day of sampling (Wald statistic = 0.152, P = 0.696) and between birds that did (N = 25) and did not move (N = 765) from SAO to PV in the same year (Wald statistic = 0.017, P = 0.895) were found. However, for the sample of birds

Number of resightings of individual red knots at Península Valdés (PV) during the study period, including individuals that moved south from San Antonio Oeste (SAO).
*[Número de reavistamientos de correlimos gordos individulales en Península Valdés (PV) durante el periodo de estudio, incluyendo individuos que se desplazaron desde San Antonio Oeste (SAO).]*

| Year | N resightings | N individuals resighted | N individuals moved from SAO to PV | % individuals resighted |
|------|------|------|------|------|
| 2006 | 197 | 78 | 25 | 32.1 |
| 2007 | 110 | 45 | 21 | 46.7 |
| 2009 | 44 | 39 | 9 | 30.0 |
| 2010 | 97 | 64 | 33 | 51.6 |
| **Total** | 448 | 162[*] | 63[*] | |

[*] Some birds were resighted in more than one year

on which hematocrits were taken at capture the GLZ showed a highly significant effect (Wald statistic = 24.7, P = 0.00001) for day of sampling (coefficient = 0.012, SE = 0.002) and between birds that did (N = 11) or did not move (N = 205) from SAO to PV (Wald statistic = 9.677, P = 0.001; fig. 3).

DISCUSSION

The flyway of *rufa* red knots in the western hemisphere is one of the longest in the world (~15,000 km), and our research took place at two staging sites used during northern migration prior to short or long-distance (jump) flights between South and North America. Resightings during four northward migration seasons of individually marked red knots in northern Patagonia, Argentina, established the previously unknown behaviour of reverse movements of ~200 km from staging sites at SAO to sites at PV. These sites differ in northward migration phenology, with migration occurring significantly later at PV. Birds making reverse movements southwards from
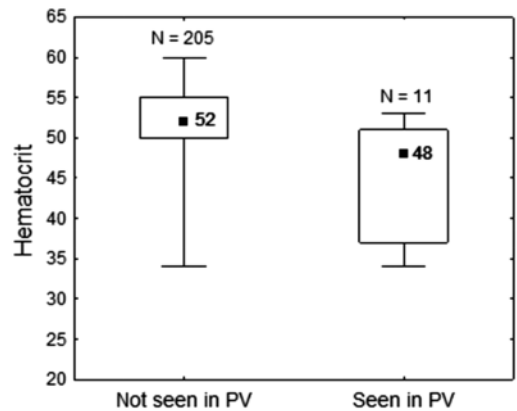


FIG. 3.— Box plot of hematocrit in red knots making or not making reverse movements from San Antonio Oeste to Península Valdés. Medians are shown as filled squares, quartiles by vertical rectangles and ranges by vertical lines. Numbers above bars indicate sample sizes.
*["Box plot" del hematocrito en correlimos gordos que hicieron o no hicieron movimientos reversos de San Antonio Oeste a Península Valdés. Las medianas se representan por cuadrados negros, los cuartiles por rectángulos verticales y los rangos por líneas verticales. Los tamaños muestrales se indican sobre las barras.]*

SAO appear to follow the later stopover phenology of red knots at PV, and there is only a low incidence of return flights to SAO (8 of 83 birds in 2006-2010). We therefore hypothesise that this more southern site provides an alternative foraging site late in the season for birds on later migration schedules. The mode of resightings at PV around April 20 occurred when numbers had been largely depleted at SAO by northward departures (fig. 2A). Flight behaviour in migratory birds, including "long jump" shorebirds like red knots, may be related to finding optimal feeding grounds for efficient acquisition of needed body stores before departure; birds in poorer condition in April, for instance, might not be able or prepared to undertake a flight to the next staging site, and might therefore move to alternative sites to find food resources (see Newton, 2008). The small number of individuals that made reverse movements to PV had similar body condition indices to other red knots when captured earlier in March at SAO, up to about one month after arrival from the migratory flight from Tierra del Fuego. However, at this time in the annual cycle red knots are in active body moult into breeding plumage (Piersma *et al*., 2005) and are unlikely to be in the rapid refuelling phase before departure to other staging sites such as Delaware Bay (Atkinson *et al*., 2007). Most red knots seemed to refuel adequately with food resources at SAO for short northward "hops" or long "jumps", and thus had no need to backtrack to PV.

Of 83 individuals seen both at SAO and PV, only 11 had been sampled for hematocrit, and they had significantly lower hematocrit levels than birds that remained at SAO (N = 205). The significant day effect for hematocrit in the nine-day period that catches were made in SAO each year from March 22-30 indicates that many birds were increasing their hematocrit before they began storing nutrients for northwards migration.

