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Foraging conditions ‘at the end of the world’ in the context of long-distance migration and population declines in red knots

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Abstract The long-distance migrant red knot (*Calidris canutus* ssp. *rufa* – Scolopacidae) alternates between the northern and southern ends of the New World, one of the longest yearly migrations of any bird and paradoxically overflying apparently suitable habitat at lower latitudes. This subspecies is sharply declining, with a major mortality event following 2000, attributed to commercial overharvesting of food resources at its Delaware Bay (USA) stop-over site. A full understanding of this peculiar migrant requires an assessment of the foraging conditions at its southern hemisphere wintering sites. Here, for a major wintering site in Argentinean Tierra del Fuego (Río Grande), we describe and compare food abundance, diet and intake rates during January–February in 1995, 2000 and 2008. The two main prey types were the burrowing clam *Darina solenoides* and three species of epibenthic mussels Mytilidae. In the year 2000, food availability and intake rate were higher than those recorded at other sites used by knots anywhere else in the world, contributing to the explanation of why red knots carry out this impressive migration. Intake rate in 2008 on the two main prey types was dramatically reduced as a result of birds eating smaller prey and strongly increased human disturbance; the same year we also found a high prevalence of a digenean parasite in *Darina*. We suggest that during the strongly enhanced winter mortality in 2000, knots did not yet face ecological problems in their southernmost wintering area, consistent with the previous evidence that problems at northern stop-overs negatively affected their numbers. However, in 2008 the ecological conditions at Río Grande were such that they would have facilitated a further decline, emphasizing the importance of a hemispheric approach to research and management.

Key words: *Calidris canutus rufa*, digenean parasite, foraging ecology, long-distance migration, population decline.

INTRODUCTION

Because they show large variation in latitudinal destinations (from the high Arctic to Australia, South Africa and South America) and in migration lengths, but at the same time occupy a restricted range of habitats – bare desert tundra during breeding and extensive coastal wetlands with good supplies of bivalves during the rest of the year (van Gils *et al.* 2005a; Piersma *et al.*

2005), red knots (*Calidris canutus* – Scolopacidae) provide an insightful global model of a migrant bird species (Piersma 2007; Buehler & Piersma 2008). The red knot subspecies that is restricted to the Americas, *Calidris canutus rufa*, not only makes the longest migration among all subspecies, but indeed makes one of the longest yearly migrations of any bird, travelling 15 000 km from its Canadian Arctic breeding grounds to the Subantarctic region of Tierra del Fuego, the southern tip of South America (Harrington 1996; Piersma 2007; Niles *et al.* 2008). At first sight this is rather paradoxical, because they overfly apparently

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suitable habitat at lower latitudes (Buehler & Piersma 2008). By doing this, not only do birds spend more time and energy on migration, but upon arrival they also encounter relatively grim weather conditions characterized by strong winds coupled with low ambient temperatures (snow during the austral summer is not rare). This leads to the expectation that there must be something attractive about Tierra del Fuego that justifies this migratory effort.

Not only is the *rufa* knot one of the longest-distance migrant shorebirds that depends on a relatively limited number of key sites for wintering, migration and breeding, it is also one of the shorebird populations that has the distinction of being in steepest decline (International Wader Study Group 2003). Based on aerial surveys on the wintering grounds, by 2003 a decrease in bird numbers of 98% was observed on the Patagonian Atlantic coast and a 50% decrease at the sites in Tierra del Fuego compared with surveys in the 1980s (Morrison *et al.* 2004).

This decline has been confirmed with capture–recapture data. A major decline event was identified around the year 2000, when annual survival of adults decreased by 37% and breeding success was also impoverished, with the number of second-year birds found in wintering flocks declining by 47% between May 2000 and May 2001 (Baker *et al.* 2004; González *et al.* 2006). All the evidence so far suggested a serious refuelling problem as a result of man-induced food shortage at the last staging site during northward spring migration, Delaware Bay, USA (Baker *et al.* 2004; Atkinson *et al.* 2007), the studies presenting the strongest evidence to date linking stop-over ecology to population dynamics of migratory birds. Nevertheless, an increase of birds arriving late and with very low weights at Delaware Bay after 2000 (González *et al.* 2006; Atkinson *et al.* 2007) suggested additional problems for knots sometime during the year. These problems could be due to seasonal carry-over of food-stress incurred at Delaware Bay, or could be related to ecological conditions earlier in the annual cycle.

This study reports on the feeding ecology of *rufa* knots in 3 years at a main southern wintering area, the Río Grande foreshore in Argentinean Tierra del Fuego. With this, we evaluate to what extent ecological conditions at southern hemisphere wintering sites may contribute to the population decline of a northern hemisphere breeding bird. Field studies in 1995 describe pre-2000 conditions, whereas the work in 2000 captures the wintering and departure conditions right at the time of the large mortality event identified by Baker *et al.* (2004). A final study in 2008 addresses recent, post-2000 conditions. We also discuss the results in the context of why Tierra del Fuego is attractive enough that it makes knots migrate between the two extreme ends of the Americas.

