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Migration of endangered Red Knots *Calidris canutus rufa* in Uruguay: important sites, phenology, migratory connectivity and a mass mortality event

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Dedication – Joaquín Aldabe, Pablo I. Rocca, Patricia M. González and Diego Caballero-Sadi dedicate this paper to the memory of the late Allan J. Baker of the Royal Ontario Museum, Toronto, Canada, who with infectious enthusiasm instigated, facilitated and supported studies of Red Knots in Uruguay.

Southern populations of Red Knots *Calidris canutus rufa* have suffered a dramatic decline since the year 2000. Although knots are one of the best known shorebird species in the Western Hemisphere, little is known about them in Uruguay. However, in 2007 the discovery of at least 312 dead knots at La Coronilla on the northern Atlantic coast of Uruguay attracted international attention to this part of the flyway. Here we present historical information gathered from museum collections, local ornithologists and literature to identify high-priority sites, as well as abundance and dates of occurrence of Red Knots along the Uruguayan coast. Information is also presented regarding the mortality event in 2007.

To establish the current role of Uruguay in the Red Knot flyway, we also investigated phenology, minimum length of stay, connectivity with nearby Argentinian and Brazilian sites, and habitat use at a main Uruguayan site during northward migration from 2009 to 2011 and in the austral summer in 2007. We identified 96 historical records from 10 localities where Red Knots were detected at least once in the period 1951–2008. The number of birds per record ranged from 1 to >2,000, but most observations (*ca.* 80%) ranged from a few to 100 birds. The sites with more records of Red Knots and the highest counts were relatively flat sandy beaches of the dissipative morphodynamic type, which have a higher abundance of potential prey for Red Knots (especially Wedge Clams *Donax hanleyanus*), for instance Barra del Chuy beach, near the Brazilian border.

Most historical observations occurred during northward migration in late austral summer and fall. The maximum count at Barra del Chuy was 1,191 birds in April 2010. However, very few birds were recorded in 2011. Median minimum length of stay of individually color-marked birds that were seen on at least two days was estimated as 5 days (range: 2–26 days). Several individual birds were observed on both sides of the Brazil-Uruguay border, suggesting that Rio Grande do Sul (Brazil) and Barra del Chuy (Uruguay) should be treated as a single staging area. Resightings of Red Knots banded at Río Grande (Tierra del Fuego non-breeding site) and San Antonio Oeste (a Patagonian stopover area) in Barra del Chuy, suggest that Rio Grande do Sul-Barra del Chuy and San Antonio Oeste function as

Keywords

Red Knot

Calidris canutus rufa

migration

stopover

conservation

mortality

parasite

Uruguay

independent moulting and fuelling areas for Red Knots en route north from Tierra del Fuego. Potential threats to the species in Uruguay are related to artificial freshwater discharge from rice fields negatively affecting Wedge Clams and other macrofauna, harmful algal blooms, and possible wind turbine establishment close to the coastline. Mass-mortality events were not recorded during the study period, and the cause of the mortality event that occurred in 2007 could not be determined.

INTRODUCTION

In recent years, systematic counts have shown a drastic decline of *rufa* Red Knots at their non-breeding areas in southern South America. In 2003, counts were about 30,000 compared to 67,500 in the mid-1980s (Morrison & Ross 1989, González *et al.* 2004, Morrison *et al.* 2004), decreasing to 13,000 in January 2012 (Andres *et al.* 2012). Local decreases have also been reported in Patagonia and Rio Grande do Sul (Baker *et al.* 2005, COSEWIC 2007, Niles *et al.* 2008). The reason for this decline was a drastic reduction of their main food resource Horseshoe Crab *Limulus polyphemus* eggs in Delaware Bay, USA (Castro

(a)

