FEATURE ARTICLES

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DECLINES IN WINTERING POPULATIONS OF RED KNOTS IN SOUTHERN SOUTH AMERICA

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Abstract. Surveys of the North American race of the Red Knot (*Calidris canutus rufa*) on its main wintering areas on the coasts of Patagonia and Tierra del Fuego (Argentina and Chile) showed a dramatic decline in the wintering population: totals in 2003 were about 30 000 compared to 67 500 in the mid-1980s. Numbers at the principal wintering site, Bahia Lomas, fell by approximately 50%, from 45 300 in 2000 to 22 000–25 000 in 2002–2003. Numbers at peripheral sites on the coast of Patagonia declined dramatically, decreasing 98% compared to numbers in the mid-1980s. The results showed that declines at core sites did not result from birds moving to other places within the known wintering (or other) areas, but reflected a general population decline, with most birds now restricted to key sites in Tierra del Fuego. This phenomenon may explain why long-term declines noted elsewhere have only recently become apparent at key wintering areas. Possible reasons for the declines are discussed. Banding studies in Delaware Bay have shown that in recent years an increasing proportion of Red Knots is unable to gain sufficient weight for migration to the breeding grounds. This is likely due to reductions in their main food resource, eggs of the horseshoe crab *Limulus polyphemus*. The resulting increase in mortality could account for the magnitude and severity of the declines we observed.

Key words: *conservation, declines, population, Red Knot, shorebirds.*

Disminuciones en las Poblaciones Invernantes de *Calidris canutus rufa* en el Sur de Sur América

Resumen. Censos de la raza norteamericana de *Calidris canutus* (*rufa*) en sus áreas de invernada principales en las costas de la Patagonia y Tierra del Fuego (Argentina y Chile) mostraron una disminución dramática en la población invernante. Los totales en 2003 fueron aproximadamente 30 000, comparados con 67 500 a mediados de los años 80. Los números en el sitio principal de invernada (Bahía Lomas) decayeron en aproximadamente un 50%, de 45 300 en 2000 a 22 000–25 000 en 2002–2003. Los números en sitios periféricos en la costa de Patagonia declinaron dramáticamente, en un 98% en comparación con los números de mediados de los ochenta. Los resultados mostraron que las disminuciones en los sitios núcleo no fueron el resultado de que las aves se movieran a otros sitios dentro del rango invernal conocido, o a otras áreas. En cambio, reflejaron una disminución general de la población; la mayoría de las aves están ahora restringidas a sitios claves en Tierra del Fuego. Este fenómeno podría explicar por qué las disminuciones poblacionales de largo plazo detectadas en otros lugares sólo se han hecho aparentes ahora en las áreas claves de invernada. Se discuten las posibles causas de las disminuciones. Estudios de anillamiento en la bahía de Delaware han mostrado que en años recientes una mayor proporción de las aves es incapaz de incrementar su peso hasta los niveles necesarios para la migración hacia las áreas

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de invernada. Esto probablemente es debido a reducciones en su principal recurso alimenticio, los huevos de *Limulus polyphemus*. El incremento en mortalidad resultante podría explicar la magnitud y la severidad de las disminuciones poblacionales que observamos.

INTRODUCTION

The Red Knot (*Calidris canutus*) is a medium-sized shorebird that undertakes spectacular long-distance migrations, from breeding grounds in the High Arctic to wintering grounds in north-temperate, tropical, and south-temperate regions of the world (Piersma and Davidson 1992). Of the six currently recognized subspecies, the Western Hemisphere population of *Calidris canutus rufa* migrates across the greatest range of latitude (70°N to 47°S), from breeding grounds in the central Canadian Arctic to wintering grounds at the southern tip of South America (Morrison and Ross 1989, Morrison and Harrington 1992, Harrington 1996). Other races of knots occurring in North America include *C. c. islandica*, which breeds in the northeastern Canadian High Arctic and Greenland and migrates to wintering areas in Europe, and *C. c. roselaari*, which breeds in Alaska and on Wrangel Island, and is thought to comprise the population wintering in Florida and on coastlines of the Gulf of Mexico, the Caribbean, and northern South America (Morrison and Harrington 1992, Piersma and Davidson 1992). Although *rufa* and *roselaari* may mix on migration in North America, they are genetically distinct (Baker 1992) and occupy widely separated wintering areas, with *rufa* occurring exclusively in southern South America (Piersma and Davidson 1992). Multiple overlapping band recoveries, color-band resightings, and tracking of radio-marked individuals have traced the migration of *rufa* from its wintering grounds to breeding grounds in the central Canadian Arctic, and nearly the entire population is thought to migrate through Delaware Bay during the northward migration (LJN, unpubl. data).