METHODS

Study area and periods

Río Grande (53°44'S, 67°44'W) is located on the Atlantic shore of Tierra del Fuego (Fig. 1A), in the Subantarctic Region (Balech 1964). The foreshore has a large tidal range with an average of 5.5 m and a maximum of 8.4 m (Servicio de Hidrografía Naval Argentina). Fieldwork was carried out from 16 to 26 February 1995, from 1 January to 5 February 2000 and from 12 to 15 February 2008.

Bird counts

Repeating the methodology of Benegas and Ramirez (1994), in 2000 we made weekly high tide counts of red knots at the shoreline between Cabo Peñas (53°50'25S, 67°33'08W) and Cabo Domingo (53°41'41S, 67°50'42W) (Fig. 1B). Only a line of gravel remains available to knots at high tide. At low tide, a broad restinga (hard substrate) and an area of soft sediments (with variable grain size from 0.004 to 2 mm) are exposed just to the east of Río Grande city's downtown, and a smaller area of fine sediment to the south of the city at the Río Grande river mouth. The biggest flocks of red knots were followed throughout the diurnal tidal cycles at the main study area (Fig. 1C); birds were counted as they arrived from the roosting places or as they flew in the air in response to disturbances. Benthos sampling and collection of faeces were carried out in the main study area as well (see below).

Feeding activity

In 2000, the proportion of birds feeding (*vs.* non-feeding) was reconstructed based on several observations at different times of the cycle (average flock size 160 birds). In 2008 every half an hour after high tide, each bird in a flock (average flock size 288 birds) was observed through a telescope and the behaviour categorized as feeding or non-feeding. The average of all the observations made for each hour after high tide is presented in the results.

Prey availability

To estimate the resource base for wintering knots, we sampled densities of bivalves over the intertidal area (Piersma *et al.* 1995). The main prey types for red knots (see below) were the buried soft-shelled clam *Darina solenoides* King, 1832 (Mactridae), hereafter called darina, and surface-living mussels (Mytilidae). Three species of mussels were present, the most abundant being *Mytilus edulis* Linnaeus, 1758 (following Seed 1992), *Aulacomys ater* Molina, 1782 and *Perumytilus purpuratus* Lamark, 1819. These two main prey types are spatially separated. The mussel beds are concentrated on restinga with only a few patches at the river mouth, whereas the darinas are found only in areas of soft sediment. Darinas were sampled by

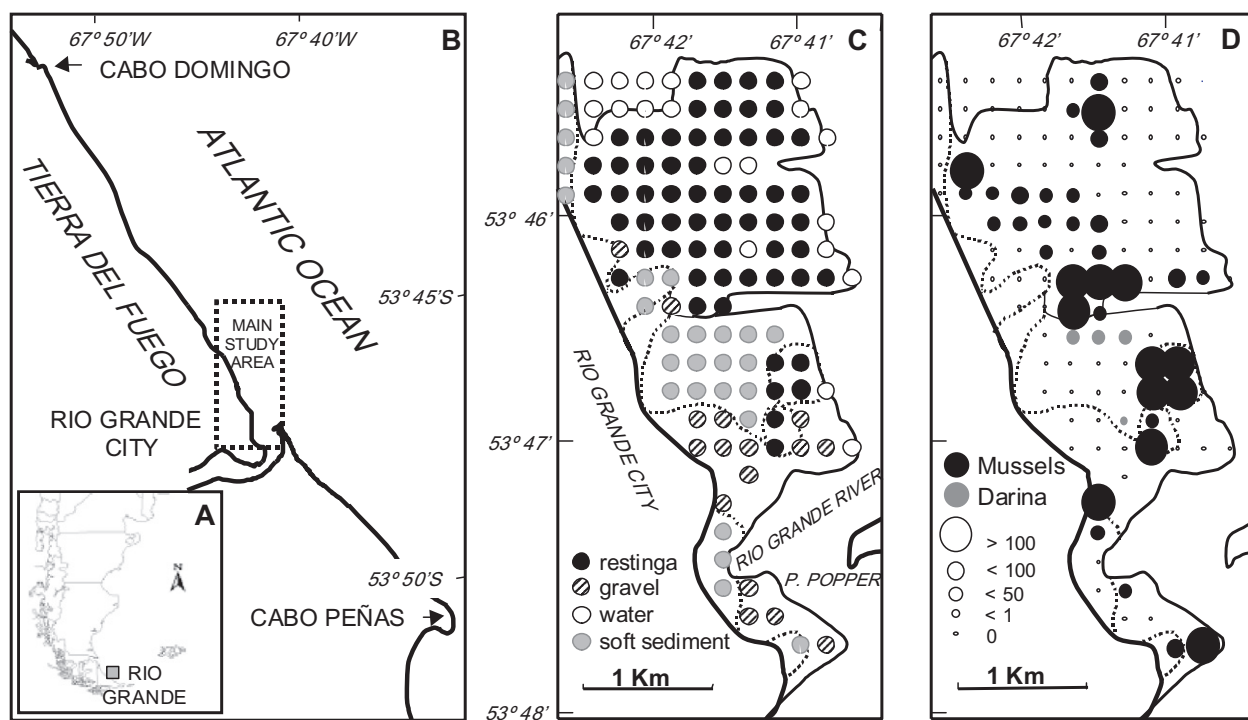


Fig. 1. Location of the study area: (A) Atlantic shore of Tierra del Fuego island, Argentina; (B) shoreline covered weekly for high tide counts from Cabo Domingo to Cabo Peñas; (C) main study area at low tide, where benthic sampling, behavioural observations and daily counts were carried out, with types of substrate indicated; (D) distribution of the two main prey types in the year 2000, expressed in grams of ash free dry mass/m².