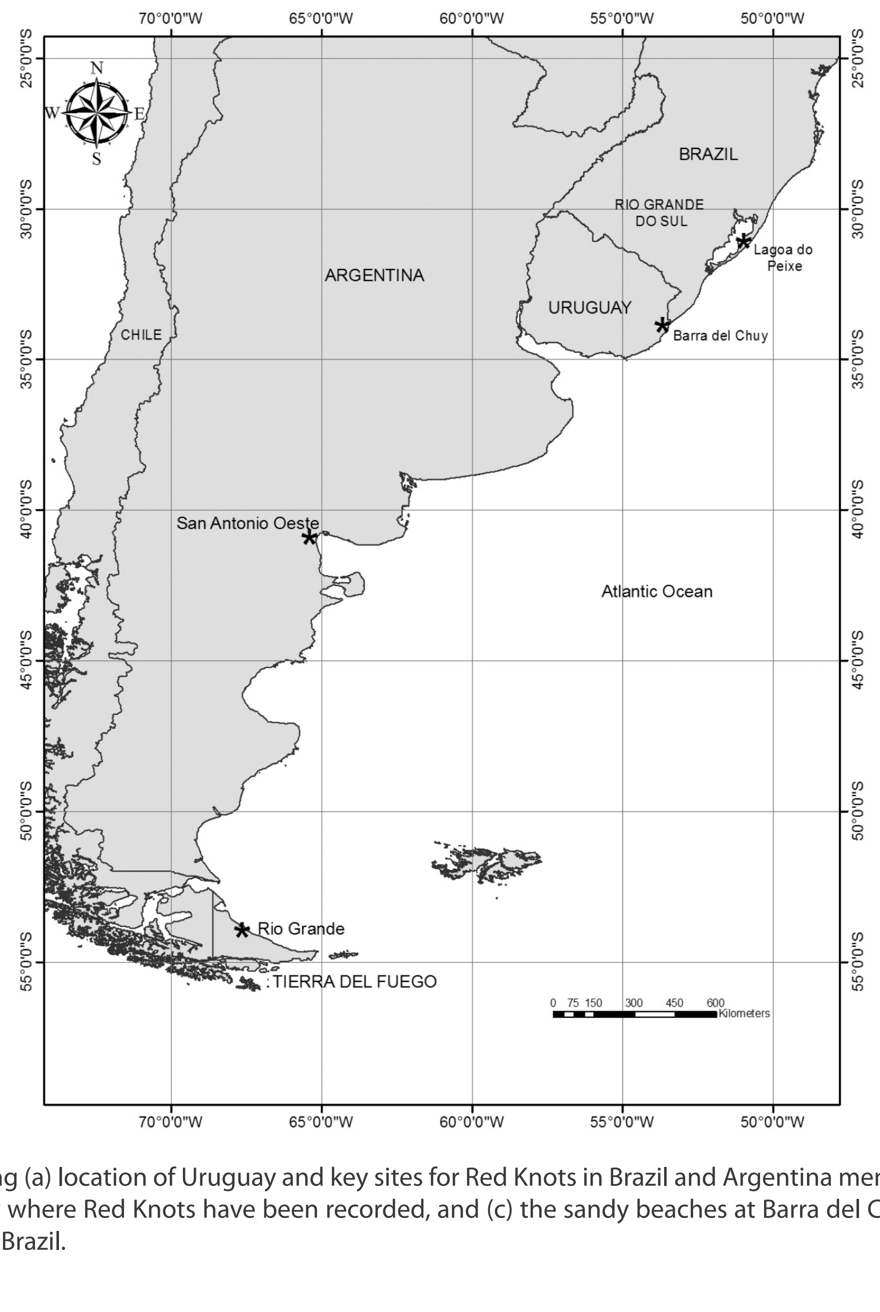
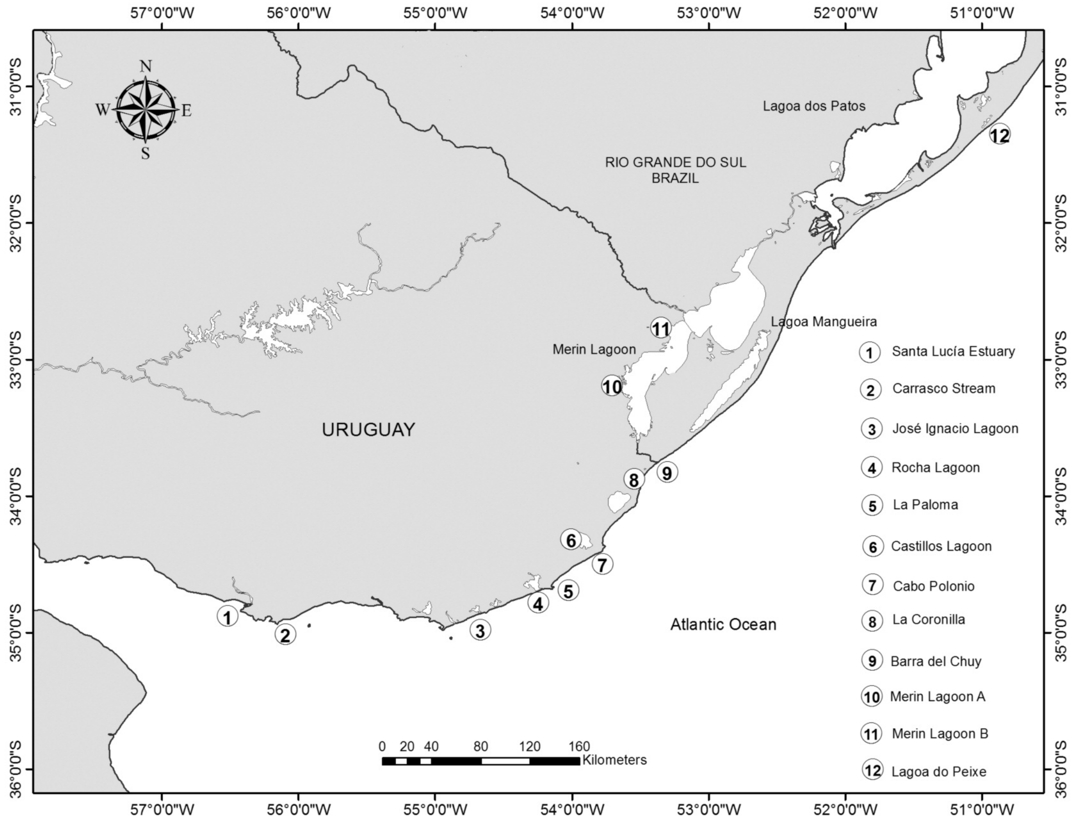


Fig. 1. Maps showing (a) location of Uruguay and key sites for Red Knots in Brazil and Argentina mentioned in the text, (b) sites in Uruguay where Red Knots have been recorded, and (c) the sandy beaches at Barra del Chuy, Uruguay, and nearby in southern Brazil.

(b)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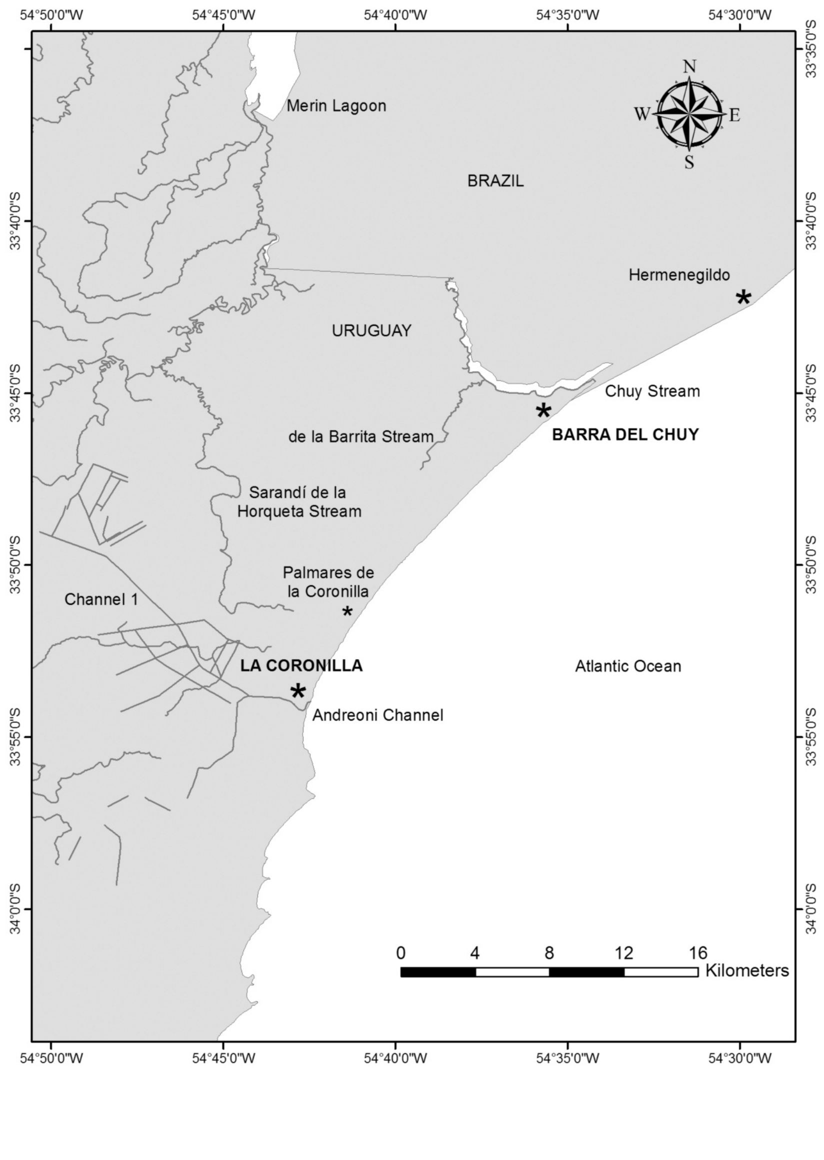
E
S
Lagoa dos Patos
RIO GRANDE DO SUL
BRAZIL
Lagoa Mangueira
Merin Lagoon
URUGUAY
Atlantic Ocean
1 Santa Lucía Estuary
2 Carrasco Stream
3 José Ignacio Lagoon
4 Rocha Lagoon
5 La Paloma
6 Castillos Lagoon
7 Cabo Polonio
8 La Coronilla
9 Barra del Chuy
10 Merin Lagoon A
11 Merin Lagoon B
12 Lagoa do Peixe
0 20 40 80 120 160
Kilometers