Red Knot conservation is of concern because, like other shorebirds, a number of features of their biology makes them vulnerable to degradation of the resources on which they depend to accomplish their migrations (Myers et al. 1987). These features include (1) a tendency to concentrate in a limited number of locations during migration and on the wintering grounds, so that deleterious changes can affect a large proportion of the population at once; (2) a limited reproductive output, subject to vagaries of weather and predator cycles in the Arctic, which in conjunction with long lifespans suggests slow recovery from population declines; (3) a migration schedule closely timed to seasonally abundant food resources, such as horseshoe crab (*Limulus polyphemus*) eggs during spring migration in Delaware Bay (Tsipoura and Burger 1999), suggesting that there may be limited flexibility in migration routes or schedules; and (4) occupation and use of coastal wetland habitats that are affected by a wide variety of human activities and developments (Bildstein et al. 1991). In addition, Red Knots show many other specializations that may put them at risk from environmental change, such as specialized food and feeding methods, impoverished genetic diversity, possible susceptibility to parasitic and other infections owing to immunospecialization, a variety of metabolic adaptations and shifts in organ sizes at various points in the year, and possible vulnerability of orientation capabilities to pesticides and pollutants (Davidson and Piersma 1992, Baker and Piersma 2000). All of these can affect adult mortality, which appears to be the most important demographic factor influencing survival of shorebirds (Hitchcock and Gratto-Trevor 1997).

Considerable concern has been expressed about possible declines in populations of *C. c. rufa*. Population trend estimates have been consistently negative over the past several decades (Howe et al. 1989, Morrison et al. 1994, Morrison, Aubry et al. 2001). Population estimates up to the early 1990s were 100 000–150 000, one of the smallest knot populations worldwide (Piersma and Davidson 1992, Morrison, Gill et al. 2001). During the 1990s this fell to around 80 000 (Baker et al. 2001, Morrison, Gill et al. 2001). This paper reports the results of surveys which suggest that numbers have fallen even further, with drastic declines of *rufa* occurring on the major wintering grounds in southern South America in recent years.

METHODS

AERIAL SURVEY PROCEDURES

Aerial surveys were conducted in late January–early February during the years 2000 to 2003 of

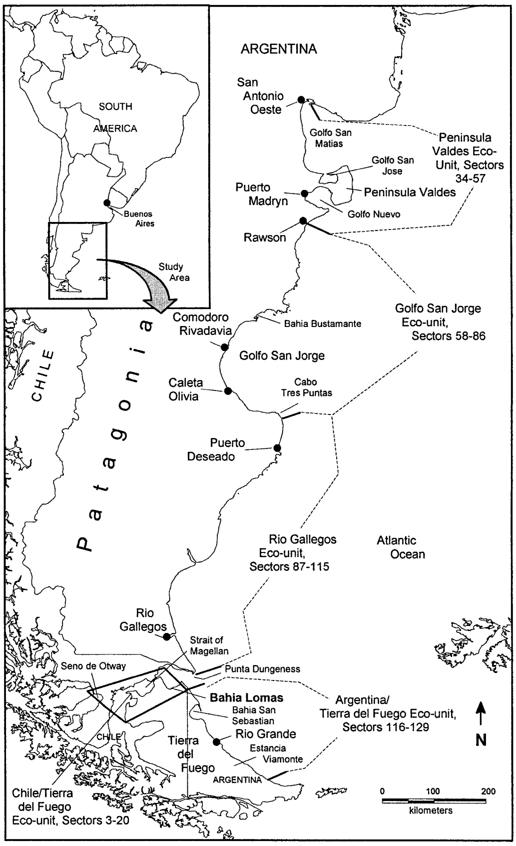

FIGURE 1. Map of Patagonia and Tierra del Fuego, Argentina and Chile, showing coastlines covered during surveys for wintering Red Knots. Eco-unit boundaries and sectors they contain are indicated, along with major geographical features and sites mentioned in the text. The main wintering site for Red Knots, Bahia Lomas in the Chilean part of Tierra del Fuego, is marked in boldface. Core sites are in Tierra del Fuego (Argentina and Chile), and peripheral sites on the coast of Patagonia. Filled circles indicate major towns and cities.