taking sediment core samples and sieving them over a mesh of 1 mm. We only included darinas that occurred up to a depth of 5 cm (the maximum depth at which knots could reach prey with their bills). If the sediment was hard (restinga) we collected a similar-sized sample consisting of all superficial material. For all shelled molluscs the maximum length was measured to the nearest 0.01 mm. In 1995 a single area of soft sediment where knots were foraging regularly was visited, and one core sample of 81.7 cm² was taken every 16 m along a 640-m long transect. In 2000 all types of substrate were examined in a grid that covered 6.8 km² with core samples of 181.8 cm² taken every 200 m, to include areas visited by knots as well as unselected patches of presumably lower quality. In 2008 we repeated one of the transects of 2000 at the soft-sediment area and one at the restinga, using the same methodology as in 2000 except that we took not one but two cores per station at the soft-sediment area in order to improve the overall estimate of food availability for the lower number of sampled stations. Collected molluscs were stored (in formalin or dried at 60°C) for later processing in the lab, where they were burned (at 560°C) to obtain ash-free dry mass (AFDM). The AFDM of the darinas collected in 1995 and 2008 was calculated from a regression of AFDM on shell length of darinas collected in 2000 ($\log \text{AFDM} = -4.966 + 2.794 (\log \text{length}), n = 104, R^2 = 0.99$). A similar regression of AFDM on shell length was made for mussels collected in 2000 ($n = 1608$) and used to obtain the AFDM of the mussels collected in 2000 and 2008. The AFDM of prey that

were accessible in the top 5 cm depth of the sediment, and that were of sizes ingestible by the red knots as estimated from remains of prey in faeces and telescope observations (see below), were taken to represent the relevant *harvestable* food biomass (*sensu* Zwarts & Wanink 1993). This metric was calculated for each station as the total AFDM of all harvestable prey per core, and then expressed as AFDM/m² by adjusting for number of cores taken and core surface. A paired *t*-test was used to compare the harvestable prey biomass for the two transects sampled in both 2000 and 2008 (1995 could not be compared as the locations of the sampling stations did not coincide).

Prey sizes taken and intake rates

In 2000 GE observed focal birds with a telescope, both on restingas ($n = 75$, average = 325 s, SD = 32 s) and at the soft-sediment area ($n = 51$, average = 293 s, SD = 60 s). In 2008 JGN and GE observed focal birds (no differences in prey size between observers: Mann–Whitney test $U = 100$; $P = 0.059$), again on both the hard ($n = 24$, average = 176 s, SD = 13 s) and the soft substrates ($n = 31$, average = 176 s, SD = 16 s). Special effort was taken to avoid pseudoreplication by selecting birds that were feeding apart from each other (Hurlbert 1984). The three species of mussels could not be distinguished from each other through the telescope. Prey size was estimated at intervals of 5 mm by comparison

with an average bill length of 36 mm (SD = 1.92; Morrison & Harrington 1992; Baker *et al.* 1999). There was no association between intake rate (mg AFDM of prey over time in s) and date (day after 1 January) in 2000 ($r = 0.068$, $P = 0.64$). Therefore we assumed that, despite the shorter observation period, we also obtained a representative estimate of intake rate for 2008.

Individual faeces were collected after feeding observations, dried at 60° and stored in individual plastic bags ($n_{2000} = 150$, $n_{2008} = 47$). In 1995, all faeces were stored together ($n = 122$). All faecal samples were processed and analysed individually (except for 1995) following the procedures described in Dekinga and Piersma (1993), whereby the length of ingested prey is estimated from the size of the hinges of the shell that remained intact in the faeces (regression of darina length on central hinge length: $r^2 = 0.89$, $n = 176$, $P < 0.001$). The length of ingested mussels could not be estimated from faeces as no useful structures remained among the broken fragments.

The size distributions of darinas taken by knots as determined by telescope observation or by analysing faeces were not significantly different in the years 2000 or 2008 (Mann-Whitney Rank test, $T_{2000} = 2924$, $n_{\text{faeces}} = 34$, $n_{\text{observed}} = 121$, $P = 0.24$; $T_{2008} = 1779$, $n_{\text{faeces}} = 31$, $n_{\text{observed}} = 53$, $P = 0.20$). Hence, field estimates of sizes of ingested darinas seemed to be accurate. On this basis, field estimates of the sizes of ingested mussels by the same observer were also assumed to be accurate.