(c)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Merin Lagoon
BRAZIL
Hermenegildo
URUGUAY
Chuy Stream
BARRA DEL CHUY
de la Barrita Stream
Sarandí de la
Horqueta Stream
Palmares de
la Coronilla
Channel 1
LA CORONILLA
Andreoni Channel
Atlantic Ocean
0 4 8 12 16
Kilometers

& Myers 1993, Tsipoura & Burger 1999). Delaware Bay is the last stopover before the Arctic breeding grounds, where the birds acquire nutrient stores that are needed not only for the final journey to the Arctic breeding grounds, but also for survival in poor weather or food shortage after arrival, and enable Red Knots to undergo physiological changes from a condition appropriate for migration to one for breeding (Morrison *et al.* 2005). Reduced departure weights/condition resulting from food shortages can lead to decreased survival and breeding success (Boyd 1992, Baker *et al.* 2004, Morrison 2006, McGowan *et al.* 2011). Climate change and other problems, such as anthropogenic disturbances, habitat destruction in other parts of the flyway, and carry over effects translating into late arrival in Delaware Bay might also have contributed to the drastic decline (Baker *et al.* 2004, González *et al.* 2006, Galbraith *et al.* 2014).

For these reasons the *rufa* subspecies of the Red Knot was listed in Appendix I (endangered) under the Bonn Convention of Migratory Species (CMS) by the Conference of the Parties in 2005 (UNEP/CMS Resolution 8.29). In April 2007, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated the southern non-breeding population of *rufa* as 'endangered' (COSEWIC 2007), and the subspecies was listed as Endangered under the Canadian Species at Risk Act in 2012. It was also categorized as 'endangered' in Argentina (López-Lanús *et al.* 2008, Resolución 348 / 2010 Secretaría de Ambiente y Desarrollo Sustentable), and in Chile by the Ministerio de la Secretaría General de la Presidencia de Chile in 2008 (Decreto 50 from 30 Jun 2008). In Uruguay it has been categorized as 'endangered' (Azpiroz *et al.* 2012) and identified as a priority species for conservation in Uruguay by the Dirección Nacional de Medio Ambiente (Aldabe *et al.* 2013). More recently in 2014, the US Fish and Wildlife Service (USFWS) designated the *rufa* subspecies of the Red Knot as 'threatened' under the US Federal Endangered Species Act (Docket ID: FWS-R5-ES-2013-0097). The French government declared the protection of the species in French Guiana (Journal Officiel n° 0235, p 16464, Arrêté 1 Oct 2014), and the Instituto Chico Mendes de Conservação da Biodiversidade, (ICMBio) confirmed its status as 'critically endangered' in Brazil (Portaria Ministério do Meio Ambiente (MMA) n° 444 on 17 Dec 2014).

Although the Red Knot is one of the best studied shorebird species in the Western Hemisphere, little is known about it in Uruguay. In 2007, however, international attention was drawn to a sudden mass mortality of Red Knots at La Coronilla on the northern Atlantic coast of Uruguay reported to the local BirdLife partner NGO, AVES URUGUAY, by a local ranger.

In this paper, we present historical information on the abundance, sites and dates when Red Knots were recorded along the Uruguayan coast. To establish the current role of Uruguay in the Red Knot flyway, we also carried out field studies of temporal fluctuation in abundance, minimum length of stay, connectivity with nearby Argentinean and Brazilian sites and habitat use at a main Uruguayan site during northward migration from 2009 to 2011 and the austral summer in 2007. We also present information regarding the mortality event in 2007. Finally, we discuss conservation implications and research needs.

METHODS

Historical review of observations of Red Knots 1951–2008 and mortality event in 2007

We created a database consisting of historical and contemporary observations of Red Knots in Uruguay, including geo-referenced locality, abundance, date and data source. Information was obtained from published and grey literature, museum collections in the National Museum of Natural History of Montevideo, and personal communications from ornithologists and bird watchers. Additionally, JA, PMG and AJB visited La Coronilla in November 2007 to interview Dante Roibal, the ranger who reported the mortality event.

Table 1. Number of historical records of Red Knots at sites in Uruguay between 1951 and 2008.

Site name	Site number (Fig. 1b)	Number of historical records
Barra del Chuy beach	8/9	22
La Paloma	5	18
St Lucia Estuary	1	16
José Ignacio Lagoon	3	15
Rocha Lagoon	4	13
Cabo Polonio	7	5
Merín Lagoon	10/11	4
Castillos Lagoon	6	2
Carrasco Stream	2	1

Study area

Based on the historical review we decided to focus surveys in the area that provided most records: Barra del Chuy beach. Regular surveys were carried out at Barra del Chuy beach, which extends for 22 km between Barra del Chuy (33°45'12"S, 53°23'01"W) and La Coronilla (33°54'27"S, 53°30'41"W). It is located on the northern Atlantic coast of Uruguay (Fig. 1a,b,c), and has been described as the southernmost of a chain of exposed sandy beaches in South America (Lercari & Defeo 2003) categorized as 'dissipative' morphodynamic type: flat beaches with wide surf zones dissipating wave force progressively as opposed to 'reflective' beaches with a relative steep slope and a narrow surf zone in which most of the wave energy is reflected from the shore morphology (Defeo *et al.* 1992; see Short 1996). The beaches experience a microtidal regime (tidal range = 0.5m), are composed of fine to very fine sand, and have a gentle slope and heavy wave action (Defeo & de Alava, 1995). High tides are infrequent and associated with strong southerly winds. The intertidal width ranges from about 60 to 66 m (Celentano & Defeo 2006), and the swash zone (the part of the beach alternatively covered and exposed by uprush and backwash) width ranges from 10 to 15 m. The beach is delimited by two freshwater discharges: a natural stream Chuy at the north end and an artificial one Canal Andreoni in the southwest (Fig. 1c). The latter is a channel that drains water from a wide plain basin used for rice crops, soybean and cattle ranching.