the principal wintering areas for Red Knots in South America. These areas extend along the coast of Patagonia, Argentina, from approximately San Antonio Oeste, southward to the eastern coast of Tierra del Fuego in Chile and Argentina (Fig. 1; Morrison and Ross 1989). The entire main wintering area was covered during flights in 2002 and 2003, while surveys were restricted to the major sites in Tierra del Fuego in 2000 (Chile and Argentina) and 2001 (Chile only). Aerial survey techniques and observers were the same as those employed during Canadian Wildlife Service shorebird atlas surveys of South America in 1982–1985 (Morrison and Ross 1989), so that results from the atlas and current surveys should be directly comparable.

Surveys were flown using a single-engined, low-winged aircraft flying at 50–80 m above sea level at approximately 160 km hr^{-1}, and covered the most important marine-influenced habitats used by shorebirds along the coast. The flights usually followed a line approximately 50 m offshore from the tideline, which allowed the two principal observers to look inshore at birds as they flushed. Surveys were scheduled to coincide with high tide for as much of the flight as possible: coverage was always completed during the upper quarter of the tidal cycle. Care was taken to fly the most important areas that have large mudflats (Bahia Lomas, Bahia San Sebastian, Rio Grande) as close to high tide as possible to count birds as they gathered in flocks to roost. Inland lagoons, upper estuaries, and salt ponds were mostly not surveyed.

Up to three observers participated in the surveys. The two principal observers (RKR, all years; RIGM, 2001–2003; and S. Meyer, 2000) recorded observations of birds directly onto cassette recorders for later transcription, along with details of locations and times from onboard Global Positioning System (GPS) equipment. Data of the two principal observers were compared after the flights and final tallies included all flocks seen by each observer. Where estimates for a flock differed between observers (differences between principal observers were mostly minor in relation to the estimated count), those of RKR were generally accepted to ensure maximum consistency between surveys, since he participated in all flights and had the best observation position. In 2000 and 2001, a third observer (LJN) in the left rear seat noted any birds on the offshore side of the aircraft, and took coordinates by GPS of major shorebird concentrations.

Numbers of shorebirds were assessed either by counting smaller groups or by estimating larger flocks. Red Knots were always identified to species, as were Hudsonian Godwits (*Limosa haemastica*); most other species were also identifiable, though general size classes were used for some medium-sized and small species where specific identification was not possible.

The coastline was divided into sectors based on landmarks and type of coastal morphology or predominant habitat (e.g., sandy ocean beach, cliffs, mixture of sandy bays separated by rocky points, mudflats, etc.; Morrison and Ross 1989). Survey data were first tabulated at the sector level, and sectors then combined into eco-units, which consisted of larger geographical regions of broadly similar habitats (Fig. 1). Principal features of the eco-units surveyed were as follows:

Peninsula Valdes Eco-unit. The west coast of Golfo San Matias south of San Antonio Oeste is generally low and rocky, with sandy beaches and stretches of *restinga,* a wave-cut, rocky, intertidal platform which can provide important shorebird habitat. The shores of the Peninsula Valdes and coast south to Rawson include mixtures of sand and gravel beaches, and rockier sections backed by cliffs.

Golfo San Jorge Eco-unit. Gravel and sandy beaches divided by rocky headlands run south from Rawson to the north end of Golfo San Jorge. Important shorebird areas are found in the marshier sections occurring around Bahia Bustamante. The northern half of Golfo San Jorge consists mostly of long gravel beaches backed by scrubland or cliff, while the southern half includes important areas of *restinga* between Caleta Olivia and Cabo Tres Puntas.

Rio Gallegos Eco-unit. Long stretches of gravel beach and cliffs extend along the southern coastline of Patagonia running south to the Strait of Magellan, providing little shorebird habitat.