Prey selection

The composition of a realized diet is a combination of which prey are on offer, and which prey a predator prefers. Selection of prey size class (measured shell lengths binned in classes of 5 mm) for each prey type and year was analysed using the Savage selectivity index $w_i = U_i/p_i$ (Ursúa *et al.* 2005), where U_i is the proportion of ingested prey of a given size class i (estimated from telescope observation and faeces when possible) and p_i is the proportion of available prey of that size class. This index varies from 0 (maximum negative selection) to ∞ (maximum positive selection), with a value of 1 indicating no selection (Manly *et al.* 1993). The statistical significance of this index was obtained by comparing the statistic $(w_i - 1)^2/\text{se}(w_i)^2$ with the corresponding critical value of a χ^2 distribution with one degree of freedom, the null hypothesis being that birds use prey size classes in proportion to their availability. The standard error of the index ($\text{se}(w_i)$) was calculated by $\sqrt{[(1 - p_i)/(u_+ p_i)]}$, where u_+ is the total number of foraging records sampled (Manly *et al.* 1993).

All statistical analyses were performed using MSYSTAT 12 (SYSTAT Software Inc, Chicago, IL, USA).

RESULTS

Bird numbers and activity

The numbers of red knots found in the main study area were estimated at 4000 and 3000 in January and

February 1995, respectively (Minton *et al.* 1996), 6000 and 3300 in January and February 2000, and 3300 in February 2008. During high tide all birds roosted at Punta Popper, or at either side of the river mouth if disturbed (Minton *et al.* 1996). In 2000 most birds were observed at the sea side (to the east) of Punta Popper, at the northern side of the river mouth, or on the gravel beach at the north of the city, thus gaining protection from the prevailing strong western winds. When the wind was from the east (or south east), the birds chose to roost at the inside of Punta Popper and the southern margin of the river (Fig. 1C). In contrast, it seemed that disturbance, although noticeable in previous years, was the main factor affecting roost site choice in 2008. The city has recently grown extensively towards the sea and river margins, and people walking or driving off road vehicles or dogs playing freely on the gravel beach during high tide made the birds fly from one spot to the other, or further to the north away from the feeding areas.

With the outgoing tide, the intertidal feeding areas uncovered progressively, and the average percentage of birds that were feeding during the course of the tidal cycle are presented in Figure 2. In 2000, 50% of the birds started eating darinas in the first strip of soft-sediment area that became available 2 h after high tide (based on observations during nine tidal cycles). In 2008, at this time of the tide the area was usually usurped by dogs, people and off road vehicles, and birds were disturbed and flushed continuously (based on observations during three tidal cycles). As a result, feeding activity started on average 0.49 h later ($F_{1,10} = 4.17$, $P = 0.068$). Feeding flocks followed the water line or remained on wet patches at the soft-sediment area until the restinga became available 5 h after high tide ($n_{2000} = 12$ tidal cycles) where the birds remained for approximately 5 h ($n_{2000} = 18$ tidal cycles). In 2008 some flocks went to feed at the restinga as soon it became available, but some remained feeding on darina at the soft-sediment area; all flocks left the soft-sediment area 6 h after high tide ($n_{2008} = 3$ tidal cycles) and remained on the restinga for approximately 4 h ($n_{2008} = 3$ tidal cycles) until the area became completely flooded 2–3 h before the next high tide. Overall most knots started feeding half an hour later in 2008 and spent half an hour longer (3 h on average) feeding on darina at the soft-sediment area. As they stopped feeding when the restinga became covered, the time feeding at the restinga was half an hour shorter in 2008 than in 2000.

Available food

Average prey densities and harvestable biomass of prey for each of the years and types of substrate are pre-

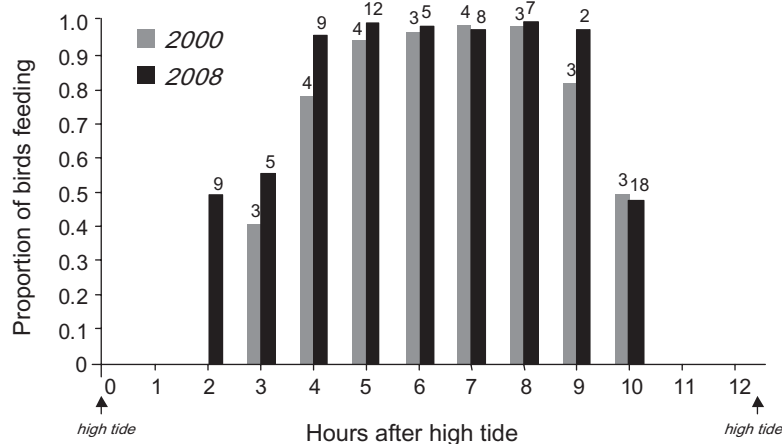


Fig. 2. Feeding activity over the tidal cycle. Presented is proportion of feeding birds grouped per hour after high tide, for the years 2000 (light grey) and 2008 (dark grey). Number of repeated observations (tidal cycles) indicated on top of the bars.