The lower hematocrits in birds that later moved south to PV therefore suggests that they were probably on later migration schedules than birds that stayed in SAO. To our knowledge, this is the first time that reverse movements on northward migration might be linked to migration phenology of late schedule birds, but larger samples are clearly required in the future to verify this finding. However, lower hematocrits in birds can be indicative of nutritional stress (Campbell, 1995; Buehler *et al*. 2009). For example, lightweight bar-tailed godwits *Limosa lapponica* that arrived late in the Dutch Wadden Sea were nutritionally stressed judging from an absence of contour feather molt, and had lower hemoglobin and hematocrit levels than earlier arriving birds. Late arriving birds therefore had to increase hemoglobin and hematocrit in the latter half of the staging period, as high red cell concentrations are required for the rapid refuelling phase prior to long distance migratory flights (Piersma *et al*., 1996). Moreover, experiments on captive red knots demonstrated that a six hour food limitation per day caused a statistically significant decline in body mass and hematocrit (Buehler *et al*., 2009). Red knots in SAO that had lower hematocrits and were not yet in the rapid refuelling phase 1-2 weeks before departure, potentially could benefit by making the southwards movement from SAO to PV where the phenology of the stopover period is delayed (fig. 2A).

The main prey (~80%) of red knots refuelling at the stopover sites in SAO is the mussel *Brachidontes rodriguezi* (González *et al*., 1996), whereas the presence of red knots at PV occurs during the peak in abundance and condition of the clam *Darina solenoides* (Musmeci *et al*., 2012). In oceanic beaches at PV this species of clam has twice the biomass/shell mass ratio of mussels growing on the rocky platforms called restinga at SAO (Hernández *et al*., 2004), and thus PV offers an opportunity to refuel rapidly later in the

season. Another additional benefit for birds foraging on intertidal clams at PV is that the potential daily foraging window is increased by about two hours due to the six-hour difference in tidal cycles between San José Gulf and Nuevo Gulf (fig. 1). This allows birds to move from one gulf where the tide is rising or high to feed in the other as the tide falls (Bala *et al.*, 2001), and thereby to maximise food intake. In contrast, red knots at SAO do not have this option because the rising tide more synchronously covers their feeding areas. Because red knots ingest bivalves whole, intake rates are constrained by the amount of shell that their gizzard and intestines can process, which in turn enlarges during the rapid refuelling stage to increase mass gain (Van Gils *et al.*, 2003). In the week before departure from staging sites on long-distance flights of thousands of kilometres, however, their stomach and liver are reduced in mass, resulting in their digestive capacity becoming more limited (Piersma *et al.*, 1999a, b). Thus, it may be advantageous for the small numbers of SAO birds that are time-constrained and on a later migratory schedule to spend ~3 g of body mass/stores to fly ~200 km to PV (based on a flight speed of approximately 60 km/h and fuel use of ~0.83 g/h as calculated by Pennycuick and Battley (2003) for the closely related great knot *C. tenuirostris*). In PV they potentially could increase their intake rate by eating thinner-shelled food during a wider daily window of foraging time, as has been demonstrated in red knots in the Dutch Wadden Sea (Van Gils *et al.*, 2005a, b).

The southward movements that we report in this study were repeated by some individuals in more than one year, in contrast with reverse movements of passerines and non-passerines detected with radar in response to abnormal circumstances unfavourable for migration such as severe weather (e.g. Richardson, 1978; Komenda-Zehnder *et al.*, 2002). During the stopover periods in our four-year study in Patagonia, we encountered no severe storms with freezing temperatures or gale force northerly winds in SAO that might have caused some birds to fly south to PV. Tests on pathogens (avian influenza, Newcastle disease virus, St. Louis encephalitis virus and avian malaria), conducted on captured red knots in SAO were negative before and during the study (D'Amico *et al.*, 2007; V. D'Amico *et al.*, unpublished), so this factor can also be discounted as a cause for reverse movements to PV. Instead, we hypothesise that the relatively small percentage (3.4%) of red knots captured or resighted at SAO that flew southwards to PV from SAO during the northward migration in 2006-2010 were probably behind schedule, and thus traded-off the small cost of a ~200 km flight for the increased foraging time and higher quality soft-shell prey late in the season in PV. This hypothesis helps to explain the later staging phenology at PV, and its role as an alternative staging area late in the northward migration. Furthermore, our results indicate that multiple stopover sites are likely required to maximise the number of red knots in the southernmost wintering population that make the arduous 15,000 journey to the breeding sites in the Canadian Arctic. Conserving only one of these sites would probably have fitness consequences for individuals in this declining population in southern South America, and reduce the number that could make a full migration.

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