Tierra del Fuego (Argentina) Eco-unit. Important shorebird habitats on the Atlantic coast of Tierra del Fuego in Argentina include the extensive mudflats found in Bahia San Sebastian, and the large areas of productive *restinga* found near Rio Grande.

Tierra del Fuego (Chile) Eco-unit. This eco-unit contains the most important wintering area for Red Knots in South America, comprising the extensive mudflats and sandflats of Bahia Lomas at the eastern mouth of the Strait of Magellan. Smaller muddy intertidal areas are found along the Strait of Magellan itself.

The major habitats in the Tierra del Fuego eco-units, particularly Bahia Lomas, Bahia San Sebastian, and Rio Grande, may be considered core wintering areas for knots, while the more scattered habitats along the Patagonian coast of Argentina may be considered peripheral wintering areas.

Conditions were generally good for the flights, except for one flight in Argentinian Tierra del Fuego in 2000 and flights along the southern part of the Patagonian coast in 2003, when there was high turbulence and glare. The areas concerned were generally not known to support notable numbers of knots, and conditions during these flights are not considered to affect interpretation of the overall results. Full details of areas covered, dates, and survey conditions are available from the authors.

STATISTICAL ANALYSES

In view of the coarse nature of the survey data, we used a nonparametric sign test to assess differences between counts obtained in each sector during the atlas surveys in 1982–1985 (Morrison and Ross 1989) and during the recent surveys (2000–2003). In addition to testing individual survey results against one another, we compared atlas counts with (a) maximum numbers within a site from 2000–2003 and (b) minimum numbers within a site from 2000–2003. These tests were conducted with the full unadjusted dataset, and after excluding sectors in which between year differences were $\leq$100 birds, using Statistica software (StatSoft Inc. 2003). Results of the two sets of tests were identical, so we present results only of the conservative test excluding small differences in counts.

RESULTS

Bahia Lomas. Counts at the most important wintering site, Bahia Lomas in the Chilean sector of Tierra del Fuego (Morrison and Ross 1989), indicated major decreases in the populations of knots using the site between 2000 and 2003 (Table 1, 2). The total at this site in 2000 (45 250) was similar to that from the same area during the South American atlas surveys during the mid-1980s (41 910), but counts fell progressively in 2001 (29 745) and 2002 to 21 855, a loss of approximately 52% over the three years. Counts in 2003 (25 500) were similar to those in 2002, confirming the major decline at the site, though suggesting the drastic reduction in numbers had not continued.

Tierra del Fuego. Survey totals for all the major sites in Tierra del Fuego, which include Bahia Lomas, Bahia San Sebastian, and Rio Grande, in the mid 1980s (53 232) and in 2000 (51 255) were similar, with numbers decreasing to 27 242 in 2002 and 29 915 in 2003 (the Ar-

TABLE 1. Counts of North American Red Knots (*Calidris canutus rufa*) on the coast of Argentina and Chile. Eco-unit boundaries and locations are indicated in Figure 1. Counts for 1982–1985 are from atlas surveys in Morrison and Ross (1989).

Country Eco-unit	Location	Sector numbers[a]	Survey year 1982–1985	2000	2001	2002	2003
Peripheral areas							
Argentina							
Peninsula Valdes	various	various (19)	0			—[b]	0
	north of Peninsula Valdes	38–40	1223			650	350
	Peninsula Valdes	45,48,50,55	3800				0
	various						
Golfo San Jose	Bahia Bustamante	various (47)	0			0	0
	Caleta Olivia to Cabo Tres	71–72	7400			0	0
	Puntas	80–84,86	1291			679	210
	coast south of Puerto Deseado						
Rio Gallegos	seado	93,97	550			0	0
	Rio Gallegos estuary	112				700	0
Core areas							
Argentina							
Tierra del Fuego	various	various (8)	0			—[b]	—[b]
	Bahia San Sebastian	118–120	4440	2250		50	900
	Rio Grande	123	5100	3300		5020	3500
	Estancia Viamonte and coast south	125,129	930	0		—[b]	—[b]
Chile							
Tierra del Fuego	north shore, Strait of Magellan	3,5	240	100	410	700	0
	various	various (8)	0	—[b]	—[b]	—[b]	
	coast north of Argentine border	11	100	0	0	0	0
	Bahia Lomas	12	41 700	45 150	29 335	21 155	25 500
	south shore, Strait of Magellan	13–15,17,18	722	455	—[b]	239	
	east shore, Seno de Otway	(1)[c]				78	15