Table 1. Overview of densities and biomass of harvestable fractions of the main prey (*Darina solenoides* and mussels Mytilidae) of red knots at Río Grande (Argentina) in the years 1995, 2000 and 2008

Prey type	1995	2000	2008
Density (mean in number/m ² , with SD)			
Darina	215 (245)	66 (64)	179 (83)
Mussels		1289 (1966)	3822 (6579)
Biomass (mean in grams AFDM/m ² , with SD)			
Darina	16.4 (20.0)	1.6 (4.6)	1.6 (2.4)
Mussels		34.3 (51.0)	58.7 (93.6)

sented in Table 1. The much higher biomass obtained in 1995 than in 2000 and 2008 is best explained by the fact that sampling was restricted to an area preferred by foraging knots. The harvestable biomass of the two main prey was not significantly different between 2000 and 2008 (paired t -test_{soft-sediment area} = 1.64, d.f. = 5, P = 0.16; paired t -test_{restinga} = -1.46, d.f. = 10, P = 0.17). The overall average biomass of harvestable prey in 2000, when we sampled the entire study area, was 20.4 g AFDM/m².

We found significant differences in the available sizes of darinas between years (Kruskal–Wallis test H = 79.6, d.f. = 2, P < 0.0001); darinas were smaller in the year 2008 than in either 1995 or 2000 (Fig. 3, Multiple comparison Dunn's method, $Q_{(1995 \& 2008)} = 81.2$, P < 0.05, $Q_{(2000 \& 2008)} = 76.7$, P < 0.05), and the same pattern was observed for the available sizes of mussels (Fig. 4) ($F_{(1,2673)} = 140.6$; P < 0.0001). This decrease in prey size explains why, despite an apparent increase in prey densities in 2008, biomass did not differ between 2000 and 2008.

Prey taken, prey selection and food intake rates

At the soft-sediment area red knots almost exclusively fed on buried darinas and on the restinga only

on mussels, during all 3 years. Faeces, depending on where they were collected, normally contained either one prey type or the other. In 2000 only 1.33% of 150 individual faeces had prey remains other than darinas or mussels. However, in 2008 at least 25% (n = 47) of the faeces also contained fragments of prey other than darina or mussels, such as snails (likely *Pareutria plumbia*, *Trophon geversianus* and *Buccinanops globulosum*), chitons (*Plaxiphora aurata*), isopods (*Exosphaeroma* sp.), crabs (*Cyrtograpsus* sp.) and insects.

Red knots ingested darinas varying in length from 5 to 35 mm, and mussels from 5 to 25 mm (Figs 3 and 4). We found significant positive selection of darina size class 25–30 mm in 1995, 20–30 mm in 2000, and 20–25 mm as well as 30–40 mm in 2008 (Fig. 3). Birds positively selected mussel sizes of 10–20 mm in 2000 and 5–15 mm in 2008 (Fig. 4).

The intake rate of red knots (Fig. 5) feeding on darinas was higher in 2000 (0.70 mg AFDM/s) than in 2008 (0.49 mg AFDM/s) (Mann–Whitney U = 1118, n = 82, P = 0.002). The lower intake rate in 2008 was not due to a lower number of prey captured per unit time (Mann–Whitney U = 690, n = 82, P = 0.33), but because ingested darinas were significantly smaller in 2008 compared with