Additionally, surveys were conducted along two different transects of 7 km and 2.5 km in Merín Lagoon (33°12'29"S, 53°39'46"W), a nearby coastal lagoon adjacent to the Brazil-Uruguay border (Fig. 1b), and along 10 km of shoreline in Brazil north from the Uruguayan border to Hermenegildo (33°40'1"S, 53°15'45"W) (Fig. 1c).

Surveys, resightings and habitat use

We surveyed Barra del Chuy beach during the non-breeding season on 23 Nov and 5–6 Dec 2007.

During northward migration, we surveyed Barra del Chuy beach every 1–3 days from 21 Mar to 6 May 2009; from 18 Mar to 28 Apr 2010; and from 18 Mar to 12 Apr 2011. We also surveyed Merín Lagoon on 15–16 Apr 2009, and 11 Apr 2011. Surveys were carried out by two observers from a car driving along the beach during mid to low tide; stops were made to count birds every time a flock was found. Number of birds passing back or forward were recorded to adjust for movements of the birds along the beach.

To investigate the connectivity of the Red Knots stopping in Uruguay with the main non-breeding grounds and stopover sites to the south, we looked for birds that had been individually marked in Argentina, using 20–60x telescopes. In Argentina, Red Knots have been banded annually by international expeditions coordinated by Fundacion Inalafquen of San Antonio Oeste (SAO, Argentina), Royal Ontario Museum, Toronto (Canada) and Virginia Choquintel Museum Río Grande, Tierra del Fuego (Argentina) at two main sites: the Río Grande, Tierra del Fuego, non-breeding site during November and December 2000–2009 (n = 2,350) and SAO during March 2006–2010 (n = 1,057), a major stopover site 1,300 km south of Uruguay, where 25–50% of the Tierra del Fuego population of *rufa* Red Knots refuel between February and early May (González *et al.* 2004, Baker *et al.* 2005). Birds were marked with orange flags engraved with a unique alphanumeric code or a combination of a flag and colour-bands. We also recorded resightings of Red Knots with colour flags from other countries, including Chile (red), USA (green or lime) or Canada (white). In 2010 we made resightings along Brazilian beaches north from Barra del Chuy to Hermenegildo (Fig. 1c), to check whether individuals that used the Uruguay side of the border were also using the Brazilian side. We estimated the minimum length of stay as the median of the number of days between first and last sighting of an individual seen at least twice during 2010 (we did not calculate this for 2009 as most birds were observed just once, nor for 2011 because of low numbers).

We recorded the behaviour of flocks of Red Knots (feeding or resting) and the part of the beach they were using (swash zone, upper-mid-low intertidal).

RESULTS

Historical observations of Red Knots

Our search identified 96 records, of which 23 occurred between 1951 and 1999, 71 between 2000 and 2008, and two records were undated. No records were found for the periods 1961–1970 and 1980–1989, probably due to low field effort during those periods. Seventy eight of the 96 observations were direct counts of Red Knots, 14 involved museum specimens with no supplementary count data, and four consisted of subjective assessments of numbers such as 'few' or 'many' (see Appendix).

Historical records came from 10 localities (Fig. 1b), with Barra del Chuy beach being the most important site (Table 1). The number of birds recorded at each locality ranged from 1 to >2,000, but typical observations (*ca.* 80%) ranged from a few to 100 birds (Appendix). These records suggest that Red Knots mainly use the Uruguayan coast during northward migration (March and April), and to a lesser degree during southward migration (October and November) (Fig. 2).

Mortality event

On the morning of 23 Apr 2007, Dante Roibal found 312 dead Red Knots at La Coronilla (Fig. 1b) distributed along 500 m of sandy beach. He noted that the birds were not there the previous night, and the tide might have brought them ashore. In the interview with JA, PMG and AJB he said there had been rainstorms, including large hail, during the previous three days, and that morning it was raining. Carcasses of only Red Knots were found deposited by the tide or floating in the water; none was on the upper beach away from the tide edge. They

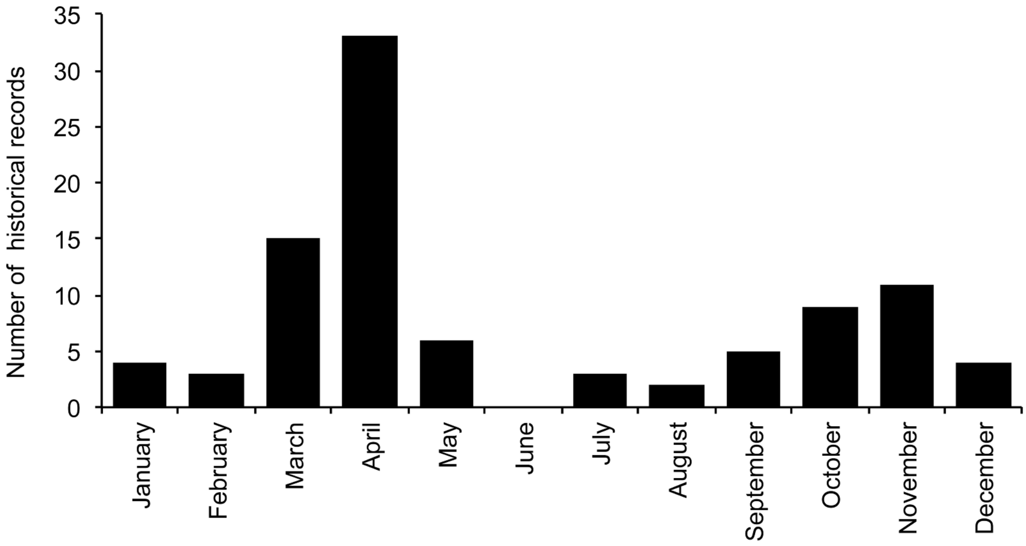

Fig. 2. Number of historical records of Red Knots in Uruguay per month between 1951 and 2008.