[a] Where sectors are listed as ''various,'' the number in parentheses is the total number surveyed.
[b] Population not estimated; includes unsurveyed sectors and surveyed sectors that contained no knots.
[c] No sector number; one sector surveyed.

gentinian sectors of Tierra del Fuego were not surveyed in 2001). Counts at Bahia San Sebastian (sectors 118–120) dropped from 4440 in 1985 to 900 in 2003 (Table 1). Numbers at Rio Grande, which appears to be the most important area on the Argentinian Atlantic coast of Tierra del Fuego, fluctuated between 3500 and 5000 over the course of the surveys, consistent with previous records from the site (Devillers and Terschuren 1976, Harrington and Morrison 1980). A flock of 900 knots was observed at Estancia Viamonte in 1985 (sector 125, Morrison and Ross 1989); this had been reduced to 30 birds in 1995 (Minton et al. 1996), and no knots were found here in 2002 on the aerial survey or on subsequent ground surveys, nor on the aerial surveys in 2003.

Coast of Patagonia. Surveys in 2002 and 2003 of the entire Patagonian coast of Argentina south of San Antonio Oeste indicated declines had also occurred at most previously recorded wintering sites in this region. This clearly demonstrated that the losses at the major sites in Tierra del Fuego were not due to a large-scale redistribution of birds within their known wintering area (Table 1, 2). For instance, substantial reductions in numbers of knots occurred in the coastal sectors north of Peninsula Valdes, around Peninsula Valdes itself, and in sectors south of Comodoro Rivadavia between Caleta Olivia and Cabo Tres Puntas (Table 1). No knots were found at Bahia Bustamante in 2002 or 2003, despite careful searching and good survey conditions; this site had held 7400 knots in 1982. No

TABLE 2. Summary of counts of Red Knots wintering on the coast of Argentina and Chile. Subtotals are shown for the core sites in Tierra del Fuego (Argentina and Chile) and for the principal wintering site for this subspecies of Red Knot, Bahia Lomas. Counts from 1982–1985 refer to atlas counts in Morrison and Ross (1989). Eco-units and locations are shown in Figure 1.

Country Eco-unit	Survey years				
	1982–1985	2000	2001	2002	2003
Argentina					
Peninsula Valdes	5023			650[a]	350
Golfo San Jorge	8691			679	210
Rio Gallegos	550			700	0
Tierra del Fuego	10 470	5550		5070	4400
Chile					
Tierra del Fuego	42 762	45 705	29 745	22 172	25 515
Total all sectors	67 496	51 255	29 745	29 271	30 475
Subtotals for core areas					
Argentina and Chile					
Tierra del Fuego	53 232	>51 255		27 242	29 915
(% of total)	(79)			(93)	(98)
Chile					
Bahia Lomas	41 910	45 250	29 745	21 855	25 500
(% of total)	(62)			(75)	(84)

[a] Not all sectors surveyed.

knots were found on outer coastal sectors between Cabo Tres Puntas and the Strait of Magellan in 2002 or 2003. Seven hundred knots were found in the Rio Gallegos estuary in 2002; this area was not surveyed in 1982, and none were observed during difficult windy conditions in the estuary in 2003.

Overall survey results. For the entire survey region, nonparametric sign tests comparing atlas sector totals with those from the full coastal surveys in 2002 and 2003, as well as with maximum and minimum sector totals for combined 2000–2003 surveys, indicated that decreases predominated in all comparisons (Table 3).

Decreases at sites on the Patagonian coast were proportionally larger than those at the core wintering sites in Tierra del Fuego. Comparing atlas surveys with minimum sector totals from 2000–2003, decreases in Patagonian sectors containing knots (n = 15) totaled 14 004 birds, or 98% of the atlas total of 14 264, whereas for sites in Tierra del Fuego, decreases totaled 28 727 (n = 14), or 54% of the atlas total of 53 232. These losses at the peripheral areas in Patagonia resulted in an increasing percentage of the birds being found at the core wintering sites in Tierra del Fuego. The percentage of the overall survey total found at the principal site in Ba-

TABLE 3. Significance of Red Knot declines between 1985 and 2003 on their wintering grounds in southern Patagonia and Tierra del Fuego. Nonparametric sign tests compared counts from 1982–1985 (atlas surveys) with counts conducted in 2000–2003. Atlas counts were compared with survey results in each year and with maximum and minimum counts observed in each sector over the 2000–2003 surveys. Sector counts that differed by ≤100 birds were excluded from the analysis.