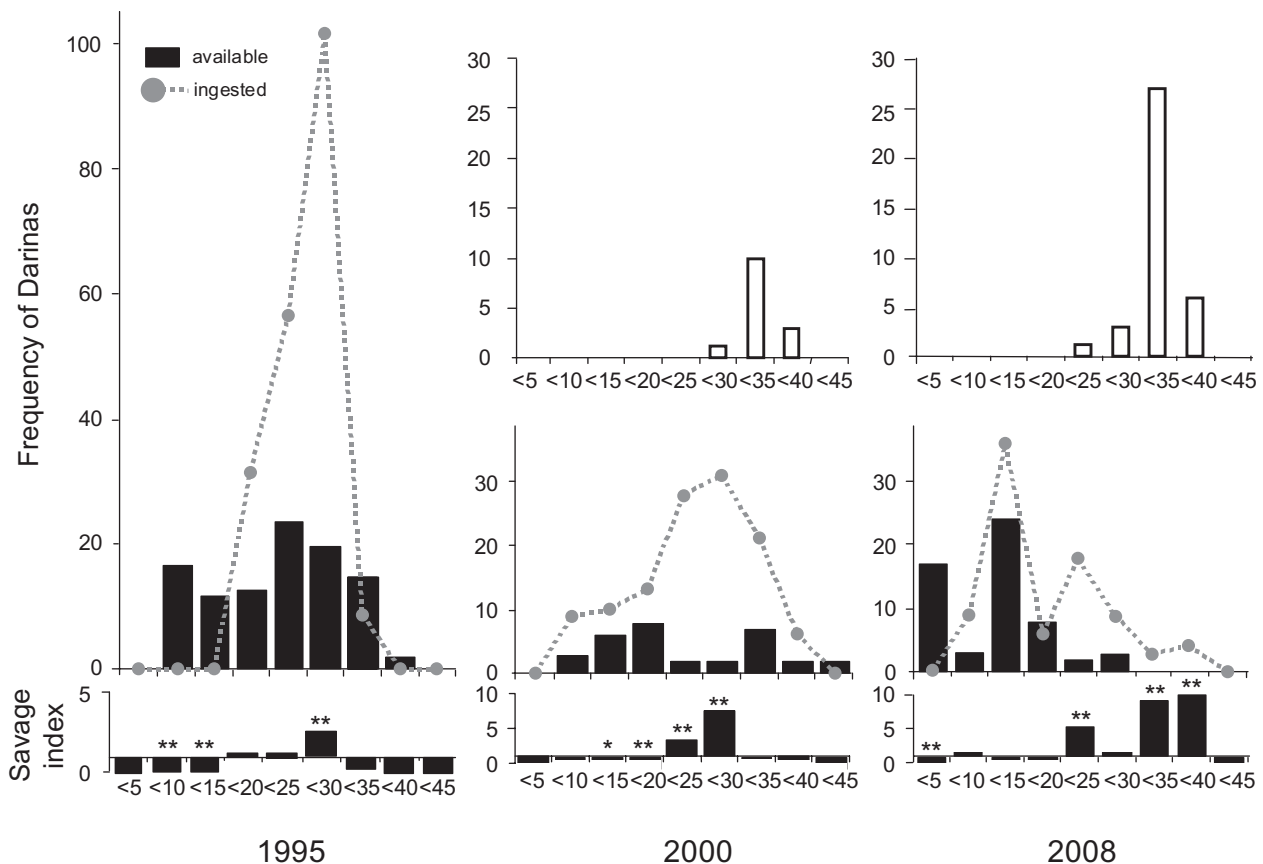


Fig. 3. Comparison between *Darina solenoides* size classes (5 mm) available and taken by knots in 1995, 2000 and 2008. Black histograms indicate the number of darina available in the sediment and grey dots indicate the number of prey ingested (sum of faeces and observations) per size class. Upper panels with white-barred histograms indicate the number of darinas found unburied in 2000 or 2008. The lower panels show prey choice using the Savage selectivity index, with level of significance indicated as * $P < 0.05$ and ** $P < 0.001$.

2000 (Mann–Whitney $U = 4607$, $n = 166$, $P < 0.0001$).

The intake rate of knots feeding on mussels (Fig. 5) was also higher in 2000 (0.76 mg AFDM/s) than in 2008 (average = 0.20 mg AFDM/s) (Mann–Whitney $U = 1772$, $n = 99$, $P < 0.0001$). These low intake rates in 2008 were explained by the lower number of prey ingested per unit foraging time (Mann–Whitney $U = 1772$, $n = 99$, $P < 0.0001$) as well as by the smaller sizes of mussels eaten in 2008 (Mann–Whitney $U = 1.6 \times 10^6$, $n = 1852$, $P < 0.0001$).

DISCUSSION

The number of red knots in February at Río Grande remained similar at 3000 to 3300 from 1995 to 2008, despite the large decreases reported for the entire subspecies (Baker *et al.* 2004; Morrison *et al.* 2004). We interpret this to mean that Río Grande is a favourite

and key wintering site, and that other, less favourite wintering sites are abandoned first with a decline in total population size. In support of this, the general pattern is that the surviving knots are more and more concentrated on Tierra del Fuego, and that more northern sites along the Atlantic coast are no longer used for wintering (Escudero *et al.* 2003; Morrison *et al.* 2004).

Our data show that the intertidal area of Río Grande has a very abundant food base. In fact, it shows a higher harvestable prey biomass for red knots than measured at sites used by knots anywhere else in the world (Table 2). However, the suitability of a given feeding site for knots not only depends on prey quantity, but may also depend on prey quality (van Gils *et al.* 2005b). Compared with other wintering sites (Table 2), prey quality at Río Grande also ranks among the higher values, suggesting that the overall food base is exceptional. Indeed, by feeding on darinas at an intake rate of 0.70 mg AFDM/s for 2.5 h and feeding on mussels at an intake rate of 0.76 mg