appeared to have died 2 or 3 days before: none had fresh eyes, and many had signs of destruction perhaps by fishes, predators or scavengers. Crested Caracaras *Polyborus plancus* and Chimango Caracaras *Milvago chimango* were observed eating some birds. Sr. Roibal did not observe other common predators such as foxes, wild or domestic cats, gulls or other bird species. He subsequently dissected four of the specimens that were in better condition: their guts were full of the small Mole Crab *Emerita brasiliensis* of ~6 mm size. All birds were very fat with large deposits of fat on the abdomen, sides and breast. His son surveyed another 2 km of beaches south of the Andreoni channel finding a similar number of Red Knots in various states of decomposition. Other observers saw carcasses along the 20 km coast north up to Barra del Chuy. The next day Sr. Roibal returned to the beach, finding only a few carcasses left by the tide, all in a state of advanced deterioration. He mentioned that the Andreoni channel was not releasing water so there was no possibility that agrochemicals were running into the sea from the rice fields at that time of the year.

Two specimens were collected (one was lost and the other was deposited in the Museo Nacional de Historia Natural-Montevideo as a skeleton specimen) but no analysis could be carried out to determine the cause of the mortality. The only photographs taken were of these two specimens.

At the time the mortality was reported, the dead birds had already been washed away by the tide. The sea-surface temperature was ~28°C in the area at the time of the mortality; this is at least 2–3°C greater than the average for late April (*http://www.ospo.noaa.gov/data/sst/anomaly/2007/ anomnight.4.21.2007.gif*). Hugo Sena (a local fishermen at La Coronilla) was consulted in 2013 about this event, and remembered an important Red Knot mortality in La Coronilla four or five years previously.

Apart from the mortality of April 2007, there have been several observations in different years of 1–20 Red Knots looking ill and apparently having difficulty walking and/or flying and subsequently dying (Paula Laporta, Sebastián Álvarez & Carlos Romero pers. comm., Aldabe & Rocca pers. obs.). There is one historical record of a few knots unable to fly on 16 Feb 1953 (Vaz-Ferreira & Gerzestein 1961). No red tide toxins were found in the stomach content of one dead Red Knot in 2010, but this is not conclusive as the bird may have metabolized the toxins before dying (María Salhi pers. comm.). The cause or causes of all these mortalities are therefore unknown. A necropsy of a Red Knot found dead on 24 Apr 2002 at Laguna de Rocha (34°39'S, 54°15'W), showed a heavy infestation with ~100 Nematoda: Acuarioidea in the esophagus, and 20 Acanthocephala, *Profilicollis* sp. of 1–2 cm length in the intestine with a proboscis deeply inserted in the intestine wall, several tens of Trematodes: Microphallidae plus other parasite taxa (Castro *et al.* 2002, Díaz *et al.* 2005). Additionally, during our visit in November 2007 we found many (>100) skeletons of fishes of different sizes washed up on the beach, mostly Catfish (Siluridae) mixed with the peat in the area around the mouth of Andreoni Channel.

Surveys

In the summer count that we carried out in November and December 2007 along Barra del Chuy beach, we found only one flock of knots comprising 22 juveniles (age based on greenish-yellow legs, relatively worn edges of primary feathers and first basic plumage with most of the black subterminal bars on upper wing coverts worn off, Hayman *et al.* 1986, Baker *et al.* 2013).

Counts during the northward migration in 2009 ($n = 25$) peaked on 22–23 March (820 individuals), and in 2010 ($n = 26$) on 8 April (1,191 individuals) (Fig. 3). In 2011, only four birds were counted in the 14 surveys made

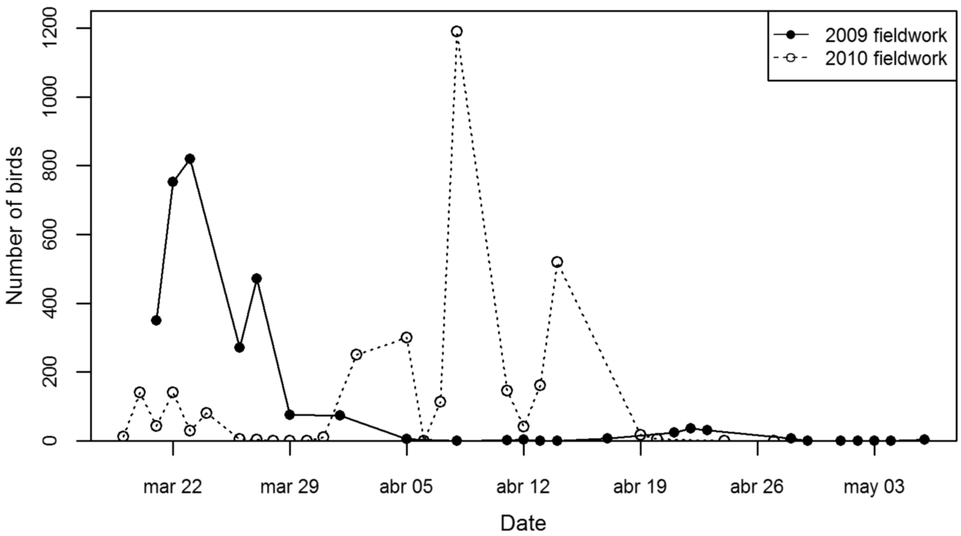

Fig. 3. Number of Red Knots recorded on surveys during the northwards migration of Red Knots along the Barra del Chuy coastline in 2009 and 2010.

within the expected peak of migration window. In Merín Lagoon we counted 33 birds in two surveys in 2009 but no Red Knots were found in one survey in 2011.

Resightings and minimum length of stay

Eighty-nine resightings of 65 different individually-marked birds were made during 2009: 20 with orange flags (Argentina) from Río Grande but none from SAO; we also observed 40 Red Knots with lime flags (USA), 4 red flags from Tierra del Fuego (Chile) and 1 white flag from Mingan Archipelago, Quebec (Canada).

In 2009, four individually-marked birds were seen on two occasions, first during 22–30 March and then from 21–23 April, when most birds had already disappeared, indicating a length of stay exceeding 22 days.