Atlas survey compared with counts from	No. of non-ties	No. sectors with atlas count > survey count	Z	P
2000	7	6	1.5	0.13
2001	3	2	0	1.00
2002	16	14	2.8	<0.01
2003	19	18	3.7	<0.01
2000–2003 maximum	20	17	2.9	<0.01
2000–2003 minimum	20	19	3.8	0.01

hia Lomas rose from 62% to nearly 84%, and at all the major sites in Tierra del Fuego from 79% to over 98%, between 1982–1985 and 2003 (Table 2).

DISCUSSION

Aerial surveys conducted throughout the main known wintering range of Red Knots in South America in 2000–2003 indicated that a drastic decline has occurred in the population using those areas. Declines were apparent not only at the major sites in Tierra del Fuego, but also throughout the rest of the main wintering areas on the Patagonian coast of Argentina, where knots declined substantially or in some cases disappeared from many areas where they had been observed in the 1980s. The broad scale of the surveys clearly demonstrated that the losses at the major sites were not the result of a redistribution of the birds on their wintering grounds.

IS THE DECLINE REAL?

Other reports also suggest Red Knot populations are declining. In Argentina, ground observations have confirmed the disappearance of knots from the Bahia Bustamante area, in contrast to other species of shorebirds which remained common at the site (Escudero et al. 2003). At Peninsula Valdes, peak numbers of knots on northward migration have fallen from as many as 20 000 in the early 1980s to about 3000 in recent years (Bala et al. 2002). Peak numbers have also fallen at the important stopover area at San Antonio Oeste (Gonzalez et al., unpubl. data). Declines in numbers using Lagoa do Peixe in southern Brazil have also been reported (Nascimento, unpubl. data).

In the United States, major declines have occurred at the most important spring stopover area in Delaware Bay, especially in the past several years, with counts falling from over 100 000 in the mid-1980s to fewer than 10 000 in 2003 (Clark et al. 1993; LJN, unpubl. data).

Trend analyses of counts of Red Knots in eastern North America also indicate that populations of Red Knots are declining. Analyses of International Shorebird Survey (eastern USA) and Maritimes Shorebird Survey (eastern Canada) data have consistently shown negative, though not always significant, trends (Howe et al. 1989, Morrison et al. 1994). Paired *t*-tests of counts of Red Knots at sites in Atlantic Canada showed significant declines in numbers of both adult and juvenile birds in recent years (Morrison and Hicklin 2001). In Quebec, analyses of checklist data covering the period 1978–1996 showed a statistically significant decline in numbers of knots (Aubry and Cotter 2001). These trends appear to be part of a wider pattern of declines observed in many Arctic-breeding, long-distance-migrant shorebirds, especially in eastern North America (Morrison 2001, Morrison, Aubry et al. 2001).

Concern about declining numbers of Red Knots has also surfaced through recent attempts to estimate the population size of *C. c. rufa* in the Western Hemisphere (Morrison, Gill et al. 2001). Estimates up to about 1990 based on banding and counts in eastern North America suggested the population was in the range of 100 000–150 000 (Harrington et al. 1988, Morrison and Harrington 1992, Morrison, Gill et al. 2001). In the late 1990s, Baker et al. (2001) pointed out that estimates of the population from resightings of banded birds in North and South America and counts in eastern North America were more consistent with a figure of 80 000. The population estimate now appears to be even lower, perhaps as low as 35 000–40 000, as suggested both by the present aerial survey data and by very similar population estimates made from resightings of birds banded in Tierra del Fuego (Gonzalez et al., unpubl. data).