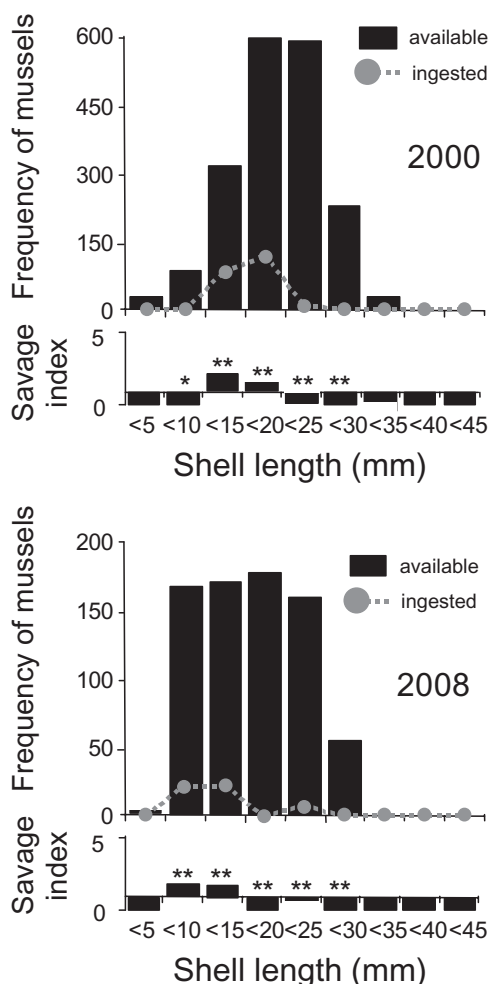


Fig. 4. Comparison between mussel size classes (5 mm) available and taken by knots in 2000 and 2008. Black histograms indicate the number of mussels available and grey dots indicate the number of prey ingested (estimated by telescope observations) per size class. The lower panels show prey choice using the Savage selectivity index, with level of significance indicated as * $P < 0.05$ and ** $P < 0.001$.

AFDM/s for 5 h, knots achieved a very high overall intake rate of 0.44 mg AFDM/s over the entire cycle (which includes 5 h of non-feeding time) in the year 2000.

Few reliable estimates of intake rate are published, but Piersma *et al.* (2005) compiled an extensive overview of red knot fuelling rates across the world, based on changes in individual or average body mass over time. We used these fuelling rates to derive intake rates, so we can place our intake rates of 2000 and 2008 into a global context. The rate of fuelling depends on how much energy is taken up, minus how much is spent on maintenance. Following González *et al.* (1996), we back-calculated how high the intake rate at a given site

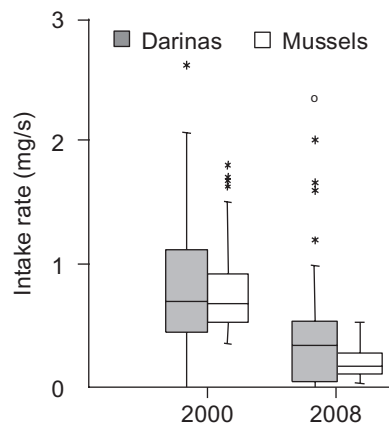


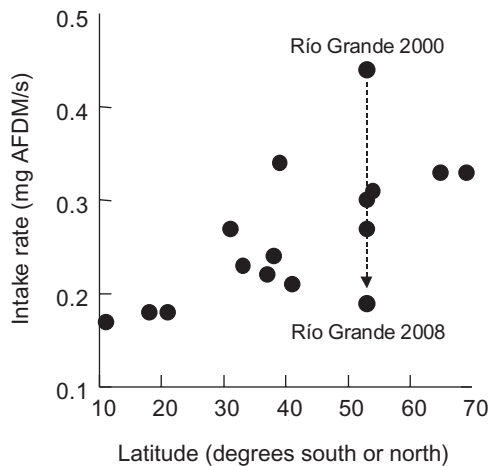
Fig. 5. Box plots showing the intake rates (mg s^{-1}) achieved by red knots on *Darina solenoides* or mussels for each of the study years.

must have been in order to allow for the observed fuelling rate. For this we assumed the same standard parameter values of the energy budget as González *et al.* (1996) for all sites. We did take into account the important increase in maintenance costs as a result of lower ambient temperature, using the model of Wiersma and Piersma (1994) and site temperatures reported in Piersma *et al.* (2005). We decided to treat these resulting derived intake rates as indicators of intake rate rather than accurate values, although the derived value of 0.21 mg AFDM/s for San Antonio Oeste in 1998 is actually quite close to the observed value of 0.235 mg AFDM/s in 1992/1993 (González *et al.* (1996)). As expected by Piersma *et al.* (2005), these intake rates show a strong positive relationship with absolute latitude (Fig. 6). Hence, the high intake rate we observed at Río Grande in 2000 is partly explained by its high latitude. However, even for its latitude, intake rate is very high, in fact higher than achieved anywhere else in the world (Fig. 6). This would likewise result in the highest fuelling rate ever recorded in the wild (6.7 g per day) if we applied the energy budget using the assumptions used in our derivations of intake rate. Yet Tierra del Fuego is not only cold but also windy which increases maintenance costs (Wiersma & Piersma 1994), and after correcting for the strong winds at Río Grande (on average 15.7 m s^{-1} instead of the 5 m s^{-1} used for all other sites), fuelling rate declines to a more realistic value of 4.7 g per day. This is still very high, and only matched by the fuelling rate at Delaware Bay, where knots gorge themselves on dense concentrations of highly available horseshoe crab eggs. Therefore, the super-abundant food base at Río Grande seems to be of great benefit to the knots despite the poor climatic conditions, and this very likely contributes to the explanation of why these birds

Table 2. Harvestable biomass and prey quality for red knots on a number of wintering (*w*) and stop-over (*s-o*) sites, based on studies that used comparable methodology to sample prey

Harvestable biomass (g AFDM/m ²)	Prey quality	Site (country, migratory status)	Reference
20.4	2.03	Río Grande (Argentina, <i>w</i>)	This study, year 2000
10.9	–	San Antonio Oeste (Argentina, <i>s-o</i>)	González <i>et al.</i> (1996)
3.4	0.89	Banc d'Arguin (Mauritania, <i>s-o</i>)	Piersma <i>et al.</i> , 1993
2.9	2.10	Wadden Sea (Netherlands, <i>w + s-o</i>)	Piersma <i>et al.</i> , 1993
2.1	2.22	Roebuck Bay (Australia, <i>w</i>)	Piersma <i>et al.</i> , 1993