During northward migration in 2010, we recorded 302 observations of 146 different individually-marked birds: 45 orange flags from Argentina (44 from Río Grande and only 1 from SAO); 88 lime flags from USA, including the flagged Red Knot Y0Y with geolocator (Niles *et al.* 2010); 10 red flags from Chile and 3 white flags from Canada. Of these, 31 birds were seen in both the Uruguayan and the Brazilian study sites, representing 23.8% of the 130 individually marked birds recorded during 21 surveys in Uruguay and 65.9% of the 47 birds recorded during seven surveys in Brazil. The median of the minimum lengths of stay was 5 days (range 2–26 days, n = 72 birds). At Barra del Chuy in 2010, we recorded one individually-marked Red Knot that we had seen the previous year in Merín Lagoon, and 20 of the 89 Red Knots seen in 2009, representing a return rate of 23.6%. We also recorded several cohort-flagged birds from Argentina, Chile, and the USA, as well as 10 banded in Lagoa do Peixe, Brazil, in 1997, 1999 and 2001.

Behaviour and habitat use

During our observations at Barra del Chuy the knots were seen feeding, but never resting. They usually walked quickly or ran about in the swash zone until they found a prey item (mostly Wedge Clams) (Fig. 4); occasionally they fed in the mid-littoral zone when groups of Wedge Clam remained stuck in the sand possibly because of a sudden drop in the water level.

DISCUSSION

Important sites for Red Knots in Uruguay

The historical review indicated that the most important sites for Red Knots in Uruguay are Barra del Chuy beach followed by La Paloma (especially the beaches of La Aguada and Costa Azul), Santa Lucía Estuary and José Ignacio Lagoon. These results come from a non-systematic survey, and observational effort is unknown, making them suggestive rather than conclusive. Our recent field surveys confirm the importance of Barra del Chuy beach, and although other sites were not assessed equally, there is good evidence (i.e. high availability of potential food; see below) to conclude that this coastline is an important refuelling site for Red Knots in Uruguay. Nevertheless, Red Knots did not use this site in all years of the field surveys, as only four birds were seen in 2011.

Phenology of migration and role of Uruguay for Red Knots

During northward migration in 2009, the first arrival dates of Red Knots at Barra del Chuy could not be determined as more than 300 birds were already present on the first survey day. Very few were found on the first survey in 2010, but the following day numbers increased substantially. The combined historical and recent records suggest that Red Knots arrive at Barra del Chuy any time

Fig. 4. Group of Red Knots in the swash zone of the sandy beach at Barra del Chuy soon after their arrival in March 2009. Note their low abdominal profile score (sensu Wiersma & Piersma 1995) (photo: Pablo Rocca).

during the first three weeks of March. Movements to other nearby areas occur regularly (see Length of stay).

After the first week of May, Red Knots numbers decrease on the Uruguayan coast. This migration window is similar to those described for Brazilian beaches in Rio Grande do Sul such as Cassino Beach and Lagoa do Peixe. Earlier in the season Red Knots complete their alternate body moult and then refuel increasing their body mass up to >190 g before departing on a long distance migration around late April or early May (Harrington *et al.* 1986, Vooren & Chiaradia 1990, Antas & Nascimento 1996, Baker *et al.* 1999). These authors showed evidence from the 1980s and 1990s that Red Knots moved north in short flights along the 500 km coast of Rio Grande do Sul and Uruguay (see Habitat use). The phenology pattern for Uruguay, showing earlier peaks in late March–early April, is consistent with these northward movements as most birds leave our study area before the typical migration departures dates in Rio Grande do Sul.

Observations of previously banded birds 370 km north in Lagoa do Peixe (Fig. 1b), suggest movement from the south. In addition, photographs of Red Knots on migration in Uruguay show low abdominal profile scores (≤3; Wiersma & Piersma 1995), indicating the birds were not ready for long distance migration and probably completed their fuelling at another place. In contrast, there is one record of a Red Knot carrying a geolocator (Lime green flag YOY) that arrived in the Barra del Chuy–Southern Brazil region on 2 April coming from SAO and did not depart until 8 May, remaining near the Uruguayan-Brazilian border (Niles *et al.* 2010). Previous work suggested Red Knots departing from non-breeding grounds in Tierra del Fuego could either reach Rio Grande do Sul directly, or in two stages, flying 1,400 km to the major stopover area in Golfo San Matías (SAO) and then continuing 1,700 km to reach Rio Grande do Sul (Piersma *et al.* 2005). Our results show that the connectivity between SAO and N Uruguay is minimal, which implies that SAO connectivity may also be low with Rio Grande do Sul, given the regular movements between sites in Uruguay and Rio Grande do Sul. Despite the large numbers of birds banded at SAO (see Methods), in 2009 we did not see any of them in Uruguay and only one was resighted in 2010 (plus the geolocator bird YOY). In contrast, the other 64 resightings of orange flagged Red Knots from Argentina came from the Río Grande non-breeding site. In both Rio Grande do Sul and SAO, Red Knots complete alternate body moult (Piersma *et al.* 2005) and then increase their body masses to levels enabling them to make long distance flights. Examples include a Red Knot with a geolocator (Red flag JUT) which flew 5,800 km from SAO to Maracaibo (Venezuela) (Ron Porter pers. comm., González 2014) and yearly records of orange flagged birds resighted by PMG in SAO and photographed 9–11 days later in early May in Florida after flying 8,000 km (Patrick & Doris Leary pers. comm.; flags H3H, MX1, P3A and others).

Since northward passage at SAO ends at the same time as in the N Uruguay–Rio Grande do Sul area, we conclude that both are important but separate areas with the same role for Red Knots: that is they are both used for moulting and refuelling before the long distance migration to the Northern Hemisphere. This also implies that most birds arriving in Barra del Chuy come directly from Tierra del Fuego, although the use of other stopover sites on the Argentinian coast cannot be excluded (Baker *et al.* 1999).

Length of stay

The median minimum length of stay in 2010 was 5 days. Several individual birds were recorded both in Barra del Chuy and on the southernmost Brazilian beaches close to the Uruguay border, and all birds staying more than 5–26 days were not detected every day. As noted above, the Red Knot with a geolocator YOY remained in the border region for 36 days, but this bird was only seen in Barra del Chuy and southern Brazil on 10,11 and 12 April, indicating that other nearby sites were used later until its departure on 8 May. Such areas could include the huge Merin Lagoon where Red Knots were reported during our study (field surveys and historical observations), as well as other sandy beaches of northern Uruguay and southern Brazil. Other birds could leave the area moving north in short flights along the coast of Rio Grande do Sul.