It might at first sight appear inconsistent that counts at the major wintering areas only appear to have fallen rapidly since 2000, whereas trend estimates and counts at other areas have suggested declines have been taking place for some time, perhaps since the 1980s. This would not necessarily be the case, however, if losses first occurred at peripheral sites in preference to core sites, a phenomenon described as the buffer effect by Gill et al. (2001). In fact, our survey data suggest that this is precisely what has happened on the wintering grounds, where numbers at peripheral sites on the Patagonian coast have fallen by 93–98% compared to atlas counts, in contrast to decreases of 2–54% at core areas in Tierra del Fuego. The long-term declines that have been described for *rufa* populations thus might not be initially apparent at the core wintering sites such as Bahia Lomas. This suggestion appears plausible: if we assume the atlas total of 67 500 wintering birds was present in the late 1980s, and that the population has been declining by 3% per year (Bart et al., unpubl. data) for the 12 years since then, the population would have fallen to 46 800 by 2000, a number similar to those found at the major wintering sites (Bahia Lomas: 45 700; all Tierra del Fuego: 51 250).

Could the observed declines be caused by a redistribution of the wintering population? Results from the 2002 and 2003 surveys showed that the decreases at Bahia Lomas did not result from a redistribution of the birds to other sites within the currently known wintering area as described by Morrison and Ross (1989). We consider it unlikely that a larger-scale redistribution has taken place for several reasons. Large increases in numbers of wintering knots in potentially suitable habitats would likely have been detected in areas such as Bahia Samborombon in Argentina, where there is a bird observatory, or at Lagoa do Peixe, a national park in southern Brazil where shorebirds have been monitored in recent years (Nascimento, unpubl. data). There is no suitable habitat for large numbers of knots between southern Brazil and the north coast of Brazil (Morrison and Ross 1989). Small numbers of knots (8200) were found wintering on the north coast of Brazil during Atlas surveys, though there appears to have been no major change in the status of this population (Rodrigues and Lopes 2000; Nascimento, unpubl. data). In any case, if large numbers of knots were wintering undetected in South America or elsewhere, they would almost certainly still be seen during spring migration through the east coast of North America, where numbers have fallen dramatically in recent years. The widespread and consistent decreases observed in numbers of knots throughout their range argues against a general redistribution causing the observed declines.

Decreases observed during the surveys also appear unlikely to be due to biases in survey methodology. Survey conditions, dates, personnel, and techniques were similar for all surveys, including those in 1982–1985, and results should therefore be directly comparable. Although it is not possible to exclude some movements between sites or differences in timing of birds starting their migration northward from Tierra del Fuego, the fact that we covered the entire likely range within which the birds would be found indicates that overall totals should be comparable.

POSSIBLE CAUSES OF THE DECLINE

The sudden and dramatic decrease in numbers during the past several years may be related to problems knots are encountering during their northward migration (Baker et al., unpubl. data). Red Knots are highly specialized long-distance migrants, and many features of their biology indicate that they are likely to be highly susceptible to environmental changes, especially changes that could affect adult mortality (Baker and Piersma 2000). Small reductions in refueling rates at stopover areas, for instance, could lead to disproportionate increases in mortality during the next leg. Such effects would be particularly drastic at the final stopover area (Delaware Bay for *rufa*) before the birds reach the breeding grounds (Davidson and Piersma 1992). These final sites are not only refueling stops, where the birds accumulate the fuel and undergo other physiological changes required for the final stage of the journey (Piersma 1998, Piersma and Gill 1998, Piersma et al. 1999), but they also provide key resources enabling the birds to acquire additional reserves needed in preparation for breeding in the Arctic (Morrison and Hobson 2004).

In this context, the major reduction in food resources used by Red Knots during migration through Delaware Bay is of special concern. Heavy harvesting has led to reductions of horseshoe crabs and more particularly crab eggs, the major food resource used by knots at Delaware Bay (Botton et al. 1994, Tsipoura and Burger 1999). In a baywide survey of crabs conducted by Delaware Division of Fish and Wildlife, the mean numbers of crabs per tow fell from 6.8 in 1991 to 0.2 in 2002, while the harvest of crabs increased from just over 363 600 kg in 1993, the first year of reported harvest, to over 2.9 million kg in 1998 (Fig. 2, Atlantic States Marine Fisheries Commission 1998, Michels 2000). Fewer breeding crabs produce fewer eggs, reducing their overall volume on the bayshore. Egg availability to shorebirds also declines because there are fewer crabs to unearth previously laid eggs as they dig to lay new egg masses (Botton et al. 1994). As a result, the availability of eggs on the beach has fallen significantly (Tsipoura and Burger 1999), especially in the last four years (LJN, unpubl. data). This decline would affect Red Knots more than other species because they rely mostly on horseshoe crab eggs found on the