Prey qualities are based on Van Gils *et al.* (2005b)

**Fig. 6.** Direct observations of intake rate at Río Grande (Argentina) in 2000 and 2008 (this study) compared with derived intake rates of red knots across the world. Intake rates (in mg AFDM/s over the entire day, including non-feeding periods) are derived from daily fuelling rates reported in Piersma *et al.* (2005).

fly such incredibly long distances between their breeding and non-breeding areas, from one end to the other end of the New World (Buehler & Piersma 2008). Similar evaluations of the harvestable biomass at potential but unused wintering sites at lower latitudes along the same flyway could test this interpretation.

A capture–recapture analysis revealed a dramatic drop in annual survival during the 1999/2000 non-breeding period (Baker *et al.* 2004). This was attributed to poor feeding conditions during stop-over at Delaware Bay. Although it could be argued that the mortality – that apparently occurred away from Delaware Bay – was due to poor conditions at southern wintering sites, our data firmly establish that at the time red knots at Río Grande lived in a world of relative plenty and achieved very high intake rates. Hence our study underpins the conclusion of Baker *et al.* (2004) that problems at stop-over sites can play a deciding role in the popu-

lation dynamics of long-distance migrants, in turn calling for increased conservation of such stop-over sites.

The findings that after 2000 increasing proportions of birds arrived late and with low weights at stop-over sites in South (San Antonio Oeste; González *et al.* 2006) and North America (Delaware Bay; Atkinson *et al.* 2007), suggested that recently red knots face additional problems somewhere *en route*. Our observations from 2008 indeed indicate that southern wintering conditions seemed to have changed for the worse. First, red knots had to cope with increased disturbance by humans during roosting and feeding. Because of increased disturbance, they must have faced increased energy expenditures (Rogers *et al.* 2006). Additionally, energy income was reduced because of the half hour loss of feeding time. Second, size distributions of the preferred prey have moved towards smaller sizes, which resulted in a lower intake rate across an entire tidal cycle (0.19 mg AFDM/s). Compared with the derived intake rates of other sites across the world (Fig. 6), this is extremely low. The results from the faecal analysis imply that the birds indeed had to incorporate other prey into their diet in order to increase intake rate. They also tried to increase their daily intake rate by feeding for longer on darina, which in 2008 yielded a higher intake rate than feeding on mussels. However, as the tide receded, knots were driven towards feeding on less profitable mussels (Fig. 5). This is because due to their specialized prey detection mechanism, knots no longer find buried bivalves effectively once the sediment dries out (Piersma *et al.* 1998).

An additional recent problem encountered by the red knots that warrants more attention is the apparent increase in exposure to parasites. When walking on the mudflats in 2000 and 2008, we observed darinas laying alive on the mud surface. Such darinas were collected ($n_{2000} = 14$, $n_{2008} = 37$), kept frozen and measured. Because burrowing bivalves close to or at the surface are often parasitized (Edelaar *et al.* 2003), all darinas collected in 2008 (including those obtained by benthos sampling) were inspected for parasites. In

2008, when darinas lying on the surface of the sediment were common, 100% of unburied clams were parasitized: the subarticular space contained several sacs of infective metacercariae of *Bartolius pierrei* Cremonte (Digenea) (Cremonte 2001). Of the buried clams (from the benthos samples) 17.8% ($n = 45$) had sacs with metacercarias as well (difference in parasite prevalence between buried and unburied clams: Fisher exact test, $P < 0.0001$). All unburied (=infected) clams were larger than 24 mm (Fig. 3) whereas the sizes of infected buried clams varied between 4 and 19.3 mm. Figure 3 shows that in 2008 large darinas were virtually absent in our benthos sampling, yet positively selected and commonly included in the diet. This strongly suggests that knots also fed upon the large superficial darinas that were infected with this digenean parasite, possibly because of the lower intake rates compared with 2000. While digenean parasites may be part of the normal helminthofauna of knots, parasites are detrimental by definition. It is likely that the adult stage of this digenean parasite lives in the stomach and intestine of its host (Cremonte 2001; 2004), causing either damage or an immunological response, thus affecting the condition of the birds. Including alternative prey species into the diet as observed in 2008 may also have increased exposure to unusual parasites, to which knots may be poorly adapted.

The recent negative impacts on resting, feeding time, food intake rate and parasite exposure are expected to affect the energy balance, health status and ultimately survival of *rufa* knots. Río Grande is part of the natural reserve Costa Atlántica Tierra del Fuego, and the biological diversity of migratory and endemic birdlife justified its inclusion as a Ramsar site, an Important Bird Area and a Hemispheric Site of the Western Hemisphere Reserves Network. A reduction in the disturbance of roosting and feeding areas and further research of the biology of prey and parasites should be top priorities for the conservation of the ecosystem and therefore the migratory bird community inhabiting this key site.

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