Habitat use

We did not find any roosting Red Knots during our surveys at Barra del Chuy, probably because our surveys were carried out at mid or low tide (necessary for driving along the beach). Birds fed mostly in the swash zone. Preliminary analysis of Red Knot faeces collected at Barra del Chuy revealed that the most frequent food item was the Wedge Clam (Aldabe *et al.* unpubl. data). This is consistent with reports from S Brazil, where Red Knots feed on Wedge Clams and other macroinfauna in the swash zone (Harrington 1986, Vooren & Chiaradia 1990, Fedrizzi 2008). The Wedge Clam as well as the Mole Crab and the Yellow Clam *Mesodesma mactroides* consumed by Red Knots (Aldabe *et al.* unpubl. data) characterize the saturation zone (which includes the swash zone) of the sandy beach at Barra del Chuy (Defeo *et al.* 1992).

Red Knots used both sandy beaches and coastal lagoons, but the largest flocks and most of the observations were on the beaches. All sandy beaches where Red Knots were observed had an intermediate to dissipative morphodynamic type, and those with the largest Red Knot numbers (Barra del Chuy and La Aguada at La Paloma) have the highest dissipative indices of any beaches along Uruguayan coastline (Lercari & Defeo 2006). Dissipative beach types show higher macroinfauna diversity and abundance than reflective beach types (Brown & McLachlan 1990). Barra del Chuy is the most dissipative beach on Uruguayan coastline and also had the highest richness, diversity, abundance and biomass of sandy beach macrofauna on the Uruguayan Atlantic coast (Lercari & Defeo 2006). This is consistent with Barra del Chuy being one of the most important sites for the Red Knots in Uruguay. Similar beaches extend northwards to the Lagoa do Peixe region of Brazil, which is well known as a refuelling site for Red Knots on the annual northwards migration (Harrington *et al.*1986, Fedrizzi 2008). Vooren & Chiaradia (1990) observed that big numbers of Red Knots fed exclusively in a narrow strip of the swash zone, and speculated that the movement of the birds was generated by their impact on prey depletion. Coincident with these observations, our observations in Barra del Chuy also indicate that the birds mainly feed on a narrow strip of the swash zone and that their abundance changes very sharply over time.

Conservation concerns

The Canal Andreoni freshwater discharge in La Coronilla has reduced abundance and increased mortality rates of potential food resources (Wedge Clam, Mole Crab and Yellow Clam) close to the disturbance source (Lecari & Defeo 2003). Furthermore, harvesting has affected densities of both Yellow Clams and Wedge Clams (Defeo & de Alava 1995), which raises concerns of depletion of food supplies for Red Knots. An additional possible threat is the presence of humans and domestic animals, as the area is heavily used by fishermen and tourists. During the field surveys, Red Knots did not use areas when human concentrations were high. In fact during surveys at Barra del Chuy, flocks of Red Knots were observed turning in the opposite direction they were flying when human concentrations were encountered; these observations are consistent with the study of Cestari (2008) who found Red Knots were highly sensitive to human concentration areas.

Some wind farms have been installed along the Uruguayan coast, in particular over the southeastern hills, while many more are in the process of being installed. Wind turbines can affect birds through direct mortality or lethal injury when collisions occur (Drewitt & Langston 2006). The distance between the southeastern hills and the marine coast can be 20 km; this distance increases towards the Uruguayan northern Atlantic coast. As shown by the observations presented in this paper, Red Knots can use habitats up to 80 km inland from the coast (e.g. Merín Lagoon) during their northward passage. Inland movements of Red Knots increase the potential for collisions with wind turbines, especially in stormy weather when visibility is low. This is especially important in the northern coast of Uruguay, where Red Knots concentrate.

Although mass mortality events of Red Knots were not recorded during the study period at Barra del Chuy, at least two such episodes have been described for the beaches of southern Brazil (Buehler *et al.* 2010). Despite the fact that the causes of the mortalities could not be identified, dead Red Knots in Brazil showed a significant degree of intestinal parasite infection by Acanthocephala, just like the individual found dead at Rocha in 2002 (Castro *et al* 2002). Acanthocephalans can use Mole Crabs (*Emerita* sp) as an intermediate host (Goulding &

Cohen 2014). *E. brasiliensis* constitutes a prey item for Red Knots in Brazil (Buehler *et al* 2010) and in Uruguay where we found it in the gut of dead birds during the mass mortality episode. In Uruguay, harmful algal blooms occur quite frequently and may affect animals that feed on molluscs (Méndez 2006) like Red Knots. The Sand Crab *Emerita analoga* can accumulate measurable amounts of algal neurotoxin domoic acid during toxic diatom *Pseudo-nitzschia* blooms in California, while the sentinel sea mussel *Mytilus californianus* shows no detectable toxin (Powell *et al.* 2002). This suggests that Mole Crabs may play a similar role, potentially acting as a source of toxins for Red Knots that feed on them during algal blooms in Uruguay; this deserves to be investigated further. Given the northward passage of substantial numbers of migratory shorebirds which depend on the food supplies offered by these beaches, a priority for conservation of the birds is to develop a protocol for the thorough monitoring and investigation of mortalities.

Additional research is also needed along the entire Uruguayan coast, to better characterize the differential intensity of site use by adult and juvenile Red Knots throughout the year. Historical data show that Red Knots used the Uruguayan coast during southward migration and small numbers were found during the austral winter (when most adults are in their Arctic breeding areas) and summer (e.g. the juveniles we saw in November and December 2007), but the regularity of these patterns is not known. Food resources (both species and biomass) and their availability are key factors that need to be assessed in order to understand parasite loads, food and feeding dynamics, energy budgets, movements and abundance trends in the context of a climate change scenario (Galbraith *et al.* 2014). The underlying reasons why Red Knots prefer dissipative sandy beaches should be studied, this could have important implications for sandy beach management and the conservation of the species. Last, if Red Knots numbers recover to past abundances, there must be available habitat to sustain them. In this sense, it is of paramount importance to protect the current and potential habitats of Red Knots in Uruguay.

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Appendix. Red Knots recorded in Uruguay between 1951 and 2008. See Fig. 1b for location of each site.