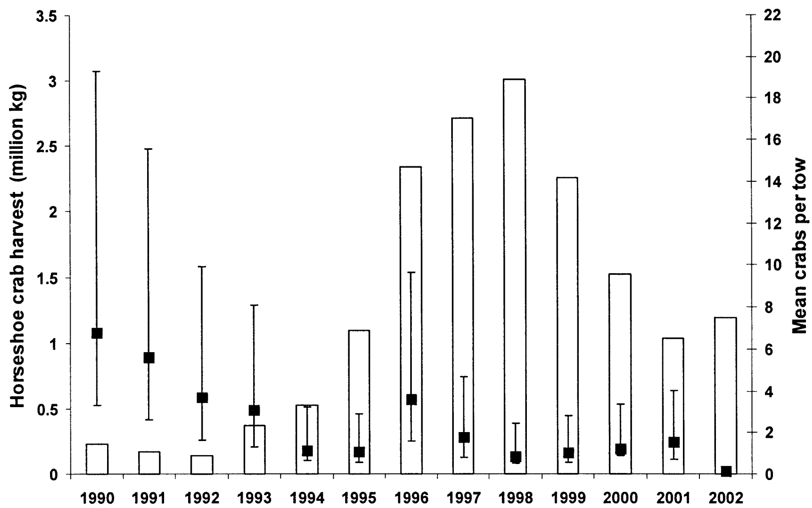

FIGURE 2. The annual harvest of horseshoe crabs (million kg; open bars) from 1990 to 2002 compared to the results of a baywide trawl of crabs (filled squares, ±95% confidence intervals) during the same period conducted by the Delaware Division of Fish and Wildlife (Atlantic States Marine Fisheries Commission 1998; S. Michels, unpubl. data). The first mandatory reporting of the horseshoe crab harvest was in 1993, so previous harvest estimates are probably underestimates. Harvest restrictions were applied in 1996 and 1998.

beach surface (Tsipoura and Burger 1999). As a result, an increasing proportion of knots in recent years has been unable to achieve weight levels required for successful migration and breeding (Baker et al., unpubl. data). This has led to a measurable increase in annual adult mortality rates between the mid- and late 1990s, with annual survival decreasing from an average of 87% to 55% (Baker et al., unpubl. data). Projected population trends using the latter figure closely follow the observed survey numbers in Tierra del Fuego, demonstrating that the increased annual mortality could lead directly to the observed 50% decrease in the population, and implying that the population could become extinct or nearly so by 2010 if survival remains at the depressed level.

The extent to which knots face problems in other parts of their migration range is currently unknown. Potential problems in the wintering range might include oil pollution resulting from exploration and transportation (Harrington and Morrison 1980) or effects on food supplies. Little is known about food resources on wintering or southern migration areas.

Whereas Red Knot populations are declining, populations of the Hudsonian Godwit (*Limosa haemastica*), a species that shares habitats and major wintering sites with Red Knots in Tierra del Fuego (Morrison and Ross 1989), are stable or increasing (Morrison et al., unpubl. data). The two species share migration paths through James Bay in northern Canada and winter in similar areas in Tierra del Fuego, but the Hudsonian Godwit does not migrate through Delaware Bay (Morrison 1984). In addition, trend estimates for two of the other major shorebird species using Delaware Bay in the spring, Semipalmated Sandpiper (*Calidris pusilla*) and Sanderling (*Calidris alba*), indicate significant declines (Clark et al. 1993).

In conclusion, aerial surveys of the main wintering grounds of the *rufa* subspecies of the Red Knot, in southern South America, have shown dramatic declines in population size over the past three years. These declines do not appear to be the result of redistribution of wintering birds. While further investigations of possible reasons for the declines are needed, studies in Delaware Bay suggest that increased adult mortality of Red Knots resulting from inability to gain sufficient weight prior to migration to the breeding grounds could account for the magnitude of the observed declines.

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