Map location (Fig. 1b)	Department	Locality	Coordinates	Count[a]	Month	Year	Reference[b]
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	1 Skin	Nov	1952	MNHN Collection Vaz-Ferreira & Gerzenstein (1961)
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	2 Skin	Nov	1958	MNHN Collection Vaz-Ferreira & Gerzenstein (1961)
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	4 Skin	Nov	1959	MNHN Collection
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	1 Skin	Sep	1959	MNHN Collection Vaz-Ferreira & Gerzenstein (1961)
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	>30	Jan	1960	MNHN Collection
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	>50	Nov	1960	MNHN Collection
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	1 Skin	Jul	1971	MNHN Collection
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	1 Skin	Aug	1971	MNHN Collection
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	1 Skin	Sep	1979	MNHN Collection Vaz-Ferreira & Gerzenstein (1961)
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	30	Oct	1993	MNHN Collection
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	2	Jul	2006	Aldabe pers. obs.
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	2	May	2007	Caballero-Sadi pers. comm.
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	2	Oct	2007	Caballero-Sadi pers. comm.
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	1	Nov	2007	Caballero-Sadi pers. comm.
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	15	Oct	2008	Caballero-Sadi pers. comm.
1	San José	Santa Lucía Estuary	34°45'S, 56°26'W	7	Oct	2008	Caballero-Sadi pers. comm.
2	Canelones	Arroyo Carrasco	34°52'S, 56°01'W	1 Skin	Dec	1958	MNHN Collection
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	>200	Undated	Undated	Vaz-Ferreira en Scott & Carbonell (1986)
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	3	Sep	1992	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	2	Apr	1997	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	2	Apr	2000	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	80	Apr	2001	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	24	Apr	2001	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	5	Apr	2002	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	6	Apr	2002	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	1	Dec	2002	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	1	Jan	2003	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	10	Apr	2003	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	3	Mar	2004	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	1	Apr	2004	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	24	Nov	2006	Rabau pers. comm.
3	Maldonado	Laguna José Ignacio	34°50'S, 54°40'W	3	Feb	2007	Lenzi & Alfaro (database in Central Ornitológica Uruguaya)
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	1 Skin	Apr	2002	MNHN Collection

Appendix. Red Knots recorded in Uruguay between 1951 and 2008. See Fig. 1b for location of each site, continued.

Map location (Fig. 1b)	Department	Locality	Coordinates	Count[a]	Month	Year	Reference[b]
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	19	Mar	2004	Abreu pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	10	Nov	2005	Abreu pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	9	Mar	2006	Abreu pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	1	Apr	2006	Abreu pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	1	May	2006	Abreu pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	4	Oct	2006	Abreu pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	1	Nov	2006	Rabau pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	7	Feb	2007	Rabau pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	1	Apr	2007	Rocchi pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	6	Jan	2008	Rabau pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	3	Oct	2008	Abreu pers. comm.
4	Rocha	Laguna de Rocha	34°40'S, 54°15'W	1	Oct	2008	Aldabe pers. obs.
5	Rocha	La Paloma	34°39'S, 54°09'W	1 Skin	Undated	Undated	MNHN Collection
5	Rocha	La Paloma	34°39'S, 54°09'W	7	Dec	1951	Teague (1955)
5	Rocha	La Paloma	34°39'S, 54°09'W	1 Skin	Sep	1960	MNHN Collection
5	Rocha	La Paloma	34°39'S, 54°09'W	1	Mar	2002	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	many groups	Apr	2002	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	1	Aug	2003	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	several individuals	Mar	2004	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	54	Apr	2004	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	27	Apr	2004	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	70	Apr	2004	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	70	May	2004	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	10	May	2004	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	7	May	2005	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	95	Apr	2006	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	18	Mar	2008	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	8	Mar	2008	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	1	May	2008	Abreu pers. comm.
5	Rocha	La Paloma	34°39'S, 54°09'W	2	Oct	2008	Abreu pers. comm.
6	Rocha	Cabo Polonio	34°24'S, 53°48'W	2 Skin	Sep	1953	ZVC-A Collection Vaz-Ferreira & Gerzenstein (1961)
6	Rocha	Cabo Polonio	34°24'S, 53°48'W	groups of 20–30 individuals	Mar	2006	Calimares pers. comm.

Appendix. Red Knots recorded in Uruguay between 1951 and 2008. See Fig. 1b for location of each site, continued.

Map location (Fig. 1b)	Department	Locality	Coordinates	Count[a]	Month	Year	Reference[b]
6	Rocha	Cabo Polonio	34°24'S, 53°48'W	groups of 20–30 individuals	Apr	2006	Calimares pers. comm.
6	Rocha	Cabo Polonio	34°24'S, 53°48'W	26	Apr	2007	Calimares pers. comm.
6	Rocha	Cabo Polonio	34°24'S, 53°48'W	35	Apr	2007	Calimares pers. comm.
7	Rocha	Laguna de Castillos	34°21'S, 53°52'W	a few individuals each count	between Oct & Mar	1991–1998	Gambarotta *et al.* (1999)
7	Rocha	Laguna de Castillos	34°21'S, 53°52'W	2	Mar	2002	Rabau pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	numerous specimens	Feb	1953	ZVC-A Collection Vaz-Ferreira & Gerzenstein (1961) Vaz-Ferreira (1956)
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	>2,000	Jan	1953	Vaz-Ferreira & Gerzenstein (1961)
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	1 Skin	Oct	1972	MNHN Collection
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	2 Skin	Apr	1990	MNHN Collection
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	9	Apr	2003	Rabau pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	50	Apr	2004	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	3 groups of 25–30 individuals	Mar	2005	Azpiroz & Rodríguez-Ferraro (2006)
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	4	Mar	2005	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	40	Mar	2005	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	200	Mar	2005	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	400	Apr	2005	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	11	Apr	2005	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	140	Apr	2005	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	71	Apr	2007	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	3	Apr	2007	Álvarez pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	174	Nov	2008	Abreu pers. comm.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	163	Mar	2008	Martínez & Fallabrino (2009)
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	1	Apr	2008	Aldabe pers. obs.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	2	Apr	2008	Aldabe pers. obs.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	3	Apr	2008	Aldabe pers. obs.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	4	Apr	2008	Aldabe pers. obs.
8/9	Rocha	La Coronilla-Barra del Chuy	33°49'S, 53°27'W	2	Apr	2008	Aldabe pers. obs.
10	Treinta y Tres	Laguna Merín	33°04'S, 53°36'W	3	Nov	2004	Blanco *et al.* (2006)
10	Treinta y Tres	Laguna Merín	33°04'S, 53°36'W	116	Apr	2008	Paulo Angonese pers. comm.
11	Cerro Largo	Laguna Merín	32°46'S, 53°18'W	60	Mar	1997	Rocha (2000)
11	Cerro Largo	Laguna Merín	32°46'S, 53°18'W	7	Jul	1997	Rocha (2000)

[a] Total counts are listed where available; otherwise subjective information on the numbers of birds is given. 'Skin' refers to a study skin in a museum collected from the locality.
[b] Abbreviations for museum include: National Museum of Natural History (NMNH) of Montevideo. Zoología Vertebrados Colección Aves (ZVC-A). Bird collection of the Facultad de Ciencias, Universidad de la República, Uruguay.